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# Wing morphing allows gulls to modulate static pitch stability during gliding

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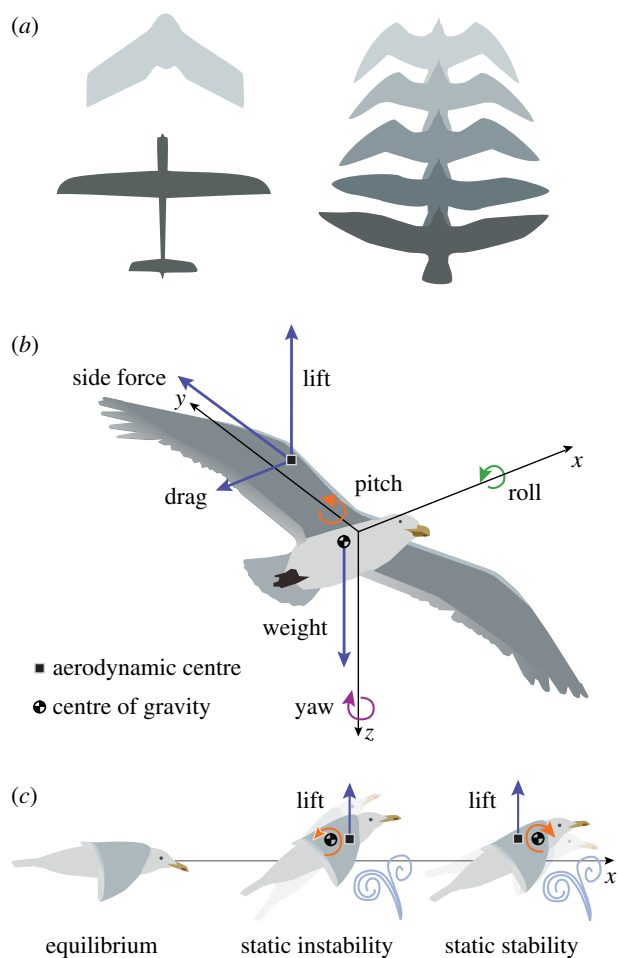
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A gliding bird's ability to stabilize its flight path is as critical as its ability to produce sufficient lift. In flight, birds often morph the shape of their wings, but the consequences of avian wing morphing on flight stability are not well understood. Here, we investigate how morphing the gull elbow joint in gliding flight affects their static pitch stability. First, we combined observations of freely gliding gulls and measurements from gull wing cadavers to identify the wing configurations used during gliding flight. These measurements revealed that, as wind speed and gusts increased, gulls flexed their elbows to adopt wing shapes characterized by increased spanwise camber. To determine the static pitch stability characteristics of these wing shapes, we prepared gull wings over the anatomical elbow range and measured the developed pitching moments in a wind tunnel. Wings prepared with extended elbow angles had low spanwise camber and high passive stability, meaning that mild perturbations could be negated without active control. Wings with flexed elbow angles had increased spanwise camber and reduced static pitch stability. Collectively, these results demonstrate that gliding gulls can transition across a broad range of static pitch stability characteristics using the motion of a single joint angle.

## 1. Introduction

The Wright brothers were not the first to design an aircraft that produced sufficient lift to fly, but they were the first to successfully control and stabilize a powered aircraft [1]. Similarly, it is not enough for birds to simply produce sufficient lift and thrust; birds must also control and stabilize their flight paths to be able to successfully forage and migrate [2,3]. Flight stability can be maintained passively due to the morphology of a flyer, actively by adjusting control inputs or by a combination of both passive and active stability [2]. It has been proposed that birds have lost their passive stability through evolution in favour of unstable morphologies that require active control [3]. However, recent theoretical and anatomical work has suggested that, like most modern aircraft, birds use a combination of passive and active stability [2]. Yet, unlike modern aircraft, birds do not have discrete control surfaces such as ailerons and flaps. Instead, birds actively change the shape of their wings, known as wing morphing (figure 1*a*). To date, there are relatively few data on avian flight stability, and there is no empirical evidence demonstrating how wing morphing affects avian stability characteristics. Understanding if, and how, avian wing morphing stabilizes their flight provides both a broader understanding of how birds fly and inspiration for novel controls for unmanned aerial vehicles.

Flight stability is the study of the moments that develop about the main body axes of a flyer after perturbation (figure 1*b*) [6]. In flapping flight, this analysis is complicated by unsteady forces and moments. In gliding flight, stability analyses can be decoupled into pitch stability (longitudinal stability, about the *y*-axis in figure 1*b*) and roll–yaw stability (lateral stability, about the *x*- and *z*-axes in figure 1*b*) [7]. Of these two modes, pitch stability is often considered to be the most important stability characteristic because of the risk of stall, which



**Figure 1.** Birds can dynamically morph the shape of their wings. (a) Aircraft are designed with fixed wing shapes that satisfy pre-defined stability and performance requirements, thereby restricting their ability to adapt to changing environmental conditions. By contrast, birds can vary their wing configuration during flight. Aircraft figures were adapted from photographs of existing unmanned aerial vehicles with wing spans approximately equivalent to gulls [4,5], and gull figures were adapted from photographs of gliding gulls in the Pacific Northwest. (b) The main forces and moments acting on a gull during steady, gliding flight are summarized as point loads acting on the aerodynamic centre. The pitching moment about the aerodynamic centre is, by definition, independent of the angle of attack. A bird is at equilibrium if all forces and moments about the centre of gravity are balanced. (c) Static pitch stability is the passive or inherent tendency for a glider to return to its equilibrium after perturbation such as a wind gust.

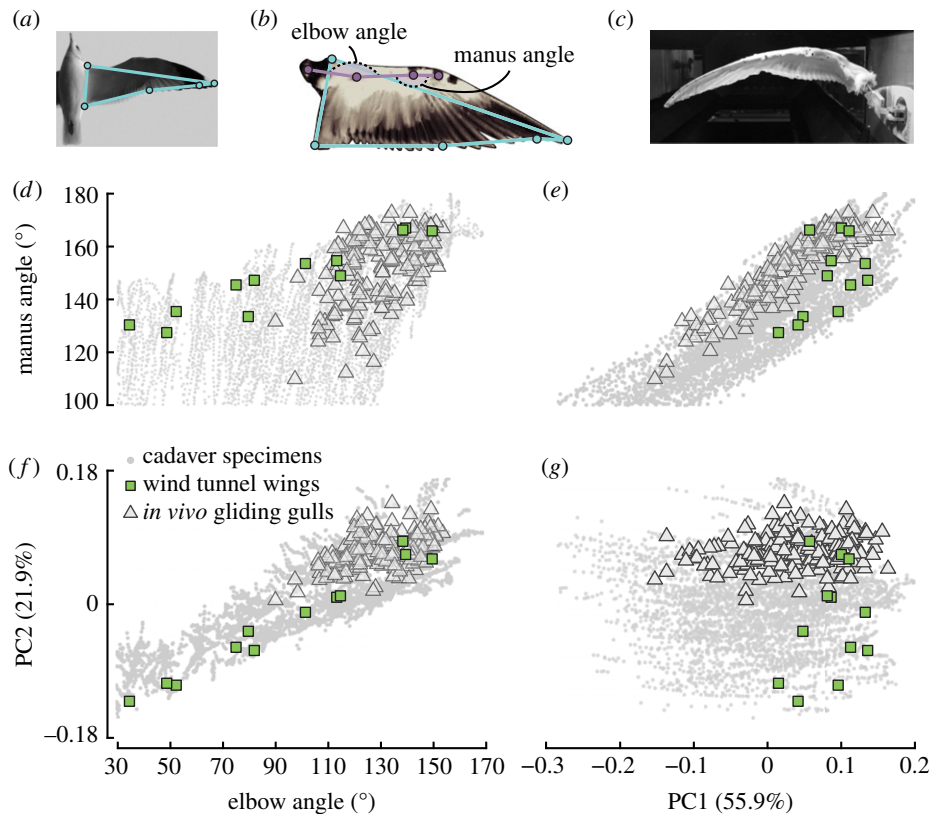
can lead to loss of control [6]. Despite its importance, only two empirical studies have measured the pitch stability characteristics of a bird posed in a single position [8,9]. These studies focus on static pitch stability, which is the time-invariant, inherent tendency for the flyer to return to an equilibrium state after an initial disturbance such as a gust [6,7] (figure 1c). A glider that is statically stable is considered to be passively stable, whereas a glider that is statically unstable must use active control to stabilize its flight path. Static stability is a necessary but insufficient condition for full flight stability, because it is possible that a statically stable flyer will continually oscillate about an equilibrium point; a time-dependent process that requires a complete dynamic analysis to evaluate the motion [7]. However, to develop a comprehensive picture of stability in steady flight conditions, such as gliding, it is necessary to first understand static stability [10]. To develop the

foundations of bird flight stability analyses, we evaluate the consequences of wing morphing on the static pitch stability of a gliding bird.

A glider's static pitch stability depends on the pressure distribution along its wings, specifically the location of the aerodynamic centre of the wings relative to the centre of gravity of the entire bird [2,7,10] (figure 1b). The aerodynamic centre differs from the centre of pressure as it represents the location on the wing where the pitching moment is independent of the angle of attack. For symmetric aerofoils, the theoretically determined aerodynamic centre and the centre of pressure are both located at the wing's quarter chord. However, as the aerofoil shape and wing geometry change, the aerodynamic centre can shift relative to the centre of pressure and the centre of gravity. If a bird experiences a perturbation when the centre of gravity is in front of the aerodynamic centre, the developed moments will inherently tend to return the bird to its equilibrium state (figure 1c). These restorative moments are required for static and, consequently, passive stability [10]. If the same perturbation occurs but with the centre of gravity behind the aerodynamic centre, the resultant forces will be destabilizing (figure 1c). In this case, the bird would be statically unstable and would need to use active control to maintain its equilibrium state. In a comparative survey with 15 bird cadavers, 11 of the posed specimens had a centre of gravity in front of the theoretical aerodynamic centre [2]. This finding suggests that, for some birds, the contribution of the wings alone may be sufficient to provide a passively stabilizing moment, and that the contributions of the tail are not required to gain passive stability [2]. It follows that if a morphing wing can shift the aerodynamic centre relative to the centre of gravity, a bird may be able to modulate between a passively stabilized state and an unstable, and thus actively stabilized, state.

One type of wing morphing that may allow such a transition is a wing that adjusts the curvature along its span, known as spanwise camber. Spanwise camber has been found to adjust the pressure distribution of aircraft wings, and thus the location of the aerodynamic centre along the wing [11,12]. An iconic example of a bird with spanwise camber is the gull. Photographs and previous observations of their gliding flight suggest that these birds can morph their spanwise camber in flight [13].

To determine if and how morphing spanwise camber affects a gull's static pitch stability characteristics, we studied the gliding flight of glaucous-winged (*Larus glaucescens*) × western (*Larus occidentalis*) gulls. We first photographed freely gliding gulls from below to determine the wing shapes used over a range of wind conditions. To then identify the *in vivo* skeletal joints from photographs of gliding gulls, we derived a relationship between skeletal joints and wing shape using the wings of gull cadavers. Next we prepared gull wings posed over the anatomical range of elbow angles to allow us to measure the static pitch stability characteristics of the anatomically possible wing configurations as well as the identified *in vivo* wing configurations. We used the elbow angle as the independent variable in the study because we found that elbow extension led to a measurable change in the spanwise camber (electronic supplementary material, figure S1). The prepared wings were tested in a wind tunnel on a six-axis force sensor that allowed us to measure the developed pitching moment as well as the lift and drag produced by each configuration. The wings



**Figure 2.** Joint angles can be predicted from wing shape. (a) Five peripheral landmarks were identified on photographs of gulls' ventral surface mid-glide (blue points). (b) Wings of gull cadavers were manipulated through the full range of extension and flexion of the elbow and manus joints. Cameras tracked the same five peripheral landmarks (blue points) as well as the position of the humerus, elbow, manus and carpometacarpus (purple points). This allowed us to determine the elbow and manus angles, and the corresponding wing outlines. (c) Wings spanning the full identified elbow angle range were prepared and dried for wind tunnel tests. (d) The range of viable elbow and manus angles was determined for the cadaver wings. (e) A morphospace of cadaver wing shapes was generated, and the *in vivo* (grey triangles) and prepared (green squares) wing shapes were projected into the space. (f) The first principal component scales with manus angle (f) and the second scales with elbow angle. The relationship between principal component data and the known joint angles of cadavers allowed us to predict the elbow and manus angles used in flight (translucent grey triangles).

were tested at varied turbulence intensities to account for possible variation in stability and performance caused by a fluctuating environment.

## 2. Material and methods

### 2.1. *In vivo* gliding wing configurations

To identify the wing configurations adopted during gliding flight, we first determined the wing shapes used by gulls as they glided directly above a camera (Sony  $\alpha$ -350 equipped with 75–300 mm lens or 18–70 mm lens/iPhone 5S) at five locations on the Pacific Northwest coast. This allowed us to capture time-stamped photographs of the ventral view of the wings during gliding flight (figure 2a). Photographs were taken in conditions with wind speeds ranging from 2.2 to 16.9 m s<sup>-1</sup>, and maximum wind gusts ranging from 3.9 to 25.6 m s<sup>-1</sup> based on time-specific reports from local weather stations. Although weather station measurements could not match the precise wind speeds and maximum wind gusts that the gulls would have encountered during each photograph, these values provide an average of each hour's conditions. From the photographs, we identified five landmarks on the ventral wing perimeter using ImageJ [14] to provide a measure of wing shape (landmarks include: shoulder, 10th primary feather tip, seventh primary feather tip, first secondary feather tip and the location where the feathers rejoined the body; blue dots in figure 2a). Prior to digitization and data analysis, the photographs were checked

by two independent investigators to ensure that they were approximately perpendicular to the camera screen. This verification was informed by an analysis of how sensitive the elbow angle prediction is to the orientation of the wing relative to the camera lens (see the electronic supplementary material for further details). In total, we selected and analysed 182 photographs from the observational study.

### 2.2. Cadaver manipulation study

We next asked if the skeletal joint angles could be predicted from the photographs of the *in vivo* wing shapes. Using gull cadavers ( $n = 3$ ), we manually manipulated the wings through the full range of extension and flexion of the elbow and manus joints, while three cameras recorded the position of markers on the humerus head, elbow, manus and distal carpometacarpus (purple dots in figure 2b). Wing motion was recorded at 50 frames s<sup>-1</sup> at 640 × 480 pixel resolution using three synchronized Allied Vision Technologies Prosilica GE680 cameras equipped with 4–8 mm lenses. To calibrate the three camera views, we filmed a moving wand prior to each recording session to obtain direct linear transformation coefficients from the easyWand5 software [15]. The three-dimensional positions of the skeletal markers were digitized using the DLTdv5 software [16], and then used to calculate the elbow and manus angles of the wing at each time point. One of the cameras was oriented to record perpendicular to the ventral surface of the wing. From this view, we digitized the same five points on the wing perimeter as in the observational photographs (blue dots in figure 2b).

### 2.3. Prediction of *in vivo* joint angles from wing perimeter shape

We used geometric morphometrics to determine the diversity of shapes associated with the five landmarks on the wing's perimeter from the cadaver videos and observational photographs (figure 2*a,b*). We performed a generalized Procrustes analysis [17] using the R package geomorph [18]. This superimposes the landmark sets to remove effects of size variation, orientation and location. We then used the aligned landmarks from the perimeter of the cadaver wings (pooled together) to perform a principal components analysis (figure 2*g*). The first and second principal components explained approximately 56% and 22% of the variation in wing shape and scaled with manus and elbow angle, respectively (figure 2*d–g*). Using the computed eigenvectors from this morphospace, we then projected the observed *in vivo* wing shapes into the cadaver-defined morphospace and used a machine learning framework (see the electronic supplementary material for further details) [19] to predict the joint angles used by the freely gliding gulls (figure 2*d*). The error of this analysis was investigated using the wings prepared for the wind tunnel (figure 2*c*; see the electronic supplementary material).

### 2.4. Wind tunnel investigation

To determine the aerodynamic consequences associated with a variation of skeletal joint angles, we focused all measurements on the elbow angle because of its relationship with spanwise camber (electronic supplementary material, figure S1). Wings from gull cadavers ( $n = 12$ ) were positioned and dried at elbow angles spanning from 34° to 149° (figure 2*d*) and the maximal manus angle. This range was selected to allow us to explore the effects of the elbow across a biologically viable range of wing shapes and not only the shapes used in flight. Each wing had a steel rod threaded and epoxied into the shaft of the humerus to permit mounting in the wind tunnel. The wings were mounted to the side of the wind tunnel with the hand wing position near perpendicular to the flow. This mounting configuration does not capture all possible wing orientations that live birds use, but allowed us to isolate the aerodynamic effects of changes in the elbow angle independent of changes in wing sweep.

We performed the measurements in the University of Toronto, Canada, variable-turbulence low-speed wind tunnel [20] at a biologically relevant glide speed of 10 m s<sup>-1</sup> [21] (Reynolds numbers 92 000–179 000 based on the root chord) at three turbulence intensities (0.04%, 1.42%, 4.61%). These specific turbulence intensities were tested because they could be homogeneously generated in the wind tunnel with turbulent length scales smaller than the root chord (see the electronic supplementary material for further details). Thus, the investigated turbulent conditions do not replicate large-scale turbulence (such as gusts), which can be approximated, to first order, as a series of quasi-steady states [22]. Rather, the effect of the turbulence introduced here is expected primarily to change the state of the boundary layer on the wing and the separation process when approaching stall.

To measure aerodynamic forces and moments, wings were rotated about the humerus attachment over a range of 80–100°. Beginning at a horizontal position (approximately 0°), wings were first rotated up to +40° (or +50°), then down to -40° (or -50°) and then back up to 0°. The set angle range was reduced for wings that stalled at a lower humerus angle. We measured the loads generated by each wing with a six-axis load cell (AMTI FS6) sampling at 4000 Hz for 10 s, amplified (AMTI Gen5, force gain = 2000, moment gain = 500) to the data acquisition system (National Instruments NI 6529 PX). The load cell axes were independently calibrated by using a series of 11 weights

from 0 to 2.5 kg and fitting a linear model to the voltage output. Tare runs (mounting system only, without the wing installed) were completed so that effects of the support system could be removed from the final measurements. During the tests, the load cell was installed such that it rotated with the stepper motor. The results were corrected accordingly so that the measured forces were returned to the inertial frame of reference, which was defined relative to the main wind tunnel axes. Additionally, the weight of the wing was subtracted from the results, allowing us to isolate the aerodynamic forces and moments. The pitching moment was defined relative to the humerus head of each wing, which was approximated as the location of the joint between the steel rod and humerus bone. We pooled the data from the 'up' and 'down' portions of the angle of attack because there was minimal hysteresis in the pre-stall readings (electronic supplementary material, figure S6). From the final force and moment data, we then determined the normalized coefficients of lift ( $C_L$ ), drag ( $C_D$ ) and pitch ( $C_M$ ) from the load cell data, wing geometry and the measured flow conditions.

## 3. Results

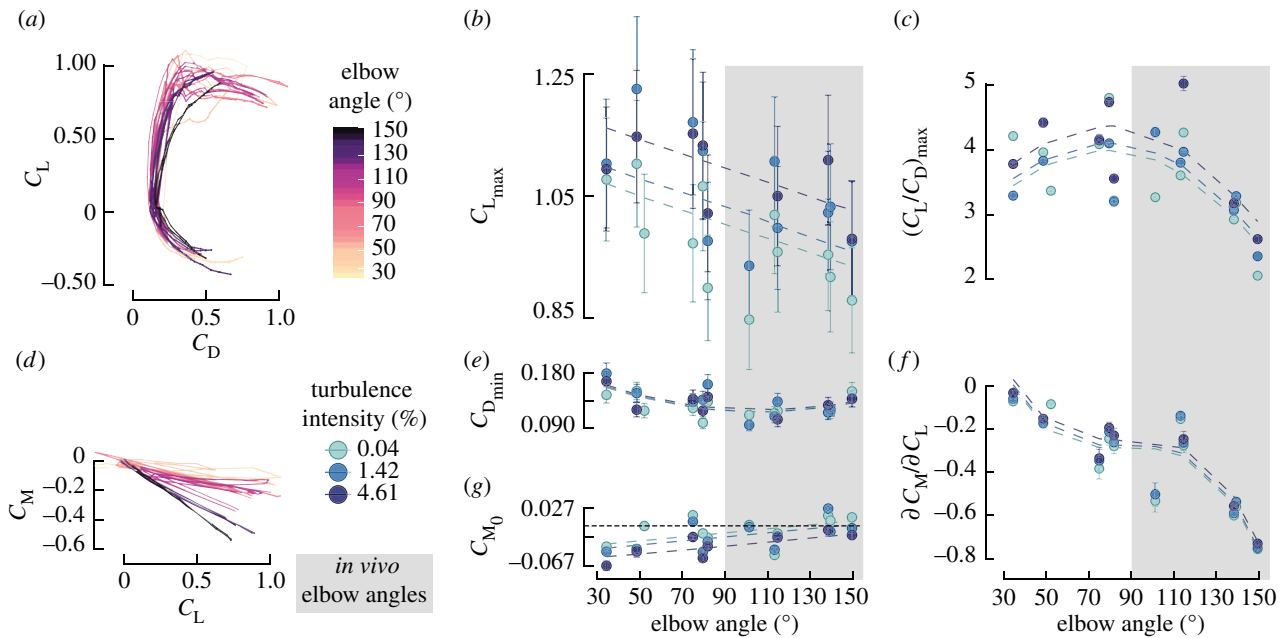
### 3.1. *In vivo* gliding wing configurations

The observational study, combined with the morphometric analysis of the gull wings, allowed us to predict the joint angles used by gliding gulls. This technique revealed that gliding gulls used elbow and manus angles that ranged from 90° to 154° and from 110° to 173°, respectively (figure 2*d*). In addition, we found that gulls used lower elbow angles as wind speeds and maximum wind gusts increased (wind speed:  $-0.61^\circ/(\text{m s}^{-1})$ ,  $t_{180} = -3.415$ ,  $p < 0.001$ ; wind gust:  $-0.40^\circ/(\text{m s}^{-1})$ ,  $t_{180} = -3.253$ ;  $p = 0.00136$ ).

### 3.2. Aerodynamic consequences of the morphed wing configurations

The wind tunnel force data revealed that aerodynamic performance was highest at intermediate elbow angles. This result can be explained by examining the relationship between lift and drag across the investigated angle of attack range, which can be visualized with a lift–drag polar plot (figure 3*a*) [23]. The polar plots revealed that the maximum lift coefficient ( $C_{L_{\max}}$ ) decreased as the elbow angle increased (figure 3*b*), but minimum drag ( $C_{D_{\min}}$ ) was lowest at an intermediate elbow angle (figure 3*e*). We found that intermediate elbow angles were the most aerodynamically efficient wing configuration, where maximum aerodynamic efficiency is defined as the maximum ratio of lift produced to drag incurred ( $(C_L/C_D)_{\max}$ ) (figure 3*c*). Additionally, turbulence intensity had a modest positive effect on maximum lift and aerodynamic efficiency, consistent with experimental turbulence studies on engineered rigid wing models [24].

We next investigated the effects of the elbow angle on static pitch stability by evaluating two necessary conditions that are derived from the relationship between the pitching moment coefficient and lift coefficient (figure 3*d*). The first condition for static pitch stability is that the pitch stability derivative ( $\partial C_M/\partial C_L$ ) must be negative (for non-stalled flight conditions) [2,6,10]. This can be evaluated as the slope of the pitching moment, which was calculated about the humerus head versus lift. We found that the pitch stability derivative was entirely below zero, satisfying the first stability condition (figure 3*f*). This value becomes increasingly negative as the



**Figure 3.** Elbow extension across the *in vivo* range decreases aerodynamic efficiency but increases static pitch stability. (a) Wings with high elbow angles show reduced aerodynamic performance. Elbow extension across the *in vivo* range (grey shading) significantly (b) decreases maximum lift coefficient, (e) increases minimum drag coefficient and (c) decreases aerodynamic efficiency. Turbulence intensity increases aerodynamic efficiency and maximum lift. (d) Passive pitch stability increases as the elbow extends, illustrated by (g) the increasing zero lift pitching moment (intercept of (d)) and (f) the decreasing pitch stability derivative (slope of (d)). The data in (d) are restricted to the pre-stall region, and thus are exclusively linear. Turbulence intensity had a destabilizing effect on both stability parameters. The horizontal dashed line in (g) represents zero. Error bars on (b), (c), (e) and (g) represent the uncertainty due to bias and precision errors. Error bars on (f) represent 95% confidence intervals of the linear model slope prediction.

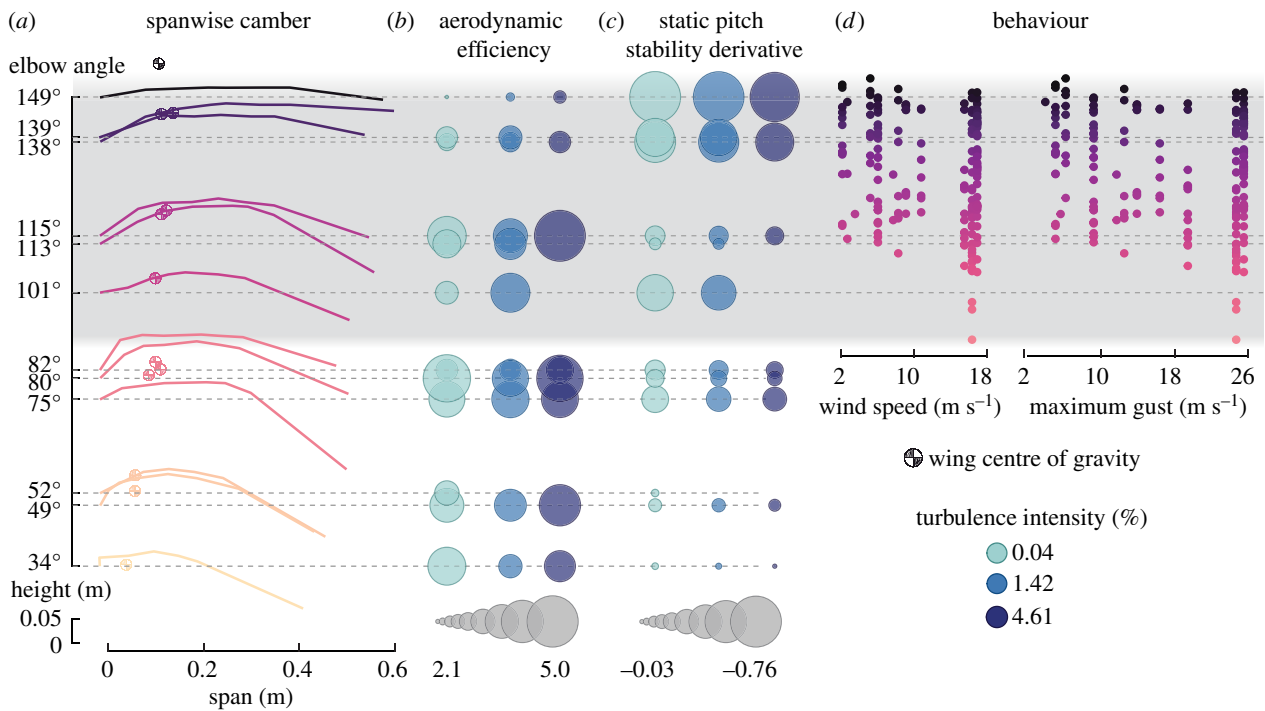
elbow extends, providing a larger restorative moment (figure 3f). The second condition is that the flyer must be able to trim, defined as the ability to produce positive lift in its equilibrium state [6]. Assuming the first condition is also satisfied, this will only occur if the zero-lift pitch moment ( $C_{M_0}$ ) is positive [6,10]. This can be visualized as the  $y$ -intercept of the pitching moment versus lift (figure 3d). We linearly interpolated the measured pitching moment values to estimate the pitching moment that would occur when lift is equal to zero. The wing's contribution alone for the majority of tested wings did not meet this condition due to a negative zero-lift pitch moment (figure 3g). However, the most extended wings had positive zero-lift pitch moments, which would make it easier for the bird to trim. Finally, we found that increasing the turbulence intensity caused a slight but statistically significant reduction in the static pitch stability for all wing configurations (figure 3f,g).

## 4. Discussion

In this study, we investigated the consequences of wing morphing on a bird's static pitch stability during gliding flight. We first identified the wing shapes used in gliding flight by combining observations of freely gliding gulls and measurements of gull cadaver functional anatomy. As wind speed and maximum gust increased, the range of elbow angles used by gulls shifted to lower values (figure 4d). Although visualization of these trends may suggest an increase in elbow angle range at higher wind speeds/gusts (figure 4d), quantile regressions (evaluated at 10% quantile intervals) indicate that trends at the upper, middle and lower ends of each data range did not differ (electronic supplementary material, figure S8). Further

measurements on gull cadavers revealed that, as the elbow flexes within the *in vivo* range, the leading edge of the wing transitions from nearly planar configurations to those with large spanwise camber (figure 4a; electronic supplementary material, figure S1).

Wind tunnel measurements suggest that elbow angle modulates the gull wing's contribution to the static pitch stability. This capability can be quantified by calculating the location of the aerodynamic centre relative to the location of the humerus, which is possible owing to the linear relationship between the lift and pitching moment (figure 3d). In this case, the aerodynamic centre can be calculated as the product of the root chord and the pitch stability derivative [25]. As the elbow extends, the aerodynamic centre shifts towards the trailing edge travelling approximately 12 cm (60% of the mean wing chord). During this same extension, the wing's centre of gravity shifts only 2 cm towards the trailing edge of the wing (10% of the mean wing chord). This disparity suggests that, through the modulation of the elbow angle alone, gulls are able to actively adjust the location of the aerodynamic centre relative to the centre of gravity of the bird, and thus gain control over their static pitch stability characteristics. Most surprisingly, we found that the fully extended elbow configurations satisfied both static pitch stability conditions and may alone be sufficient to provide passive stability to a gull gliding in this configuration. It is important to note that this conclusion relies on the full bird's centre of gravity being less than 12 cm aft of the humerus head along the bird's body [26]. We did not measure the location of the centre of gravity because our specimens were frozen cadavers, and we were not convinced that such measurements would be reliable. A detailed investigation of how a bird's centre of gravity shifts over a range of wing, tail and body positions would be highly informative.



**Figure 4.** Gulls can actively control elbow angle to adjust spanwise camber, potentially negotiating trade-offs in aerodynamic efficiency and static pitch stability. (a) Across the *in vivo* range (grey band) the spanwise camber reduces as the elbow angle increases, and encompasses two divergent aerodynamic characteristics. First, wings with the highest elbow angles (138–149°) have the least spanwise camber characterized by (b) reduced aerodynamic efficiency but (c) increased static pitch stability. By contrast, wings with intermediate elbow angles (101–115°) have (b) increased efficiency but (c) reduced static stability and, thus, would require active control. These diverse sets of aerodynamic parameters may allow the same wing to navigate between trade-offs in stability and efficiency. (d) Gulls use lower elbow angles during glides as wind speeds and wind gusts increase, which suggests gulls glide with reduced static pitch stability in unsteady environments.

The possibility that avian wings may provide passive stability during gliding flight differs from conclusions drawn previously in the avian literature, which suggests that birds have lost passive stabilizing mechanisms in favour of active flight control [2,3,9]. Previous empirical studies have indicated that avian wings are statically unstable in pitch, but these findings are based on measurements of a singular wing configuration [8] or on constant mass models that displace the centre of gravity [9]. Instead, our results are consistent with a theoretical study that suggests that some birds may have passive stability and use a combination of passive and active stability in flight [2]. When the wind tunnel measurements are compared with the *in vivo* gliding observations, our results indicate that gulls may extend their elbows into a more planar configuration in calm conditions and take advantage of increased passive stability. In windy and gusty conditions, gulls can reduce their elbow angle to morph into a more unstable configuration characterized by high spanwise camber. Previous observational work has noted herring gulls (*Larus argentatus*) transitioning to wing configurations with increased spanwise camber while gliding in gale force winds [13]. The reduced stability of this configuration may be beneficial for a glider in fluctuating conditions because high passive stability can cause a constant ‘overshooting’ effect that results in an erratic flight pattern [2].

Turbulence intensity had a minimal, but statistically significant, effect on both the aerodynamic performance and static pitch stability. The turbulence intensities investigated can be characterized as a statistically steady flow phenomenon because the length scale of the turbulence is smaller than the chord of the wing. Our results indicate that turbulence on this level may be largely negligible to

gulls. Furthermore, previous work has shown that changes in the turbulence intensity of the same order of values that we investigated had an insignificant effect on a gliding gull’s energy expenditure [26]. As we found the wing was statically stable in pitch about the humerus, it is possible that across these low levels of turbulence gulls require less force, and thus less energy, to maintain the wing at the desired angle of attack relative to the body’s position. However, gulls often encounter unsteady, large-scale turbulence while flying in the wake of buildings or convective air flows over open water. Atmospheric turbulence in these conditions is expected to be larger than the turbulence intensities investigated in our study and, consequently, it is possible that gull flight stability is affected by larger scale turbulence. Given our findings that the static pitch stability decreases as turbulence increases, it is possible that there is a critical level of turbulence intensity that would cause the wings to become statically unstable in pitch about the humerus, requiring a gull to spend more energy to maintain the equilibrium angle of attack.

In this study, we focus solely on the wing’s contribution to static pitch stability. To construct a complete picture of a morphing wing glider’s stability, it will be necessary to perform a full dynamic analysis across varied perturbations. In addition, although wings are a major contributor owing to their large lifting area, the contributions of the tail and body are often not negligible and will have an additive effect on stability [6]. The tail is the most significant of the two and serves to increase a glider’s passive stability because its aerodynamic centre is always behind the centre of gravity [2,6]. The highly coupled nature of a bird’s wings makes it difficult to fully isolate how independent kinematic parameters affect aerodynamic stability and performance. It is

likely that other features of wing morphing, such as wing sweep or digit positioning, affect the location of the aerodynamic centre and, thus, the overall stability of the flyer. Future work with particle image velocimetry and rigid wing models may allow us to further decouple the complex kinematics of morphing wings to identify the aerodynamic benefits associated with each kinematic parameter. Despite these qualifications, understanding the static pitch stability contributions of the wings is necessary to develop the framework for future avian flight stability studies.

In addition to reducing static pitch stability in favour of actively controlled stability, flexed elbow angles with increased spanwise camber also led to improved aerodynamic efficiency (figure 4*b,c*). Could spanwise camber lead to a second trade-off, one between stability and efficiency during avian gliding? It has been previously demonstrated that engineered wings with spanwise camber do have increased aerodynamic efficiency, but there is no empirical evidence of the effects on static pitch stability [11,27]. Coupling of stability and efficiency is well established for certain aircraft configurations, including box wings and flying wings [28,29]. For birds, varying spanwise camber could lead to a trade-off between stability and efficiency if the modified pressure distribution causes a shift in both the aerodynamic centre and the orientation of the force vector. In this study, we found that extending the gull elbow both shifts the aerodynamic centre and impacts the maximum lift-to-drag ratio and, consequently, the orientation of the force vector. Our results are therefore consistent with the hypothesis that varying spanwise camber leads to a trade-off between static pitch stability and efficiency. However, spanwise camber was not an independent variable in our study and is linked to changes in aspect ratio and wing area, among other geometric properties. A direct test of this hypothesis will require high-quality flow visualization of engineered wing models that vary only in spanwise camber to reveal specific aerodynamic mechanisms [30,31].

The aerodynamic efficiency, which is here considered as equal to the maximum lift-to-drag ratio, is expected to be high for gliding birds. High lift-to-drag ratios allow birds to maximize the glide range without additional energy input. The highest lift-to-drag values (greater than 10) that have been directly measured for birds come from prepared swift wings that were tested over a range of wind speeds [23,32]. The maximum lift-to-drag values obtained in the present study were 5, which is similar to what has been measured

in several other studies with different avian taxa, and for some of the wind speed combinations with prepared swift wings [23,32]. The lower lift-to-drag values from the gull wing configurations tested in this study are unlikely to represent the maximum that gulls can achieve when attempting to maximize glide distance. Instead, the lift-to-drag values likely reflect that wings were prepared to explore the effects of variation in spanwise camber and to match configurations observed for gulls flying in windy conditions, without concern for whether the birds were ascending or descending.

Can the insight from gulls' static pitch stability during gliding flight be used to improve the stability of aircraft flying in challenging conditions? The range of the pitch stability derivative (approx.  $-0.03$  to  $-0.75$ ) provided by adjusting a gull's elbow angle is extensive. This range is substantially larger than the range that can be achieved when varying a rigid wing across different configurations of conventional wing sweep, aspect ratio, taper ratio and chordwise camber (static pitch stability derivative range of  $-0.01$  to  $-0.26$ ) [33]. Our results suggest that morphing a wing in a way that is similar to a gull's elbow motion may expand the operating range of unmanned aerial vehicles flying at a similar Reynolds number. Furthermore, the implementation of a single joint angle, functionally similar to the gull elbow, may provide a novel, effective design for a morphing wing, without sacrificing design simplicity. Such a mechanism may permit enhanced control by allowing an aircraft to adapt its wing configuration and static pitch stability characteristics to variable environmental conditions.

**Data accessibility.** All datasets, custom code and observational photographs are available on figshare at <https://doi.org/10.6084/m9.figshare.c.3977505>.

**Authors' contributions.** C.H. and D.L.A. designed the study and wrote the manuscript. D.L.A. and P.L. provided conceptual and technical guidance. C.H. collected and analysed the experimental data. C.H. and V.B.B. collected and analysed the observational and specimen manipulation data. All authors edited the manuscript.

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