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Aerial Righting, Directed Aerial Descent, and Maneuvering in the Evolution of Flight in Birds

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Aerial Righting, Directed Aerial Descent, and Maneuvering in the Evolution of Flight in Birds

by

Dennis José Evangelista

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy

 in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Robert Dudley, Chair Professor J. A. McGuire Professor Ronald Fearing

Spring 2013

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Abstract

Aerial Righting, Directed Aerial Descent, and Maneuvering in the Evolution of Flight in Birds

by

Dennis José Evangelista Doctor of Philosophy in Integrative Biology University of California, Berkeley Professor Robert Dudley, Chair

This thesis consists of four major studies: a study of incipient flight behaviors in young birds over ontogeny (chapter 1); a detailed study of maneuvering using physical models of a likely ancestral bird morphology (chapter 2); a comparative study of maneuvering ability in several stem-group birds, within a phylogenetic context (chapter 3); and development of basic engineering theory to quantify the turbulence sensitivity of shapes to environmental turbulence of given scales and spectral content. The studies have identified: 1) shifts in function from asymmetric to symmetric movements in young birds, contrary to predictions from alternative hypotheses and occurring before wing-assisted incline running; 2) shifts in function, tied to angle of attack, of asymmetric appendage postures in creating yawing and rolling moments; and 3) migration of control effectiveness as tails are shortened and other features change, during the early evolution of birds. The work plugs some considerable gaps in current prevailing theories (e.g. Dial, 2003; Tobalske et al., 2011) and provides a test of hypotheses of flight evolution not based in outdated "trees-down" or "ground-up" paradigms from the past, but rather based on the universal need of airborne animals to maneuver (Dudley and Yanoviak, 2011; Maynard Smith, 1953).

This work seeks to understand early flight evolution from a maneuvering perspective; every animal in the air must maneuver, and by understanding "powered" flight as simply a point along a spectrum of *maneuvering* flight (Dudley and Yanoviak, 2011), unifying breakthroughs are made. It is hoped that the multifaceted approach taken here, with ontogenetic series, aerodynamic studies, and phylogenetic approaches, is robust against the shortcomings of any one approach individually: confounding ontogeny with evolution (as may be the case in others' studies of alternative hypotheses, e.g. (Dial, 2003)); inferring implausible functions from paleontological material in the absence of proper benchmarking against live animals; or misdiagnosis of how forms work in the absence of functional studies. Dedicated to my family

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¹"I will never surrender of my own free will... I will continue to resist by all means available. I will make every effort to escape and to aid others to escape. I will accept neither parole nor special favors from the enemy... I will keep faith with my fellow prisoners. I will give no information or take part in any action which might be harmful to my comrades..."

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Introduction

This thesis examines the role of aerial righting, directed aerial descent, and maneuvering in general in the early evolution of flight in birds. To address this question, four main studies were conducted: a study of incipient flight behaviors in young birds over ontogeny; a detailed study of maneuvering using physical models of a likely ancestral bird morphology; and a comparative study of maneuvering ability examining several stem-group birds; as well as a study of the sensitivity of airborne shapes to environmental noise to compliment measurements of stability and control effectiveness. This introduction provides a roadmap to the work presented in the chapters that follow.

Everything in the air must maneuver. Failure to do so risks colliding with objects, capture by predators, failure to land in a desired spot, or crashing hard in a very bad spot. It is curious, then, that this perspective is not considered more often in the evolution of vertebrate flight. Too often, "true" flight, restricted to birds, bats, and pterosaurs, is seen as a separate and unrelated thing to the many instances of gliding; one professor instructs students in an evolution class that "studies of extant gliders will tell you nothing about the evolution of flight." Nothing could be further from the truth. Consider the shift in perspective, that everything in the air must maneuver, and that even "parachuting" and "gliding" (which are far more dynamic and unsteady than their names seen) require production of forces and torques to change the position and orientation of the body in the air. "True, powered" flight, which was once a separate entity, is now simply a case of maneuvering flight where the magnitude of the forces and moments produced is large enough to be self-supporting (Dudley and Yanoviak, 2011). When one is open to such a shift in perspective, careful examination of the role of aerial righting, directed aerial descent, and maneuvering in the early evolution of flight in birds becomes the next logical step to understanding flight evolution. The maneuvering perspective suggests a generalized biomechanical scenario (maneuvering hypothesis) for the acquisition of aerial behaviors (Dudley and Yanoviak, 2011), shown in table 1.

This thesis will further test maneuvering hypotheses of the evolution of flight, specifically by testing for incipient maneuvering ability in young birds during ontogeny (chapter 1, figure 1), and by examining maneuvering ability in birds and their theropod ancestors (chapters 2 and 3, figure 2). Chapter 1 provides the first systematic exploration of aerial righting and directed aerial descent in birds, including shifts in function that correspond with the transitional stages identified in (Dudley and Yanoviak, 2011). Chapter 2 examines the funcTable 1: Generalized biomechanical scenario for the acquisition of aerial behaviors and flight, repeated from (Dudley and Yanoviak, 2011)

- 1. Arboreality; residence on elevated substrate
- 2. Jumping (either volitional or via startle reflex); falling
- 3. Aerial righting and landing reflexes
- 4. Parachuting (drag based descent)
- 5. Directed aerial descent (lift-based and drag-based; steep glide angles)
- 6. Gliding (predominantly lift-based; shallow glide angles)
- 7. Elaboration of wings and maneuvers
- 8. Flapping flight

tional consequences of early bird forms for maneuvering, and how function shifts with glide angle. These are then examined in a phylogenetic and historical context in Chapter 3. An additional chapter examines the sensitivity (in a control theory sense) of an airborne shape to environmental disturbances (chapter 4). The results provide multiple lines of evidence in support of the scenario of (Dudley and Yanoviak, 2011). Furthermore, the many-pronged approach is expected to be robust against the shortcomings of either approach individually: confounding ontogeny with evolution (as may be the case in (Dial, 2003)); or inferring implausible functions from paleontological material in the absence of proper benchmarking against live animals.

1 Biomechanics of the aerial righting response and directed aerial descent during ontogeny in young birds

An aerial righting response allows falling animals to reorient the body dorsoventrally, presumably to initiate gliding/parachuting and subsequent landing without injury. As fliers must fly in unpredictable environments, subject to disturbances from wind gusts, navigational hazards, predators, or widely spread desirable resources, an animal in the air may need to further direct its descent by maneuvering.

The focal species for this chapter 1 is the Chukar Partridge (*Alectoris chukar*), a grounddwelling game bird native to Asia introduced to the United States. *Alectoris chukar* was also the model system in studies of wing-assisted incline running (WAIR) (Dial, 2003; Dial et al., 2008); this allows comparison of our results with existing data purportedly in support of an alternate hypothesis. Comparisons were conducted with Ducks (*Anas platyrhynchos*) in order to examine aerial righting and directed aerial descent in a species with a slower developmental trajectory and an endpoint of long distance migratory flight. Both species have



Figure 1: Shift in aerial righting behaviors during ontogeny in Chukar Partridge (*Alectoris chukar*) from asymmetric rolling to symmetric pitching (chapter 1)



Figure 2: Model tests and comparative study of maneuvering (chapters 2 and 3)

received considerable attention for ground-based, symmetric use of wings (wing-assisted incline running) prior to flight Dial (2003); Geist and Feduccia (2000); Tobalske et al. (2011). My study identified asymmetric movements that precede WAIR in development and accomplish maneuvering functions such as righting and control of descent. The findings here highlight the importance of maneuvering during development and in the origin of flight.

Aerial righting in Chukar Partridges (Alectoris chukar)

Chukar Partridge chicks were hatched from eggs and subjected to drop tests from 1 day post hatching (dph) through 30 dph. Aerial righting was observed through use of 500 frame/s high speed video and 60 frame/s high definition (HD) video to obtain detailed kinematics and trajectories. Initially, at 1 dph, chicks do little to alter their fall compared to a falling passive projectile. By 4 dph, birds exhibit righting by rolling using asymmetric flapping, in which one wing is strongly flapped while the other wing is flapped weakly or not flapped at all. At 10 dph, chicks begin transitioning to righting in pitch, using symmetric flapping with protracted wings. Manipulations were also carried out during the experiment to show that righting is not visually mediated and that righting requires use of the wings.

Directed aerial descent in Chukar Partridges (Alectoris chukar)

Directed aerial descent was studied using the same techniques as for aerial righting. Chukar Partridge chicks were hatched and subjected to drop tests, which were filmed with 500 frame/s high speed video and multiple 60 frame/s HD video. Trajectories were compared to a null model of a passive projectile to detect onset of directed aerial descent. After onset of directed aerial descent, flight abilities are examined over ontogeny. By 14 dph, chicks were able to slow their descent and exhibit clear modification of their trajectory to head towards targets of interest; strong directed aerial descent ability becomes apparent shortly thereafter. The techniques used to maneuver do not change much during subsequent development from directed aerial descent to full flight ability. Manipulations were attempted to augment tail inertia; manipulations were also carried out to trim wings and to check that directed aerial descent is visually mediated.

2 Maneuvering capabilities and the effect of morphology in feathered theropod dinosaurs

Chapter 2 reports the effects of posture and morphology on the static stability and control effectiveness of physical models based loosely on a feathered four-winged dinosaur, \dagger *Microraptor gui* (Xu et al., 2003), from the Cretaceous of China. Stability and control effectiveness are quantified from force and torque measurements on physical models using previously established techniques (McCay, 2001a; Park and Choi, 2010). The results give a first-order approximation of what the reconstructed organism may have been capable of, bearing in mind that flapping and closed-loop control mean we will, in general, under-predict aerial abilities.

Models were placed in different proposed reconstruction postures and with varying degrees of leg and tail feathers. Postures had largely similar lift and drag characteristics but vastly different pitching moment and stability properties. While some leg postures render $\dagger M.~gui$ unstable, and thus quick to maneuver, others are stable, slower to maneuver but resistant to perturbation by wind gusts. Depending on body posture, asymmetric leg positions can cause roll but have surprisingly little effect on yaw, while raising and lowering the tail or the hind limbs can alter pitch. More importantly, the data show shifts in stability and shifts and reversal in function of appendages as glide angle and angle of attack are changed.

While $\dagger M$. gui lived after $\dagger Archaeopteryx$ and likely represents a side experiment with feathered morphologies, the general patterns of stability and control effectiveness as leg and tail morphologies are changed may help elucidate the evolution of flight control aerodynamics in vertebrates. Additionally, recent evidence confirms the four-winged (Beebe, 1915; Lippin-cott, 1920) morphology as ancestral to the Avialaes (Hu et al., 2009; Xu et al., 2011; Zheng et al., 2013). Furthermore, in chapter 3, these results are applied in a phylogenetic context, to further understand potential biomechanical constraints on extinct flyers or gliders arising from the need to maneuver.

While previous thinking regarding aerial hypotheses focused on lift and drag coefficients and glide angles (Beebe, 1915; Bock, 1986; Bunnell, 1930; Chatterjee and Templin, 2003; Emerson and Koehl, 1990; Emerson et al., 1990; Feduccia, 1979; Feduccia and Tordoff, 1979; Gatesy and Dial, 1996; Heilmann, 1926; Heptonstall, 1970; Long et al., 2003; Norberg, 1990) the focus here is on maneuvering (Dudley and Yanoviak, 2011; Dudley et al., 2007; Maynard Smith, 1953).

Additional benchmarking studies

Model tests require benchmarking and validation, however this has been lacking in previous model studies (Alexander et al., 2010; Chatterjee and Templin, 2007). As part of this effort, benchmarking data was obtained for models of three taxa, which also serendipitously allowed further testing of ideas regarding maneuvering and stability. While I do not report these in detail in this thesis, a brief sketch is helpful here.

Model tests of Anna's Hummingbirds (*Calypte anna*, a high performance, low angle of attack glider) during display dives was conducted to test how the tail and wings are used during an extreme selective maneuver (Evangelista et al., in prep). Model tests of *Draco* lizards (a moderate performance glider) focused on the aerodynamic consequences of two postures (cambered initial and flat mid glide), as well as testing of stability, control effectiveness, and the effect of partial and extended patagia (Evangelista et al., in prep). For both of these, data collection and analysis is complete; additional simulations for comparison to previously published trajectories will be performed.

Tests of human skydivers (a poor glider with no obvious aerial adaptations) were also conducted, as human free fall is an understudied and important point of comparison: humans use both inertial and aerodynamic mechanisms to accomplish maneuvers and direct their descent and they are the largest vertebrate known to perform aerial behaviors (Cardona et al., 2011; Evangelista et al., 2012). Tests suggest that maneuvers at skydiving speeds are dominated by aerodynamic torques (vice inertial, as in human gymnasts tumbling at low speed). Human use of limbs as aerodynamic surfaces is consistent with those of smaller animal skydivers like ants (Munk, 2011) or stick insects (Zeng, in prep). Stability varies depending on axis of motion and glide angle and stability shapes which behaviors are effective in accomplishing maneuvers, suggesting the results are valid for the range from the smallest aerial maneuverers (Munk, 2011; Zeng, in prep), through the middle of the range (this thesis), to some of the largest and fastest (Cardona et al., 2011; Evangelista et al., 2012).

3 Comparative study of maneuvering within the Avialaes

Maneuvering hypotheses posit that aerial maneuvering was a pervasive force shaping the evolution of flying animals. Chapter 1 examines maneuvering during an ontogenetic series in an extant bird; Chapter 2 examines maneuvering in one extinct bird ancestor. In chapter 3, I analyze the physical effects of structural changes on aerial maneuvering as they present themselves in fossils and along evolutionary lineages. This chapter directly addresses criticisms of maneuvering hypotheses (e.g. Padian, 1985, 1987, 2001) stemming from Bock's notion of paradigms (Bock, 1965) and the need to examine fossils and phylogeny by working from a phylogeny to see what the biomechanical patterns are.

To accomplish this, I measured the aerodynamic maneuvering characteristics of a series of models based on Mesozoic birds and avian ancestors to determine whether or not measures of aerodynamic performance correlated with morphological changes. Maneuvering characteristics during glides were quantified by measuring static stability $(\partial C/\partial \alpha)$; the tendency to experience righting moments when deflected from equilibrium) and control effectiveness $(\partial C/\partial \delta)$; the amount of force or moment generated for each degree of movement of a limb or control surface).

As in Chapter 2, tests on a broader range of feathered theropods confirms that changes in planform, such as the presence or absence of a feathered tail or of leg feathers or the reconstructed posture of the animal, can drastically alter static stability. In addition, appendage function (e.g. as an elevator, rudder, or aileron, generating control forces and torques in different directions) also depends on posture and glide angle, and the function of appendages can shift dramatically due to reversal or cross-coupling effects. When stability and control effectiveness were mapped onto phylogenies, the patterns showed migration of control from tails and hind-limbs to more effective and larger forelimbs during the early evolution of birds from their dinosaur ancestors. The patterns also showed loss of stability as (fore)wings increased. This immediately suggests a role for flapping as control responses to increasing body instability.

4 Sensitivity of shapes to turbulent incident velocity noise

Chapter 4 considers the effects on maneuvering of in-flight perturbations due to turbulent environments, building on (McCay, 2001a). Airborne objects (animals, plants, and vehicles) flying in real environments may feel disturbances from turbulence in the air they are flying through. The shape of an object and its size relative to turbulent eddies affects the magnitudes and frequencies of the disturbances felt, in other words, the sensitivity to turbulence. I empirically measured this using models in a wind tunnel and an ultrasonic anemometer Kwong et al. (2013). I also developed some basic engineering theory to predict how turbulence sensitivity should change with shape, in order to compare with the empirical measurements. Elongated shapes with low aspect ratio are better filters of turbulent noise, while high aspect ratio shapes experience larger turbulent disturbance forces.

Turbulence can be described as eddies of various sizes and frequencies impinging upon an object. The size and shape of the object should alter which eddies are able to exert forces and the magnitude of the forces. For a flying animal, these result in force and torque disturbances which must be controlled or damped in order to remain on course. Two factors affecting the transfer function were examined: (1) relative size between body and eddy size and (2) shape (size, area, aspect ratio). While previous chapters dealt with stability and control effectiveness, this chapter evaluates the sensitivity to noise already in the environment, e.g. the first level of filtering and transduction.

Chapter 1

Aerial righting and directed aerial descent during ontogeny in young birds

I filmed aerial behaviors of Chukar Partridge (*Alectoris chukar*) and Mallard Duck (*Anas platyrhynchos*) from hatching through fledging as they were presented with aerial maneuvering challenges. Both species have received considerable attention for ground-based, symmetric use of wings (wing-assisted incline running) prior to flight (Dial, 2003; Jackson et al., 2009; Tobalske et al., 2011). I observed asymmetric movements that precede WAIR in development and accomplish maneuvering functions such as righting and control of descent. These findings highlight the importance of maneuvering during development and in the origin of flight.¹

1.1 Introduction

Flight among vertebrates is widespread (Dudley et al., 2007). Flight can be advantageous to fliers, enabling rapid or long distance travel and access to new resources. Clades that fly are able to disperse and colonize, possibly enhancing diversification. While historically, some may have considered "powered" flight restricted to birds, bats, and pterosaurs, Dudley and Yanoviak (2011), citing (Norberg, 1990; Rayner, 1988) noted that gliding using obvious aerodynamic structures has evolved independently at least 30 times in mammals, reptiles, and amphibians. Furthermore, aerial behaviors can occur in the absence of obvious aerodynamic surfaces, such as in directed aerial descent in canopy ants (Munk, 2011; Yanoviak et al., 2005, 2011), bristletails (Yanoviak et al., 2008), stick insects (Jusufi et al., 2011; Zeng, in prep), geckoes (Jusufi et al., 2008, 2010), or even human skydivers in free fall (Cardona et al., 2011; Evangelista et al., 2012); or in aerial righting or other attitude control in cats

¹This chapter is intended for *PNAS*, J exp Biol or *Proc R Soc B*, possibly in three parts: a short piece on righting in Chukar, a longer piece with the detailed mechanics of righting and directed aerial descent, and a third on Ducks. Methods have been presented in public as a conference poster (Cam et al., 2013).

Table 1.1: Predicted sequence of aerial behaviors in baby birds presented with aerial challenges, modified from (Dudley and Yanoviak, 2011).

- 1. Falling and jumping
- 2. Aerial righting and landing reflexes
- 3. Detectable slowing of descent
- 5. Detectable turns or motion to desired targets, e.g. directed aerial descent
- 6. Further elaboration of wings and maneuvers

(Frohlich, 1970; Kane and Scher, 1969; Liu and Nelson, 1985), geckoes (Jusufi et al., 2008, 2010), or human springboard divers (Edwards, 1986).

Previous literature includes many entrenched, yet arbitrary, definitions of terms such as "powered" flight, parachuting, and gliding, all of which have muddled the comparative picture. When one considers that all of these aerial behaviors require production and control of forces and moments in the air, it becomes clear that these are all a continuum of behaviors which vary primarily in the magnitude of the forces produced (Dudley and Yanoviak, 2011). This shift in perspective suggests a sequence for the acquisition of aerial behaviors (Dudley and Yanoviak, 2011), shown in Table 1.1².

The maneuvering hypothesis predicts that incipient maneuvering ability will be observed early on in the development of flight. Specifically, righting is expected to occur first, using asymmetric appendage motions to effect changes in orientation (attitude) using either inertial or aerodynamic mechanisms (unsteady) (Dudley and Yanoviak, 2011). The maneuvering hypothesis also predicts that as the animal grows, its ability to create forces and torques will increase (Dudley and Yanoviak, 2011), resulting in detectable directed aerial descent³ that results in body trajectories and orientations that are not described by passive ballistic models. A corollary to this is that, as they grow, birds should switch to symmetric mechanisms that are primarily aerodynamic (force $\sim \rho U^2 A$) as areas, frequencies, and speeds increase. Another corollary is that birds with delayed developmental trajectories necessitating long times on the ground should still follow the same stages suggested in (Dudley and Yanoviak, 2011).

In contrast, an alternative set of hypotheses (ontogenetic transitional wing (OTW) and wing-assisted incline running (WAIR)) focus on putative uses of protowings in theropod bird ancestors who are assumed to be cursorial⁴. Ground-based symmetric uses of wings

²Dudley and Yanoviak's original list identifies parachuting and gliding (in the sense of fixed-wing gliding); I suspect there may be some branching decisions in such a functional taxonomy, and a simple list does not effectively communicate these notions.

³I use the term directed aerial descent as opposed to controlled flapping descent (CFD) (Jackson et al., 2009). CFD presumes flapping and is less general of a term. In addition, the term directed aerial descent (Dudley et al., 2007) precedes the term controlled flapping descent (Jackson et al., 2009). CFD also confuses with the more widely used acronym for computational fluid dynamics.

⁴The maneuvering hypothesis and the alternate WAIR-based hypotheses are sometimes cast in the light

to navigate obstacles and high-angle terrain are well documented (Dial, 2003; Dial et al., 2008; Dial and Carrier, 2012; Jackson et al., 2009; Tobalske et al., 2011); the prediction from these hypotheses are that initial aerial behaviors, possible only once an animal has WAIRed up some surface of interest, should primarily be symmetric. Additionally, symmetric aerial behaviors should primarily slow descent and should not effect maneuvers until later in development. Furthermore, WAIR should be most evident in ground-based birds, including ones with chicks that spend a long time on the ground prior to developing flight.

Given the widespread occurrence of aerial righting and other "sub-powered flight"⁵, e.g. aerial maneuvering behaviors in a wide range of vertebrates and invertebrates, I set out to examine young birds to see if they perform aerial righting or directed aerial descent. I also wish to know the mechanism used in any such maneuvers, and how aerial abilities change during ontogeny. The patterns should help discern if development of flight is more consistent with aerial maneuvering hypotheses (Dudley and Yanoviak, 2011) or OTW and WAIR (Dial, 2003; Dial et al., 2008; Dial and Carrier, 2012; Jackson et al., 2009; Tobalske et al., 2011).

In this chapter, I test hypotheses of the origin of bird flight by examining wing use during aerial challenges over ontogeny. Previous workers have used the Chukar Partridge (*Alectoris chukar*), a ground-dwelling game bird native to Asia but imported to the US, as a model system to explore the use of the wings to assist incline running (Dial, 2003). For comparison to this existing data set, chukars are a logical candidate for these experiments. For further comparison, I also examined one batch of Mallard Duck (*Anas platyrhynchos*), in order to provide contrast with a slower developing species that reaches an endpoint of long distance migration on the wing (Dial and Carrier, 2012). Two general methods are used. In drop tests, the birds are dropped from an inverted position to observe their righting response and any subsequent motions. In tosses, birds are thrown at a random orientation. The birds are compared to a null model of a passive ballistic ping pong ball, to allow visible detection of when birds are producing significant forces and torques in the air. Computational methods are also applied to closely check trajectories for the earliest detectable directed aerial descent.

1.2 Methods and materials

1.2.1 Study animals

A total of 26 Chukar Partridges (*Alectoris chukar*) in five batches, 15 male and 10 female, aged one day-post-hatching (dph), were obtained by hatching eggs from a local game bird farm (Fall Creek Game Birds; Felton, CA). Clean, unwashed eggs were placed in a forced air incubator (HovaBator, GQF Manufacturing; Savannah, GA) equipped with a turning tray. Eggs were held at 37.5 °C (99.5 °F) for 24 d; turning was discontinued at 21 d. Upon hatching, chicks were allowed to dry in the incubator for 12 h and transferred to a brooder bin. During

of antiquated "trees-down" and "ground-up" ideas; I feel these are not productive distinctions. Rather, it is more important to ask what the patterns are and what they are consistent with.

⁵ "Powered" flight is an artificial distinction based on a specious analogy with powered airplanes.

the course of experiments, chicks were housed in $53 \text{ cm} \times 38 \text{ cm} \times 30 \text{ cm}$ brooder bins heated with two 100 W floodlamps to maintain a brooder temperature of 29.4 °C the first week, 26.7 °C the second, and 23.9 °C for subsequent weeks. Birds were kept on wood shavings and offered crumbled chick starter rations (Purina; St. Louis, MO) and water *ad libitum*. Birds were also offered grit, freshly cut grass and mealworms. Chukars were studied at ages between 1 dph to 28 dph. All handling of chicks and eggs was under protocols (appendix A) approved by the UC Berkeley Animal Care and Use Committee (ACUC).

To provide comparison with a species with slower wing development, a single batch of five Mallard Ducks (*Anas platyrhynchos*), 2 male and 3 female, was obtained as day-old-hatchlings from a local waterfowl farm (Metzer Farms; Gonzales, CA). Ducklings were housed on absorbent bedding in a large fiberglass tub and were fed on higher-protein waterfowl starter (Mazuri, PMI Nutrition International, St. Louis, MO). Care of ducklings was similar to care for Chukar chicks, using protocols approved by the UC Berkeley ACUC. Ducks were studied at ages between 1 dph to 70 dph.

All birds were re-homed in private homes at the end of the study with ACUC permission.

For all birds, body mass was measured daily using a digital balance (Scout Pro; Ohaus, Parsipanny, NJ). Wings were also photographed daily, to measure areas, wingspan, aspect ratio, second moment of area, and wing loading. Birds were restrained by hand against a board and photographed using a digital camera (Canon PowerShot SD550). The photos were then digitized using a script written in Python. The resulting morphometric data were plotted and analyzed in R (R Development Core Team, 2013) to examine trends with age and mass. Aspect ratio, second moment of area, and wing loading were calculated as:

$$AR = s^2/A \tag{1.1}$$

$$I_s = \int \int_{wing} |\vec{r} - \vec{r}_{root}|^2 dA \tag{1.2}$$

$$WL = \frac{mg}{2A} \tag{1.3}$$

In addition to wing morphometrics, masses and lengths of appendage segments were taken from a dead Chukar chick (bird 31) that died at 11 dph of natural causes while under OLAC care. The bird was frozen immediately upon discovery. Parts were trimmed into segments using dissecting scissors, weighed using a digital mass balance and measured for length. Measurements were also made for one bird that died while hatching under OLAC care, and for three birds who died shortly after hatching obtained *post mortem* from a breeder.

1.2.2 General filming setup

Aerial behaviors were filmed using methods similar to (Jusufi et al., 2008, 2011; Munk, 2011). Birds were dropped in several different initial orientations (described below), from heights ranging between 0.5 m to 2.5 m (described below). Aerial behaviors were captured using a
suite of high speed and conventional digital video cameras. High speed cameras consisted of between one and three cameras (AOS Technologies AG, Baden Daettwil, Switzerland; or Fastec Imaging, San Diego, CA) operated at 500 frames/s, with one camera filming from the front and additional cameras filming from above or to the side. Conventional cameras consisted of up to seven high definition (HD) cameras (FlipHD, Cisco Systems, San Francisco, CA), typically with four cameras filming at different angles from the front and additional cameras filming from above or to the side. Illumination was provided by 16 100 W flood lights hung from the ceiling. The lights, in conjunction with additional oil heaters, were able to warm the entire filming area to the same temperature as the brooder area.

For 2D analyses, cameras were calibrated with a scale held in frame at the same position as the birds. For 3D reconstruction, camera parameters were estimated by filming a calibration object (chessboard) and using a Python script to implement single-camera and stereo camera calibration routines from the OpenCV library (see appendix B). Body positions (center or individual limbs) were then digitized frame by frame using ImageJ (NIH, Bethesda, MD) with the MTrackJ plugin (Meijering et al., 2012), and the resulting kinematics were analyzed as described below.

1.2.3 Aerial righting drop tests, righting success, and mode

The first batch of Chukars and the batch of Mallard Ducks were dropped with upright, 90° , and inverted (180°) orientations presented at random. It was found that righting from the fully inverted position occurred very quickly in both (Section 1.3, within 4 dph) and that drops from upright position always remained upright. Accordingly, subsequent drops for the remaining four Chukar batches were conducted only from the 180° inverted position. As required by the animal use protocol, birds younger than 4 dph were dropped from no higher than 0.5 m; birds older than 5 dph were dropped from 1 m.

Aerial righting drop tests were scored by two observers recording if birds landed on their feet. In addition to this, high speed videos were reviewed to confirm righting. Typically, the final bird position was also visible on Flip cameras. For all high speed videos, we recorded righting success, drop distance, final angle reached, and wingbeat frequency for the wing showing largest motions. Drop distance was the distance fallen before righting was complete. Final angle was the angle of the body attained at the end of the maneuver or when the body hit the ground if righting was not successful. Wingbeat frequency was recorded as the frequency of the wing with the largest motion during the maneuver (averaged over 2 to 5 beats during the course of the maneuver). Results were plotted and analyzed in R (R Development Core Team, 2013).

Mode used during righting was identified from the high speed videos for batch 2. Mode was clearly identifiable as either (1) righting by rolling using asymmetric wing and leg motions or (2) righting by pitching using symmetric wing and leg motions. These are discussed further in Section 1.3.

To test if righting and directed descent are visually mediated, drops were conducted with normal, blindfold, and sham treatments. Symmetric and asymmetric clipping of wings (all remiges proximal to the outermost secondaries) and complete clipping of the tail (all retrices) were also performed at the end of all other runs⁶. The results were analyzed using Pearson's χ^2 test in R (R Development Core Team, 2013).

1.2.4 Identifying the onset of directed aerial descent

We examined the onset of directed aerial descent during ontogeny and changes in directed aerial descent performance by dropping birds from 5 dph to 15 dph, 1 m away from a desirable target: the brooder with the rest of the brood, food, and water. The brooder was a suitable target because birds removed from it would typically exhibit a distress call and when released on the ground would walk towards the brooder. Other previous research also made use of the brooder to elicit movements (Jackson et al., 2009).

In batch 2 and later, birds were dropped along with standard ping pong balls. The ping pong ball provided a null model of the expected behavior under gravity alone in an indoor, still-air environment (simple ballistic model). Under ballistic assumptions, trajectories should be parabolic with the second order derivative reflecting gravitational acceleration (e.g. $\ddot{y} = g$ where $g = -9.81 \text{ m s}^{-1}$) (Galilei, 1638, reviewed in Naylor, 1980). The ping pong ball also allowed quick scoring of videos to identify if the birds fell slower than the ping pong ball and if birds made visible horizontal progress towards the brooder. For each high speed video, we identified (1) righting success; (2) if birds visibly yawed towards the brooder; (3) if birds visibly slowed their descent in relation to the ping pong ball; (4) if birds visibly made horizontal progress to the brooder and (5) if birds landed at the brooder. Results were plotted and analyzed in R (R Development Core Team, 2013).

Along with scoring of directed aerial descent performance in relation to falling ping pong balls, a quantitative analysis of the 2D kinematics of the body was conducted using maximum likelihood estimation (MLE) and an Akaike Information Criterion (AIC) (Akaike, 1974; Burnham and Anderson, 2002; Burnham et al., 2011) implemented in R (R Development Core Team, 2013) using the bbmle package. 2D analysis used a single side- or front view high-speed camera calibrated using scales within the image. Body position was digitized during the entire maneuver using ImageJ (NIH, Bethesda, MD) with the MTrackJ plugin (Meijering et al., 2012).

The onset of aerial behaviors was detected by examining where the observed behaviors are no longer well-described by a passive ballistic null model consisting of simple gravity in y and zero acceleration in x. To accomplish this, the likelihood of a given 3D trajectory was computed based on several candidate models for the behavior. These were then compared using an Akaike Information Criterion (AIC), which compares the likelihood of a model to the number of parameters needed by the model:

$$AIC = 2k - 2\ln(\mathcal{L}) \tag{1.4}$$

⁶In Chukar, manipulations to augment tail inertia were attempted by attaching plastic prosthetic long tails using veterinary wrap. Tail augmentation was not successful; birds tended to foul the prosthetic tail or mounting vet wrap with feces or groom it off. Tail augmentation tests are not reported further here.

The candidate models were obtained from normal distributions around expected trajectories:

$$g_{0}: x = X_{0} + \mathcal{N}(0, \sigma) \qquad (stationary)$$

$$g_{1}: x = X_{0} + Vt + \mathcal{N}(0, \sigma) \qquad (constant velocity)$$

$$g_{2}: x = X_{0} + Vt + \frac{1}{2}at^{2} + \mathcal{N}(0, \sigma) \qquad (constant acceleration)$$

$$g'_{2}: x = X_{0} + Vt - \frac{1}{2}9.81t^{2} + \mathcal{N}(0, \sigma) \qquad (Earth gravity)$$

$$g_{3}: x = X_{0} + Vt + \frac{1}{2}at^{2} + \frac{1}{6}bt^{3} + \mathcal{N}(0, \sigma) \qquad (constant jerk)$$

$$(1.5)$$

Models up to the sixth derivative of position (constant snap, crackle, and pop) were considered. The benefits of this method are that it explicitly identifies the measurement noise (as the σ term in the normal distribution in these examples) and that it provides an estimate of higher order derivative terms without the need to numerically differentiate measured kinematic data (which injects large amounts of noise, masking any effect we wish to observe, as it likely does in (Dial and Carrier, 2012). The derivation of these methods is given in Appendix C⁷.

1.2.5 Bird tosses, three-dimensional analyses and inertial contribution to turns

For a subset of runs, a three-dimensional analysis was conducted to examine more extreme examples of directed aerial descent not visible in 2D movements, as well as to examine the relative role of inertia versus aerodynamic forces and torques during righting. For these tests, birds were dropped as before. In addition, birds older than 10 dph were thrown at random orientations and directions. As in drop tests, tossed birds were thrown with a ping pong ball to provide ready visual indication of departures from simple ballistic behavior.

In addition to quantifying performance relative to a visible passive ballistic trajectory, a few runs with multiple high speed cameras were used in a detailed 3D kinematic analysis. The 3D kinematic analysis used a camera calibration technique that was developed based on (Bradski and Kaehler, 2008; Munk, 2011). The calibration made use of homography transforms for multiple views of a two-dimensional chessboard calibration object to obtain camera poses (3D position and rotation), focus (intrinsic) parameters, and relative positions to one another. With the camera parameters and with homologous points digitized in each image from each camera, a minimization routine was used to minimize the 2D reprojection error of the estimated 3D position. The method differs from (Munk, 2011) in the use of

⁷This method was also benchmarked against autorotating seeds in a collaborative side project with Stevenson et al. (Stevenson et al., 2013).

homography transforms and a 2D, repositionable calibration object (chessboard) compared to the large and fixed frame of (Munk, 2011); this makes the method here more field-portable and easy to setup. Details of the method are given in Appendix B.

The relative role of inertia in accomplishing maneuvers was examined using a numerical method to predict how the maneuver would unfold in the absence of any aerodynamic forces. The method is derived in Appendix D. For a subset of videos, six landmarks (head, right wing, left wing, right leg, left leg, and body) were digitized to allow computation of angular velocity and angular momentum during the righting maneuver.

Point masses were assigned 3D positions based on digitized body and limb positions obtained as described above. The mass values were scaled from measurements from a dead chukar of the same age. These were then used in a forward calculation, to calculate the angular momentum and examine if it is constant (as would be predicted in a maneuver dominated by inertia) or if it is time-varying (as would be predicted where aerodynamic forces and torques are large). The same data were also used in a reverse calculation, to obtain the whole body rotation that would result in a solely inertia case (i.e. in the case of a bird falling in a vacuum). The methods here are superficially similar to (Jusufi et al., 2008, work by Bergou) but avoid the need to derive explicit analytical expressions for multi-axis constrained linkages. By numerically performing this calculation, this method is more applicable to a wider range of geometries and situations where the inertia acting to accomplish the maneuver is not straightforward to identify and lump into a single rotating element.

1.2.6 Checking for wing-assisted incline running and other uses of proto-wings

To examine aerial righting and directed aerial descent in the context of other behaviors, we attempted to observe the onset of wing-assisted incline running (WAIR) (Dial, 2003) in Chukar batches 1 and 2 (n = 15 birds) and in Duck batch 1 (n = 5). Following (Dial, 2003), we attempted to run birds up inclines ranging from 15° to vertical, using surfaces covered in coarse grit sandpaper (Dial, 2003; Dial et al., 2008; Dial and Carrier, 2012; Jackson et al., 2009; Tobalske et al., 2011), corrugated cardboard, fabric (person's arm for Chukar; fabric-covered cardboard for Ducks), or hardware cloth (wire). The goal of these measurements was not to completely re-do previous work (Dial, 2003) but to check if our batch was tracking these previous observations.

Several methods were attempted to motivate birds to run up the incline. We attempted to scare birds by hand, by threat of capture, or simulated predator (plastic snake, tame retriever dog). We also placed birds on a level surface and then raised it. The most effective methods, as described in (Jackson et al., 2009), were to place other birds or mealworms or both at the top of the incline, or by placing the incline to lead from the outside to the wall of the brooder.

In addition to testing for WAIR (which we found to be hard to elicit), we examined use of wings during both vertical and long jumps. Both were elicited by suspending mealworms



Figure 1.1: Chukar mass (mean \pm standard deviation) versus age. During the 30 d experiment period, birds increased from around 10 g to around 100 g, a tenfold difference.

above or across from birds; or by placing birds on a platform with a gap to an identical platform on which the rest of the brood was placed. For Chukar, we also observed use of wings for wing-assisted balancing, on level but narrow cylinders (PVC pipe, person's arm). For Ducks, we observed wing flapping when drying and during swimming.

1.3 Results

1.3.1 Morphometrics during ontogeny

Figure 1.1 shows chukar mass as a function of age. Wing morphometrics are given in figure 1.2. Wing loading and wingbeat frequency are shown in figure 1.3. Mass, area, span, second moment of area, and wing loading all increased monotonically through ontogeny. Area and span increased linearly with age. Aspect ratio did not change significantly with age (linear regression, p = 0.07), though it did show a slight decrease with mass (linear regression, p = 0.03). Second moment of area appeared to increase with age².5 (linear regression, $p = 2.2 \times 10^{-5}$).

Wing morphometrics revealed some breakpoints with age or body mass. Area had a breakpoint at 6 dph; analysis of variance showed that a model with two different lines was a better fit than one with one line (ANOVA, $p = 2 \times 10^{-4}$). Similarly, against body mass, breakpoints were found in mass, span, and second moment of area at 30 g (ANOVA, minimum $p = 4.1 \times 10^{-5}$).



Figure 1.2: Wing morphometrics as a function of age (left) and mass (right). Wing area, span, and second moment of area increase steadily with age and with increasing body mass. Aspect ratio remains relatively constant.



Figure 1.3: Wing loading and wingbeat frequency. Wing loading decreases abruptly prior to 10 dph, and may reach a minimum at around 20 g, where birds develop 100% righting and at the onset of directed aerial descent. Wingbeat frequency increases steadily with age.

As in wing morphometrics, breakpoints were observed in wing loading at 7 dph and 30 g body mass (ANOVA, $p = 2.2 \times 10^{-16}$). Prior to these, wing loading is decreasing steadily; wing loading decreases less after birds reach 7 dph or 30 g.

Masses and lengths of appendage segments of an 11 dph Chukar chick are given in table 1.2. Table 1.2: Masses and lengths of body parts of an 11 dph Chukar chick (bird 31), total mass 17.41 g, total length 9.7 cm. Chukar died of natural causes under OLAC care.

segment	mass, g	length, cm
femur	0.58	1.9
tibiotarsus	0.57	2.8
tarsometatarsus	0.21	2.2
pes	0.18	2.0
digits I-III	0.26	2.9
radius-ulna	0.21	2.4
humerus	0.27	1.7
neck	1.13	3.2
head	2.72	3.2

1.3.2 Righting success and mode

Basic aerial righting performance is shown in figures 1.4 through 1.7. As mentioned above, birds dropped in initial upright positions stayed upright all the time. Birds dropped in inverted position began to right by using asymmetric wing and leg movements to accomplish aerial righting by rolling (figure 1.5A, purple in figure 1.4 bottom). Rolling with asymmetric wing and leg movements typically took 3-5 wing beats to accomplish, by which time birds had fallen about 1 m (figure 1.6 left side).

After 9 dph, every bird righted during every drop. Around this same time, birds began to use symmetric wing and leg movements for aerial righting by pitching (figure 1.5B, blue in figure 1.4 bottom). Pitching with symmetric wing and leg movements typically took 1 wing beat to accomplish, with birds falling less distance (figure 1.6 right side).

The mode (asymmetric/rolling versus symmetric/pitching) of righting was clearly diagnosed from high speed video. Asymmetric rolling consisted of large amplitude movements of one wing, with the other wing tucked or making only small amplitude motions and with considerable phase difference between wings. Asymmetric rolling was also characterized by asymmetric leg kicking during rolling, and took 3 to 5 wingbeats in order to reach a fully upright position. Asymmetric rolling movements never included rotations in pitch.

In contrast, symmetric pitching consisted of large amplitude, in-phase movements of both wings. Leg kicking was absent or was confined to symmetrical movements of both legs, during the end portion of the movement as the bird reached fully upright. While some symmetric pitching movements included a roll component, the symmetric nature of the movement was always apparent; figure 1.4 shows only a small number of trials (pink) in which the mode could not be clearly identified.

Figure 1.5 also shows that some early birds may have pushed off during drops (green); push off was readily apparent because 1 dph birds who pushed off moved no appendages, and often rotated beyond 180°. This was corrected for in older birds, but was difficult to fix in the youngest because of difficulty manipulating such tiny animals; it is included in the plot to show the absence of handling difficulties in the bulk of the dataset.

Figures 1.8 and 1.9 show the pronounced wing asymmetry during righting by rolling. One wing is held fixed or tucked, while the other is flapped. Legs are also kicked asymmetrically during this maneuver.

Results from tests with blindfolded and sham-treatment birds are given in table 1.3. All birds righted, with or without blindfold; blindfold also did not affect the mode of righting used. Results from tests with wing and tail clipping are given in table 1.4. Wing or tail clipping did not affect righting; all birds righted regardless of clipping.

1.3.3 Directed aerial descent onset and performance

Figure 1.10 shows the percentages that birds exhibit righting, turning to the brooder, slowing of their descent, moving towards the brooder, and landing in it as viewed in high speed videos. The figure shows a gradual progression to full directed descent capability around



Figure 1.4: Percent righting and righting mode versus age in Chukar. By 9 dph, Chukars right every bird every time. A rolling maneuver accomplished by asymmetric wing and leg movements is used prior to 14 dph (purple (see figure 1.5A)). Starting around 9 dph, birds switch to pitching using a symmetric wing movement (blue) (figure 1.5B). The onset of righting by 9 dph corresponds to an increase in wing area and span and a decrease in wing loading (refer to Figure 1.3).



Figure 1.5: Example composite images of righting. Photos are 100 ms apart. A. Righting by rolling using asymmetric wing and leg movements, used prior to 14 dph. This mode of righting is readily recognized by strong motions of one wing and absent or weak motions of the other, as well as asymmetrical leg kicking during the righting. It is accomplished in 3 to 5 wingbeats and a drop of about 1 m. B. Righting by pitching using symmetric wing movements, prevalent after 9 dph. This mode is distinguished from rolling by strong, symmetric movements of both wings. Leg movements are symmetric as well and occur after pitching. Typically, pitching maneuvers were accomplished in 1 wingbeat and 0.25 m to 0.5 m drop.

Table 1.3: Righting results for control, blindfold, and sham-treatment birds at 15 dph. Mode differences are not significant (Pearson's χ^2 test, p = 0.09949).

righting mode	blindfold	$\operatorname{control}$	sham
symmetric, pitch	0	2	0
asymmetric, roll	5	3	5



Figure 1.6: Drop distance during righting versus age in Chukar, for birds that successfully righted. Drop distance decreases as birds switch from rolling to pitching (linear regression, p = 0.0189).

20 dph. This corresponds to the onset of the ability to make unassisted takeoffs from the ground from rest (results in section 1.3.5).

Figures 1.11 through 1.16 show the results of using the maximum likelihood estimation (MLE) and an Akaike Information Criterion (AIC) to detect onset and continuing directed aerial descent. These confirm the findings from gross observation of trajectory in comparison to ping pong balls thrown as passive tracers.

The MLE and AIC method was used to examine acceleration and force production in Chukar batch 2 from 1 dph to 14 dph (figures 1.17 and 1.18). Results show all trajectories after 4 dph show significant support for a vertical model with $a < 9.81 \text{ m s}^{-2}$ and a horizontal model with measurable acceleration (figure 1.17), indicating a lower bound for the onset of directed aerial descent. Force production increases steadily during this period (figure 1.18).

Figures 1.19 and 1.20 show extreme examples of directed aerial descent in which the birds are thrown at random angles. In each they perform major righting and yawing movements, then make progress to a desired target, slow their descent, and land at the desired target.



Figure 1.7: Final roll angle versus age in Chukar. This plot includes birds that do not successfully right, to illustrate progress in righting over the first 5 dph. Following 7 dph to 10 dph, birds are righting every time from fully 180° inverted position.



Figure 1.8: Additional example of righting by rolling using asymmetric wing and leg movements, bird 23, 7 dph, mass 18.51 g. In this bird, the left wing is held fixed while the right wing flaps. In addition, the right leg is kicked near the start of righting. The left wing and left leg are moved only near the end of the maneuver.



Figure 1.9: Body angle to horizontal and wing angles relative to body for the maneuver depicted in figure 1.8. At the start of the maneuver, the left wing is held fixed (stroke amplitude not visible), while the right wing is flapped (stroke amplitude about 180°, wingbeat frequency about 10 Hz for 3.5 wingbeats). Righting is not confined to a single wingbeat but proceeds over the entire maneuver.

Table 1.4: A. Righting results for wing clipping at 29 dph. Mode differences are significant (Pearson's χ^2 test, p = 0.03045). B. Righting results for tail clipping; mode differences are not significant (p = 0.3671). C. Directed aerial descent results for wing clipping; results significant ($p = 1.625 \times 10^{-8}$). D. Directed aerial descent results for tail clipping; results not significant (p = 0.2177).

	righting mode	both wings	wings	right wing	
۸		clipped	intact	only	
A.	symmetric, pitch	7	29	5	
	asymmetric, roll	5	7	7	
	righting n B. symmetric asymmetric	node ta clipj c, pitch 3 ic, roll 1	il ta ped int 1 1 7 2	ail act 2	
С.	lands in brooder	both wings clipped	ngs wings right wing d intact only 5 10		
	yes	12	0 31	10	
	lands in b D. yes	prooder ta		ail $\frac{tact}{3}$	



Figure 1.10: Directed aerial decent percentages of righting, turning to the brooder, slowing descent, moving to the brooder, and landing in the brooder, versus age in Chukar.



Figure 1.11: 1 dph bird 21, mass 14.2 g. The bird's fall is well described by ballistics with $g = 9.81 \,\mathrm{m\,s^{-2}}$; at 1 dph it is not detectably altering its trajectory in the air. A: Digitized position (black dots) and MLE/AIC analysis result (red line). B: Composite image

of maneuever. Bird has adopted a sprawled, reversed skydiving position.



Figure 1.12: 5 dph bird 6, mass 14 g. The bird is flapping and has detectably slowed its downward acceleration to $9.4 \,\mathrm{m\,s^{-2}}$. This is the onset of directed aerial descent. A: Digitized position (black dots) and MLE/AIC analysis result (red line). B: Composite image of maneuever.



Figure 1.13: 10 dph bird 21, mass 23.6 g. Downward acceleration has slowed to $8.9 \,\mathrm{m\,s^{-2}}$. A: Digitized position (black dots) and MLE/AIC analysis result (red line). B: Composite image of maneuever.



Figure 1.14: 10 dph bird 21, mass 23.6 g. Downward acceleration at $8.4 \,\mathrm{m\,s^{-2}}$. This is readily visible as the bird lands after the ball. A: Digitized position (black dots) and MLE/AIC analysis result (red line, bird; magenta line, ping pong ball). B: Composite image of maneuever.



Figure 1.15: 10 dph bird 24, mass 26.6 g. The bird is falling visibly slower than the ball. A: Digitized position (black dots) and MLE/AIC analysis result (red line, bird; magenta line, ping pong ball). B: Composite image of maneuver.



Figure 1.16: 11 dph bird 21, mass 25.4 g. The bird is falling visibly slower than the ball. A: Digitized position (black dots) and MLE/AIC analysis result (red line, bird; magenta line, ping pong ball). B: Composite image of maneuever.



Figure 1.17: Acceleration and forces from MLE and AIC analysis from 1 dph to 14 dph in Chukar batch 2 (n = 5 birds). Following 4 dph, AIC indicates all trajectories show significant support for a vertical model with $|a| < 9.81 \text{ m s}^{-2}$ and a horizontal model with measurable acceleration. The null model for passive ballistics without drag is gravitational acceleration $|g| = 9.81 \text{ m s}^{-1}$ and constant horizontal velocity.



Figure 1.18: Overall force, from MLE and AIC analysis from 1 dph to 14 dph in Chukar batch 2 (n = 5 birds). Force production increases over the entire period, illustrating continuously increasing capacity for directed aerial descent over ontogeny.



Figure 1.19: 17 dph bird 2, mass 39 g. Bird is obviously directing its descent. The bird falls slower than the ball, visibly yaws, and extends its trajectory to the brooder.



Figure 1.20: 19 dph bird 41, mass 66 g. Bird is obviously directing its descent. If the bird were not directing its descent, it would follow the passive ballistic path outlined. By turning 180° towards a preferred location and slowing its descent, it has shown it is using directed aerial descent.



Figure 1.21: Example three-dimensional analysis for bird 5, 14 dph, 46 g. Trajectory here includes rolling, reversal of direction, yawing, and slowing of descent that cannot be explained by a passive ballistic parabolic trajectory. Likelihood is vanishingly small and ballistic models fail as explanations of the entire behavior.

1.3.4 Tosses, three-dimensional analysis, and inertial contributions

An example three-dimensional analysis is shown in figure 1.21. As in the 2D shots, the trajectory here is demonstrably different from the passive trajectory of the ball thrown with the bird.

Figure 1.22 gives the digitization of additional points in the aerial righting maneuver of figure 1.8. In addition to wing angles, leg angles and extension are plotted in figure 1.23.

Following the methods derived in appendix D, additional analyses of a roll and a pitch maneuver are shown in figures 1.24, 1.28, and 1.27. The roll and pitch maneuvers are shown in figure 1.24A and B, respectively. Figure 1.28 gives the angular momentum calculated from the maneuver and the predicted body angle in a vacuum for the roll maneuver. Figure 1.27 gives these same quantities for the pitch maneuver.



Figure 1.22: Digitized positions of head (black dot), wings (blue lines) and legs (green lines) for the righting maneuver of figure 1.8, bird 23, 7 dph, 18.51 g. In this maneuver, the bird holds the left wing fixed while flapping the right wing. There is a kick by the right leg at the start of righting. The left leg and left wing are moved only at the end of the maneuver.

1.3.5 Wing-assisted incline running and other uses of proto-wings

We attempted to observe wing assisted incline running (WAIR), in order to help benchmark our aerial behaviors with previous work (Dial, 2003; Dial et al., 2008; Jackson et al., 2009). Within Chukar, we found it difficult to elicit WAIR behaviors. Batch 1 (n = 8) Chukars showed no WAIR during 3 h of trials at 4 dph. At 6 dph to 7 dph, WAIR was weak and rare, with two bouts observed during 2 h of trials, all at inclines below 45°. In Batch 2 (n = 6) at 12 dph, we were only able to elicit WAIR in 1 out of 4 trials. At 19 dph, we observed WAIR at 45° in five of eight birds. During all trials, we obtained six successful high speed videos of WAIR, all at angles below 45°. Above 45°, birds flapped briefly, and then jumped off the incline and headed down it. During tosses to observe directed aerial descent, we threw five Chukars at a felt covered wall; birds never WAIRed up the wall, but did remain flapping prior to pushing off the wall to continue their descent. Chukar chicks placed on hardware



Figure 1.23: Body angles, wing and leg angles, and leg extension for the righting maneuver of figure 1.8. The start of rolling corresponds to both right wing downstroke and a kick-ing/abduction movement of the right leg (around t = 0.1 s). Righting is not confined to this period, however, and takes place over the course of several more wingbeats of the right wing. The left wing and leg and moved only near the end of the maneuver.

cloth failed to WAIR, however I observed one adult Chukar performing WAIR up hardware cloth, and one performing WAIR up an avocado tree (*Persea americana*), in an outdoor enclosure after the end of experiments.

In contrast to WAIR, we were able to observe several other uses of wings, concomitant with the development of aerial righting and directed aerial descent. At 2 dph, Chukars were observed to use their wings to control pitch during voluntary jumps for mealworms. 7 dph Chukar were observed to use their wings when balance was challenged, such as when placed at the narrow lip of the brooder, or on a PVC pipe, or on a researcher's arm, hand, or finger. At 16 dph, Chukars made voluntary jump takeoffs from the ground, to cover horizontal distance across gaps. At 24 dph, Chukars made voluntary vertical ascending flights from rest of up to 1 m, to rejoin the brooder.

With Ducks, we were unable to elicit WAIR at all, in contrast to (Dial and Carrier, 2012). As incline angle increased, Ducks would place their belly on the incline and attempt



Figure 1.24: (left) Roll maneuver in 10 dph bird 25, mass 27.0 g. (right) Pitch maneuver in 10 dph bird 53, mass 36.3 g.

to kick up it; at higher angles they would not attempt to ascend. Ducks also showed wing use during jumping, and increasing wing frequency during flap-drying and during bathing movements.

1.3.6 Ducks

Ducks developed more slowly than Chukars but exhibited the same stages in the development of aerial behaviors. While Chukars reached 100 g over a 19 d period, Ducks attained 1.2 kg over 62 d (figure 1.29).

As in Chukar, Duck wing morphometrics revealed breakpoints with body mass. Area had a breakpoint at 30 dph; analysis of variance showed that a model with two different lines was a better fit than one with one line (ANOVA, $p = 6.33 \times 10^{-7}$). Similarly, against body mass, breakpoints were found in mass, span, and second moment of area at 300 g (ANOVA, minimum $p = 2.2 \times 10^{-16}$).

For Ducks, breakpoints were observed in wing loading at 20 dph (ANOVA, $p = 1.0 \times 10^{-10}$) and 300 g body mass (ANOVA, $p = 2.2 \times 10^{-16}$). Prior to 20 dph, wing loading is increasing,



Figure 1.25: Body positions and angular momentum during roll maneuver in figure 1.24A, 10 dph bird 25, mass 27.0 g. A. Measured positions of wings (blue) and legs (green). B. Position predicted from inertial-only model. C. Angular momentum of each element in model. D. Total angular momentum, which is not constant.

unlike in Chukar. Wingbeat frequency is also decreasing slightly prior to 30 dph, unlike in Chukar.

Ducks used the same asymmetric wing and leg movements as Chukar to attempt righting early in ontogeny, however they were not successful in righting until much later (30 dph for Ducks versus 6 dph to 7 dph in Chukar). The mode of righting did not show as clear a division between rolling and pitching in time; Ducks continued to use rolling motions later in ontogeny.

As in Chukar, for Ducks, directed aerial descent was observed to progress from righting, to turning to the brooder, slowing descent, moving towards the brooder and landing in it. Ducks completed this progression much later (60 dph) and at larger body mass (1.2 kg).



Figure 1.26: Measured body angle (dots) and body angle predicted for zero angular momentum righting, 10 dph bird 25, mass 27.0 g (maneuver in figure 1.28). Only the first part of the maneuver appears to fit a zero angular momentum turn. A model with only inertia overpredicts the final body angle reached; aerodynamic mechanisms are necessary for control of righting and are dominant contributors at higher speeds.



Figure 1.27: Body positions and angular momentum during pitch maneuver in figure 1.24B, 10 dph bird 53, mass 36.3 g. A. Measured positions of wings (blue) and legs (green). B. Position predicted from inertial-only model. C. Angular momentum of each element in model. D. Total angular momentum, which is not constant.



Figure 1.28: Measured body angle (dots) and body angle predicted for zero angular momentum righting, 10 dph bird 53, mass 36.3 g (maneuver in figure 1.27). Only the first part of the maneuver appears to fit a zero angular momentum turn. A model with only inertia overpredicts the final body angle reached; aerodynamic mechanisms are necessary for control of righting and are dominant contributors at higher speeds.



Figure 1.29: Duck mass (mean \pm standard deviation) versus age. During the 60 d experiment period, birds increased from around 40 g to around 1.2 kg, a 30-fold difference.


Figure 1.30: Wing morphometrics as a function of age (left) and mass (right). Wing area, span, and second moment of area increase steadily with age and with increasing body mass.



Figure 1.31: Wing loading and wingbeat frequency. Wing loading increases prior to 20 dph, unlike Chukars, and reaches a maximum at around 300 g. Righting is greatly delayed in Ducks. Wingbeat frequency during righting decreases with age in Ducks as wing areas increase.



Figure 1.32: Percent righting and righting mode versus age in Ducks. By 37 dph, Ducks right every bird every time. A rolling maneuver accomplished by asymmetric wing and leg movements is used prior to 60 dph (purple) (see figure 1.34). Very late in ontogeny, Ducks switch to pitching using a symmetric wing movement (blue) (figure 1.35). The onset of righting between 11 dph to 28 dph corresponds to increases in wing area and span and a decrease in wing loading.



Figure 1.33: Duckling attempts to righting by rolling using asymmetric wing and leg movements. Left wing is flapping, right wing is not. Legs are also kicked in an asymmetric motion. Duck does not successfully right.



Figure 1.34: Righting by rolling using asymmetric wing and leg movements, used prior to 50 dph in Ducks. This mode of righting is readily recognized by strong motions of one wing and absent or weak motions of the other, as well as asymmetrical leg kicking during the righting. It is accomplished in 3 to 5 wingbeats and a drop of about 1 m.



Figure 1.35: Righting by pitching using symmetric wing movements, prevalent after 50 dph in Ducks. This mode is distinguished from rolling by strong, symmetric movements of both wings.



Figure 1.36: Final roll angle versus age in Duck. This plot includes birds that do not successfully right, to illustrate progress in righting over the first 37 dph. Following 37 dph, Ducks are righting every time from fully 180° inverted position.



Figure 1.37: Directed aerial decent percentages of righting, turning to the brooder, slowing descent, moving to the brooder, and landing in the brooder, versus age in Ducks.



Figure 1.38: Directed aerial descent in a Duck. Duck is thrown in inverted position, rights by pitching using asymmetric wing movements, steers towards the brooder, slows its descent, and lands in the brooder.

1.4 Discussion

1.4.1 Observed sequence is consistent with aerial hypotheses

During ontogeny, birds grew progressively better at responding to aerial challenges. In Chukar, at 1 dph, birds did little to alter their fall compared to a falling passive projectile. Aerial righting developed first (4 dph, figures 1.4, 1.6, and 1.7) using an asymmetric rolling mode. Starting at 9 dph, birds began transitioning to righting in pitch, using symmetric flapping. Righting was followed by an expanding suite of behaviors (yaws to preferred targets, slowing of descent, horizontal progress, and landing at preferred targets; figures 1.10, 1.17 and 1.18) along a continuum of directed aerial descent. At 10 dph, descents were visibly slowed compared to a passive reference (ping pong ball). During ontogeny, ability to use the wings in other contexts (jumps, short vertical flights) also increased. These are all consistent with aerial hypotheses of the origin of flight (Dudley and Yanoviak, 2011). Manipulations were also carried out during the experiment to show that righting is not visually mediated and that righting requires use of the wings.

The aerial responses, especially maximal accelerations identified from trajectories (figure 1.17), agree well with Jackson et al's descriptions of controlled flapping descent (CFD) (Jackson et al., 2009). Accelerations identified in other previous work (Dial and Carrier, 2012) are less clearly interpreted because the other work's use of finite differences injected large amounts of noise.

1.4.2 Observed sequence precedes WAIR

Righting was first accomplished with asymmetric wing and leg motions that caused the body to roll (figure 1.5)⁸. This preceded the onset of wing-assisted incline running and is in good agreement with the "asymmetric flapping / quadrupedal crawling" stage identified in (Jackson et al., 2009). By the time WAIR was observed, birds had already been capable of the first stages of directed aerial descent for several days, and had already exhibited righting by pitching using symmetric movements of the wings and legs.

The shifts in preferred directions of maneuvering and methods used to accomplish aerial righting, by left-right asymmetric movements, inertial movements, or symmetric movements as predicted by maneuvering hypotheses (Dudley and Yanoviak, 2011). Furthermore, the prediction that all the same stages would occur in a bird of a vastly different size and delayed developmental trajectory (Duck) is also supported. In contrast, the predictions of an alternative hypothesis (Dial, 2003; Dial et al., 2008; Tobalske et al., 2011) are not borne out in our observations; during both evolution and ontogeny, organisms maneuver early on, using left-right asymmetries; while the symmetrical flapping needed for wing-assisted incline running only comes later.

This suggests that WAIR is a by-product of flight, rather than a cause of or early phase of it. This is supported by the relative rarity of WAIR in these experiments, markedly in

⁸Roll-first may correspond to model test and stability results in chapter 3.

contrast with claims of "every bird, every time" in (Dial, 2003). Onset WAIR did correspond to the use of wings for other tasks (balancing, pitch control during jumps, etc), and it is not to suggest that WAIR for an animal with capable wings is an effective way to navigate an obstacle. However, flight is an aerial behavior, and it is most parsimonious to consider its development driven by aerial tasks. As further support for this, we know of no study that has demonstrated WAIR in chicks in any ecologically relevant context in the field⁹. On the other hand, behaviors in which newly hatched chicks jump from trees or other high places appear in wood ducks (*Aix sp.*), guillemots (*Uria sp.*), and murrelets (*Synthliborhamphus sp.*) (Attenborough, 1998); other undescribed examples certainly exist.

1.4.3 Inertial mechanisms important early, largest inertias are head and legs; aerodynamic mechanisms dominate later

Birds lack a massive tail (unlike geckos) and their axial skeleton is stiffened by imbricated ribs and by the widespread fusion at the synsacrum (unlike mammals). I expected the avenues available to other vertebrate taxa for generating zero-angular-momentum turns would not be present in birds. This was not supported; young birds still appear partially capable of using inertia from wings and legs. However, zero-angular-momentum mechanisms appear only to be effective at the start of maneuvers while at low speed. The remainder of the maneuver is not zero angular momentum; inertial-only models over-predict motion in late stages, and righting maneuvers took much longer to complete than would be anticipated if they were solely inertial.

Despite the limitations of inertial mechanisms, their importance early in maneuvers supports maneuvering hypotheses of the origin of flight. Early in a maneuver (or in ontogeny or in evolution), a wide range of mechanisms (each of which may only be moderately effective) are used to accomplish righting and turns. The inertias associated with limbs are significant: wings are 8% of body mass in 10 dph Chukar (table 1.2); while the head and neck are 22% and the legs are 17%. Wing inertia increases relatively quickly (for example, wing second moment of area, figure 1.2D, scales as $J_a \sim t^{2.5}$). It remains to be seen if there is a "sweet spot" where inertia is briefly dominant before aerodynamic forces take over.

Theropod ancestors of birds had similar hips but lacked the rib cage stiffening; they also possessed long tails, and studies of falling bird chicks alone may not fully address this. While manipulations to increase tail inertia by adding a prosthesis were not successful here, we predict that aerial righting reflexes are present in other archosaurs. This would provide a (somewhat weak) extant phylogenetic bracket for the presence of aerial righting in bird ancestors.

An area not yet addressed is the size-scaling of aerial righting ability. Chukars (10 g to 100 g) developed aerial righting very quickly; this was much delayed in Ducks (0.04 kg to 1.2 kg). Duck wings were much smaller initially in comparison to body size, however

⁹According to hunter's accounts, Chukar adults use WAIR to run up trees in order to glide down slopes and drops (O'Toole, 2003); adult WAIR use would follow development of all other aerial behaviors.

Ducks were able to use inertia associated with other appendages (namely the head, neck, and legs) for maneuvers. Many phylogenetic reconstructions of size in the clades leading to birds suggest they were small, perhaps small enough that both inertia and aerodynamics are important in the initial aerial righting given the phylogenetic constraints on axial body movement.

1.4.4 Evolutionary significance for the origins of bird flight

WAIR has received much attention because of the assertion, via the ontogenetic transitional wing (OTW) hypothesis, that it was a major ancestral function in the theropod ancestors of birds. I state two reservations here. First, there is no guarantee that "ontogeny recapitulates phylogeny," though here I entertain the idea in response to previous work (Bundle and Dial, 2003; Dial, 2003; Dial et al., 2008; Dial and Carrier, 2012; Jackson et al., 2009; Tobalske et al., 2011). Second, the assertion by some WAIR proponents that raw force generation by symmetric wing movements comes first and that aerial maneuvering and control come later is wrong. We have seen here that aerial righting (a maneuver) precedes WAIR in ontogeny. Every animal in the air, whether it took off from the ground, jumped off the top of an incline it had run up, or fell from a tree, must maneuver, and early ability to maneuver (righting, directed aerial descent) is evidence of this. WAIR may be important, but maneuvering is more important and informative in understanding the evolution of flight in birds.

Aerial righting and some degree of maneuverability has been demonstrated in a wide range of animals, including ones without wings or other obvious aerial features such as ants (Munk, 2011), geckoes (Jusufi et al., 2008, 2010), stick insects (Jusufi et al., 2011; Zeng, in prep), or even skydiving humans (Cardona et al., 2011; Evangelista et al., 2012). It should not be surprising to see similar sequences among vastly different taxa; flight is constrained by physics. Physics is independent of phylogenetic history, so some degree of convergence should be reassuring, but it is still important to also test such hypotheses against what we know of the phylogenetic history to provide robustness against the sins of conflating ontogeny with phylogeny or of making too much out of a single species. This will be the focus of Chapters 2 and 3.

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Chapter 2

Aerodynamic characteristics of a feathered dinosaur shape measured using physical models, part I: effects of form on static stability and control effectiveness

I report the effects of posture and morphology on the static aerodynamic stability and control effectiveness of physical models based loosely on a feathered dinosaur, $\dagger Microraptor gui$, from the Cretaceous of China. While some leg postures render $\dagger M$. gui unstable, and thus quick to maneuver, others are stable, slower to maneuver but resistant to perturbation by wind gusts. Depending on body posture, asymmetric leg positions can cause roll but have surprisingly little effect on yaw, while raising and lowering the tail or the hind limbs can alter pitch. These results may help bound speculation and inform debate regarding $\dagger M$. gui specifically, which has attracted much attention due to its leg and tail feathers. Furthermore, while $\dagger M$. gui lived after $\dagger Archaeopteryx$ and likely represents a side experiment with feathered morphologies, the general patterns of stability and control effectiveness as leg and tail morphologies are changed may help understand the evolution of flight control aerodynamics in vertebrates. As further fossils with different morphologies or postures are found, these results could be applied in a phylogenetic context to understand potential biomechanical constraints on extinct flyers or gliders arising from the need to maneuver.¹

¹This chapter is intended for *PLoS*. Methods were previously presented in public at a conference as (Koehl et al., 2011; Tisbe et al., 2011) and in public talks by a faculty member without my knowledge.

2.1 Introduction

The evolution of flight in vertebrates, and particularly in birds, is the subject of lively debate and considerable speculation. Furthermore, flight ability of extinct vertebrates is often inferred from very simple parameters (such as lift and drag coefficients and glide angles (Emerson and Koehl, 1990; Emerson et al., 1990)); these alone may not be sufficient as anything flying in a real environment will experience perturbations and the need to maneuver around obstacles (Dudley and Yanoviak, 2011).

Discoveries (Xu et al., 2003; Zhou and Zhang, 2006; Zhou et al., 2003) during the last decade of a diversity of feathered dinosaurs and early birds from the Cretaceous of Liaoning, China have led to considerable speculation about the roles that the feathers played on these extinct animals. Fossil forms are important in biomechanical studies because they may indicate "missing links", transitional forms within a lineage, between ancestral and derived taxa, or they may record "experiments" in form in side-branches; both are informative for questions of biomechanics. Although we cannot observe the behavior of extinct animals, we can measure the aerodynamic forces on dynamically-scaled physical models in a wind tunnel to quantify the broader effects on performance of different postures and morphologies. Since physical laws apply the same to all taxa, regardless of history, knowing about the physical implications of shape can suggest "priors" that would apply to anything in the air.

The Jiufotang Formation has been interpreted as a forest based on pollen data and plant fragments (Duan et al., 1995; Zhou et al., 2003). The inference that $\dagger M$. gui was arboreal solely based on pollen is not terribly strong, given that not everything that lives in a forest lives in the trees and that processes after death (taphonomy) that occur during fossilization also tend to wash everything together. However, quite many things in forests make use of the trees even if they don't appear particularly arboreal (Jenkins and McClearn, 1984). In addition, the vertebrate diversity includes several species of pterosaurs (Wang and Zhou, 2003; Wang et al., 2008) as well as numerous feathered theropod dinosaurs and enantornithine birds (He et al., 2004; Norell and Xu, 2005; Xu, 2006; Zhou, 2004; Zhou and Zhang, 2003; Zhou et al., 2003), many with small size (Turner et al., 2007) and similar feathered forms, suggesting that at least some might have been in the trees and performing aerial behaviors.

I used physical models (Reynolds, 1875), loosely based on $\dagger Microraptor gui$ (Figure 2.1), a cat-sized dromaeosaur with flight feathers on its forelimbs, hindlimbs, and tail, enabling us to investigate effects of diverse aerodynamic surfaces in the aft/posterior of a body. By measuring not just lift and drag, but also side forces and moments in pitch, roll, and yaw, I can assess static aerodynamic stability (tendency to experience righting torques when perturbed) and control effectiveness (moments generated by motions of control surfaces), both of which affect the ability to maneuver while gliding or parachuting through a complex forest habitat (McCay, 2001a, 2003).

I compared the lift, drag, and side forces, and the pitch, roll, and yaw moments on models with versus without leg feathers, and I tested the models in different symmetric and asymmetric postures that have been proposed by various researchers. In some cases leg feathers had no effect, and in others they did (e.g. leg feathers reduced drag for some



Figure 2.1: \dagger *Microraptor gui* Xu et al. (2003), a dromaeosaur from the Cretaceous Jiufotang Formation of Liaoning, China. Holotype specimen IVPP V13352, scale bar 5 cm. Notable features include semilunate carpal bones, a boomerang-shaped furcula, a shield-shaped sternum without a keel, uncinate processes on the ribs, unfused digits, an intermediate angle of the scapulocoracoid, and a long tail of roughly snout-vent length. In addition, there are impressions of feathers on the forelimbs, hindlimbs, and tail.

postures at some angles of attack). Therefore, whether or not leg feathers affected gliding, parachuting, or maneuvering performance depended on the posture and orientation of the dinosaur. These results will contribute to our understanding of the role of empennage in animal flight control.

In this chapter, I seek to examine the role of shape in static aerodynamic stability. I hypothesize that shape and posture will have large effects on stability, larger than traditional metrics considered (Emerson and Koehl, 1990). Vertebrate fliers (birds, bats, pterosaurs) seem to converge on a two-wing high aspect ratio geometry, although larger variation in geometry is seen when considering all vertebrate taxa with aerial behaviors. In particular, the multiple surfaces of \dagger *Microraptor* might be expected to have large impacts for maneuvering (Lehmann and Pick, 2007; Standen and Lauder, 2005, 2007; Wang and Sun, 2005). In engineering practice, snap rolls up to dangerously large angles in 7800 long ton nuclear submarines can be caused by interactions between the sail (upstream appendage) and rudder (downstream appendage)². In biology, interactions between median or paired fins can enhance maneuvering in fish (Fish and Lauder, 2006; Lauder et al., 2002; Standen and Lauder,

²In the submarine case, dihedral planes are sometimes added to stabilize the ship; I hypothesize that leg feathers may have such a stabilizing role here.

2005, 2007). A four-(or more) flipper planform is widely seen in aquatic creatures, and also occurs in some "gliders" like frogs (McCay, 2001a) and four-winged flying fish (Park and Choi, 2010).

I also seek to determine which appendage movements are effective in creating forces and torques that might be used for maneuvering, and which appendage movements are not effective. A two-year-old pretending to be a ballerina might imagine several postures that could cause yaws or rolls. Other possibilities emerge when considering the use of wings in fixed wing behaviors in *Draco*, *Calypte anna*, or of appendages in frogs, bristletails, stick insects, or ants. I hypothesize that symmetric appendage movements will be most effective in pitch, while asymmetric movements will create rolling and yawing movements (see also chapter 1). Based on intuition from activities like skydiving³ and windsurfing⁴, the most effective control movements should make large movements of large surfaces far from the center of mass such as long tails or large wings.

Finally, I wish to test if the function of appendages varies with the aerodynamic environment, e.g. speed and Reynolds number, or angle of attack and glide angle. Among invertebrates, directed aerial descent performance at high glide angles is widely distributed even among taxa without obvious aerial features (Dudley and Yanoviak, 2011; Munk, 2011; Zeng, in prep). During a transition between high glide angle directed aerial descent and lower angle behaviors, functions of appendages in creating aerial forces and moments may shift. High angle of attack aerodynamics can be vastly different from low angle of attack, with shifts in stability expected. Another phenomenon in engineering practice is control plane reversal, in which a control surface acts the opposite of what it "normally" does; for example, at low speed ship's rudders acting opposite to their normal direction have caused collisions.

This is the first of two chapters dealing with the $\dagger M$. gui aerodynamics. In this chapter, I discuss results of a systematic survey of stability and control effectiveness in a four-winged (Beebe, 1915; Lippincott, 1920; Xu et al., 2003) basal morphology, originally inspired by $\dagger M$. gui but now considered to be ancestral to the Avialae (Xu et al., 2011; Zhang and Zhou, 2004; Zheng et al., 2013). In chapter 3, I will look beyond a single specimen or single shape to examine how stability and control effectiveness change during evolution.

2.1.1 Review of previous model tests in dinosaurs

Dynamically similar model tests of animal shapes have long been used; Reynolds' original work included ducks (Reynolds, 1875). Dinosaur flight mechanics have been previously

³For human skydivers in freefall, several stable and unstable postures are possible. The effectiveness of symmetric movements in controlling pitch and asymmetric movements in generating yaws and rolls was demonstrated in (Cardona et al., 2011; Evangelista et al., 2012) and is awaiting publication in a journal article.

⁴Windsurfers create yaw by protracting or retracting the entire sail relative to the keel center of pressure, using a universal joint roughly comparable to the glenoid. For developing an intuitive understanding of how forces and torques can be modulated by fine deflections of a wing, I highly recommend it.

studied using both computational and experimental approaches. Generally, fluid mechanics can be idiosyncratic enough to require both approaches.

Heptonstall (1970) examined $\dagger Archaeopteryx$, and later Gatesy and Dial (1996) examined $\dagger Archaeopteryx$ tails using computational approaches, both without benchmarking against experiment. Longrich (2006) later recognized the presence of leg feathers in $\dagger Archaeopteryx$ and provided the first estimates of dinosaur maneuvering capabilities via computations based on (Emerson and Koehl, 1990; McCay, 2001a). Chatterjee and Templin (2003) used computer simulations for assumed aerodynamic coefficients to identify phugoid mode gliding in $\dagger Archaeopteryx$; these were later extended to a particular configuration of $\dagger Microraptor$ (Chatterjee and Templin, 2007)⁵. All of these suffer from being purely computational studies, using coefficients and assumptions drawn from fixed wing aircraft at low angle of attack.

Model tests have been used in more recent dinosaur studies. Xu, Jenkins, Breuer, et al. used full-scale wind tunnel models constructed by professional preparators to examine flight characteristics of \dagger *Microraptor* (Provided in a TV documentary by Davis, 2008; data not yet published). The results of that program focused on lift and drag and only briefly addressed stability. The methods here mare most similar to that effort.

Alexander et al. (2010) also used full-scale flying models constructed from styrofoam gliders, intending to test the biplane hypothesis of (Chatterjee and Templin, 2007). The methods include some very nose-heavy ballasting for which I am unsure what the biological basis is.

An effort was started by Karen Yang and other UC Berkeley biomechanics undergraduates around 2005, after the discovery of the fossils (Xu et al., 2003). That previous effort focused on lift and drag coefficients with some consideration of moments but no moment data collected. While this study developed from the remnants of that study, here I add major technical and measurement improvements, deeper consideration of the paleontology, actual data in large quantities on forces and moments and at usable step-sizes in angle (5°), analysis of the resulting data and understanding of its functional and paleontological significance⁶.

 $^{{}^{5}}I$ discuss their reconstruction in section 2.2.

⁶Over two years of undergraduate effort, no moment measurements were collected, and maneuvering data consisted only of lift or drag coefficients. Only 140 measurements total were collected. The models used in that effort were made of sewn foam and are not replicable even between trials, and a coating of covert feathers was used as wing primaries. The sensors, derived from (McCay, 2001a), showed extreme flow-induced vibration and used strain gauges that were wildly out of calibration; the wind tunnel was unsafe and was condemned by UC Berkeley EHS in 2012. Finally, angle runs were very coarse (20°) due to antiquated, manually adjusted sensor mounts, so any attempt to compute derivatives would have failed even if the data existed.



Figure 2.2: Physical models of $\dagger M.$ gui, wingspan 20 cm, snout-vent-length 8 cm. Reconstruction postures (a-d) used for constructing physical models: a, sprawled, after (Xu et al., 2003); b, tent, after (Davis, 2008); c, legs-down, after (Davis, 2008); d, biplane, after (Chatterjee and Templin, 2007). Additional manipulations (e-h): e, sprawled without leg or tail feathers; f, tent without leg or tail feathers; g, example asymmetric leg posture with 90° leg mismatch (*arabesque*); h, example asymmetric leg posture with 45° dihedral on one leg (*dégagé*).

2.2 Materials and Methods

2.2.1 Models and postures

Scale models of $\dagger M$. gui (snout-vent length 8 cm) were constructed from published reconstructions and photographs (Chatterjee and Templin, 2007; Davis, 2008; Xu et al., 2003). The models are shown in Figure 2.2A. Model construction was guided by dissection of Starlings (Sturnus vulgaris), reference to preserved specimens of birds, bird wings, and lizards, teaching casts of $\dagger Archaeopteryx$, and illustrated textbooks on vertebrate functional morphology and vertebrate paleontology (Benton, 1997; Liem et al., 2000). Photographs of the $\dagger M$. gui holotype IVPP V13352 were printed on a laser printer (Xerox, Norwalk, CT) at full scale and at model scale to further guide model construction. Models were built on an aluminum plate with polymer clay (Polyform Products Co., Elk Grove, IL) to fill out the body using methods described in (Koehl et al., 2011). Removable tails and heads, to allow repositioning, were constructed using polymer clay over steel rods. The forelimbs were constructed by bending 26-gauge steel wire scaled to the lengths of the humerus, radius and ulna, and digits as seen in published photographs of the holotype. Similarly, hindlimbs were constructed with wire scaled to the lengths of the femur, tibiotarsus, tarsometatarsus, and digits. For the appendages and tail, feathered surfaces were modeled using paper and surgical tape (3M, St. Paul, MN) stiffened by addition of monofilament line at the locations of the individual feather rachises. This method of creating wing surfaces was compared to wings with craft feathers individually sewn onto them and seen to provide equivalent results (Koehl et al., 2011). In addition, models of Anna's Hummingbirds (*Calypte anna*) constructed using the same techniques have been shown to faithfully reproduce the aerodynamic properties of diving hummingbirds (Evangelista, in preparation).

Model reconstruction postures (Figure 2.2B-E) were chosen based on those previously published (Chatterjee and Templin, 2007; Davis, 2008; Xu et al., 2003). Some of these postures are anatomically dubious; in particular the sprawled posture drawn in (Xu et al., 2003) has been criticized because of interference between the trochanter on the femur and the surrounding structures of the ilium and ischium (Benton, 1997; Davis, 2008; Liem et al., 2000), while a feasible mechanism for maintaining feathers in the biplane / muffed feet posture of (Chatterjee and Templin, 2007) under load has never been proposed. I also tested models in postures more strongly inferred for theropods, including a legs-down posture with no more than 45° leg abduction (Davis, 2008), and a tent posture in which the legs are extended caudad with the feathered surface extending over the proximal part of the tail ⁷

I recognize that some of the reconstruction postures are less feasible than others. The approach taken here is to test all previously proposed reconstructions, in order to examine the aerodynamic implications of these shapes from a purely physical standpoint. With the uncertainties inherent in applying a physical modeling approach to an extinct animal with only a single published skeleton, statements about aerodynamic performance in $\dagger M$. gui should always be taken with a grain of salt.

2.2.2 Conditions for dynamic similarity and Reynolds number sweep

To achieve dynamic similarity (Koehl et al., 2011; Kundu and Cohen, 2004) in these models, it would be nice to match the Reynolds number ($\text{Re} = uL/\nu$), the nondimensional ratio of viscous to inertial forces. Based on pilot studies we estimated Re for the full scale $\dagger M$. gui to be approximately 200 000. Limitations on the wind tunnel size and speed required the Reynolds number of the model to be 32 000. To test this, I performed a sweep of Re to check if scale effects needed to be considered⁸ The expectation is that the Reynolds number is high and that many of the runs approach bluff-body conditions so that coefficients should be independent of Re.

 $^{^{7}}$ Xu never intended the sprawled posture as an actual reconstruction per se but rather just a convenient way to illustrate the planform (Xu et al., 2005). In the absence of fossil material illustrating otherwise there is no reason to assume extraordinary hip anatomy not seen in any other theropod.

⁸Results of the Reynolds number sweep were published previously as part of (Koehl et al., 2011).



Figure 2.3: Sign conventions, rotation angles, and definitions for model testing, after (Emerson et al., 1990; McCay, 2001a,b; McCormick, 1995).

2.2.3 Force measurements

As described in (Koehl et al., 2011), models were mounted on a six-axis force transducer (Nano17, ATI Industrial Automation, Apex, NC), which was in turn mounted on a 1/4-20 threaded rod damped with rubber tubing, and attached to a tripod head used to adjust angle-of-attack. The force sensor and sting exited the model on the right side of the body mid-torso at approximately the center of mass.

Wind tunnel tests were conducted in an open jet wind tunnel with a 15 inch \times 15 inch \times 18 inch (38.1 cm \times 38.1 cm \times 45.7 cm) working section used previously for studies of gliding frogs (McCay, 2001a,b). Tunnel speed was controlled using a variable autotransformer (PowerStat, Superior Electric Company, Bridgeport, CT) and monitored using a hot wire anemometer (Series 2440, Kurz Instrument Co., Monterey, CA).

Force transducer readings were recorded at 1000 Hz sampling frequency using a National Instruments 6251 data acquisition card (National Instruments, Austin, TX). Raw measurements were rotated from a frame fixed to the model to one aligned with the wind tunnel and flow using the angle-of-attack. Transformed measurements were then averaged over a one-minute recording. For each measurement, wind tunnel speed v was recorded and used to compute Reynolds number (Re = vL/ν , $\nu = 15.0 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$). The sign convention for forces and moments is shown in Figure 2.3

Aerodynamics forces and moments were normalized to obtain nondimensional coefficients

according to the following (using notation from (McCormick, 1995)):

$$lift = C_L 0.5 \rho u^2 A_p \tag{2.1}$$

$$drag = C_D 0.5 \rho u^2 A_p \tag{2.2}$$

side force =
$$C_S 0.5 \rho u^2 A_p$$
 (2.3)

pitching moment =
$$C_m 0.5 \rho u^2 A_p \lambda_{SVL}$$
 (2.4)

rolling moment =
$$C_r 0.5 \rho u^2 A_p \lambda_{SVL}$$
 (2.5)

yawing moment =
$$C_y 0.5 \rho u^2 A_p \lambda_{SVL}$$
 (2.6)

where $\rho = 1.204 \text{ kg m}^{-3}$ is the air density, A_p is the model planform area, and λ_{SVL} is the snout-vent length of the model. To allow comparisons among models, a single, consistent baseline configuration is needed. Accordingly, nondimensional coefficients are referenced to the planform area of the four-winged, sprawled position originally proposed in (Xu et al., 2003) unless specially noted. The questions of interest for this study are tied to the absolute value of forces and moments produced and differences that occur from the same animal in different postures; our choice of normalization preserves these distinctions in most cases.

2.2.4 Static stability coefficients

To assess static stability, we calculated nondimensional static stability coefficients from fixedwing aircraft stability and control theory (notation from McCormick, 1995, see also Anderson, 2007; Etkin and Reid, 1996; Phillips, 2004; Stengel, 2004) and previously used in studies of gliding frogs (McCay, 2001a,b).

The pitching stability coefficient $C_{m,\alpha}$ is defined as (McCay, 2001a)

$$\partial C_m = C_{m,\alpha} \partial \alpha \tag{2.7}$$

where α is the angle-of-attack and C_m is the pitching moment coefficient as defined above. It is the local slope of the pitching moment curve, and is thus an indication of the sense (restoring or non-restoring) and magnitude of the torque generated in response to a perturbation in angle-of-attack. If $C_{m,\alpha} < 0$, the response torque will be opposite the direction of perturbation; this is the condition for static stability.

Similarly, for roll:

$$\partial C_r = C_{r,\phi} \partial \phi \tag{2.8}$$

where ϕ is the roll angle and $C_{r,\phi} < 0$ is the condition for static stability in roll. By symmetry, models at zero angle-of-attack have neutral rolling stability, and we did not calculate roll stability for most cases.

For yaw,

$$\partial C_y = C_{y,\psi} \partial \psi \tag{2.9}$$

where ψ is the yaw angle and $C_{y,\psi} < 0$ is the condition for static stability in yaw (also known as directional stability).

Pitching stability coefficients were obtained from angle-of-attack (α) runs taken from -15° to 90° at 5° increments. Yawing stability coefficients were obtained from yaw angle (ψ) runs from -30° to 30° at 10° increments. For each series, central differences were used to estimate the slopes at each point for each replicate run.

2.2.5 Control effectiveness

I also calculated nondimensional control effectiveness coefficients using methods from aerodynamic engineering (Etkin and Reid, 1996) used in previous studies of gliding frogs (McCay, 2001b). In general, control effectiveness for a control surface whose angular orientation relative to the flow can be changed is the partial derivative of the moment generated with respect to the angle. High control effectiveness means a large amount of moment generated for a small movement of the surface.

I calculated the pitching control effectiveness for the tail, forewings, and legs as follows:

$$\partial C_m = C_{m,\delta} \partial \delta \tag{2.10}$$

where δ is the angle of the control surface in question. Similarly, we calculated yawing control effectiveness for these surfaces as follows:

$$\partial C_y = C_{y,\delta} \partial \delta \tag{2.11}$$

as well as rolling control effectiveness for asymmetric movements of the wings and legs:

$$\partial C_r = C_{r,\delta} \partial \delta \tag{2.12}$$

2.2.6 Other flight performance metrics

To allow comparison with previous studies, two additional measures of maneuvering performance were computed: the banked turn maneuvering index and crabbed turn maneuvering index (Emerson et al., 1990; McCay, 2001a,b). The banked turn maneuvering index assumes turns accomplished by banking is computed in two ways, both of which assume that some component of lift generated is used to provide the force necessary for turning:

$$MI_{\text{banked},1} = \frac{C_{L,\text{max}}}{mg/A_P} \tag{2.13}$$

after (Emerson et al., 1990) (note this is not a nondimensional index), and

$$MI_{\text{banked},2} = \frac{L\cos\phi}{mg} \tag{2.14}$$

where $\phi = 60^{\circ}$ is arbitrarily chosen with no reasonable basis for picking it, after (McCay, 2001a,b). Similarly, for crabbed turns, a nondimensional index is the horizontal component of side force normalized by body weight (McCay, 2001a,b):

$$MI_{\text{crabbed}} = \frac{F_{\text{side}} \sin \psi}{mg} \tag{2.15}$$

again with $\psi = 60^{\circ}$ arbitrarily chosen based on frogs (McCay, 2001a,b)⁹.

Several flight performance metrics not immediately tied to maneuvering were also computed (Emerson and Koehl, 1990; Emerson et al., 1990; McCay, 2001a,b). As a measure of horizontal glide performance, we computed $(C_L/C_D)_{\text{max}}$ for each posture (Emerson et al., 1990). Minimum glide speed, a measure of the ease of which gliding can be initiated, was also computed as $U_{\text{min}} = [2mg/(A_P\rho C_L)]^{1/2}$ (Emerson et al., 1990). As a measure of parachuting ability, we also compared D_{90} , the full scale drag for parachuting (Emerson et al., 1990), as well as a nondimensionalized parachuting index D_{90}/mg^{10}

2.2.7 Estimation of mass and centers

The mass of a live $\dagger M$. gui was estimated by scaling using data from some sources in two ways. One estimate was formed by scaling body parts and systems and summing (Colbert, 1962; Henderson, 1999), methods identical to estimation of weights and centers for traditional naval architecture and other engineered systems. Another estimate was formed using scaling from many taxa based on long bone measurements (Angst et al., 2011). Mass and center estimates fell within what has been published recently for very detailed estimates (Allen et al., 2013). Masses (ranging from 1 kg to 1.4 kg, full scale snout-vent-length ~ 35 cm) were used here only to estimate wing loadings and required glide speeds.

2.3 Results

During the fall of 2010, we collected a dataset of 12,810 measurements for 180 combinations of postures and positions. The raw data require approximately 5.3 GB of storage. The work

⁹A valid criticism of these indices from (Emerson et al., 1990; McCay, 2001a,b) is that they are just scaled versions of other numbers that are more informative without manipulated by arbitrary choices of ϕ or ψ . These are included only for comparison to past literature.

¹⁰Gliding and parachuting are considerably more dynamic and unsteady than their names would imply; these coefficients may be oversimplifications but are included here only for comparison to past literature.

was accomplished during approximately 350 hours of wind tunnel time by a team of ten undergraduates¹¹ led by one graduate student.

For the plots given here, color represents the base posture: red for sprawled, blue for tent, green for biplane, and purple for down. All sign conventions are as in (McCay, 2001a) and as shown in Fig 2.3. Symbols, where used, represent variations in position from the base posture, such as movement of legs, wings, or tail. All units are SI unless otherwise noted.

2.3.1 Baseline longitudinal plane aerodynamic data and effects of posture and the presence/absence of leg and tail feathers

Fig 2.4 gives the nondimensional coefficients of lift, drag, and pitching moment for $\dagger M$. gui with full feathers. Scaling with the coefficients, the full scale forces for $\dagger M$. gui at 12 m s^{-1} are plotted in Fig 2.5.

For comparison with previous work (Emerson et al., 1990), various other gliding performance metrics are compared in figures 2.6 and 2.7.

A Reynolds number sweep (Fig 2.8, Table 2.1) was also conducted to check for scale effects.

Table 2.1: Dynamic similarity parameters for model and full scale *†Microraptor gui*

2.3.2 Effect of leg and tail feathers

The effects on longitudinal plane coefficients of the presence or absence of leg and tail feathers are shown in figures 2.9 and 2.10.

2.3.3 Yaw stability and the effects of shape and angle of attack

Figure 2.11 shows how yaw stability varies between postures. To examine the effect of aerodynamic environment (*vis-a-vis* glide angle, or angle of attack as a loose proxy for glide angle), figure 2.12 shows how yaw stability changes as angle of attack increases from 0° to

¹¹I thank Griselda Cardona, Chang Chun, Eric Guenther-Gleason, Tony Huynh, Austin Kwong, Dylan Marks, Neil Ray, Adrian Tisbe, and Kyle Tse. We are sad to have lost one member of our team to tragedy, Alex Lowenstein. I intend that all of them should be co-authors when this chapter is published as a journal article.



Figure 2.4: Nondimensional coefficients for all models. Red is sprawled, blue is tent, green is biplane, purple is down. α from -15° to 90° in 5° increments, with 5 or more replicates per treatment. a: Lift coefficient. b: Drag coefficient. c: Lift drag polars. d: Pitching moment coefficient.

 60° to 90° (or how yaw stability would change in going from falling from a tree at high angle of attack to gliding from one at low angle of attack). The presence or absence of empennage feathers (figure 2.13) also alters yaw stability (Tisbe et al., 2011).



Figure 2.5: Full scale forces and moments for $\dagger M$. gui at $12 \,\mathrm{m \, s^{-1}}$. Red is sprawled, blue is tent, green is biplane, purple is down. α from -15° to 90° in 5° increments, with 5 or more replicates per treatment. a: Full scale lift at $12 \,\mathrm{m \, s^{-1}}$, all models. This figure must be annotated to show the band of $\dagger M$. gui body weight. b: Full scale drag at $12 \,\mathrm{m \, s^{-1}}$, all models. c: Lift-drag polars. d: Full scale pitching moment at $12 \,\mathrm{m \, s^{-1}}$ versus angle of attack, all models.



е

Figure 2.6: Red is sprawled, blue is tent, green is biplane, purple is down. α from -15° to 90° in 5° increments, with 5 or more replicates per treatment. a: Lift to drag ratio. b: Glide angle. c: Minimum glide speed. d: Terminal velocity (assuming stability). e: Pitching stability coefficient (note pitching moment must also be zero for stable equilibrium).



Figure 2.7: Comparison of simple glide metrics after (Emerson et al., 1990) suggests the metrics are not informative. Red is sprawled, blue is tent, green is biplane, purple is down. a:Maximum lift to drag ratio, by posture, without regard to stability. (Emerson et al., 1990)'s minimum ratio is never achieved because the models are not stable at the point where L/D is maximum. There is no difference in maximum lift to drag ratio among postures (Kruskal-Wallis, P = 0.1740). b: Minimum glide initiation speed, by posture, without regard to stability. The minimum speed is never achieved because the models are not stable at the point where U_{min} is lowest. There is no difference in U_{min} among postures (Kruskal-Wallis, P = 0.575). c: Parachuting drag, by posture, without regard to stability. This drag is never achieved because the models are not stable at a 90° angle-of-attack. There are significant differences in D_{90} among postures (Kruskal-Wallis, $P = 9.2 \times 10^{-5}$); sprawled position has higher parachuting drag.



Figure 2.8: Reynolds number sweeps for lift, drag, and pitch coefficients. There are not large changes in aerodynamic coefficients over the ranges shown here. This is similar to what is seen in *Draco* lizard and Anna's Hummingbird (*Calypte anna*) models. The coefficients are roughly constant in the range of \dagger *Archaeopteryx* and are constant enough for these results to be applicable to \dagger *Microraptor*.



Figure 2.9: Presence or absence of leg and tail feathers can drastically alter longitudinal plane aerodynamics (first presented as Tisbe et al., 2011). Sprawled and tent postures with and without feathers, all coefficients shown versus angle-of-attack, solid squares with empennage feathers, open squares without empennage feathers. a: Lift coefficient. Stall occurs at higher angle-of-attack when leg feathers are present. b: Drag coefficient. Leg feathers increase drag at high angle-of-attack, improving parachuting performance. c: Lift coefficient versus drag coefficient. d: Lift to drag ratio. Lift to drag ratio is improved slightly without the additional drag and less-efficient lift generation of hind wings. e: Pitching moment coefficient. Without leg feathers, stability is not achieved in either posture. f: Pitching stability coefficient.



Figure 2.10: Presence or absence of leg and tail feathers has effects on (Emerson et al., 1990) metrics, although the usefulness of (Emerson et al., 1990) is questionable (see figure 2.7). Feathers present (black outline) or absent (grey outline) a: Maximum lift to drag ratio, by sprawled and tent postures with and without feathers. The maximum lift to drag ratio for tent without leg or tail feathers is significantly higher than for other postures (ANOVA, P < 0.003), however, this improvement is never achieved because the tent posture is never stable without leg feathers. b: Minimum glide speed, by sprawled and tent postures with and without feathers in minimum glide speed between postures (ANOVA, P > 0.08). c: Parachuting drag, by sprawled and tent postures with and without feathers. There are significant differences in parachuting drag between postures (ANOVA, P < 0.04), however, the straight-down parachuting position is not stable in any posture.



Figure 2.11: At 0° angle-of-attack, there are clear differences in yaw stability between postures. In particular, with legs down, the legs strongly act as weathervanes to stabilize the body in yaw (purple line, high slopes near 0°). Color represents the base posture: red for sprawled, blue for tent, green for biplane, and purple for down.



Figure 2.12: There are also clear differences in yaw stability at different angles-of-attack. At 0° , some postures are more stable in yaw than others. At 60° , postures that were stable at 0° may go unstable, such as tent posture. At 90° , all postures are marginally stable due to symmetry (lines flat, yawing does not alter position relative to flow). Color represents the base posture: red for sprawled, blue for tent.



Figure 2.13: The differences in yaw stability at different angles-of-attack also depend on the presence or absence of leg feathers. At 0° , some feathered-leg postures are more stable in yaw than others. At 60° , postures that were stable at 0° may go unstable, such as tent posture with leg feathers. At 90° , all postures are marginally stable due to symmetry. Results first presented as (Tisbe et al., 2011). Color represents the base posture: red for sprawled, blue for tent, green for biplane, and purple for down.



Figure 2.14: Tail control effectiveness for biplane posture for tail angles of -15° (down triangle), 0° (square), and 15° (up triangle). At low angle-of-attack, tail up produces a nose up moment relative to zero tail angle, while tail down produces a nose down moment relative to zero tail angle. The small effect on lift suggests the tail is primarily effective because of moments generated by its long length.

2.3.4 Control effectiveness of tail, symmetric wing and leg movements

The control effectiveness for symmetric movements of several appendages is given in figures 2.14 through 2.21. Figures 2.14-2.17 give the control effectiveness of dorsoventral tail flexion for biplane, down, sprawled, and tent posture. Figures 2.18 and 2.19 give the control effectiveness of symmetric leg movement. Figure 2.20 gives the control effectiveness for symmetric wing fore-aft sweep (protraction and retraction). Figure 2.21 gives the control effectiveness for symmetric wing pronation/supination.


Figure 2.15: Tail control effectiveness for down posture for tail angles of -15° (down triangle), 0° (square), and 15° (up triangle). At low angle-of-attack, tail up produces a nose up moment relative to zero tail angle, while tail down produces a nose down moment relative to zero tail angle. At high angle of attack, the tail experiences reversal in which tail down produces nose up moments / tail up produces nose down moments.



Figure 2.16: Tail control effectiveness for sprawled posture for tail angles of -15° (down triangle), 0° (square), and 15° (up triangle), with empennage feathers (a,c) and without (b,d). At low angle-of-attack, tail up produces a nose up moment relative to zero tail angle, while tail down produces a nose down moment relative to zero tail angle (c). Reversal is not seen at high angle-of-attack. Without leg feathers (d), the tail is ineffective at producing lift or pitching moment.



Figure 2.17: Tail control effectiveness for tent posture for tail angles of -30° (large down triangle), -15° (down triangle), 0° (square), 15° (up triangle), and 30° (large up triangle), with (a,c) and without (b,d) empenage feathers. At low angle-of-attack, tail up produces a nose up moment relative to zero tail angle, while tail down produces a nose down moment relative to zero tail angle (c). Some reversal occurs at high angle-of-attack. Without leg feathers, the tail is ineffective at producing lift or pitching moment (b,d).



Figure 2.18: Leg control effectiveness for sprawled posture for leg angles of -15° (down triangle), 0° (square), and 15° (up triangle). At low angle-of-attack, legs up produces a nose up moment relative to zero leg angle, while legs down produces a nose down moment relative to zero leg angle. Leg movement is slightly less effective at high angle of attack.



Figure 2.19: Leg control effectiveness for tent posture for leg angles of -30° (large down triangle), -15° (down triangle), 0° (square), 15° (up triangle), and 30° (large up triangle) with empennage feathers (a,c) and without (b,d). At low angle-of-attack, leg up produces a nose up moment relative to zero leg angle, while leg down produces a nose down moment relative to zero leg angle (c). Without leg feathers, the legs still have smaller effects (d).



Figure 2.20: Symmetric wing sweep control effectiveness for tent posture for wing sweep angles of -45° (large down triangle), -22.5° (down triangle), 0° (square), 22.5° (up triangle) and 45° (large up triangle). Wing sweep is very effective at generating pitching moments. Forward sweep generates nose up moments, while backwards sweep generates nose down moments. This is like steering a wind surfing rig and is similar to what is seen in Anna's Hummingbird (*Calypte anna*) dive models (Evangelista, in preparation). This mode of control exhibits reversal at negative angle of attack. See also chapter 1, righting by pitching with symmetric movements in Chukar after 10 dph)



Figure 2.21: Symmetric wing pronation/supination control effectiveness for tent posture for wing angles of -30° (large down triangle), -15° (down triangle), 0° (square), 15° (up triangle) and 30° (large up triangle). Wing pronation/supination (wing angle-of-attack) is effective at changing the lift generated but exhibits reversal at high angle-of-attack where stall occurs.



Figure 2.22: Asymmetric wing sweep control effectiveness for tent posture for wing sweep angles of -45° (large down triangle), -22.5° (down triangle), 0° (square), 22.5° (up triangle) and 45° (large up triangle). Forward sweep generates upward pitching moments, backward sweep generates downward pitching moments. Considerable roll moments are also generated at higher angles-of-attack.

2.3.5 Control effectiveness of asymmetric wing positions

Figures 2.22 through 2.24 give the control effectiveness for asymmetric wing movements, including asymmetric wing sweep (figure 2.22), asymmetric wing pronation (figure 2.23), and asymmetric wing tucking (figure 2.24).



Figure 2.23: Asymmetric wing pronation control effectiveness for tent posture for wing pronation angles of -30° (large down triangle), -15° (down triangle), 0° (square), 15° (up triangle) and 30° (large up triangle). At low angles-of-attack, asymmetric wing pronation generates large rolling moments. At high angles-of-attack, there is a shift in function and asymmetric wing pronation tends to generate yawing moments instead of rolling moments.



Figure 2.24: Asymmetric wing tucking control effectiveness for tent posture; both wings out (solid square), no right wing (open square) and no wings (open diamond). Tucking one wing produces large roll moments but at the expense of one quarter of the lift (see also, chapter 1, righting by roll with asymmetric movements in Chukar before 10 dph). Large yaw moments are not generated except at higher angles-of-attack where the leg and tail positions become more important.



Figure 2.25: Asymmetric leg dihedral (leg dégagé) effect on yaw. Baseline down position (solid square) versus one leg at 45° dihedral (down arrow). Placing one leg at a dihedral is destabilizing in yaw and produces side force and yawing moments.

2.3.6 Control effectiveness of asymmetric leg positions in yaw

Control effectiveness of asymmetric leg positions in yaw is plotted in figures 2.25-2.27.



Figure 2.26: Asymmetric one leg down (leg arabesque) effect on yaw. Baseline tent position (solid square) versus one leg at 90° mismatch (down arrow). Placing one leg down has little effect.



Figure 2.27: Asymmetric one leg down (leg *arabesque*) effect on yaw without leg feathers. Baseline tent position (solid square) versus one leg at 90° mismatch (down arrow). Placing one leg down had little effect; with no leg or tail feathers there is no effect.



Figure 2.28: Asymmetric tail movement (lateral bending) effect on yaw, down posture. Baseline down position (solid square), tail 10° left (open square), tail 20° left (open triangle), tail 30° left (open diamond). The tail is effective at creating yawing moments but at low angles-of-attack it is shadowed by the body and larger movements are needed.

2.3.7 Control effectiveness of other asymmetric positions

The control effectiveness of some additional asymmetric tail and leg movements is given in figures 2.28-2.30.



Figure 2.29: Asymmetric tail movement (lateral bending) effect on yaw, tent posture. Baseline tent position (solid square), tail 10° left (open square), tail 20° left (open triangle), tail 30° left (open diamond). The tail is effective at creating yawing moments but at low angles-of-attack it is shadowed by the body and larger movements are needed.



Figure 2.30: Asymmetric tail movement (lateral bending) effect on yaw, down posture. Baseline down position (solid square), tail 10° left (open square), tail 20° left (open triangle), tail 30° left (open diamond). The tail is effective at creating yawing moments but at low angles-of-attack it is shadowed by the body and larger movements are needed.



Figure 2.31: Asymmetric one wing down effect on yaw, tent posture. Baseline tent position (solid square), left wing down (down triangle). Placing one wing down does not make large yawing moments. Some roll and side force is produced at low angles-of-attack, at the expense of one quarter to one half of the lift.

2.4 Discussion

2.4.1 Postures have similar lift and drag coefficients but exhibit very different pitch (longitudinal) stability

All postures have roughly similar lift coefficients at low angles-of-attack (Fig. 2.4a); at high angles-of-attack, the main differences are due to the orientation and projected area of the legs.

Examining the pitching moments reveals that only the biplane and tent postures have stable points (Fig. 2.4d). For the tent position, the stable glide angle is 35° , at roughly 12 m s^{-1} and an angle-of-attack of 27° . For the biplane position, a stable equilibrium point appears at angle-of-attack 16°. The sprawled posture, which possesses roughly equal fore and aft area, is marginally stable in pitch (in effect, the longitudinal center of pressure is at the center of mass), while the down posture is never stable because the legs are not employed in lift generation (the longitudinal center of pressure is ahead of the center of mass).

These stability results agree with (Chatterjee and Templin, 2007), who argued from simulation results (that were highly dependent on parameter selection) that the biplane posture was stable. In contrast, Xu et al. (as described on television in (Davis, 2008)), found the biplane to be unstable in wind tunnel tests except at high angle-of-attack, however, without the detailed results to review it is not possible to comment why. Xu et al. also found the tent posture to be stable, which agrees with our results. Alexander et al. (2010) found that with nose-heavy ballasting, a sprawled/biplane posture could be made stable; we agree with this, with the caveat that such ballasting may not be biologically realistic as the densities of biological tissues do not vary as greatly as the density difference between lead and styrofoam. A more recent effort by Habib et al. (in review) appears to agree with my findings regarding legs.

My predicted equilibrium glide angle for the tent position seems reasonable (Koehl et al., 2011). The animal would be fast enough to require some kind of landing maneuver to avoid injury; using an approach similar to (Tedrake et al., 2009), one could evaluate the perching or landing ability of this animal using our data. Our glide angle and speed are higher than in Alexander et al. (2010), however, their weight estimate is half ours, and their models were constructed from model airplane parts that were already designed to fly.

Based on projected full scale forces (Fig. 2.5) and stability considerations, we estimate the $\dagger M$. gui could glide in tent position. Sprawled posture and down posture are unstable in pitch. Biplane position does not appear to generate sufficient lift. We did not mechanically evaluate if feathers cantilevered out the feet in the style of muffed feet on pigeons is able to carry significant loads; however this was a common point of failure in our models suggesting it would have been a limitation for that hypothetical posture.

At first glance, there also appear to be differences in the maximum lift to drag ratio, minimum glide initiation speed, and parachuting drag for different postures (Figs. 2.6 and 2.7). It is important to note that these "optima" reflect a very narrow criteria of optimality and are not always achievable because of constraints, such as from stability or anatomy. In

particular, none of the most "optimal" configurations are stable. Blind application of gross aerodynamic performance parameters (such as Emerson et al., 1990) may be misleading if it ignores other constraints.

2.4.2 Coefficients are insensitive to Reynolds number

The Reynolds number sweep (figure 2.8, Table 2.1) shows that the models under test here are in a regime where aerodynamic coefficients are relatively insensitive to Reynolds number, so that results are valid for the full-scale $\dagger M$. gui, as well as for full-scale $\dagger Archaeopteryx$. This result was briefly discussed in (Koehl et al., 2011) but additional details are relevant here. Unlike in gliding ants (Munk, 2011) or in typical low Reynolds number structures such as crab antennas (Waldrop, 2012) or blastoid respiratory hydrospires (Huynh et al., 2013), there are not dramatic shifts in function of the wings as Reynolds number is varied over a range of sizes and speeds (figure 2.8). Reynolds number does not matter. This is similar to what is observed in wind tunnel models of *Draco* lizards (Evangelista, in preparation) and Anna's Hummingbirds (*Calypte anna*) (Evangelista, in preparation) and similar to what is expected from typical high Reynolds number aerodynamics (Hoerner, 1993; Koehl et al., 2011; Kundu and Cohen, 2004; Shapiro, 1961). The absence of scale effects here provides added assurance that these results should be broadly applicable in evaluating maneuvering during evolution or ontogeny.

2.4.3 Leg and tail feathers have important implications for aerodynamics and stability

Leg feathers forming a hindwing will experience delayed onset of stall (figure 2.9a, similar to a jib and a mainsail, or flaps on an airliner), increase drag at high angles-of-attack (figure 2.9b), and drastically alter stability (figure 2.9d). None of the shapes tested were stable without leg feathers present (figure 2.9d). This suggests that leg/tail morphology in fossils may be informative as to the stable glide angles or positions an organism can adopt in the air. The leg feathers were initially downplayed in criticism as a taphonomic artifact; however subsequent finds of a wealth of specimens with feathers on the legs beg further work to evaluate their aerodynamic significance in a comparative framework.

Leg feathers increased D_{90} and decreased the lift to drag ratio, however, without leg feathers the models were not stable (figure 2.10). Higher L/D without leg feathers may be achieved by reduced drag from surfaces whose ability to produce lift is limited by their downstream location behind the forewings. This may be a reason to shift from a feathered leg form to a larger forewing reduced leg form (as is seen in the evolution of birds). For $\dagger M$. gui in tent position with no leg feathers, it ought to glide slightly shallower, at the expense of having to go $1.4 \times$ faster (about 17 m s^{-1}) and requiring some invisible hand of optimal but unachievable L/D ratios to stabilize it. In reality, it would pitch upwards until stalling, and then tumble. This illustrates once again that assuming "better glide performance" is a single number such as L/D is an oversimplification; higher L/D means only lower steady glide angle when there's no guarantee an animal actually uses such trajectories¹²; high L/D does not mean lower glide speed, and a high L/D may be unachievable because of constraints from stability or anatomy.

Living animals differ from models in being dynamic and that the various postures evaluated in this study (and others) might have been used in different circumstances to maximize the aerodynamic potential of the living animal. Dynamic behaviors (flapping, inertial flailing) would increase the maneuvering abilities further beyond what is discussed here, but these results provide a useful first-order understanding.

2.4.4 Yaw stability depends on posture and leg feathers, and exhibits shifts based on angle-of-attack

Stability varies in different axes (pitch, versus yaw and roll); a shape which is stable in pitch at a particular operating point may not be stable in the other axes.

Some postures (notably down) were observed to be more stable than others in yaw (figure 2.11). More importantly, postures which are stable at low angle-of-attack (such as tent) were unstable at intermediate angle-of-attack, and all postures were marginally stable at 90° angle-of-attack (figure 2.12). Leg feathers were similarly seen to have different effects on stability with angle-of-attack (figure 2.13). The significance of this result is that during a shift from parachuting, through mid-AOA gliding¹³, to low-AOA flight, different plan forms have drastically different stability characteristics in yaw. The aerodynamic basis for the difference is not yet clear, though likely due to effects of vortex shedding or separation at the tips and trailing edges (such as the stabilizing mechanism for high AOA lifting bodies or surf boards). Further work is needed to examine this using flow visualization.

2.4.5 Control effectiveness varies with AOA and can exhibit reversal or shifts from one axis to another

Control effectiveness was observed to vary with AOA (figure 2.12, 2.13; figure 2.14 onwards); furthermore there were cases in which its sign completely switched, i.e. when a control surface does the opposite of what it normally does (figure 2.15, down posture with the tail in pitch; figure 2.17, tent posture with the tail in pitch; figure 2.21, wing pronation in tent posture). These happen in pitch at high angles of attack and in yaw at different angles of attack and postures. Reversal during abnormal operating conditions in vehicles/ships etc can cause collisions and crashes; in a biological system it is a complete shift in function that would happen coincident with a transition from steep angle directed aerial descent to lower

¹²Among human skydivers, steep approaches are often used to build speed in order to enable finer control near ground. This is also the logic behind steep final approaches in powered aircraft, as it reduces the impact on control of an engine failure near ground.

¹³As in chapter 1, I must state the caveat that parachuting and gliding are both more dynamic and unsteady than the terms often imply to the casual reader.

angle of attack aerial behaviors. This deserves further study; the basis for reversal is unclear in these models and flow visualization is needed.

As with the other measurements, removal of leg feathers tended to drastically reduce control effectiveness (for example, figure 2.16c versus d). This might suggest that as birds evolved and moved away from long tails and feathered legs, the control effectiveness that those surfaces once possessed became reduced, or possibly was shifted to another surface (the wings). This is bolstered by the observation that birds with partially amputated tails (such as from household cats) can still fly. In this data, wing sweep (in a manner similar to steering a windsurfing rig) was very effective at creating pitching moments, similar to patterns seen in Anna's Hummingbird (*Calypte anna*) display dive model tests (Evangelista, in preparation). Further comparative study of tails and empennage in general, including reference to convergent examples in pterosaurs, are discussed in chapter 3.

2.4.6 Some asymmetric movements are effective in rolling or yawing

For asymmetric wing movements, similar trends were observed. Asymmetric wing sweep was effective (figure 2.22). Asymmetric wing pronation, in particular, tent posture with one wing changing its pronation/supination was observed to produce large rolling moments at low angle of attack but large yawing moments at high angle of attack (figure 2.23). This is another observation of a major shift in the function of a control surface with angle of attack. Tucking one wing (figure 2.24) was effective in rolling (see also chapter 1, Chukar asymmetric righting by rolling before 10 dph).

On the other hand, certain movements fancifully postulated to have large effect, such as placing a leg *dégagé* (figure 2.25) or *arabesque* (figures 2.26 and 2.27) or placing one wing down to yaw (figure 2.31) did surprisingly little for yaw, roll, or side force, at the tremendous expense of the loss of a large portion of lift. There is no basis for such postures in the fossils and no basis for such postures in the flight of any extant creature, and no further work is needed on these.

Asymmetric tail movements (lateral bending) were only partly effective (figures 2.28-2.30); at low angles of attack, the tail is shadowed by the body.

2.4.7 Maneuvering must be considered when considering the evolution of flight in vertebrates

Taken together, these results show that morphology can have large effects on the stability and control effectiveness and also place constraints on aerodynamic performance (specifically, whether or not reduced glide angles, lower glide speeds, or improved parachuting performance can actually be achieved). The changes in tail and leg morphology during the transition from theropods to birds (and convergent changes from early pterosaurs to later pterosaurs and early bats to later bats) beg for the metrics observed here to be studied in a comparative context, to examine how they change as the morphologies are changed and to examine what skeletal or other features co-occur with changes in aerodynamics, as I will do in the next chapter.

If we move away from a false dichotomy of "ground up" versus "trees down", we are left with trying to understand flight itself. This might include the production of forces for traction (as in wing assisted incline running (WAIR) Dial, 2003), although evidence in chapter 1 suggests WAIR is less crucial to flight evolution than previously believed. Perhaps most importantly, it is vital to consider aerial maneuvering (Dudley and Yanoviak, 2011), for which a deeper understanding of stability and control attained here is essential.

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Chapter 3

Aerodynamic characteristics of feathered dinosaur shapes measured using physical models, part II: a comparative study of maneuvering

Aerial maneuvering was likely a pervasive force shaping the evolution of flying animals. Regardless of how aerial behaviors might have arisen, we can analyze the physical effects of structural changes on aerial maneuvering as they present themselves in fossils and along evolutionary lineages. To accomplish this, we measured the aerodynamic maneuvering characteristics of a series of models based on Mesozoic birds and avian ancestors to determine whether or not measures of aerodynamic performance correlated with morphological changes. Maneuvering characteristics during glides were quantified by measuring static stability $(\partial C/\partial \alpha)$; the tendency to experience righting moments when deflected from equilibrium) and control effectiveness $(\partial C/\partial \delta)$; the amount of torque or moment generated for each degree of movement of a limb or control surface). We then mapped the results of our aerodynamic study onto a phylogenetic tree of Avialae, using $\dagger Microraptor$ (Dromaeosauridae) and $\dagger Anchiornis$ (Troodontidae) as outgroups, in order to test whether or not changes in maneuvering characteristics correlated with changes in morphology during early bird evolution. We specifically examined the performance effects of the shortening of the tail and control effectiveness of leg and tail plumage compared to that of the forelimb wing. We also briefly examined similar trends in the pterosaurs and bats, which also appear to show reduction in tails in derived forms. Our analysis offers a biomechanical perspective to the evolution of avian flight that integrates morphological evidence from fossils with modeled performance in a phylogenetic framework.¹

¹Methods from this chapter have been previously presented in public as a conference talk (Chun et al., 2011).

3.1 Introduction

This is the second part of a study of maneuvering and control in birds and bird ancestors using physical models. In the first part of the study (chapter 2, based on the mid-Cretaceous dromeosaur \dagger *Microraptor gui* (Xu et al., 2003), we found that changes in planform, such as the presence or absence of a feathered tail or of leg feathers or the reconstructed posture of the animal, can drastically alter static stability. In addition, appendage function (e.g. as an elevator, rudder, or aileron, generating control forces and torques in different directions) also depends on posture and glide angle, and the function of appendages can shift dramatically due to reversal or cross-coupling effects. The results from chapter 2 are exciting, but they are based on a single specimen². Stronger conclusions can be drawn from comparative study of several species, within a phylogenetic context.

Consider some of the arguments made for alternative hypotheses, such as wing-assisted incline running in vertebrates (as the driver behind intermediate development of the flight stroke necessary to power flight). Consideration of the use of the wings in vertical behaviors is useful, but some proponents focus on it as a veiled "ground up" argument. This is propped up by phylogenetic arguments that trace the origin of three traits deemed "necessary" for flight by specious analogy to airplanes: (1) a fast metabolism "engine" (2) an airfoil "wing" and (3) a flight stroke "propeller" (Padian, 1985, 1987, 2001). Oddly, Padian (2001) criticizes Bock (1965, 1986) for arbitrarily picking a sequence³, but is just as guilty of arbitrarily picking a sequence of three easily-identifiable traits of questionable relevance. The traits Padian chooses are drawn from questionable comparison with powered flight in fixed wing aircraft, and may not actually reflect how the functions play out in real animal flight. The previous chapters here have provided ample suggestions for what functional traits should be considered.

From chapters 1 and 2, maneuvering and the production of left-right asymmetries appears very important and measurable. This is true in other taxa as well; studies of ants (Munk, 2011) and stick insects (Zeng, in prep) look at the consequences of body postures for maneuvering or other functions, and such means can produce maneuvers even in vertebrates with zero aerial history and no obvious aerial adaptations (Cardona et al., 2011; Evangelista et al., 2012). For a balanced biomechanical assessment of the origins of vertebrate flight, it is logical to expand the phylogenetic arguments in Padian (1987, 2001) by considering (1) stability; (2) control effectiveness from symmetric movements and (3) control effectiveness from asymmetric movements; these may vary also according to glide angle or angle of attack. In this chapter, we adopt the same key method suggested by Padian (2001) of cross-testing adaptive hypotheses by tracing traits on a tree to ask what the patterns are.

²There is now broad support for a four-winged morphology as ancestral to the Avialaes (see Hu et al., 2009; Xu et al., 2011; Zheng et al., 2013).

³While Padian's criticism of Bock regarding the need to consider phylogenetic context is valid, arbitrarily defining that "powered flight" is a special entity and then selecting traits based on that, in the way Padian does, is not quite right because it postulates that maneuvering-related uses of traits during "non-powered" flight are not important; by definition, Padian excludes maneuvering hypotheses from testing.

One apparent trend is the transition from long tails and feathered legs in early stem birds to extant forms with reduced tails and absence of flight feathers on the legs; such a pattern is convergently repeated in pterosaurs. The functional consequences of this have not been identified via model testing, though others have theorized about them (Beebe, 1915; Maynard Smith, 1953; Thomas, 1997). Other changes happening during the evolution of this group include changes in the shoulder and pectoral girdle, loss of teeth, development of the triosseal canal, fusion of digits, fusion of the posterior axial skeleton, and development of a carinate sternum. While many of these are typically assumed to be related to increasing flight power, they could also have had maneuvering implications, particularly regarding the shoulder girdle and the ability of a carinate sternum to allow larger left-right asymmetry in force production.

I hypothesize that aerial maneuvering was a major factor shaping the early evolution of flight in birds and that maneuvering abilities were present early in bird evolution, in the form of directed aerial descent in taxa that may have had no identifiable aerodynamic structures; and that these abilities may have shifted in form and function as planforms changed during the evolution of birds (for example from long tailed forms like \dagger *Microraptor* (Xu et al., 2003), \dagger *Anchiornis* (Hu et al., 2009), and \dagger *Archaeopteryx* (reviewed in Christiansen and Bonde, 2004; Longrich, 2006), to short-tailed forms with relatively large wings as in modern birds). The prediction of these hypotheses is that we will observe shifts in stability and control effectiveness when model test results (from engineering techniques) are mapped onto phylogenetic trees (a technique from comparative biology). The alternative is that there may be no pattern to the evolution of maneuvering-related features, or that early in evolution, maneuvering ability is absent and only develops later.

I also predict shifts in preferred directions of maneuvering and methods used to accomplish aerial righting, by left-right asymmetric movements, inertial movements, or symmetric movements; these have also already been observed in ontogenetic work with baby birds (chapter 1)⁴. While ontogeny is not guaranteed to recapitulate phylogeny, we may observe if stability and control effectiveness mirror the sequence of maneuvers seen during ontogeny.

3.1.1 Quantifying maneuvering: Stability and control effectiveness

To briefly review chapter 2, recall that a body in flight at sufficiently high speed will experience aerodynamic forces (lift and drag) from the air flow around it Etkin and Reid (1996); McCormick (1995). The body will also feel aerodynamic torques or moments that may cause it to pitch up or down, roll to one side or the other, or yaw left or right in heading ⁵. The

⁴In contrast, the predictions of an alternative hypothesis (Dial, 2003; Dial et al., 2008; Tobalske et al., 2011) were not borne out in our observations; during both evolution and ontogeny, organisms maneuver early on, using left-right asymmetries; while the symmetrical flapping needed for wing-assisted incline running only comes later.

⁵In aerodynamics usage, roll, pitch and yaw are generally used to refer to perturbations about a particular operating point given by a body's bank, elevation, and azimuth; in the interest of not confusing a general

moments, which are of primary interest for this study, can be measured and used to quantify maneuvering ability of a shape by examining stability and control effectiveness (chapter 2, Etkin and Reid, 1996; McCay, 2001a,b; McCormick, 1995). It is typical to nondimensionalize the moments, to compare primarily the effect of shape, rather than of size or speed. For example, the pitching moment coefficient is given by

pitching moment =
$$M = 0.5C_m \rho u^2 A \lambda$$
 (3.1)

where $\rho = 1.2 \text{ kg m}^{-3}$ is the density of air, u is the speed, A is a characteristic area taken here as the planform area and λ is a characteristic length taken here as the estimated snout-vent length (Koehl et al., 2011; McCay, 2001a,b). Rolling moment coefficient C_r and yawing moment coefficient C_y are similarly defined.

For a given shape or body in a particular posture, a stable equilibrium point is a fixed point (zero moments) in which the body feels a restoring moment when deflected away (see chapter 2, see also Etkin and Reid, 1996; McCay, 2001a,b; McCormick, 1995). To quantify stability, the moments acting on the body are measured as it is perturbed (in pitch, roll, or yaw). Stability is indicated by the slope; negative slope results in restoring moments and indicates static stability, while positive slope indicates that the moments are destabilizing (Etkin and Reid, 1996; McCay, 2001a; McCormick, 1995). For example, in pitch, the pitching stability coefficient is given by

pitching stability coefficient =
$$C_{m,\alpha} = \frac{\partial C_m}{\partial \alpha}$$
 (3.2)

where α is the angle of attack. Stability for roll $(C_{r,\phi} = \partial C_r / \partial \phi)$ and yaw $(C_{y,\psi} = \partial C_y / \partial \psi)$ are similarly evaluated. As a simple example, consider the case of a sphere versus a weather vane, shown in Figure 3.1. The symmetrical sphere feels no restoring moments and is marginally stable, while the weather vane is stable near zero. A backwards weathervane would show positive slope indicating instability. A weathervane with larger tail feathers would show a greater slope, indicating larger restoring torques felt for a given deflection.

Just as stability can be quantified by perturbing the position of the entire body, the control effectiveness of a particular appendage or body movement can be examined by perturbing the appendage, to measure the change in moments as the appendage moves. In aeronautical engineering, the control effectiveness measured in this way might be used to understand how much yawing torque is exerted on an airframe for every degree of rudder deflection, for example: $C_{y,\delta} = \partial C_y / \partial \delta$ (McCormick, 1995). For this study, we examine the change in aerodynamic torques for small movements of the wings, legs or tail. A graphical example for the effect of tail dorso-flexion on pitch in $\dagger Microraptor$ is given in Figure 3.2, from (Koehl et al., 2011; Tisbe et al., 2011). As the tail is deflected upwards 15° the body feels a nose-up pitching moment, while deflecting the tail downwards 15° results in a nose-down pitching moment; this fits with intuition and experience with toy gliders.

reader, we use the more widely understood terms here.



Figure 3.1: Stability of a sphere versus a weathervane



Figure 3.2: Example of control effectiveness of tail deflection in $\dagger Microraptor$. From Koehl et al. (2011); Tisbe et al. (2011). As the tail is deflected upwards the body feels a nose-up pitching moment, while deflecting the tail downwards results in a nose-down pitching moment. Equivalently, tail movement shifts the stable equilibrium point to higher or lower angle of attack, respectively.

Maneuvering ability is determined by the combination of stability and control effectiveness. A biomechanical tradeoff is inherent here; a highly stable object can resist perturbations (from disturbances in the air, impacts or collisions) with minimal control effort, but it will also have difficulty in changing direction (to right or direct its descent to safe landing areas, resources of interest, or to maneuver away from predators). Locomotion is a complex task and passive stability is often exploited to reduce control effort (Jindrich and Full, 2002; Kubow and Full, 1999; Ting et al., 1997); conversely, passive instability may be exploited in extreme (and likely selective) maneuvers when organisms do not possess enough actuator and brain to provide closed-loop control around an unstable system during a very fast or challenging maneuver (Cardona et al., 2011; Evangelista et al., 2012). It is instructive to examine the evolution of both stability and control effectiveness within a phylogenetic context, using comparative methods.

3.1.2 Examining patterns in evolution of maneuvering using phylogenetic comparative methods

To examine patterns in the evolution of maneuvering, we examined how morphological characters and performance change during the evolution of the Avialae (\dagger *Archaeopteryx* and descendants, Gauthier, 1986). The phylogeny (Figure 3.3) used was assembled from (Li et al., 2010; O'Connor et al., 2011; Zhou and Li, 2010) for extinct taxa and from (Cracraft et al., 2004) for four extant birds used in the comparison. Two outgroups (\dagger *Anchiornis* Hu et al., 2009 and \dagger *Microraptor* Xu et al., 2003) were also included in the analysis. Mapping stability, control effectiveness, and morphological traits onto the tree allows examination of patterns in the evolution of maneuvering.

3.2 Materials and Methods

Forces and torques were measured on specially constructed physical models in a wind tunnel using methods similar to chapter 2, which describes the general methods used.

3.2.1 Models

To compare maneuvering as morphology changes during the evolution of the clade, we created physical models (8 cm SVL) of four extant birds and eight theropods. Species were selected to sample available phylogenies; fossils were also selected to provide reasonable support for relative limb and body proportion and wing and tail feather planform. Table 3.1 and figure 3.4 give the source fossils and references used in construction⁶. In addition to the models discussed here, we created models of three pterosaurs, two bats, and two artificial

⁶Neither I, nor any member of my team has yet had opportunity to directly examine any of the fossils which have been the focus here. We hope to remedy this in the future. While we have made best use of papers, reprints, and remotely available resources, direct examination would enable serious re-examination of bony or integumentary features that correlate with the changes observed herein.



Figure 3.3: Phylogeny of the Avialae, after (Cracraft et al., 2004; Li et al., 2010; O'Connor et al., 2011; Zhou and Li, 2010). Assembled based on strict consensus between the most parsimonious trees.

shapes (sphere and weathervane) for checking calibration and to explore parallel evolution.

Fossil theropods were reconstructed in a position with the wings spread and the legs extended back (Xu et al., as presented in a television documentary in Davis, 2008). Models were constructed closely referencing published photographs of impression fossils and reconstructions identified in the literature. Completed models are shown in Figure 3.5 and summarized in Table 3.2. Unlike chapter 2, in this chapter I ignored the more fanciful and less supported postures (biplanes, unrealistic sprawled postures, ballet-inspired postures). I also focused on appendage movements shown in chapter 2 to have measurable effect: asymmetric wing pronation/supination and wing tucking, symmetric wing protraction/retraction, and movements of the tail.

3.2.2 Aerodynamic measurements

As in chapter 2, wind tunnel tests were conducted with a six-axis force and torque sensor (Nano17, ATI Industrial Automation, Apex, NC). The sensor was mounted to a 0.5 inch



Figure 3.4: Fossils used for comparative study. A. †*Anchiornis* (Hu et al., 2009). B. †*Microraptor* (Xu et al., 2003). C. †*Archaeopteryx*, photo from UCMP. D. †*Jeholornis* (Zhou and Zhang, 2002; Zhou et al., 2003). E. †*Zhongornis* (Gao et al., 2008). F. †*Sapeornis* (Zhou and Zhang, 2003). G. †*Zhongjianornis* (Zhou and Li, 2010). H. †*Confuciusornis* (Chiappe et al., 2008; Hou et al., 1995). I. Extant birds *Alectoris*, *Columba*, *Larus*, and *Buteo*, from Google Images.

Table 3.1: Fossil taxa sampled for aerodynamic testing and references used during model construction.

	specimen and reference	approx length	remarks
		$10^{-2}{ m m}$	
$\dagger Microraptor$	IVPP $V13352^1$	85	
$\dagger Anchiornis$	LPM $B00169^{2}$	42	
$\dagger Archaeopteryx$	$\operatorname{Berlin}^{3,4}$	40	
† Jeholornis	IVPP V13274, $13553^{5,6}$	65	feathers only in 13553
$\dagger Zhongorn is$	$D2456-2456^7$	10	weak feather impressions only
$\dagger Sape orn is$	IVPP V13275 ⁸	27	
†Zhongjianornis	IVPP $V15900^{9}$	22	
<i>†Confuciusornis</i>	$\mathrm{multiple}^{10,11}$	30	

References: ¹(Xu et al., 2003) ²(Hu et al., 2009) ³(Benton, 1997) ⁴(Longrich, 2006) ⁵(Zhou and Zhang, 2002) ⁶(Zhou et al., 2003) ⁷(Gao et al., 2008) ⁸(Zhou and Zhang, 2003) ⁹(Zhou and Li, 2010) ¹⁰(Chiappe et al., 2008) ¹¹(Hou et al., 1995)

 $(1.27 \times 10^{-2} \text{ m})$ aluminum sting damped with sand and rubber (figure 3.5B). The force sensor and sting exited the models at mid-torso, at approximately the center of mass, on the right side (for pitch measurements), dorsally (for yaw measurements) and posteriorly (for roll measurements). In some measurements, use of a 2 mm steel extension rod was necessary to avoid interferences between the model and sensor.

Wind tunnel tests were conducted as in chapter 2, primarily at 6 m s^{-1} resulting in a Reynolds number of around 32 000. The Re here corresponds to full-scale $\dagger Archaeopteryx$, however we do not anticipate major scale effects. In this regime and at high angles of attack, the aerodynamic constants of interest are reasonably constant with Re (chapter 2, see also Koehl et al., 2011).

Force transducer readings were recorded at 1000 Hz sampling frequency using a data acquisition card (PCI-6251, National Instruments, Austin, TX), as in chapter 2. In these experiments, the sting was mounted to a standard-size digital servo modified for 180° operation (HS-5485HB, Hitec USA, Poway, CA) and interfaced to the data acquisition computer via a specially constructed interface box based on an Arduino microcontroller (SparkFun, Boulder, CO) using specially written code in Python. This allowed the computer to automatically position the sting, zero the sensor, control wind tunnel speed, and take measurements. As in chapter 2, raw measurements were rotated from a frame fixed to the model to one aligned with the wind tunnel and flow using the sting angle; the transformation also accounted for any additional mounting rods used (translation and rotation matrix; identical to those given in appendix B).

Using the automated sting, we obtained 13,792 points for 247 positions (86 pitch, 69 roll,

	area, S	SVL	TL	span, s	AR
	$10^{-4}{ m m}^2$	$10^{-2}\mathrm{m}$	$10^{-2}\mathrm{m}$	$10^{-2}\mathrm{m}$	
$\dagger Anchiornis$	87.11	7.1	18.0	19.6	2.2
$\dagger Archae optery x$	94.57	8.0	10.5	17.7	1.7
$\dagger Confucius orn is$	50.53	6.8	9.2	19.9	3.9
$\dagger Jeholorn is$	77.03	7.7	19.0	22.7	3.4
$\dagger Microraptor$	114.60	9.3	22.5	19.2	1.6
$\dagger Sape orn is$	54.44	6.6	7.6	20.7	3.9
$\dagger Zhong jian orn is$	61.87	8.3	10.1	21.3	3.7
$\dagger Zhongorn is$	44.73	7.7	11.5	15.4	2.7
Alectoris	57.89	7.1	9.8	15.0	2.0
Buteo	98.55	8.3	9.9	23.8	2.9
Columba	80.71	7.3	9.8	19.3	2.3
Larus	72.62	7.9	10.5	24.0	4.0
†Onychonycteris	194.70	9.6	13.4	29.5	2.2
Pteropus	201.20	8.4	12.4	35.1	3.1
$\dagger Pteranodon$	42.13	6.4	6.5	22.1	5.8
$\dagger Pterodactylus$	51.15	8.4	8.9	19.0	3.5
$\dagger Rham phorynchus$	78.56	8.0	18.4	29.7	5.6
Sphere	11.34		3.8	3.8	0.6
Weathervane	39.30		24.0	5.0	0.3

Table 3.2: Geometry data for physical models of eight extinct theropod dinosaurs, four extant birds, two bats, three pterosaurs, and two shapes for checking calibration

92 yaw total). The positions focused on static stability in pitch, roll, and yaw; control effectiveness of symmetric wing, leg, and tail movements; and control effectiveness of asymmetric wing and tail movements.

3.2.3 Phylogenetic comparative methods

A Nexus file without branch lengths was prepared representing the topology of trees assembled from (references) and shown in Figure 3.3. Mapping of the discrete maneuvering traits was performed in Mesquite citepMesquite with the built-in ancestral state reconstruction routines, using unordered parsimony with no branch length information.

The aerodynamic measurements were coded into two character matrices. The first character matrix gave 8 discretized (stable, marginal, unstable) stability values for each taxa. The matrix also included 10 discrete morphological traits and 12 discretized control effec-





Figure 3.5: Models used for comparative study. A. Example model design working directly from fossil. B. Completed model mounted on robotic sting, *†Archaeopteryx* based on Longrich (2006) reconstruction. C. Dinosaur models plus *Larus*, SVL 8 cm. Photo credit Tony Huynh.

tiveness values. Control effectiveness was discretized as two states (effective or not effective), using a threshold coefficient value of 0.09. The value was set based on the restoring moment felt by the weathervane model, and so is expected to represent a reasonably large achievable control moment. A second character matrix gave the continuous character states based on the mean values reported here.

3.3 Results

3.3.1 Aerodynamic measurements

Typical data for a series is given in Figures 3.6-3.8. Figure 3.8 also illustrates how stability and equilibrium point are read from a given run from the slope of the neutral position line and the spread between control movement in opposite directions. The results for all runs are summarized in tables 3.4-3.10.



Figure 3.6: Example raw aerodynamic measurements. All pitch data for all taxa, all positions, all runs.

Pitch stability data for all runs and models are given in Table 3.3. Control effectiveness in pitch of tail dorso-flexion and symmetric wing protraction are given in Tables 3.4 and 3.5.

Roll stability data for all runs and models are given in Table 3.6. Control effectiveness in roll of asymmetric wing tucking is given in Table 3.7.

Yaw stability data for all runs and models are given in Table 3.8. Control effectiveness in



Figure 3.7: Example raw aerodynamic measurements. All wing control effectiveness runs.

yaw of tail lateral movement and asymmetric wing pronation/supination is given in Tables 3.9 and 3.10.



Figure 3.8: Example raw aerodynamic measurements. Long-tailed taxa in A, short-tailed taxa in B. Square shows straight tail, upward triangle 15° tail up, downward triangle 15° tail down. Long-tailed taxa have a stable equilibrium point at $10-25^{\circ}$, and the tail is effective at low angles of attack. Short-tailed taxa have an unstable equilibrium point at $0-5^{\circ}$ and the tail is ineffective at low angles of attack.
Table 3.3: Pitch stability coefficients $\partial C_m/\partial \alpha$, measured using physical models. Results are shown as mean \pm standard deviation, n = 15.

	$\frac{\partial C}{\partial \alpha}$ at low ar	nd high angle of attack		pitch ϵ	equilibrium point
	$\alpha = 0^{\circ}$	$lpha=15^{\circ}$	$\alpha = 75^{\circ}$	equilib α	equilib $\frac{\partial C}{\partial \alpha}$
$\dagger Anchiornis$	-0.005 ± 0.013	-0.067 ± 0.012	-0.13 ± 0.03	29 ± 2	-0.170 ± 0.028
$\dagger Archae optery x$	-0.134 ± 0.013	-0.221 ± 0.020	-0.18 ± 0.03	9 ± 2	-0.190 ± 0.012
$\dagger Confucius ornis$	0.142 ± 0.009	0.039 ± 0.020	-0.06 ± 0.02	0 ± 2	-0.030 ± 0.073
$\dagger Jeholornis$	0.011 ± 0.018	-0.108 ± 0.010	-0.10 ± 0.02	25 ± 1	-0.120 ± 0.044
$\dagger Microraptor$	-0.039 ± 0.006	-0.071 ± 0.009	-0.17 ± 0.02	20 ± 2	-0.070 ± 0.029
$\dagger Sape ornis$	0.109 ± 0.010	0.007 ± 0.011	-0.11 ± 0.02	5 ± 2	-0.100 ± 0.052
$\dagger Zhong ji a nornis$	0.305 ± 0.036	0.195 ± 0.027	-0.15 ± 0.16	5 ± 1	0.180 ± 0.078
$\dagger Zhongornis$	0.237 ± 0.021	0.084 ± 0.017	-0.11 ± 0.09	0 ± 2	0.060 ± 0.089
A lector is	0.206 ± 0.006	0.090 ± 0.020	-0.37 ± 0.16	0 ± 1	0.120 ± 0.013
Buteo	0.187 ± 0.010	-0.042 ± 0.009	-0.13 ± 0.02	0 ± 3	-0.140 ± 0.030
Columba	0.046 ± 0.014	-0.047 ± 0.017	-0.18 ± 0.16	0 ± 6	-0.050 ± 0.088
Larus	0.352 ± 0.028	0.092 ± 0.015	-0.10 ± 0.02	0 ± 1	0.150 ± 0.049
$\dagger Onychonycteris$	-0.011 ± 0.011	-0.112 ± 0.005	-0.12 ± 0.02	10 ± 2	-0.110 ± 0.033
Pteropus	-0.118 ± 0.014	-0.055 ± 0.008	-0.10 ± 0.02	0 ± 2	-0.080 ± 0.015
$\dagger Pteranodon$	0.054 ± 0.023	0.004 ± 0.018	-0.07 ± 0.04	5 ± 3	-0.050 ± 0.029
$\dagger Pterodactylus$	-0.020 ± 0.020	-0.050 ± 0.009	-0.05 ± 0.03	0 ± 4	-0.040 ± 0.009
$\ddagger Rhamphorynchus$	-0.062 ± 0.013	-0.192 ± 0.024	-0.05 ± 0.01	15 ± 1	-0.180 ± 0.044
Sphere	-0.037 ± 0.023	-0.020 ± 0.022	-0.03 ± 0.01	50 ± 1	-0.050 ± 0.006
Weathervane	-0.333 ± 0.040	-0.347 ± 0.020	-0.03 ± 0.04	0 ± 2	-0.210 ± 0.055

Table 3.4: Control effectiveness $(\frac{\partial C}{\partial \delta})$ in pitch using tail dorsoventral flexion, at low and high angle of attack. For bats, control effectiveness using leg and tail deflections is shown instead. Results are shown as mean \pm standard deviation, n = 5 for all points.

	$\frac{\partial C}{\partial \delta}$ at lo	w and high angle of att	ack
	$\alpha = 0^{\circ}$	$lpha=15^{\circ}$	$\alpha = 75^{\circ}$
$\ddagger Anchiornis$	0.168 ± 0.002	0.191 ± 0.006	0.0467 ± 0.0120
$\ddagger Archaeopteryx$	0.219 ± 0.007	0.190 ± 0.010	0.0649 ± 0.0240
$\dagger Confucius ornis$	0.011 ± 0.003	0.013 ± 0.003	0.0178 ± 0.0050
$\dagger Jeholornis$	0.268 ± 0.019	0.223 ± 0.001	0.0678 ± 0.0050
$\dagger Microraptor$	0.174 ± 0.023	0.125 ± 0.002	0.0891 ± 0.0140
$\dagger Sapeornis$	0.054 ± 0.001	0.064 ± 0.005	0.0817 ± 0.0060
$\dagger Zhongjianornis$	0.023 ± 0.004	0.019 ± 0.004	0.0124 ± 0.0260
\dagger Zhongornis	0.049 ± 0.006	0.048 ± 0.002	0.0455 ± 0.0030
Alectoris	0.011 ± 0.004	0.012 ± 0.005	0.0443 ± 0.0070
Buteo	0.018 ± 0.003	0.033 ± 0.012	0.0491 ± 0.0060
Columba	0.044 ± 0.004	0.050 ± 0.003	0.0085 ± 0.0020
Larus	0.014 ± 0.008	0.016 ± 0.003	0.0137 ± 0.0080
$\ddagger Onychonycter is$	0.029 ± 0.004	0.032 ± 0.002	0.004 ± 0.004
Pteropus	0.053 ± 0.009	0.026 ± 0.003	0.026 ± 0.002
$\ddagger Pteranodon$	0.016 ± 0.005	0.015 ± 0.002	0.0158 ± 0.0030
$\dagger Pterodactylus$	0.015 ± 0.002	0.025 ± 0.004	0.0388 ± 0.0050
$\ddagger Rhamphorynchus$	0.347 ± 0.016	0.245 ± 0.032	0.0288 ± 0.0100

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Table 3.5: Control effectiveness $(\frac{\partial C}{\partial \delta})$ in pitch using symmetric wing protration/retraction (wing sweep), at low and high angle of attack. Results are shown as mean \pm standard deviation, n = 5 for all points.

	$\frac{\partial C}{\partial \delta}$ at low	and high angle of attack	
	00	15°	75°
$\dagger Anchiornis$	0.00 ± 0.02	0.05 ± 0.02	0.070 ± 0.004
$\ddagger Archaeopteryx$	-0.00253 ± 0.01600	0.060 ± 0.018	0.12800 ± 0.00367
$\dagger Confucius ornis$	0.00640 ± 0.03400	0.117 ± 0.023	0.22900 ± 0.00150
+ Jeholornis	0.04239 ± 0.00900	0.072 ± 0.006	0.08800 ± 0.00204
$\ddagger Microraptor$	0.01784 ± 0.00800	0.037 ± 0.003	0.05100 ± 0.00362
$\ddagger Sapeornis$	0.02174 ± 0.03800	0.173 ± 0.039	0.32900 ± 0.00113
$\dagger Zhongjian ornis$	0.02522 ± 0.02700	0.119 ± 0.023	0.22100 ± 0.00063
$\ddagger Zhongorn is$	0.02976 ± 0.01200	0.069 ± 0.010	0.10000 ± 0.00062
Alectoris	-0.00095 ± 0.01700	0.124 ± 0.020	0.11900 ± 0.00168
Buteo	0.04297 ± 0.03400	0.142 ± 0.021	0.21300 ± 0.00130
Columba	0.07612 ± 0.02700	0.151 ± 0.013	0.16800 ± 0.00019
Larus	-0.00706 ± 0.03000	0.110 ± 0.032	0.23100 ± 0.00123
$\dagger Onychonycteris$	0.03101 ± 0.03000	0.152 ± 0.031	0.23500 ± 0.00254
Pteropus	-0.00490 ± 0.04100	0.131 ± 0.030	0.23000 ± 0.00229
$\dagger Pteranodon$	0.16728 ± 0.05000	0.315 ± 0.033	0.48000 ± 0.00137
$\dagger Pterodactylus$	0.00492 ± 0.02600	0.088 ± 0.018	0.14100 ± 0.00231
$\ddagger Rhamphorynchus$	0.01197 ± 0.02500	0.045 ± 0.020	0.17500 ± 0.00070

Table 3.6: Roll stability coefficients measured using physical models. Results are shown as mean \pm standard deviation, n = 15 for all points except sphere. For sphere (tested only in pitch), roll stability is 0 (exact) due to symmetry.

	15°	75°
$\dagger Anchiorn is$		
$\dagger Archae optery x$	0.009 ± 0.060	-0.200 ± 0.019
$\dagger Confucius orn is$	-0.020 ± 0.020	-0.20 ± 0.09
$\dagger Jeholorn is$	0.073 ± 0.030	-0.400 ± 0.025
$\dagger Microraptor$	0.132 ± 0.030	-0.300 ± 0.019
$\dagger Sape orn is$	0.043 ± 0.040	-0.300 ± 0.026
$\dagger Zhong jian orn is$	0.030 ± 0.020	-0.200 ± 0.012
$\dagger Zhongorn is$	0.017 ± 0.040	-0.10 ± 0.08
Alectoris	0.009 ± 0.060	-0.100 ± 0.016
Buteo	0.028 ± 0.050	-0.400 ± 0.022
Columba	-0.030 ± 0.050	-0.300 ± 0.014
Larus	-0.009 ± 0.020	-0.400 ± 0.028
†Onychonycteris		-1.000 ± 0.044
Pteropus	-0.027 ± 0.050	-0.700 ± 0.064
†Pteranodon	0.011 ± 0.020	-0.200 ± 0.014
$\dagger Pterodactylus$	-0.002 ± 0.060	-0.300 ± 0.016
$\dagger Rham phorynchus$	-0.069 ± 0.030	-0.400 ± 0.021
Sphere	0	0

Table 3.7: Control effectiveness $(\frac{\partial C}{\partial \delta})$ in roll using asymmetric wing tucking, at low and high angle of attack. Results are shown as mean \pm standard deviation, n = 5 for all points.

	15°	75°
$\dagger Anchiorn is$		
$\dagger Archae optery x$	0.090 ± 0.005	0.200 ± 0.018
$\dagger Confucius orn is$	0.050 ± 0.002	0.100 ± 0.012
†Jeholornis	0.080 ± 0.004	0.120 ± 0.024
$\dagger Microraptor$	0.050 ± 0.007	0.170 ± 0.021
$\dagger Sape orn is$	0.080 ± 0.002	0.130 ± 0.016
$\dagger Zhong jian orn is$	0.050 ± 0.001	0.140 ± 0.015
$\dagger Zhongorn is$	0.030 ± 0.001	0.050 ± 0.007
Alectoris	0.060 ± 0.002	0.080 ± 0.007
Buteo	0.170 ± 0.012	0.240 ± 0.055
Columba	0.180 ± 0.007	0.180 ± 0.027
Larus	0.150 ± 0.004	0.200 ± 0.038
$\dagger Onychonycter is$	0.810 ± 0.036	0.880 ± 0.100
Pteropus	0.680 ± 0.020	0.830 ± 0.088
†Pteranodon	0.070 ± 0.002	0.100 ± 0.010
$\dagger Pterodactylus$	0.100 ± 0.003	0.110 ± 0.027
$\dagger Rham phorynchus$	0.160 ± 0.007	0.210 ± 0.030

Table 3.8: Yaw stability coefficients measured using physical models. Results are shown as mean \pm standard deviation, n = 15 for all points except sphere and weathervane. Sphere and weathervane values not measured; based on symmetry, pitch values given for comparison purposes (not significantly different from 0).

	15°	75°
$\dagger Anchiornis$	-0.09690 ± 0.00293	0.00640 ± 0.00595
$\dagger Archae optery x$	-0.06970 ± 0.00436	0.00960 ± 0.00440
$\dagger Confucius orn is$	-0.02590 ± 0.00215	0.00350 ± 0.00212
$\dagger Jeholornis$	-0.09100 ± 0.00286	0.00160 ± 0.00091
$\dagger Microraptor$	-0.10060 ± 0.01577	0.03900 ± 0.01001
$\dagger Sape orn is$	0.00190 ± 0.00253	0.00470 ± 0.00042
$\dagger Zhong jian orn is$	0.02070 ± 0.00310	0.00830 ± 0.00200
$\dagger Zhongorn is$	0.01410 ± 0.00215	0.00 ± 0.81
Alectoris	0.02200 ± 0.00084	0.00140 ± 0.00213
Buteo	0.02700 ± 0.00583	-0.00190 ± 0.00412
Columba	0.04760 ± 0.00204	0.00270 ± 0.00158
Larus	0.01730 ± 0.00394	0.00230 ± 0.00150
†Onychonycteris	0.02450 ± 0.00796	-0.04000 ± 0.00741
Pteropus	0.03976 ± 0.02476	-0.16000 ± 0.00545
†Pteranodon	0.02630 ± 0.00199	0.00160 ± 0.00042
$\dagger Pterodactylus$	-0.00190 ± 0.00071	0.00180 ± 0.00084
$\dagger Rham phorynchus$	-0.05210 ± 0.00366	-0.03400 ± 0.00388
Sphere (pitch)	-0.020 ± 0.022	-0.03 ± 0.01
Weathervane (pitch)	-0.346 ± 0.020	0.03 ± 0.04

Table 3.9: Control effectiveness $\left(\frac{\partial C}{\partial \delta}\right)$ in yaw using left-right asymmetric tail flexion, at low and high angle of attack. Results are shown as mean \pm standard deviation, n = 5 for all points. Tails on model *Pteropus*, $\dagger Pteranodon$, and $\dagger Pterodactylus$ too small to bend.

	15°	75°
$\dagger Anchiornis$	0.23860 ± 0.07042	0.06860 ± 0.01319
$\dagger Archae optery x$	0.22010 ± 0.07074	0.06640 ± 0.00355
$\dagger Confucius orn is$	0.00240 ± 0.00077	-0.00420 ± 0.00088
$\dagger Jeholorn is$		-0.02740 ± 0.00673
$\dagger Microraptor$	0.51960 ± 0.08315	-0.07580 ± 0.00985
$\dagger Sape orn is$		
$\dagger Zhong jian orn is$	-0.00140 ± 0.00193	-0.00710 ± 0.00125
$\dagger Zhongorn is$	0.00720 ± 0.00205	-0.01120 ± 0.00143
Alectoris	0.01930 ± 0.01246	-0.04960 ± 0.00146
Buteo	-0.00680 ± 0.00337	-0.02900 ± 0.00296
Columba	0.00480 ± 0.00194	-0.02230 ± 0.00056
Larus		-0.01230 ± 0.00193
†Onychonycteris	-0.01110 ± 0.00453	-0.01180 ± 0.00317
<i>Pteropus</i> (no tail)		
† <i>Pteranodon</i> (no tail)		
† <i>Pterodactylus</i> (no tail)		
$\dagger Rham phorynchus$	0.16990 ± 0.00790	0.12760 ± 0.00212

	15°	75°
$\dagger Anchiornis$	0.1990 ± 0.0300	0.3300 ± 0.0042
$\dagger Archae opter yx$	0.4200 ± 0.0152	0.3830 ± 0.0155
$\dagger Confucius orn is$	0.2060 ± 0.0254	0.1840 ± 0.0073
$\dagger Microraptor$	0.2590 ± 0.0130	0.3730 ± 0.0075
$\dagger Zhong jian orn is$	0.2960 ± 0.0153	0.2620 ± 0.0149
$\dagger Zhongorn is$	0.1150 ± 0.0059	0.1130 ± 0.0020
Alectoris	0.0810 ± 0.0134	0.0930 ± 0.0041
Buteo	0.5650 ± 0.0598	0.4310 ± 0.0246
Columba	0.4550 ± 0.0416	0.2040 ± 0.0034
$\dagger Ony chonycter is$	0.8700 ± 0.0929	0.6270 ± 0.0487
$\dagger Pteranodon$	0.2710 ± 0.0130	0.2340 ± 0.0036
$\dagger Pterodactylus$	0.1960 ± 0.0141	0.1390 ± 0.0130
$\dagger Rhamphorynchus$	0.2790 ± 0.0270	0.3190 ± 0.0240

Table 3.10: Control effectiveness $\left(\frac{\partial C}{\partial \delta}\right)$ in yaw using asymmetric wing supination, at low and high angle of attack. Results are shown as mean \pm standard deviation, n = 5 for all points.

Table 3.11: Control effectiveness $\left(\frac{\partial C}{\partial \delta}\right)$ in yaw using the head, at low and high angle of attack. Results are shown as mean \pm standard deviation, n = 5 for all points.

	15°	75°
$\dagger Pteranodon$	0.1200 ± 0.0021	-0.00330 ± 0.00049
$\dagger Pterodactylus$	0.1900 ± 0.0030	0.00220 ± 0.00137
$\dagger Rham phorynchus$	-0.0330 ± 0.0091	

3.3.2 Mapping onto trees

The aerodynamic measurements were coded into two character matrices. The first character matrix gives discretized (stable, marginal, unstable) values for each taxa. The second character matrix gives the continuous character states based on the mean values reported here.

Mapping of the discrete character states onto the phylogeny of Figure 3.3 gives the results in Figures 3.9-3.12.



Figure 3.9: Pitch stability at equilibrium changes within the tree. Long-tailed taxa are stable in pitch at equilibrium; short-tailed taxa are not.



Figure 3.10: Control effectiveness of the tail changes within the tree. Long-tailed taxa have large tail control effectiveness; short-tailed taxa do not.



Figure 3.11: Control effectiveness of symmetric wing protraction changes within the tree. Wing control effectiveness increases in later taxa.



Figure 3.12: Evolution of pitch maneuvering within the tree. Consilience between three traits (pitch stability, tail control effectiveness, and wing control effectiveness). Early in the tree, taxa are stable and with some amount of tail control effectiveness. Later in the tree, taxa are unstable and control effectiveness has been lost in the short tails. However, it has migrated to the wings.



Figure 3.13: Evolution of roll maneuvering within the tree. Characters shown are stability at low angle of attack (mostly unstable due to symmetry; $\dagger Zhongornis$ and $\dagger Sapeornis$ marginal); stability at high angle of attack (all stable); and control effectiveness of asymmetric wing tucking in roll (always effective).

Figure 3.13 shows the results of mapping roll-related maneuvering performance onto the tree. At low angle of attack, most models in roll are unstable, while $\dagger Zhongornis$ and $\dagger Sapeornis$ marginal). At high angle of attack, all models are stable. Asymmetric wing tucking is always effective in producing roll for these measurements.

In yaw, there are clear differences between high angle of attack (figure 3.14) and low angle of attack (figure 3.15) situations. At high angle of attack, models are mostly marginally stable, with a few that are unstable. Wing asymmetric movements are always effective at creating yawing moments at high angle of attack.

On the other hand, at low angle of attack, long tailed models are stable in yaw, while short tails render the model marginal or unstable. As with the pitch case, tails are only effective in generating yawing moments in organisms with long tails. Wing asymmetric movements are always effective at creating yawing moments at low angle of attack.



Figure 3.14: Evolution of yaw maneuvering within the tree, high (75°) angle of attack case. Models are mostly marginally stable (left), as might be expected from symmetry. Wing asymmetric movements are always effective at yawing.

3.4 Discussion

3.4.1 Long tails and stability

Figures 3.8 and 3.9 give a clear example of stabilization by a long tail. In figure 3.8A, organisms with long tails are stable in pitch. Notably, the figures show the same shapes for the basal pterosaur $\dagger Rhamphorynchus$ along with $\dagger Archaeopteryx$ and $\dagger Jeholornis$ plus the later dromaeosaur $\dagger Microraptor$. In figure 3.8B, a completely different shape is observed for four short tailed organisms. Long tailed organisms were more stable in pitch (and yaw, see figure 3.15) and the long tail was effective in generating pitching and yawing moments.

3.4.2 Shifts in stability and control in pitch during evolution

Morphologically, the clade shows progressive tail loss as well as loss of leg-associated control surfaces along with a concomitant increase in forward wing size and bony features associated with the pectoral girdle. While traditionally these are assumed to be related to generation of a power stroke, an alternative explanation may be that they are related to shifts in control.

Figures 3.9-3.12 depict this. In pitch (figure 3.9), the models shift from ancestrally stable to unstable in derived taxa. Control effectiveness also appears to migrate from ancestral large and feathered after surfaces (tail and legs, figure 3.10) to the wings (figure 3.11),



Figure 3.15: Evolution of yaw maneuvering within the tree, low (15°) angle of attack case. Long tailed organisms are stable, while short tailed organisms are marginal or unstable. Tail movements are only effective at yawing in long tailed organisms. Wing asymmetric movements are always effective at creating yawing moments at high angle of attack.

which become larger in derived taxa. Consilience between all three traits (figure 3.12) is an indication that as stability and tail length decrease, control is migrating to increasingly capable wings.

The transition appears to initiate as the coracoid becomes elongated, along with other changes in the scapula; in addition, the sternum becomes modified (though the strong keel has not yet developed) (Benton, 1997; Heers and Dial, 2012; Homberger, 2003; Hutchinson and Allen, 2009; Hutchinson and Gatesy, 2000). As the transition proceeds, the tail becomes much reduced into a pygostyle. Other shared derived features appear later (mid-Cretaceous): strut-like coracoid, triosseal canal, synsacrum and carinate sternum. While the latter features are likely more important for power production, the former ones appear to be consistent with maneuvering. That the ontogenetic tests (chapter 1) show young birds are capable of maneuvers before strong development of a carinate sternum (ontogeny of bone growth in Dial et al., 2012; Heers and Dial, 2012; Heers et al., 2011) suggests this interpretation is correct.

3.4.3 Roll and yaw during evolution

In roll (figure 3.13), there are fewer easily recognizable trends during evolution because most models appear to behave the same. In roll, most models were stable at high angle of attack,

and unstable or marginal at low angle of attack. Large asymmetric wing movement (wing tucking) was always effective in creating rolling moments. Recalling results from chapter 1, young birds righted by rolling first, using large asymmetric wing movements. Also, young birds dropped upright tended to stay upright. Very young birds dropped inverted, before development of asymmetric wing movements, were also unable to right and tended to fall (stably) inverted.

In yaw (figures 3.15 and 3.14), models at high angle of attack were marginally stable as might be expected from symmetry. Asymmetric wing pronation/supination was always able to create yawing moments, so organisms were likely maneuverable in yaw early on. This mirrors what was seen in chapter 1 with young birds yawing towards the brooder. At low angle of attack in yaw, similar trends are seen as with pitch. Organisms with long tails are stable but the tail is effective at creating yawing moments; as the tail becomes shorter, organisms become marginal or unstable, and control effectiveness migrates from the shortening tail to the growing wings.

Note that in roll and yaw, the stable mode shifts with angle of attack, which could be a proxy for glide angle or the steepness of descent. At high angle of attack, roll is the more stable direction, while at low angle of attack, yaw is more stable. Wing asymmetrical movements are always effective, while wing symmetrical movements are not. The tail is only useful in long-tailed organisms. These results also mirror the results with baby birds from chapter 1.

3.4.4 Incipient flapping as a control response to instability?

The results here suggest that incipient flapping may have become elaborated as a control response to growing instability. Movements were needed to control body movement as static stability was reduced and eventually lost. Such movements would also have enhanced aero-dynamic force production and provided a means for inertial attitude adjustment. Once the transition to wing-mediated maneuverability and control begins, larger surfaces and increased musculature make it is easier to incorporate dynamic force production. Alternatively, perhaps as ancestral birds made the switch from a stable system to a wing-mediated controlled-instability that enhanced maneuverability, what was originally a control stroke became a power stroke (as seen in chapter 1). This could be tested further with flapping robots (e.g. Peterson, in preparation).

3.4.5 Support for maneuvering hypotheses of the origin of flight in birds

The findings are most consistent with a maneuvering based hypotheses (Dudley and Yanoviak, 2011). Early in evolution, the tail possesses large aerodynamic control effectiveness and the body possesses some degree of stability. Combined with likely dynamic forces and torques generated by tail whipping (Jusufi et al., 2008) or asymmetric or symmetric incipient flap-

ping (chapter 1), this suggests that the ancestral organisms were very capable of righting or directed aerial descent.

Stable directions are consistent with the sequence of righting observed in chapter 1. Early in evolution, the long tail was stabilizing and was a large inertia that would have made it difficult to right in pitch. By rolling with asymmetric wing use, righting would avoid the inertia of the tail; removing the asymmetry would allow stable continued descent. Later in evolution, tails become shorter and control shifts to the wings. In derived forms, wing protraction/retraction is one of the largest available sources of pitching moment (see also chapter 2) and would allow fastest righting; this is indeed seen in later stage baby birds (chapter 1).

Performance mapping onto phylogenies shows that early in evolution, the control system functions well at high angles of attack expected during flight at steep glide angles. Later, the shifts in control system function are consistent with lower glide angles.

3.4.6 Additional support for maneuvering hypotheses

Amazingly, the same trends hold in the three pterosaur models we tested, which also exhibit long tails in ancestral forms ($\dagger Rhamphorynchus$) shifting to shorter tails in derived forms ($\dagger Pteronodon$, $\dagger Pterodactylus$). Pterosaurs are very distant from dinosaurs and birds. This is evidence that the performance trends in evolution seen here are not the result of historical accident, but rather, they are a sign of the physical constraints on flight. Since physics is invariant to ancestry, we might expect convergence in highly physically constrained tasks like aerial righting, directed aerial descent, flight and other aerial behaviors.

The trends observed here could not be observed in our bat models, probably because the earliest bat (†*Onychonycteris*) is mostly a modern bat with only a slightly longer tail, well within tail lengths seen in other extant bats. The fossil record of bats does not provide a sufficiently transitional form to perform the tests we used here, however others have noted the same sequence in baby bats (for example, Padian, 2013). If the as-yet-undiscovered ancestral bat had a flying squirrel-like patagium and long tail, the results here would predict elongation of the forelimbs followed by reduction in tail length as control shifts primarily to the fore; so we anxiously await the discovery of such a fossil as a further test of these hypotheses.

3.4.7 Aerial maneuvering was a major factor shaping the early evolution of flight in birds

As predicted, we observed shifts in stability and control effectiveness during evolution. Morphological changes appear linked with these shifts and are convergent across two very distant volant clades. Contrary to WAIR-based predictions (Dial, 2003; Gatesy and Baier, 2005), maneuvering abilities of some sort were evident early in evolution. The changes seen also mirror those observed during ontogeny in baby birds.

3.5 Acknowledgments

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Chapter 4

Disturbance forces and sensitivity of simple and biological shapes to turbulent incident air velocities

Airborne objects (animals, plants, and vehicles) flying in real environments experience disturbances from turbulence in the air they are flying through. The shape of an object and its size relative to turbulent eddies should affect the magnitudes and frequencies of the disturbances felt, in other words, the sensitivity to turbulence. To test this, I quantified the sensitivity of simple two- and three-dimensional models to turbulent incident air velocity using simultaneous measurements of forces and torques and air velocities in a wind tunnel. Preliminary results compare well with theoretical predictions of the disturbances an airborne organism of a given shape might experience in a particular environment. We also found good general agreement between simplified geometric shapes and 2D animal planforms of equivalent aspect ratio. Elongated shapes with low aspect ratio are better filters of turbulent noise, while high aspect ratio shapes experience more of the turbulence. This may have important consequences for maneuvering and noise pickup from a turbulent environment as body plans evolve.¹

4.1 Introduction

Consider the case of an airborne object translating through the air. In most real environments, the air is not perfectly still but instead has some velocity that can vary in time and space. The variation is often due to turbulence, i.e. blobs of vorticity that advect, diffuse, and stretch in complicated and unpredictable ways (Davidson, 2004; Tennekes and Lumley, 1972). We can go outdoors on windy days and experience this: a light breeze, or heavy gusts, for example.

¹This chapter is intended for J Fluid Mech; portions have been presented in public as a conference poster (Kwong et al., 2013).

Turbulent eddies have length and time scales associated with the swirling fluid they contain (Davidson, 2004; Tennekes and Lumley, 1972). The eddies in a cup of tea are on the scale of millimeters, while larger scale eddies may be of the size of entire weather systems. How an airborne object experiences the turbulence should depend on size. For example, consider a large aircraft and a bee. When experiencing large eddies around the size of the large aircraft, the crew, passengers and cargo experience disturbance forces and torques, and as a consequence are asked to remain seated with seatbelts fastened. When eddies of such large size are experienced by the bee, the bee feels slow, uniform disturbances. Eddies the size of the bee are simply not felt on the large aircraft because they average out over the large size of the airframe. The eddies also give rise to a cascade of energy from large eddies to smaller eddies and down² (Davidson, 2004); the cascade will also play a role in understanding size effects.

The size and shape of the object should alter which eddies are able to exert forces and the magnitude of the forces (Fig 4.1), which for a flying or swimming animal or robot represent force and torque disturbances which must be controlled or damped in order to remain on course. To my knowledge, I know of no widely accepted method to quantify this, so I developed the methods described herein. First, I describe an empirical method in which I correlate force recordings from a stiff six degree-of-freedom (6DOF) force/torque sensor with recordings of the turbulent velocity from a sonic anemometer. I then compare this to theory based on considering the effect of shape as the result of spatial filtering of the eddies.

4.1.1 Relevance of turbulence to biological processes and animal flight

Turbulence is of critical importance to many biological processes. Turbulence enhances mixing and transport phenomena that are vital to nutrient exchange, respiration, etc (Denny et al., 1998). Turbulence can affect dispersal of seeds, gametes, propagules, or organisms both in water and in air (Denny et al., 1998). In the case of flying organisms, turbulence is of biological interest in two ways. The sensitivity of an animal or plant shape to incident eddies could affect its dispersal distance, its ability to navigate (McCay, 2003; Webb and Cotel, 2010), or provide limits on conditions during which it cannot fly (e.g. birds in severe storms) or during which dispersal might be "optimal" (e.g. plants releasing aerial propagules on gusty days).

Another consideration is the evolution of flight itself. If we consider the role of maneuvering and flight control throughout the evolution of animal flight (Dudley and Yanoviak, 2011; Dudley et al., 2007; Maynard Smith, 1953), the nature of disturbances becomes of key importance. Maneuvering refers to the ability of a gliding animal to change its flight path, which is important for safely navigating to a given destination, avoiding obstacles and evading predators, and may be important for impressing potential mates (Dudley et al., 2007). Animal studies have characterized some of the overall body kinematic effects of turbulence

 $^{^{2}}$ Until viscosity becomes dominant and dissipates the energy, at the Kolmogorov scale.



Figure 4.1: A. Thinking model of turbulence as a distribution of eddies of varying sizes. After (McCay, 2003). B. In this paper, the distribution of eddies is modeled as stationary, correlated random variables corresponding to velocities resulting from the eddies; the velocities result in forces and torques. The "transfer function" from velocity to forces/torques is expected to depend on shape and size (compare with filter shape and window size.)

on "large" animals such as fish (Feitl et al., 2010; Lupandin, 2005; Pavlov and Skorobogatov, 2009; Tritico and Cotel, 2010; Webb and Cotel, 2010), flying frogs (McCay, 2001a,b, 2003), orchid bees (Combes and Dudley, 2009), and hummingbirds (Ortega et al., in preparation).

Maneuvering and control in animals makes use of passive stability where available or as afforded by posture (Full et al., 2002; Jindrich and Full, 2002; Kubow and Full, 1999; Ting et al., 1997); it is reasonable to expect this to be true in flight and swimming too (Bartol et al., 2005; Fish, 2004; Fish and Lauder, 2006). As we have seen in previous chapters, flight control uses static and dynamic asymmetries to effect turns, rolls, and righting (chapter 1 in baby birds; chapter 2 and 3 in bird ancestors; see also Cardona et al., 2011; Evangelista et al., 2012; Munk, 2011; Zeng, in prep). As we have also seen, it is reasonably straightforward to measure both stability and control effectiveness, for example in model tests with perturbations in attitude and body position (chapters 2 and 3, see also McCay, 2001a; Park and Choi, 2010).

These address two of the key aspects (and a major tradeoff) of any flight control system (McCormick, 1995); stability means an organism is able to resist perturbations (perhaps with reduced requirements for active control from a complicated nervous system), while control effectiveness means body motions can generate the necessary forces and torques; the tradeoff is balancing ease of control with speed of response.

A third major part of a classical control system, the sensitivity of the system to external noise (Siebert, 1985), is what we seek to address quantitatively here. In this context, the noise to consider is environmental noise incident on an organism from turbulent eddies (Davidson, 2004). An organism may simply accept the resulting disturbance forces, opt not to fly, or alter body position or behavior to ameliorate the disturbance. For example, orchid bees in high turbulence are known to extend their hind legs (Combes and Dudley, 2009); while hummingbirds in turbulence are able to compensate to a point, beyond which major alterations in body kinematics are observed (Ortega et al., in preparation). In water, eddies of certain sizes may be exploited to save energy (Liao et al., 2003), or may reduce the effectiveness of forward swimming (Webb and Cotel, 2010). A general theoretical framework is needed: what are the broad patterns of sensitivity versus body size or shape?

4.1.2 Empirical and reduced-order methods for identifying sensitivity to incident eddies

To answer the biological questions, we must use or expand engineering methods. Two ways to identify the patterns of sensitivity versus shape and size are to empirically measure it or to model it. The empirical measurement is obtained using a series of model tests to systematically vary shape (in this case, a simple nondimensional shape parameter like aspect ratio) and relative size of the model to the eddies (here taken as the size of the model relative to the size of an upstream cylinder initiating the eddies). Velocities, forces, and torques are then recorded and correlated to identify a transfer function³.

Typical design guidelines (Naval Air Systems Command, 1996; Parris, 1975; Phillips, 2004) ignore size and shape dependence and instead prescribe a given level of disturbance (aircraft is a point, entire wind changes instantaneously, and a large aircraft is the same as a bee), which is not helpful for our biological questions. The spatial filtering alluded to in figure 4.1B immediately suggests a more precise way to consider shape and size. If we treat the turbulence as a stationary stochastic process with a distribution chosen to match typical turbulence cascade models, we can examine the effect of spatial filtering computationally (e.g. a reduced-order model that does not explicitly consider eddy structure but does consider the distribution of the resulting velocities) and compare it to our empirical results.

³I use the term "transfer function" here only to mean something relating input noise to output disturbances, without meaning to imply linearity. Several methods are possible; some authors use auto- and cross-correlation (Fox et al., 2010; Marmarelis, 1977, 1993), while here I choose to discard all phase information and consider only ratios of magnitudes.

	l	w	S_{plan}	l/w
rect1	$7.0 imes 10^{-2}$	$7.0 imes 10^{-2}$	49×10^{-4}	1
rect2	9.9×10^{-2}	5.0×10^{-2}	49×10^{-4}	2
rect4	14.1×10^{-2}	$3.5 imes 10^{-2}$	49×10^{-4}	4
rect6	17.3×10^{-2}	2.8×10^{-2}	49×10^{-4}	6
rect8	20.0×10^{-2}	$2.5 imes 10^{-2}$	$50 imes 10^{-4}$	8

Table 4.1: Flat plate model data.

	l	w	S_{plan}	S_{front} l/w
pong1	4.00×10^{-2}	4.00×10^{-2}	12.5×10^{-4}	$12.5 imes 10^{-4}$ 1
pong2	5.65×10^{-2}	2.82×10^{-2}	12.5×10^{-4}	$6.3 imes 10^{-4}$ 2
pong4	8.00×10^{-2}	2.00×10^{-2}	$12.5 imes 10^{-4}$	$3.1 imes 10^{-4}$ 4
pong6	9.80×10^{-2}	1.63×10^{-2}	12.5×10^{-4}	2.1×10^{-4} 4
pong8	11.31×10^{-2}	1.41×10^{-2}	$12.5 imes 10^{-4}$	$1.6 imes 10^{-4}$ 8
pong2A	8.00×10^{-2}	4.00×10^{-2}		12.5×10^{-4} 2
pong4A	16.00×10^{-2}	4.00×10^{-2}		12.5×10^{-4} 4

Table 4.2: Ellipsoidal model data.

4.2 Methods and materials

4.2.1 Models

I prepared a series of two-dimensional (2D) flat plate models consisting of rectangles of equal area $(50 \times 10^{-4} \text{ m}^2)$ and varying aspect ratios (1, 2, 4, 6, and 8). Models were designed using a vector graphics program (Illustrator 5.5; Adobe Systems Inc., San Jose, CA). The models were cut out of 3 mm acrylic stock (McMaster-Carr, Los Angeles, CA) using a laser cutter (VLS6.60; Universal Laser Systems, Scottsdale, AZ). 2D model dimensions are given in table 4.1.

To check for three-dimensional (3D) effects, a series of 3D ellipsoidal models was also constructed using the same aspect ratios (1, 2, 4, 6, and 8). The three-dimensional models were based on a standard table tennis ball (40 mm diameter), stretched to preserve planform area. Two models were also designed to preserve frontal area. 3D models were designed using a solid modeling program (Solidworks; Dassault Systems, Waltham, MA) to prepare stereolithography (STL) files, which were then output to a 3D printer (ProJet HD 3000; 3D Systems Corp., Rock Hill, SC) and printed in acrylic. 3D model dimensions are given in table 4.2.

To examine a simple case of biologically relevant geometries, two Avialae (the extant sea gull (*Larus*) and the extinct Jurassic feathered dinosaur \dagger *Anchiornis*), and three teleost





Figure 4.2: A. Flat plate and ellipsoidal physical models used during testing. B. Example test setup. C. Diagram of setup.

fish (salmon (*Oncorhynchus*), butterflyfish (*Chaetodon*), and seahorse (*Hippocampus*)) were designed using methods identical as for the 2D models. *Larus* and \dagger *Anchiornis* were chosen to examine the effect of tail reduction during the evolution of flying vertebrates and for use with the stability and control effectiveness data of chapter 3. The fish were chosen to examine the effect of an ancestral morphology (*Oncorhynchus*, *L/D* 6 similar to "optimal" submarine teardrop hulls) versus two extremely derived modified body forms (*Chaetodon* and *Hippocampus*) that both perform station-keeping in cluttered environments (Eschmeyer and Paxton, 1994). 2D biological model dimensions are given in table 4.3.

4.2.2 Generation of a turbulent incident flow

Models were placed in the $18 \operatorname{inch} \times 18 \operatorname{inch} \times 36 \operatorname{inch} (45.7 \operatorname{cm} \times 45.7 \operatorname{cm} \times 91.4 \operatorname{cm})$ working section of an Eiffel-type wind tunnel (Engineering Laboratory Design, Lake City, MN) and subjected to turbulent flow in the wake of an upstream obstruction. The time-averaged airspeed in the wind tunnel ranged from 0 to approximately $7 \operatorname{m s}^{-1}$. Two types of obstruction

	l	w	S_{plan}	l/w
sea gull (Larus)	$7.0 imes 10^{-2}$	19.3×10^{-2}	49.99×10	$^{-4}$ 0.4
$\dagger Anchiornis$	16.4×10^{-2}	14.5×10^{-2}	49.99×10	$^{-4}$ 5.4
salmon (Oncorhynchus)	16.5×10^{-2}	$6.5 imes 10^{-2}$	49.99×10	$^{-4}$ 2.5
butterflyfish (Chaetodon)	10.3×10^{-2}	$7.9 imes 10^{-2}$	49.99×10	$^{-4}$ 1.3
seahorse (<i>Hippocampus</i>)	$6.1 imes 10^{-2}$	$13.0 imes 10^{-2}$	49.99×10	$^{-4}$ 0.5

Table 4.3: Animal profile plate model data.

were used to simulate biologically relevant situations: a cylinder (simulating a branch or other structure) or a screen (simulating leafy cover or other porous obstruction).

Cylinders were placed 10×10^{-2} m upstream of the model leading edge. Cylinders were vertical sections of pipe in one of three sizes: large (3-inch schedule 40, OD 88.9 × 10^{-3} m), medium (3/4-inch schedule 40, OD 26.7 × 10^{-4} m) and small (1/2-inch schedule 40, OD 21.3 × 10^{-3} m). At the airspeeds used in this experiment, vortex shedding frequencies from the von Kárman instability are expected to be in the range 5 Hz to 15 Hz for the large cylinder. Cylinders were identical to those used in other studies of hummingbirds in turbulence (Ortega et al., in preparation).

Screens consisted of no screen, coarse $(1/4\text{-inch } 6.35 \times 10^{-3} \text{ m spacing})$, fine $(1/16\text{-inch } 1.69 \times 10^{-3} \text{ m spacing})$, and middle $(1/8\text{-inch } 3.18 \times 10^{-3} \text{ m spacing})$. Coarse and middle screens also had a $1/16\text{-inch smaller mesh stretched across the left side of the tunnel to generate turbulence via Helmholtz-Kelvin instability.$

4.2.3 Measurement of forces and velocities

A six degree-of-freedom (6DOF) force and torque sensor (Nano17; ATI Industrial Automation, Apex, NC) provided measurements of the forces and torques acting on the model. Sensor axes were aligned with the wind tunnel at the start of runs. A data acquisition card (PCI-6251; National Instruments, Austin, TX) recorded sensor readings at a sample rate of 10 000 Hz. The sensor was zeroed immediately before each measurement. To eliminate high frequency electrical noise and avoid aliasing in downstream processing, force and torque data were filtered using a 16-point moving average filter, reducing the effective sampling rate to 625 Hz.

A three-axis ultrasonic anemometer (Model 81000, R. M. Young Co., Traverse City, MI) provided non-contact measurements of the streamwise and both crosswise velocities as well as ambient temperature and speed of sound to verify calibration. Anemometer axes were aligned with the wind tunnel at the start of runs. The sampling rate for the anemometer was 32 Hz. The anemometer was connected to the host computer via a serial connection.

For each combination of model, upstream obstruction, and tunnel speed, measurements were taken simultaneously during a 3 min interval. Additional measurements of velocity for each upstream obstruction were recorded at speeds between $0 \,\mathrm{m\,s^{-1}}$ to $9 \,\mathrm{m\,s^{-1}}$, to further characterize the downstream flow.

4.2.4 Additional velocity measurements

Particle imaging velocimetry (PIV), in which paired images of particles suspended in the flow are used to obtain two-dimensional flow fields, was used to visualize flow and confirm spatial scales. The flow was seeded using an olive oil mist created by a pressurized oil container equipped with a perforated tube atomizer (LaVision, Göttingen, Germany). Models were illuminated in the sagittal plane using a vertical 532 nm wavelength laser sheet generated by a double-pulsed Nd:YAG laser (New Wave Research model 25185, Fremont, CA) equipped with a 20° sheet optic. The sheet was filmed with a LaVision ImagerPro X 2M camera and a Nikon 50 mm f/1.8 lens to obtain paired images at 15 pairs/s. To obtain velocity fields, images were post-processed in DaVis (LaVision, Göttingen, Germany) with multiple passes up to 64×64 pixel windows at 75% overlap⁴).

I also used a microphone (Snowball USB, Blue Microphone; Westlake, CA; range 20 Hz to 20 000 Hz, sampling at 44.1 kHz) placed within the tunnel to record a measure of velocity at frequencies higher than the anemometer was able to sample (Blake and Chase, 1969; Rubinstein and Zhou, 1997). The power spectral densities of microphone sound cuts were used to check that the flow showed a turbulence cascade as expected from theory and also allowed verification of frequencies for noises within the tunnel (notably, motor noise and blade passing frequency, duct and cavity resonances associated with the tunnel itself, and inverter switching noise).

4.2.5 Data analysis

The resulting recordings were analyzed using Python scripts utilizing the Scipy libraries as well as the statistical program R (R Development Core Team, 2013). R was used to examine distributions of velocity noise, force, and torque disturbances.

The power spectral density (PSD) of each signal was computed using a Python script implementing Welch's method (Welch, 1967). PSD results were also integrated over one-third-octave bands. Transfer functions were obtained from the ratio of the magnitudes.

I also examined data using both time domain and spatial domain assuming frozen turbulence. Frozen turbulence assumes that the velocity field is stationary (in a statistical sense) and advected at the mean flow velocity, and hence can be modeled as a stationary random process. The frozen turbulence assumption was implemented by exchanging the time vector for a spatial vector constructed from the average downstream velocity for each run. Consideration of spatial domain is important for understanding spatial filtering effects of shape.

⁴PIV results are being prepared for publication separately as part of (Ortega et al., in preparation).

4.3 Results

4.3.1 Example raw measurements

Figures 4.3-4.5 show raw measurements of velocity, force, and torque. The raw measurements themselves are unremarkable except that they appear sufficiently described statistically by a random variable with an approximately normal distribution.

Figure 4.6 shows the power spectral density (PSD) of velocity measurements, given as functions of frequency f and wavenumber k. One-third-octave band sums are also shown (lower plots).

4.3.2 Time-averaged forces, velocities, and overall transfer functions

Figure 4.7 gives the means of force and velocity as well as a nondimensionalized force coefficient (drag coefficient) versus Reynolds number.

To examine overall relationship between incident noise and the resulting disturbance forces and torques, figures 4.8 and 4.9 give the fluctuations (standard deviations) of force and torque, e.g.:

$$f'_{y,rms} = \sqrt{E(f_y - \overline{f_y})} \tag{4.1}$$

$$t'_{y,rms} = \sqrt{E(t_y - \overline{t_y})} \tag{4.2}$$

4.3.3 Spectral and one-third-octave band transfer functions

To examine spectral variation in the relationships between incident velocity noise and disturbance forces and torques, figures 4.10, 4.11, and 4.12 give power spectral density (PSD) and one-third-octave band sums for velocity, force, and torque, respectively.



Figure 4.3: Example data for velocity measurements axial and cross-stream (normal to model).



Figure 4.4: Example data for force measurements axial and cross-stream (normal to model).



Figure 4.5: Example data for torque measurement in yaw.



Figure 4.6: Example data for velocity measurements from anemometer (solid line) and from microphone (dotted line) showing that measured responses are consistent with what is expected for a turbulent cascade of eddies. Energy is injected at low frequency, cascades down; the sharp decrease at highest frequencies corresponds to the Kolmogorov scale (Davidson, 2004; Kolmogorov and Levin, 1941a,b) (B). Peaks correspond to known acoustic noises in the tunnel, including the motor, inverter, and duct resonances. Left plots (A,C) are in frequency domain, right plots (B,D) are corresponding data in wavenumber (spatial frequency) domain assuming frozen turbulence, lower plots (C,D) are for one-third-octave-band data.



Figure 4.7: Check of setup for time-average force and velocity. Time-averaged (a) drag versus speed and (b) nondimensional drag coefficient versus Reynolds number, for flat rectangular plates with an empty screen. Grey scale indicates model aspect ratio (l/w), from $\frac{1}{8}$ (dark) to 8 (light), indicating that shorter plates achieve fully turbulent boundary layers at relatively slower speed, thus experiencing higher drag than longer plates of the same area.



Figure 4.8: Overall transfer of turbulent velocity fluctuation to disturbance force. Rootmean-square (rms) (a) side disturbance force versus side velocity fluctuation and (b) nondimensional rms side disturbance force versus Reynolds number, for flat rectangular plates with upstream cylinders, size medium (circles) or small (triangles). Grey scale indicates model aspect ratio (l/w), from $\frac{1}{8}$ (dark) to 8 (light). At the lowest speeds, the noise floor of the force sensor dominates the signal. However, when speed is high enough $(u'_{y,rms} > 0.2 \,\mathrm{m\,s^{-1}})$ to provide measurable force fluctuations, the resulting nondimensional disturbance force takes values between 0.1 and 0.5 and also exhibits dependence on aspect ratio, with shorter models experiencing higher disturbance forces.



Figure 4.9: Overall transfer of turbulent velocity fluctuation to disturbance torque. Rootmean-square (rms) (a) yawing disturbance torque versus side velocity fluctuation and (b) nondimensional rms yawing disturbance torque versus Reynolds number, for flat rectangular plates with upstream cylinders, size medium (circles) or small (triangles). Grey scale indicates model aspect ratio (l/w), from $\frac{1}{8}$ (dark) to 8 (light). At the lowest speeds, the noise floor of the force sensor dominates the signal. However, when speed is high enough $(u'_{y,rms} > 0.2 \,\mathrm{m\,s^{-1}})$ to provide measurable force fluctuations, the resulting nondimensional disturbance torque shows strong dependence on aspect ratio, with shorter models experiencing lower disturbance torques.



Figure 4.10: Power spectral density and one-third-octave band spectra for incident flow, upstream cylinder, medium size. (a,c) side velocity fluctuation versus frequency (b, d) side velocity fluctuation versus wavenumber (assuming frozen turbulence). Grey scale indicates motor speed.



Figure 4.11: Power spectral density and one-third-octave band spectra for side disturbance force, upstream cylinder, medium size. (a,c) side disturbance force versus frequency (b, d) side disturbance force versus wavenumber (assuming frozen turbulence). Grey scale indicates model aspect ratio (l/w) from $\frac{1}{8}$ (dark) to 8 (light). Short models (low l/w) experience more disturbance force.



Figure 4.12: Power spectral density and one-third-octave band spectra for yawing disturbance torque, upstream cylinder, medium size. (a,c) yawing disturbance torque versus frequency (b, d) yawing disturbance torque versus wavenumber (assuming frozen turbulence). Grey scale indicates model aspect ratio (l/w) from $\frac{1}{8}$ (dark) to 8 (light). Long models (high l/w) experience more disturbance torque.



Figure 4.13: Transfer function magnitude from incident velocity noise to disturbance force for flat rectangular plates of varying aspect ratio (l/w). Grey scale indicates model aspect ratio (l/w), from $\frac{1}{8}$ (dark) to 8 (light). (A,C) frequency and one-third-octave bands. (B,D) wavenumber and one-third-octave bands.

4.3.4 Flat plates

Figures 4.13 and 4.14 give the transfer function magnitude from incident velocity to disturbance force and torque, respectively. The results shown were obtained from the ratio of the disturbance force (figure 4.11) or torque (figure 4.12) and the incident velocity (figure 4.10).

4.3.5 Biological and 3D shapes

As a quick check of the relevance of the flat plate models to more biological shapes, figure 4.15 gives the relationships between force and velocity fluctuations. The overall shape of the plot is the same as figure 4.8; trends with aspect ratio follow those of the simple flat plates and fit within the results from them.



Figure 4.14: Transfer function magnitude from incident velocity noise to disturbance torque for flat rectangular plates of varying aspect ratio (l/w). Grey scale indicates model aspect ratio (l/w), from $\frac{1}{8}$ (dark) to 8 (light). (A,C) frequency and one-third-octave bands. (B,D) wavenumber and one-third-octave bands.

4.4 Discussion

4.4.1 Instrumentation appears to be working

Measured flows (figures 4.3 and 4.6) appear to be within expected values. Figure 4.3 shows the turbulent fluctuation as a histogram centered on a mean value; the mean values correspond to 0 m s^{-1} cross-stream and -6 m s^{-1} downwind, which is expected for the tunnel settings. Figure 4.6 shows energy injected at low wavenumber and traveling down the cascade as expected (Davidson, 2004; Kolmogorov and Levin, 1941a; Taylor, 1938; Tennekes and Lumley, 1972), with an abrupt downturn at the Kolmogorov scale. Furthermore, high frequency peaks in microphone data of figure 4.6 are as expected for known acoustic noise sources in the tunnel, including the inverter, rotor blade passing frequency, and tunnel wall resonances (determined via impulse tests with a microphone and a hammer).

Measured forces and torques (figures 4.4 and 4.5) appear to be responding correctly as well. In addition, the measured drag is as expected (figure 4.7). For force, see figure 8. It gives exactly what is expected for drag, even including small and known effects of changing



Figure 4.15: Disturbance force fluctuation (standard deviation) versus incident velocity fluctuation (standard deviation) for medium and small cylinders and biological or 3D shapes. (a) Sea gull *Larus* and $\dagger Anchiornis$; (b) Salmon *Oncorhynchus*, butterflyfish *Chaetodon*, and seahorse *Hippocampus*; (c) stretched ellipsoid 3D table tennis ball series all follow same trends with aspect ratio L/D and relative size of model versus cylinder size (turbulent eddy size).
4.4.2 Shape and size alter turbulence sensitivity

Figures 4.8 and 4.9 show the effect of changing shape (aspect ratio) and relative size (triangles versus circles) on turbulence sensitivity. For a given environment (triangles versus circles), as the incident velocity noise in the environment increases, the disturbance forces and torques increase (series of J-shaped curves in figures 4.8a and 4.9a). The toe of the J-shaped curve has yet to be explained but could be the noise floor of the torque sensor; more work is needed to confirm this.

Considering a nondimensionalization of the variables of interest, the nondimensional groups are similar to those constructed for the nondimensionalized drag plot of figure 4.7 $(C_f = f/(0.5\rho u^2 A), \text{Re} = ul/\nu, \text{ and } AR = l/w)$. The plots become families of parallel horizontal lines (figures 4.8b and 4.9b), suggesting these are a useful set of dimensionless variables.

If the cartoons of figure 4.1 are correct, we should see that for low aspect ratio shapes, the incident velocities "sum" over a longer length, averaging out higher frequency components and leaving only low frequency components. For a turbulent cascade (in which energy content decreases with frequency), longer shapes should have lower forces. Figure 4.8a confirms this. On the other hand torques "sum" as the differential force times a moment arm, as a result, longer shapes should experience higher torques. This is also apparent from figure 4.9a.

The effect of relative size between the object and the flow should follow the same logic. Small objects (the bee) experience disturbances from high and low frequency velocity components; large objects (the C-17) only experience disturbances at lower frequencies. The biggest transfer should occur when the turbulence is the same size or larger than the object. For different size cylinders acting as turbulence initiators, the plots of figures 4.8a and 4.9a appear to show this. However, Reynolds and Strouhal number effects (e.g. vortex shedding frequency) mean that the relationship between cylinder size and resulting velocity fluctuations are more complicated, and the spectra should also be examined (empirically or computationally). The cylinder size sets the low frequency bump in the E(k) curve; trends with size are determined by where this bump occurs relative to the shape's spatial bandwidth.

Biological shapes appear suitably approximated by flat plates with matching aspect ratios (figure 4.15). This suggests that simplified models may be useful in understanding, to first order, the disturbances that physically reach a flying animal, e.g. the first level of transduction before any active control or response is necessary.



Figure 4.16: Thought experiment: spatial filtering of turbulent velocity. In the spatial domain, the force or torque acting on an object is like a convolution of the body shape function with the spatial velocity distribution. In the wavenumber domain, the convolution becomes multiplication and the size and shape effects are understood as the bandwidth (based on body length) and the wavenumber content of the incident velocity spectrum.

4.4.3 Proposed filter theory

The cartoon of figure 4.1 suggests considering the transfer of turbulent incident velocity noise to disturbance forces and torques as a spatial filter, in which the incident velocity is considered to be a stationary random process impinging on the body. The center of mass of the body then experiences forces and torques which are scaled and shifted versions of the velocity field, though the functions involved may be nonlinear. To understand this, consider the simplified situation below in which a turbulent spectrum in the environment is filtered by a simple rectangular shape approximated as a pulse.

Recall the Fourier transform of a rectangular pulse is a sinc function (figure 4.16), so that a narrow body in space should be a very broadband filter in wavenumber. Conversely, an elongated body in space should pass only low wavenumbers.

$$\operatorname{rect}(x) \Leftrightarrow \operatorname{sinc}(k) = \frac{\sin \pi k}{\pi k}$$
(4.3)

The theory is complicated by two things. The spectrum of the turbulent noise is not trivial, but empirical results and scaling have resulted in spectra that can be used (Davidson, 2004). Furthermore, the form of the filtering kernel is probably nonlinear and depends on the shape of the body. To address these, I adopted a model spectrum from (Davidson, 2004):



Figure 4.17: Spectrum from equation 4.4 (a) and simulated velocity (b) in blue. Simulated result illustrates short term correlation between velocities ("sweeps" and "bursts") expected by having colored rather than white noise, as expected for a turbulent velocity.

$$E(k) = \hat{k}^4 (1 + \hat{k}^2)^{-17/6} \exp\left[-\hat{k} \operatorname{Re}^{-3/4}\right], \hat{k} = kl$$
(4.4)

and a filtering kernel motivated from simple drag coefficients and strip theory:

$$df = 0.5\rho u^2 w dx \tag{4.5}$$

. The window function for torque is similar:

$$df = 0.5\rho u^2 w x dx \tag{4.6}$$

To simulate this, I constructed a magnitude vector from equation 4.4. With the phase set to a random, uniform distribution around the unit circle, I took the inverse fourier transform to obtain a simulated velocity signal which I then filtered using the kernel of equation 4.5. The full derivation of this is in appendix E.

As a filter kernel, I created rectangular windows corresponding to a $10 \,\mathrm{cm}^2$ flat plate similar to what was measured. The window functions are shown in figure 4.18

The result of applying these to u|u| is:

Figure 4.19 roughly compares with the measured transfer functions (magnitude ratios) of figures 4.13 and 4.14. The higher frequency behavior is difficult to observe in the empirical results because of the time response of the sensors and the inertias present, though I tried to minimize these as much as possible by minimizing the model mass and using a very stiff mounting; further measurements would require laser Doppler anemometry or a very fast hotwire anemometer and a redesign of the force/torque sensor.

Figure 4.20 shows the result as the model parameters are varied for different aspect ratio and incident turbulent velocity fluctuation. The shape of the model predictions is similar



Figure 4.18: Window function for force (a) and torque (b). (b) is related to (a) by a multiplication by x in the spatial domain, or differentiation by k in the wavenumber domain. Red l/w = 8, green l/w = 1, blue l/w = 1/8.



Figure 4.19: Filter output (unscaled) for force (a) and torque (b). (b) is related to (a) by a multiplication by x in the spatial domain, or differentiation by k in the wavenumber domain. Red l/w = 8, green l/w = 1, blue l/w = 1/8.



Figure 4.20: Filter output (unscaled) for force (a) and torque (b). Force/torque fluctuation (standard deviation) versus incident velocity fluctuation. Grey indicates aspect ratio l/w from 1/8 to 8.

to the overall results of figures 4.8 and 4.9. As turbulent velocity fluctuation increases, the disturbance forces and torques increase (nonlinearly so). The aspect ratio behavior is also modeled, with short models experiencing larger forces and smaller torques. The model does not exhibit the J-shaped toe because sensor response (specifically, dead zones in the force/torque transducer at low amplitude) was not modeled. Future work will extend this formulation to a full stochastic differential equation model of the control system (Øeksendal, 2010).

4.4.4 Biological significance of turbulence sensitivity

Overall turbulence sensitivity results compare well with predictions of the disturbances an airborne organism of a given shape might experience in a particular environment. We also found good general agreement between simplified geometric shapes and 2D animal planforms of equivalent aspect ratio (figure 4.15). Elongated shapes with low aspect ratio (e.g. long tailed dinosaur ancestors like $\dagger Anchiornis$) filter the turbulent noise by reducing the disturbance force they experience. High aspect ratio shapes (e.g. broad winged, anteroposteriorly compressed forms for extant birds like *Larus*) feel more of the turbulence as forces, but transmit less of it as torques on the body. This result is notable when considering that the ancestral long-tailed forms tended to be stable in pitch and have high control effectiveness (chapter 3), while the short-tailed extant birds have reduced stability and large control effectiveness particularly in torque.

These results bolster the observations in chapters 1, 2, and 3 that maneuvering is critical to any organism in the air, and that understanding the components of aerial maneuvering (stability, control effectiveness, and sensitivity to environment) is useful for making sense of changes in shape that may happen over ontogeny or during evolution.

4.5 Acknowledgements

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Appendix A

Alectoris chukar Animal Use Protocol

The following are excerpts from UC Berkeley Animal Use Protocol R282, revision 1 for the use of Chukars (*Alectoris chukar*) in studies of directed aerial descent and righting.

A.1 Research goals

Existing paleobiological scenarios for the origin of flapping flight in bats, birds, and pterosaurs strongly implicate transition from a gliding and maneuvering form, but the biomechanical and aerodynamic correlates of this transition are unclear. To examine biomechanical constraints relevant to such a transition, recent and past work includes studies of falling geckos (Jusufi et al., 2008), gliding frogs (Emerson and Koehl, 1990; McCay, 2001a), extinct feathered dinosaurs (Xu et al., 2003), and flying squirrels. Other parallel work in invertebrate taxa, such as gliding ants (Yanoviak et al., 2005) and gliding stick insects also strongly implicate transition from a gliding and maneuvering form.

An alternate scenario for the origin of flapping flight in vertebrates involves the use of wings to assist running and traction up steep terrain (wing-assisted incline running, Bundle and Dial, 2003; Dial, 2003; Dial et al., 2008). Studies in support of this alternative scenario have observed that hatchling birds utilize flapping movements when running up inclines (Dial et al., 2008). However, these studies ignore use of the wings during other aerial-related behaviors, for example, use of the wings when descending vertically. Using the same species and general experimental setup, we plan to address this gap by determining limb and body kinematics, both symmetric and asymmetric, that contribute to aerial righting and directed aerial descent maneuvers, and that may have historically led to bilateral limb flapping in birds. Wind tunnel studies of static and flapping models and computer simulations based on aerodynamics and inertial mechanics will complement these kinematic studies.

A.2 Justification for animal use

A.2.1 Rationale for use of animals

Flying and gliding animals are paradigmatic examples of the generation and control of unsteady aerodynamic forces, and exhibit both neuromuscular regulation and multimodal sensory integration that far surpass current technological capacities. To understand both generation and control of these aerodynamic phenomena, it is necessary to study living animals as they naturally locomote in the air.

A.2.2 Rationale for choice of species and numbers

Chukar Partridges are a model system for wing-assisted inclined running; as this work examines a gap in WAIR theory and seeks to extend it, they are a logical choice to start with as the data obtained will be directly comparable to previous studies (Bundle and Dial, 2003; Dial, 2003; Dial et al., 2008). Chukars are widely available through the poultry trade (Heinrichs, 2009; O'Toole, 2003; Willis and Ludlow, 2009). The number of study birds is based on our labs previous work in similar kinematic studies and should provide sufficient replicate measurements.

A.3 Description of laboratory research

With Chukar Partridges, we seek to determine 1) the presence or absence of an aerial righting reflex over ontogeny; 2) the presence or absence of directed aerial descent ability over ontogeny; 3) three-dimensional trajectories and limb and tail usage during such maneuvers; and 4) the impact of a limited set of non-invasive manipulations (attachment/augmentation of feathers, especially pelvic wing feathers (Evans and Hatchwell, 1992; Evans et al., 1994; Lippincott, 1920; Thomas, 1997; Xu et al., 2003) and augmentation of tail inertia (Jusufi et al., 2008).

All experiments will involve filming with video cameras illuminated with 500 W lights. Each filming event lasts up to thirty seconds. Birds may be filmed on a daily basis for periods of three hours. During all experiments, animals will be observed for signs of weakness and will be removed from the study if such signs are evident. Animals showing signs of reluctance will be given time to habituate to experimental setups. Animals may be non-destructively marked by either attachment of adhesive-backed 3 mm reflectors or use of Wite-out and black marker, both typical in other studies of bird locomotion (Daley et al., 2007; Dial et al., 2008; Essner, 2002; Hedrick and Biewener, 2007; Wischusen and Richmond, 1989). During marking, animals will be restrained by hand.

A.3.1 Presence or absence of aerial righting reflexes over ontogeny

Chicks will be placed on a platform such as a ladder and allowed to take off freely, or dropped at a random orientation by tipping out of a cup. Their vertical orientation will be observed during descent using high-speed video recording of kinematics. Gentle vibration may be applied to the cup to induce takeoff. The experimental setup will provide for a soft landing area, such as a loosely spanned, soft and elastic cloth or foam. The methods here will be identical to those we have used to study aerial righting and directed aerial descent in rain forest canopy ants, stick insects, and also in geckos (Jusufi et al., 2008).

All chukar experiments will be conducted using a ladder, ramp, or scaffold structure within a $5 \text{ m} \times 3 \text{ m}$ full-ceiling-height animal enclosure with fabric or netting walls in Haas 97/99. For runs in which voluntary bird behavior is recorded, filming will be conducted up to daily for up to three hours per day. For runs in which birds are gently stimulated, 5 min duration rest periods will be provided between glides and a 30 min rest every five glides, with an absolute maximum of 15 glides per animal per day.

A.3.2 Presence or absence of directed aerial descent ability over ontogeny

Using methods similar to (Dial et al., 2008), chicks will be allowed to run up an incline and jump off it freely; or will be placed at the top of an obstacle and gently stimulated to descend from it into a soft landing area. Filming of the descent with multiple highspeed video cameras will assess if trajectories show evidence of turns or if they are random or confined to a single plane (Essner, 2002; Socha, 2002). Most runs will film the free, volitional behavior of chicks as they explore the experimental setup.

To provide additional testing of the extent of directed aerial descent abilities, the target landing zone may be displaced over small distances after the chick jumps, as has been done in what was done in previous studies of flying squirrels (Wischusen, 1990).

A.3.3 Three-dimensional trajectories and limb and tail usage during such maneuvers

Part of this experiment will be conducted concurrently with experiments 1 and 2, which already film the animals using multiple high-speed video cameras that are sufficient to obtain three-dimensional trajectories and appendage use during maneuvers.

To obtain additional information on aerodynamic use of appendages , chicks may be placed in the working section of a vertical wind tunnel to simulate conditions of free fall (Jusufi et al., 2008; McCay, 2001a). Equilibrium gliding at terminal falling velocity is reached when the aerodynamic drag and lift forces balance the force of gravity. A small animal like a Chukar Partridge will attain terminal velocity at a ventral airflow of less than 6 m s^{-1} ,

depending on individual mass and surface area. Chicks will not be exposed to air speeds exceeding the equivalent of individual terminal velocity. To prevent chicks from maneuvering sideways out of the test section and to enable high-speed video filming, transparent acrylic sidewalls will be mounted around the opening of the wind tunnel. A safety net will be installed in the test section to prevent animals from contacting the expansion chamber of the wind tunnel.

A.3.4 Relative effects of inertia and aerodynamic forces in maneuvers

To examine the role of inertia, small weights no more than 10% of body weight will be attached to the chicks using veterinary wrap, similar to methods used in (Daley et al., 2007). Inertia will be increased by addition of a "prosthetic tail" made from a lightweight shaft (e.g. music wire, wood, plastic or cut turkey feathers) with a small weight held onto to the chicks natural tail using veterinary wrap. For control purposes, an equivalent amount of weight may be added at the hips, near the center of mass, or on a leg or wing (as in Daley et al., 2007). Weights will be removed at the end of each session.

To examine the role of aerodynamic forces, we will observe aerial behaviors over ontogeny as the birds natural feathers develop. In addition, we may clip the primary feathers and retrices, augment the primary feathers or retrices by gluing of additional feather extensions (Evans et al., 1994, approved UCB Animal Use Protocol R282), or augment feathers by gluing flight feathers at the position of other, non-flight feathers such as the pelvic "wing" plumage (Lippincott, 1920).

Feather extensions will be conducted using the method of Evans et al. (1994). Feathers will be cut near the base and new feathers glued on to vary length from between 5% to 10% of the original length. Feather extensions will be glued using a combination of pins and cyanoacrylate superglue. Attached feathers will have been frozen several months to kill any parasites that may have been present. During these manipulations, chicks will be restrained by hand. No anesthetization is necessary because the manipulations involve no living tissue; no living tissue is manipulated other than whole-body restraint for no more than 10 min during these procedures. Feathers are attached carefully so that they retain aerodynamic function; this method has been used extensively for other avian taxa (Evans and Hatchwell, 1992; Evans et al., 1994; Thomas, 1997) and these authors report that manipulated birds folded their tails naturally and did not pick at or seem to unduly notice the manipulated feathers. Maneuverability and aerodynamic performance of individuals with manipulations will be assessed using the methods described above. Upon completion of manipulation experiments, manipulated feathers will be plucked to induce their replacement. Birds that pick at extensions will have the extensions checked and adjusted as practicable and will be given time to acclimate, but extensive picking or grooming of the extensions may invalidate the experiment and such birds will be removed from study.

A.4 Method of euthanasia and disposition of specimens

Euthanasia, if needed for Chukar Partridges at study's completion: overdose of isofluorane or carbon dioxide inhalation followed by bilateral thoracotomy.

A.5 Proposed animal housing

Chukar Partridges will be maintained within the Animal Behavior Research Suites on the fifth floor of VLSB. Chukar Partridge chicks will be maintained within the Animal Behavior Research Suites on the fifth floor of VLSB. Birds will be kept on brooder bedding litter (wood shavings, sawdust, compressed wood pellets, or other suitable material) changed bi-weekly or as necessary (Heinrichs, 2009; Willis and Ludlow, 2009). Lamps will be provided to maintain a warm temperature as necessary (Heinrichs, 2009; Willis and Ludlow, 2009). Birds will be kept in an enclosure with approximately 25 chicks to a 4×3 foot area (Heinrichs, 2009; Willis and Ludlow, 2009). We will keep an individual Chukar Partridge for up to eight weeks, to allow completion study up to the point of being fully feathered and slightly beyond. Most work will be completed at approximately four weeks. Batches of chicks will not be mixed and additional space will be provided as birds age beyond four weeks (approximately 2 square feet per bird) (Heinrichs, 2009; Willis and Ludlow, 2009).

Chukar Partridge will be fed typical chick starter rations (20% protein) in suitably designed feeding containers (Heinrichs, 2009; Willis and Ludlow, 2009). OLAC personnel will feed the birds daily following standard UCB arrangements. Diet will occasionally be supplemented with grit, vegetable material, or insect larvae (Heinrichs, 2009; Willis and Ludlow, 2009). Water will be available at all times in suitably designed watering containers no more than a few inches deep (Heinrichs, 2009; Willis and Ludlow, 2009).

When Chukar Partridges are returned to fifth floor housing after flight experiments, they will be monitored one hour after return and again the following morning to ensure normal behavior. We typically check in on all of our animals one to two times daily independent of the occurrence of flight experiments.

A.6 Breeding

No breeding will be undertaken.

A.7 Capture and transportation of animals

Chukar Partridges will be obtained as one-day-old chicks and shipped via standard shipping methods for poultry (Heinrichs, 2009; Willis and Ludlow, 2009). For experiments, chicks will be transported between the Animal Behavior Research Suites on the fifth floor of VLSB and

Haas 97/99 (a one minute walk) using a small animal carrier with litter and provision for ventilation. No more than 12 chicks will be placed in one box (or less depending on size).

A.8 Description of field research

No field components are associated with studies of Chukar Partridges.

Appendix B

Camera calibration and three-dimensional reconstruction routine

This appendix describes a method to recover the three-dimensional (3D) position of birds and their appendages using several two-dimensional (2D) views, obtained from inexpensive fixed-focus FlipHD cameras. The methods are also applicable to AOS and Fastec high speed cameras used in other parts of the work.

While the techniques are similar to those used to track ants in the rain forest (Munk, 2011), and to methods I used to track ballistically launched amphipods (Evangelista, in preparation), there are some important differences incorporated here in order to simplify the calibration procedure and setup. The primary difference is the use of multiple views of multiple poses of a two dimensional calibration object (chessboard), enabled by use of homographies, freeing the setup from the need for a large, fixed calibration shape that remains present and un-moved/un-altered through all filming runs. This reduces setup time and is critical when cameras must be shared between multiple setups and must be setup and broken down each day or multiple times each day.

B.1 Camera extrinsics

In computer vision applications, it is typical to convert from world coordinates to camerafixed spatial coordinates using a translation \vec{t} , followed by rotations about \hat{z} , then the new \hat{y} , then the new \hat{x} (in that order) (Bradski and Kaehler, 2008).

$$\mathbf{R}_{\mathbf{x}}(\psi) = \begin{pmatrix} 1 & 0 & 0\\ 0 & \cos\psi & \sin\psi\\ 0 & -\sin\psi & \cos\psi \end{pmatrix}$$
(B.1)

$$\mathbf{R}_{\mathbf{y}}(\phi) = \begin{pmatrix} \cos\phi & 0 & -\sin\phi \\ 0 & 1 & 0 \\ \sin\phi & 0 & \cos\phi \end{pmatrix}$$
(B.2)

$$\mathbf{R}_{\mathbf{z}}(\theta) = \begin{pmatrix} \cos\theta & \sin\theta & 0\\ -\sin\theta & \cos\theta & 0\\ 0 & 0 & 1 \end{pmatrix}$$
(B.3)

$$\vec{x}_{cam} = \mathbf{R}_{\mathbf{x}} \mathbf{R}_{\mathbf{y}} \mathbf{R}_{\mathbf{z}} (\vec{x}_{world} - \vec{t}) \tag{B.4}$$

$$\vec{x}_{cam} = \mathbf{R}(\vec{x}_{world} - \vec{t}) \tag{B.5}$$

The inverse of this operation is given by:

$$\vec{x}_{world} = \mathbf{R}^{-1} \vec{x}_{cam} + \vec{t} \tag{B.6}$$

where

$$\mathbf{R}^{-1} = \mathbf{R}^T = \mathbf{R}_{\mathbf{z}}^T \mathbf{R}_{\mathbf{y}}^T \mathbf{R}_{\mathbf{x}}^T$$
(B.7)

Alternatives to this formulation include axis-angle and quaternion methods, which avoid problems at $\pm 90^{\circ}$ pitch angles. This is often handy, e.g. when integrating inertial sensor data, but for now we will stick to the orthogonal rotation matrix method as it is standard in computer graphics practice.

B.2 Camera intrinsics and pinhole model

It is useful at this point to introduce homogenous coordinates, in which a point in an *n*-dimensional space is expressed as an n + 1-dimensional vector; any two points whose values are proportional ("within a scale factor") are equivalent (Bradski and Kaehler, 2008). The pinhole model of camera is thus:

$$\begin{pmatrix} x \\ y \\ w \end{pmatrix}_{im} = \begin{pmatrix} f_x & 0 & c_x \\ 0 & f_y & c_y \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \\ z \end{pmatrix}_{cam}$$
(B.8)

where f is the focal length and c is the displacement of the imaging plane from optical zero. To find pixel coordinates we make use of the equivalence of homogenous coordinates, i.e. $x_{pal} = x_{im}/w_{im}$ and $y_{pel} = y_{im}/w_{im}$.

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B.3 Homography, chessboards, and calibration

Ignoring distortion, we can map real world coordinates to image coordinates using the following:

$$\begin{pmatrix} x \\ y \\ 1 \end{pmatrix}_{im} = s \begin{pmatrix} f_x & 0 & c_x \\ 0 & f_y & c_y \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \vdots & \vdots & \vdots & \vdots \\ \vec{r}_1 & \vec{r}_2 & \vec{r}_3 & \vec{t} \\ \vdots & \vdots & \vdots & \vdots \end{pmatrix} \begin{pmatrix} x \\ y \\ z \\ 1 \end{pmatrix}_{world}$$
(B.9)

Rearranging for the case of a flat chessboard on which we arbitrarily pick z = 0,

$$\begin{pmatrix} x \\ y \\ 1 \end{pmatrix}_{im} = s \begin{pmatrix} f_x & 0 & c_x \\ 0 & f_y & c_y \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \vdots & \vdots & \vdots \\ \vec{r_1} & \vec{r_2} & \vec{t} \\ \vdots & \vdots & \vdots \end{pmatrix} \begin{pmatrix} x \\ y \\ 1 \end{pmatrix}_{chessboard}$$
(B.10)

Collecting the matrices into a single homography matrix for a particular view (source and destination pair) gives:

$$\vec{p}_{dest} = \mathbf{H}\vec{p}_{source} \tag{B.11}$$

By collecting many points in a particular view, a best-fit $\hat{\mathbf{H}}$ can be found that minimizes the back projection error $\sum \|\vec{p}_{dest} - \hat{\mathbf{H}}\vec{p}_{source}\|$. Open source camera calibration routines then use numerically determined $\hat{\mathbf{H}}$ for many views, and the constraints of orthonormality to obtain camera intrinsics, as well as extrinsic parameters for each particular view (Bradski and Kaehler, 2008).

B.4 Correcting for distortion

Distortion from cheap lenses and short focal lengths is expected to be large. It is possible to run the calibration ignoring distortion, then solve for distortion parameters and iterate until convergence (Bradski and Kaehler, 2008). Radial distortion arises from the lens and is given by:

$$x_{corr} = x(1 + k_1 r^2 + k_2 r^4 + k_3 r^6)$$
(B.12)

$$y_{corr} = y(1 + k_1 r^2 + k_2 r^4 + k_3 r^6)$$
(B.13)

Tangential distortion arises from skewed mounting of the sensor and is given by:

$$x_{corr} = x + [2p_1y + p_2(r^2 + 2x^2)]$$
(B.14)

$$y_{corr} = y + [p_1(r^2 + 2y^2) + 2p_2x]$$
(B.15)

B.5 Completing the calibration

The equations given so far are combined in the OpenCV routine cvCalibrateCamera2(), which allows solving for a single camera's intrinsic and distortion parameters and the extrinsic rotation and translation associated with each view used. The next step is to combine information from multiple cameras. While most computer vision texts focus on stereo vision applications and use of epipolar geometry and fundamental matrices (Bradski and Kaehler, 2008), we are more concerned with more than two cameras, in arbitrary arrangements that make such approaches non-intuitive. The stereo vision application is also optimized somewhat for speed (by reducing search dimensionality using epipolars); while here we wish to search in 3D and find the most accurate positions possible.

From the single camera calibration, we have an initial guess of the position of the cameras relative to one another. However, we have a lot of extra parameters since the calibration shape is the same in all views. The next step is to re-run the calibration with some of these extra parameters fixed. In practice, this was not yet implemented because the results from several pairwise stereo calibrations with camera 0 have been sufficient so far.

B.6 Locating points

Once we have the calibrations, we take the approach of (Munk, 2011) to find 3D positions from multiple 2D images. To accomplish this, we assume a position and minimize the squared projection error in all images:

$$\hat{x}_{world} = \operatorname{argmin} V \tag{B.16}$$

$$V = \sum_{all \ cameras} \|\vec{x} - s\mathbf{M} \begin{bmatrix} \mathbf{R} & \vec{t} \end{bmatrix} \hat{x}_{world} \|$$
(B.17)

where s, \mathbf{M} , \mathbf{R} , and \vec{t} were all obtained from the calibration step.

In practice here, a good initial guess is needed in order to avoid local minima and converge on a good position estimate. Typically, the previous position at $t - \Delta t$ is used, but this is not possible for the first point or for when no good guess is available.

B.7 Implementation as a Python library decal

For future use by biomechanics researchers, I implemented a Python library for Dennis Evangelista's calibration routines (decal, available for download via bitbucket.org). The intent of the library is to provide routines usable by non-specialist biomechanics researchers with some coding experience.

B.7.1 Major core classes in core.py

The core classes implemented in decal include Movie, Chessboard, Corners, Intrinsics, Extrinsics, and Camera. Each is implemented as a serializable YAML object that can be output to flat text files for reading, editing, or downstream processing. Movie and Chessboard contain all necessary information about a particular movie or chessboard calibration object and are intended to be entered by users. The other objects are the result of intermediate processing steps described below.

B.7.2 Methods from corners.py, intrinsics.py, extrinsics.py, and cameras.py

These four sub packages are addressable using standard Python dot notation and implement conversions between a lower level class (e.g. Movie) and the next higher level class (e.g. Corners). The details of the conversions are fully documented in the docstring help for each sub package. intrinsics.py includes methods for both initial generation of intrinsic parameters and refinement of previous estimates of intrinsic parameters given an input list of Corners objects. extrinsics.py assembles a list of extrinsics associated with chessboard positions; this is not usually of much use for this application except that it is the necessary intermediate step for assembling camera positions in cameras.py. The list of Camera objects output by cameras.py is sufficient for any further position reconstruction given points from the various movies of an event.

B.7.3 Other methods

quaternions.py implements quaternion based rotation as a helper function. points.py implements the Levenberg-Marquardt search. In practice, points.py is very sensitive to choice of initial position; the next planned revision of decal will implement a radial basis function for estimating initial position (Gershenfeld, 1998). This method is chosen because the underlying function is expected to be a smooth mapping between R_3 and $R_{2\times n}$, and because the method has been useful before (Evangelista, 1999) in similar estimation tasks.

Acknowledgment

I thank Yonatan Munk for his assistance in implementing these improved methods. I also thank the Berkeley Center for Integrative Biomechanics Education and Research (CIBER) for providing camera availability problems that motivated this work.

Appendix C

Testing for directed aerial descent using an Akaike Information Criterion

These notes give my thoughts on how to test a recorded animal trajectory for directed aerial descent using log-likelihood functions and the Akaike Information Criterion (AIC).¹

C.1 Introduction

In studies of the comparative biomechanics of aerial behaviors, we often obtain the trajectory of an animal traveling through space and we wish to decide if it is moving as a passive ballistic projectile would, or if it is "doing something." Is it using bits of its body to generate forces and moments that change its trajectory through the air in order to right itself, land on some target, move towards some goal or away from something it wishes to avoid? More generally, we wish to test some data and see if it is well explained by a certain model with some terms, or if an alternative model with other terms is a better description. We may also need (or have) some idea of what our measurement noise is.

C.2 A toy example: estimating position of a stationary object with noisy measurements

Let us imagine we have a calibrated high speed video recording of a dead limpet on a rock. Frame by frame, we digitize the x position of the limpet for the portion of the video we wish to analyze. The data are given in Figure C.1. While digitizing such positions are tedious, they allow us to answer two questions. First, what is the position of the limpet? Second, is it still moving or is it dead?

¹Several undergraduates helped me to crystallize some of these thoughts when we were puzzling over how, using finite differences, some animals dropped from a ladder in Haas gymnasium, could reach accelerations of $\pm 900 \,\mathrm{m\,s^{-2}}$; Dave Bapst assured me that use of MLE and AIC in this manner is a reasonable thing to do.

To answer the first question, a simple-minded thing to do first would be to simply take the mean of the measured positions. We could report then the position as the mean along with the standard deviation; the limpet is at (0.423 ± 0.001) m. This frequentist approach is pretty standard in biology and biomechanics.

However, we run into problems if we try to answer the second question - is the limpet still moving? Now we must somehow approximate the derivative. We may try using a finite difference approximation, approximating the derivative $\frac{dx}{dt}$ as $\frac{x_{n+1}-x_n}{\Delta t}$, then testing to see if this is significantly different from zero using an appropriately chosen frequentist statistical test. The drawback with this is that numerical differentiation in this manner introduces noise, and since we are often after accelerations and forces, which require a second derivative, the noise can quickly mask anything interesting that may be happening in realistic data. We could employ filters (e.g. Butterworth, Chebyshev, moving average) or interpolating spline procedures, however, these add additional layers of manipulation to the data and may be unintuitive to those not used to filtering approaches. Furthermore, they do not make use of whatever we might happen to know about the noise in our measuring system.

C.3 An alternative using maximum likelihood estimation

Let us proceed by imagining a model of the process of measuring the position of a dead, stationary limpet. Unless it is being moved by something, the limpet's measured position at some discrete time n may be thought of as an actual position plus some additive measurement error:

$$x[n] = X_0 + \mathcal{N}(0,\sigma) \tag{C.1}$$

We might consider this model as a null model for a dead limpet. \mathcal{N} here is some model of the measurement noise; in this case for simplicity we will consider zero-mean, stationary, Gaussian noise. For this case, it is clear that our earlier procedure of simply taking the mean and standard deviation of our measurements should recover X_0 as the position fo the limpet and σ as the standard deviation, provided we take enough samples.

Let's consider a different approach known as maximum likelihood estimation (Burnham and Anderson, 2002; Rauch et al., 1965). Imagine we knew X_0 and σ ; then we could figure out how likely it is that we observe the actual measurements by computing P(data|model, parameters):

$$\ln(\mathcal{L}(X_0, \sigma | x, \text{stationary})) = \sum_n \ln\left(f_{\mathcal{N}(0,\sigma)}(x[n] - X_0)\right)$$
(C.2)

 $\ln(\mathcal{L})$ is the log-likelihood; it is easier for us to use because it turns the product of many small numbers into a sum of something that is more easily represented within the computational range of our computer. To figure out the most likely estimate of the position of the limpet

(and the noise of our measuring setup), we can search for the values of those parameters that maximize the likelihood:

$$\hat{X}_{0}, \hat{\sigma} = \underset{X_{0}, \sigma}{\operatorname{argmin}} \left[-\sum_{n} \ln \left(f_{\mathcal{N}(0, \sigma)}(x[n] - X_{0}) \right) \right]$$
(C.3)

The search is done in our computer, using whatever minimum-seeking routine we wish to use, such as various flavors of fmin in Matlab, Octave or Python, "GoalSeek" in Excel, etc.

At first glance, the log-likelihood approach appears to make life more complicated, but it is an improvement. With our old approach, we heavily manipulate the data to get velocities and accelerations, compute some test statistics (mean, standard deviation) and then perform some set, voodoo-like procedure (ANOVA or non-parametric test) to see if this is different from the position of another dead limpet. The test procedure is, to many biomechanics practitioners, a black box relegated to a stats course taken long ago. The old approach is "no thought required" - which is precisely its drawback. By instead modeling the process that produced the measurements, we can get a handle on both the physical process driving the measurement and the measurement noise. We can also then compare different models, to select which is a more appropriate description of what we have observed.

C.4 Comparing models

Back to the question of is the limpet moving? Our null approximating model (repeated below) was that it is stationary:

$$g_0: x[n] = X_0 + \mathcal{N}(0, \sigma) \tag{C.4}$$

A reasonable alternative approximating model is that the limpet is crawling along with some constant velocity V:

$$g_1: x_v[n] = X_0 + V \frac{n}{f} + \mathcal{N}(0, \sigma)$$
 (C.5)

where the positions are sampled at some known sample rate f; this is simply $x = X_0 + Vt$. We could perform a log-likelihood calculation for g_1 and get a decent guess for what X_0 , Vand σ are for that model, noting that we've added an additional parameter V. We might like to know if the data are better explained by g_0 or g_1 ? Additionally, if g_1 is "better", is it better by enough to justify the additional parameter V, or are we guilty of what is known as over fitting?

C.4.1 Akaike information criterion (AIC)

The Akaike information criterion (AIC) (Akaike, 1974) provides a way to compare several candidate approximating models and ask if the additional explanatory power of a given

model is worth the extra parameters (k is the number of parameters):

$$AIC = 2k - 2\ln(\mathcal{L}) \tag{C.6}$$

The AIC is computed for the maximum likelihood parameter estimate for each model. The model that best explains the data is the one with the minimum AIC value. In essence, we are searching for the model that requires as little information as necessary to describe the observed data well.

We can see that increasing the number of parameters increases the AIC. On the other hand, a model that is more likely to explain the observed data will have a smaller AIC. Models within 1-2 of the minimum have substantial support and should not be discarded; models within 4-7 have less support and models 10 and above have no support and can be discarded (Akaike, 1974; Burnham and Anderson, 2002).

C.4.2 Bayesian information criterion (BIC)

An alternative to AIC is the Bayesian information criterion (BIC) (Schwarz, 1978). It is similar in form but includes a term related to the number of observations n. This means that the penalty for having more parameters is larger than in the AIC. We can check both and see if similar answers are given with each index.

$$BIC = k \ln(n) - 2 \ln(\mathcal{L}) \tag{C.7}$$

C.4.3 So is the limpet moving?

Let us apply these to some (simulated) limpet data for two limpets, shown in Figure C.1: The simple estimate of the position of Limpet 1 is (0.423 ± 0.001) m, obtained by taking the mean and standard deviation. If we apply the maximum likelihood estimation algorithm of Equation C.3 to Limpet 1, we obtain the same, (0.423 ± 0.001) m. It's nice to get the right answer (these correspond to the "true" values for Limpet 1 in the simulation), and we can go a little further.

We wish to test if the limpets are moving, by checking which fits the data best, stationary model g_0 , or constant velocity model g_1 . Tables C.1 and C.2 summarize the maximum likelihood estimates for the limpets for each model. The table also contains the AIC and BIC values for the models. Limpet 1 is stationary and the model with a constant velocity term estimates zero speed (Table C.1). We conclude that Limpet 1 is not moving. On the other hand, there is substantial support that Limpet 2 is moving to the right (Table C.2, Δ_i AIC = 61.1). Comparing the Δ_i AIC and Δ_i BIC shows that the constant velocity model has substantially more explanatory power for Limpet 2. Limpet 2 is not dead, it is moving to the right at 0.0001 m s⁻¹ (which is also the "true" value for Limpet 2 in the simulation).

Note that taking finite differences of the data in Figure C.1 would have been hopelessly fracked by the measurement noise; the mean speed of Limpet 2 by that method is $-8.9 \times 10^{-5} \,\mathrm{m \, s^{-1}}$. The "true" values here would have been very hard to pick out of the noisy data using simple finite differences.



Figure C.1: Simulated limpet data. Limpet 1 is blue, Limpet 2 is green.

Table C.1: Maximum likelihood parameter estimates and model comparison information for
Limpet 1 in the simulated data of Figure C.1. The generating model ("truth") for Limpet 1
is stationary at $X_0 = 0.423 \mathrm{m}$.

	Parameter estimates				Model comparison information				
Model	σ , m	X_0 , m	$V,\mathrm{ms^{-1}}$	K	MSE	$\ln\left(\mathcal{L} ight)$	$\Delta_i \operatorname{AIC}$	Δ_i BIC	w_i
g_0 , stationary	0.001	0.423		2		3308.2	0.0	0.0	
g_1 , constant v	0.001	0.423	0.000	3		3308.2	2.0	6.4	

Table C.2: Maximum likelihood parameter estimates and model comparison information for Limpet 2 in the simulated data of Figure C.1. The generating model for Limpet 2 is moving right at $V = 0.0001 \,\mathrm{m \, s^{-1}}$.

	Parameter estimates				Model comparison information				
Model	σ , m	X_0 , m	$V,\mathrm{ms^{-1}}$	k	MSE	$\ln\left(\mathcal{L} ight)$	$\Delta_i \operatorname{AIC}$	Δ_i BIC	w_i
g_0 , stationary	0.0012	0.4235		2		3308.8	61.1	63.1	
g_1 , constant v	0.0009	0.423	0.0001	3		3340.3	0.0	0.0	

C.5 Real example: Angry Bird / Ping pong ball

Rather than just testing with simulated data, we wish to check our methods with a real, physical example of a passive projectile in flight. This will allow us to check the performance of our techniques given realistic noise from typical biomechanics data gathering setups.

We filmed the trajectory of a commercially available toy (Angry Birds² Knock on Wood Game, Mattel Inc., El Segundo, CA) consisting of a spring-powered catapult and (approximately) spherical, 1-inch (2.54 cm) projectile, mass 5.88 g. The trajectory was filmed at 60 frame/s using a fixed-focus HD camcorder (Flip MinoHD; Cisco Systems, San Jose, CA) placed perpendicular to the plane of movement. Calibration was provided by a 15 cm scale placed in view of the camera. Projectile positions were digitized on a MacBook Pro (Apple; Cupertino, CA) using a freely available software package (GraphClick; Arizona Software). Subsequent analysis, described in detail below, was carried out in R (R Development Core Team, 2013).

A typical trajectory is given in Figure C.2. The digitized result is shown in Figure C.3.

To continue with the analysis, we construct several physically-motivated candidate approximating models that we will then test to see which is best supported by the data:

$g_0: x = X_0 + \mathcal{N}(0, \sigma)$	(stationary)
$g_1: x = X_0 + Vt + \mathcal{N}(0, \sigma)$	(constant velocity)
$g_2: x = X_0 + Vt + \frac{1}{2}at^2 + \mathcal{N}(0,\sigma)$	(constant acceleration)
$g'_2: x = X_0 + Vt - \frac{1}{2}9.81t^2 + \mathcal{N}(0, \sigma)$	(Earth gravity)
$g_3: x = X_0 + Vt + X_1 e^{-t/\tau} + \mathcal{N}(0, \sigma)$	(linear drag terminal velocity)

For simplicity we consider similar forms for y and assume that noise in x and y are uncorrelated, stationary, zero-mean Gaussian random processes $\mathcal{N}(0,\sigma)$. Also, for a more

²The physical toy was inspired by a popular computer game in which various birds are shot by a slingshot at structures containing evil green pigs. Analysis of the game physics used shows that either the birds are 5 m tall (Allain, 2010), heights only seen in extinct, non-volant birds; or the computer game does *not* conform to our normal rules of physics; for example g is substantially less than 9.8 m s^{-2} .



Figure C.2: Trajectory of an Angry Bird. Composite image with multiple frames superimposed, 30 frame/s, elapsed time approximately 0.5 s. Scale 15 cm. Inset shows catapult device and projectile.

complicated example, we might construct and solve a system of differential equations describing the motion (Rauch et al., 1965) (or see the next section). Here we work only with the trivial known forms of the solutions for simple cases. These should be adequate to describe the motion, but if they are not, we will find out from a poor fit and a large noise variance σ .

The models were then used along with the mle2 routine in R to obtain maximum likelihood estimates and values for the log-likelihood, AIC and BIC. The results of the analysis are given in Tables C.3 and C.4. The best supported models are constant velocity (g_1) in xand Earth gravity (g'_2) in y. These are shown as the blue line in Figure C.3. In contrast, an unsupported model, such as constant velocity (g_1) in y, shown as the red line in Figure C.3 gives a poor fit as well as large Δ_i AIC and BIC values and low likelihood values (comparable to stationary in Table C.4).

Other candidate models exist. For example, a model with terminal velocity or one implementing a set of differential equations for phugoid mode gliding could be used as more complicated candidate models, at the expense of computational complexity and additional parameters.

In practice, mle2 seems not to be the best at finding a global minimum without crashing into local minima. For the results in this thesis, this is avoided by testing of several initial guesses. While this may be tedious, due to measurement noise, blindly two derivatives via



Figure C.3: Digitized trajectory of an Angry Bird. Body positions at 1/60 s intervals shown by dots. Blue line shows the best supported candidate models for x(t) and y(t). Red line shows an unsupported candidate model.

finite differences would inject hopeless amounts of noise and ask any possibility of observing the onset of directed aerial descent, as is seen in results in (Dial and Carrier, 2012).

C.6 Conclusions

The fundamental way this works is to establish *a priori* models of what one expects to see and then to test if the observations are well-explained by those models. This is fundamentally a good way to do business in science. In the context of detecting the onset of directed aerial descent in baby birds, we expect that initially birds will act like passive projectile motion. As their ability to generate forces and torques in the air grows, they will no longer be well-modeled by passive projectiles; we should see this by seeing that the models for passive projectiles are not supported by observed trajectories (\mathcal{L} and AIC comparable to uninformative models like stationary, or very large error estimates σ) or by a failure by the mle2 routine to find a suitable global minimum estimate³.

³Both of these occurred in the analyses of chapter 1.

$x \mod x$	σ , m	X_0 , m	$V,\mathrm{ms^{-1}}$	$a, \mathrm{ms^{-2}}$	X_1 , m	τ , s
g_0 , stationary	0.210	0.331				
g_1 , constant v	0.007	-0.023	1.248			
g_2 , constant a	0.005	-0.013	1.144	0.365		
g'_2 , Earth gravity	0.129	-0.279	4.031	-9.810		
g_3 , terminal v	0.010	-0.708	1.660		0.693	1.374
$x \mod x$	$k \ln$	$(\mathcal{L}) \Delta_i$	AIC Δ_i l	BIC		
g_0 , stationary	2 4	.93 20	60.2 25'	7.1		
g_1 , constant v	3 13	7.03	0.0 0.	0		
g_2 , constant a	4 12	5.75 2	0.6 19	.0		
g'_2 , Earth gravity	3 21	.98 22	28.1 220	5.5		
g_3 , terminal v	4 -3	32.16 34	40.4 34	1.9		

Table C.3: Maximum likelihood parameter estimates and model comparison information for Angry Bird trajectory x data of Figure C.3.

Table C.4: Maximum likelihood parameter estimates and model comparison information for Angry Bird trajectory y data of Figure C.3.

$y \bmod e$	σ , m	X_0 , m	$V,\mathrm{ms^{-1}}$	$a, \mathrm{ms^{-2}}$	X_1 , m	$ au, { m s}$
g_0 , stationary	0.126	6 0.238				
g_1 , constant v	0.127	0.224	0.052			
g_2 , constant a	0.010	-0.036	2.877	-9.955		
g'_2 , Earth gravity	0.010	-0.032	2.835	-9.810		
g_3 , terminal v	0.010	3.882	-4.647		-3.937	0.484
$y \bmod e$	k	$n(f) = \Delta_{f}$	AIC A. F	DIC.		
÷	10 1	$(\sim) \Delta_i$	All Δ_l I	JIC		
g_0 , stationary	$\frac{n}{2}$	$\frac{\ln(2)}{22.56}$ 17	$\frac{A10}{75.4} \frac{\Delta_i}{173}$	3.9		
g_0 , stationary g_1 , constant v	$\frac{n}{2}$	$\frac{m(2)}{22.56}$ 17 22.65 17	$ \begin{array}{cccc} & All & \Delta_i \\ & 75.4 & 175 \\ & 77.3 & 177 \\ \end{array} $	3.9 7.3		
g_0 , stationary g_1 , constant v g_2 , constant a	$\begin{array}{c} 1 \\ 2 \\ 3 \\ 4 \end{array}$	$ \frac{11(2)}{22.56} \frac{17}{17} \\ 22.65 17 \\ 11.87 ($	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	3.9 7.3 4		
g_0 , stationary g_1 , constant v g_2 , constant a g'_2 , Earth gravity	$ \begin{array}{c} 2 \\ 2 \\ $	$ \frac{11(2)}{22.56} \qquad \frac{\Delta_i}{15} \\ \frac{11.87}{11.28} \qquad (1) $	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	3.9 7.3 4 0		

To summarize, it is possible to test for aerial behaviors with a minimum of statistical voodoo. There is still some voodoo, but it is confined to a few, easy-to-understand places and one can at least rationalize the form the voodoo takes.

This method appears to work and is applied to the case of falling baby Chukar Partridge (*Alectoris chukar*) and Mallard Duck (*Anas platyrhynchos*) in chapter 1. It has also been successfully applied to studies of auto rotating seeds (Stevenson et al., 2013) and will be used in studies of human skydivers (Cardona et al., 2011; Evangelista et al., 2012).

Appendix D

Modeling multi-axis zero angular momentum turns

These notes give my thoughts on how to numerically test a recorded movement for use of zero- and constant angular momentum turning mechanics¹.

D.1 Introduction

We wish to examine the earliest instants of roll, pitch, and yaw maneuvers made by baby birds (Chukar Partridge (Alectoris chukar) and Mallard Duck (Anas platyrhynchos), from 1 dph to fledging). At this early age, the wings are not yet fully developed. In addition, during the initial instants of a fall, the body has not yet attained sufficient airspeed to develop large aerodynamic forces and torques, which scale $\sim \rho U^2 A$ and $\rho U^2 A \lambda$, respectively. Consequently we might expect these early maneuvers to involve significant contribution from other mechanisms, such as inertial mechanisms (Edwards, 1986; Jusufi et al., 2008, 2010). Inertial mechanisms are ones in which body angular position is changed by modulating body inertia, either to modulate some initial angular momentum obtained when leaving the ground, or to effect a zero- or constant angular momentum turn (Edwards, 1986). In order to answer questions of biological interest, we need general ways (numerical methods) to test if a given maneuver uses inertial mechanisms or detect when non-inertial mechanisms must be at work.

¹Tom Daniel first suggested to me the idea of predicting what an animal would do if there were no air, in the solely inertial case.

D.2 Conservation of angular momentum *H*

First, some definitions are in order. For a collection of moving particles, we can define angular momentum about an arbitrary point B as follows (after (Baruh, 1999)):

$$\vec{H}_B = \sum_i \vec{r}_{Bi} \times m_i \vec{v}_i \tag{D.1}$$

We also introduce the centroid, or center of mass G:

$$\vec{r}_G = \frac{\sum_i m_i \vec{r}_i}{\sum_i m_i} \tag{D.2}$$

which, for our collection of moving particles, may also be moving. The angular momentum about the center of mass reduces to a convenient form:

$$\frac{d}{dt}\vec{H}_G = \vec{M}_G \tag{D.3}$$

where M_G are the externally applied moments about the center of mass. In the case of an organism in free fall, where it has not yet attained sufficient speed for aerodynamic torques to be significant, and is not ejecting any mass or in contact with things that it can push off on (refer to (Baruh, 1999) for the derivation of this result)

$$\frac{d}{dt}\vec{H}_G = 0 \tag{D.4}$$

or alternatively,

$$\vec{H}_G = \sum_i \vec{r}_{Gi} \times m_i \vec{v}_i = \text{constant} \tag{D.5}$$

In other words, angular momentum is conserved.

Equation D.5 will be the main tool we use in our simulations and analyses in two ways. First, we will take observations of body position and calculate H_G , to test if angular momentum is constant and detect if a maneuver requires use of external (aerodynamic) torques. This first task is easy. Second, given a sequence of body positions in coordinates fixed to the body, we should be able to project what whole-body rotations should result in the absence of air, i.e. if the animal were magically flying in a vacuum. The second task is only a little harder.

D.3 Calculating H from observed positions, the easy way

By filming an organism with multiple calibrated cameras, it is often possible to obtain estimates of three-dimensional position for joints, markers, limbs, etc. We denote these measured positions as a set of position vectors in the rest frame $\vec{r}_{0i}[n]$, where [n] represents each discrete time frame of the video.

With each point we will also associate a point mass m_i representing the mass of each chunk of the organism. This is a simplification; organisms are not point masses in general, but small chunks of an animal can be approximated as such to simplify calculation². We can guess m_i from the shape of the animal, or by using a good balance and a meat cleaver. Unless chunks of the organism are removed or redistributed during the sequence (not usually the case for terrestrial animals), m does not depend on time [n]. Thus, our analysis model of the organism is a system of point masses with prescribed motions.

To numerically calculate the angular momentum H of the system, we proceed by finding the location of the center of mass \vec{r}_G using Equation D.2 above. We subtract to find the time-varying body positions relative to the time-varying center of mass:

$$\vec{r}_{Gi}[n] = \vec{r}_{0i}[n] - \vec{r}_{G}[n] \tag{D.6}$$

The velocity of each point mass, $\vec{v}_{Gi}[n]$, can be estimated using a simple backwards difference:

$$\vec{v}_{Gi}[n] \approx \frac{\vec{r}_{Gi}[n] - \vec{r}_{Gi}[n-1]}{\Delta t} \tag{D.7}$$

where $\Delta t = 1/\text{fps}$ is the period between frames. Taking derivatives of positional data injects noise, but this is the only derivative we need to take, and hopefully it's not as bad as differentiating twice to get accelerations³.

We now have all the pieces needed to compute H_G at each time step [n], repeated here:

$$\vec{H}_{Gi}[n] = \vec{r}_{Gi}[n] \times m_i \vec{v}_{Gi}[n] \tag{D.8}$$

$$\vec{H}_G[n] = \sum_i \vec{H}_{Gi}[n] \tag{D.9}$$

For a zero- or constant angular momentum (inertial) maneuver, $H_G[n]$ should be constant, while for a maneuver where external aerodynamic torques are important, $H_G[n]$ will vary with time. Plotting should suffice to tell, or this could be formally tested using maximum likelihood estimation plus an Akaike Information Criterion (appendix C).

The principal advantage of this numerical formulation is that it is easier to apply to more generalized shapes (e.g. a baby bird with two kicking legs, two flapping wings, wagging tail and a head on a long neck; insect with six legs) compared to analytical models of chains of inertias that must be specifically derived for each body plan (Evangelista, 2009; Jusufi et al., 2008, 2010) and which are usually only tractable for small numbers of links. Kinematics

 $^{^{2}}$ We really wish to avoid dealing with long kinematic chains where each link has large inertia; any more than two links is very hard to write and likely to induce madness.

³If this does turn out to be bad, there are other tricks we can try like spline smoothing or using more explicit models of the body.

studies naturally produce positions of points, which can easily be used to generate clouds of point masses that track the movements of the study organism and allow computation of its angular momentum.

D.4 Predicting body rotation to maintain *H* constant

We may wish to go the "opposite" way in our numerical analysis, in other words, find the expected motions if the maneuver was only inertial. In this case what we do is a little different. We begin as before, with a set of position vectors $\vec{r}_{0i}[n]$ for each joint/marker/limb/point as it moves through time [n]. We also assume or measure the mass associated with each chunk m_i , and we compute the time-varying position of the center of mass \vec{r}_G (Equation D.2). From this we use Equation D.6 to obtain $\vec{r}_{Gi}[n]$, the time-varying body positions relative to the center of mass. So far this is the same as in Section D.3.

In Section D.3, we computed $\vec{r}_{Gi}[n]$ in a reference frame that is translating with the center of mass but is not rotating. Consider instead a reference frame' that translates with the center of mass and also rotates with some logical body-fixed axes, such as in an anatomically bilaterally symmetric animal (antero-posterior, lateral, and dorso-ventral axes)⁴. We denote the body position in the new frame' as:

$$\vec{r}_{Gi}[n] = \mathbf{R}[n] \cdot \vec{r}_{Gi}[n] \tag{D.10}$$

where $\mathbf{R}[n]$ is an appropriately chosen, invertible rotation matrix. With the body positions in the new coordinate system, we continue as before to obtain the velocities and "apparent" angular momentum:

$$\vec{v}_{Gi}[n] \approx \frac{\vec{r}_{Gi}[n] - \vec{r}_{Gi}[n-1]}{\Delta t}$$
 (D.11)

$$\vec{H}'_{Gi}[n] = \vec{r}'_{Gi}[n] \times m_i \vec{v}'_{Gi}[n] \tag{D.12}$$

$$\vec{H}'_{G}[n] = \sum_{i} \vec{H}'_{Gi}[n]$$
 (D.13)

For an inertial maneuver, $H'_G[n]$ will usually *not* be constant because we removed the wholebody rotation when we transformed to a coordinate frame that rotates with the body. Using this discrepancy, we can find the whole-body rotation that would have made the "real" angular momentum H_G constant.

Recall that the "real" angular momentum for the case of no external torques $H_{Gi}[n]$ is given by

$$\vec{H}_G[n] = \sum_i \vec{r}_{Gi}[n] \times m_i \vec{v}_{Gi}[n] = \text{constant} = \vec{H}_G[0]$$
(D.14)

⁴It need not be strictly bilaterally symmetric in the posture taken during the maneuver.

Since \mathbf{R} is invertible⁵, we can expand using Equation D.10, keeping in mind that the velocities of each mass also include a component from the whole-body rotation:

$$\vec{H}_{G}[n] = \sum_{i} \mathbf{R}^{-1}[n] \cdot \vec{r}_{Gi}[n] \times m_{i}(\vec{v}_{Gi}[n] + \vec{\omega}_{G}[n] \times \vec{r}_{Gi}[n]) = \vec{H}_{G}[0]$$
(D.15)

We then rearrange terms and simplify:

$$\sum_{i} \vec{r}'_{Gi}[n] \times m_i(\vec{v}'_{Gi}[n] + \vec{\omega}_G[n] \times \vec{r}'_{Gi}[n]) = \mathbf{R}[n] \cdot \vec{H}_G[0]$$
(D.16)

$$\sum_{i} \vec{r}_{Gi}[n] \times m_i \vec{v}_{G,i}[n] + \sum_{i} \vec{r}_{Gi}[n] \times m_i \vec{\omega}_G[n] \times \vec{r}_{Gi}[n] = \mathbf{R}[n] \cdot \vec{H}_G[0]$$
(D.17)

$$\vec{H}_G'[n] + \mathbf{J}_G'[n]\vec{\omega}_G[n] = \mathbf{R}[n] \cdot \vec{H}_G[0]$$
(D.18)

$$\vec{\omega}_G[n] = \mathbf{J}_G^{\prime-1}[n] \cdot (\mathbf{R}[n] \cdot \vec{H}_G[0] - \vec{H}_G^{\prime}[n])$$
(D.19)

where $\mathbf{J}'_G[n]$ are the instantaneous moments of inertia of the body about the body-fixed (') axes and $\vec{\omega}_G[n]$ is the whole-body rotational speed. It is worthwhile to write out $\mathbf{J}'_G[n]$ and equation D.19 for the case of zero initial angular momentum $(\vec{H}_G[0] = 0)$.

$$\vec{\omega}_G[n] = -\mathbf{J}_G^{\prime-1}[n] \cdot \vec{H}_G^{\prime}[n] \tag{D.20}$$

$$\mathbf{J}_{G}'[n] = \sum_{i} \begin{bmatrix} m_{i}(r_{iy}^{2} + r_{iz}^{2}) & -m_{i}r_{ix}r_{iy} & -m_{i}r_{ix}r_{iz} \\ -m_{i}r_{ix}r_{iy} & m_{i}(r_{ix}^{2} + r_{iz}^{2}) & -m_{i}r_{iy}r_{iz} \\ -m_{i}r_{ix}r_{iz} & -m_{i}r_{iy}r_{iz} & m_{i}(r_{ix}^{2} + r_{iy}^{2}) \end{bmatrix}$$
(D.21)

where all $\vec{r_i}$ are evaluated at time [n].

Using equations D.20, D.21, and D.13, we can numerically integrate $\vec{\omega}_G[n]$ to find $\vec{\theta}_G[n]$, the angular position of the body, and then construct a new rotation matrix $\mathbf{A}[n]$ to rotate the entire body to the new predicted orientation. We also translate the center of mass according to which external conservative forces (e.g. gravity) are acting.

Equations D.20, D.21, and D.13 allow us to predict the overall motion of a body given prescribed appendage movements (flapping, kicking, tail wagging) with respect to body-fixed coordinates. To be sure the numerical methods work correctly, we can check these methods and those from Section D.3 using simple toy model simulations (Section D.5).

⁵In the case of a body with zero initial angular momentum $(\vec{H}_G[0] = 0)$ we can avoid calculating **R** entirely! Win!

D.5 Simulation of a two-dimensional toy model

Figure D.1 gives the results of several simulations of toy models to check that the code is working as desired. The first case (A) shows a simulation of an amphipod launch similar to those in (Evangelista, 2009). After contact with the ground, amphipods became passive spinning batons in the air, and this is reflected in their constant angular momentum (the momentum of each link varies but the sum is constant). In case (B) a more complicated case is shown in which the amphipod shortens the body, spinning faster. Here too, angular momentum is conserved.

In case (C), a hypothetical amphipod with rocket engines is modeled. The rocket engines are fired to spin the animal faster, resulting in an increase in H; the retrorockets are then fired and H decreases. As a final test case, (D) shows the reverse calculation for the body movements resulting from a wagging scallop, assuming zero total angular momentum.

D.6 Conclusions

This method appears to work for the cases tested here. It is applied to pitching and rolling maneuvers in Chukar partridge (*Alectoris chukar*) in chapter 1. Future uses will include human skydivers (Cardona et al., 2011; Evangelista et al., 2012) and amphipods (Evangelista, 2009).



Figure D.1: A. Tumbling amphipod with constant length body showing constant total angular momentum. B. Tumbling amphipod with body shortening at time t = 0.4, showing rotational speed up to maintain constant total angular momentum. C. Tumbling amphipod with rocket motors firing at time t = 0.4 and retro-rockets at t = 0.6, showing non-constant total angular momentum. D. Two-link "gecko" with lateral tail wagging $\pm 30^{\circ}$ at 3 Hz in body-fixed coordinates (left) and with projected motion assuming zero total angular momentum (right).

Appendix E

Derivation of filter theory for turbulence sensitivity

In this appendix, I provide further definition and derivation of the concepts behind the turbulence sensitivity measurements of chapter 4.

E.1 Definitions

I compute three quantities. I call them "sensitivity" in the sense that they characterize how external disturbances, which are measurable quantities in the flow environment, provide extraneous forcing inputs to the "plant." I choose not to call them "robustness", which in a control sense generally deals with variation of internal control parameters.

The first quantity we compute is an overall measure of turbulence sensitivity, defined as the ratio of the standard deviations $(\sigma_x = (E((x - \overline{x})^2)^{0.5}))$ of force or torque and velocity:

$$S \equiv \frac{\sigma_f}{\sigma_u} \quad \text{or} \quad \frac{\sigma_\tau}{\sigma u}$$
 (E.1)

where $S_{f_y,u_y} = \sigma_{f_y}/\sigma_{u_y}$, $S_{\tau_z,u_y} = \sigma_{\tau_z}/\sigma_{u_y}$, and so on. The dimensions of S are dimensions of mechanical impedance, i.e. N s m⁻¹ or kg s⁻¹ for forces, or N s or kg m s⁻¹ for torques. This quantity is straightforward to compute from measured data. In turbulence literature, the σ terms are sometimes called "fluctuation" (see table E.1), e.g. velocity fluctuation, but in all cases what is meant is $E((x - \bar{x})^2)$.

Alternatively we can nondimensionalize f or τ by making use of a turbulence sensitivity coefficient, C_S :

$$f_y = C_{S_{f_y, u_y}} 0.5 \rho u_y^2 A \tag{E.2}$$

$$\tau_z = C_{S_{\tau_z, u_y}} 0.5 \rho u_y^2 A l \tag{E.3}$$

where A is the planform area, l is a characteristic length, and C are expected to vary based on shape, Re, or possibly other terms. This quantity is also straightforward to compute

Total velocity field	$\mathbf{u} = \mathbf{V} + \mathbf{u}'$
Mean flow in wind tunnel	\mathbf{V}
Turbulent fluctuations	\mathbf{u}'
Size of large eddies (integral scale)	l
Typical fluctuating velocity of large eddies	u
Size of smallest eddies (Kolmogorov scale)	η
Typical fluctuating velocity of smallest eddies	v

from measured data. We choose the planform area for A and either the body length or the integral (length) scale of the turbulent flow as l. The nondimensionalization is useful in fluid mechanics to divide out the effects of other size- or flow-related parameters to focus on the key shape parameters of interest, especially in flows that are expected to be similar with respect to other key fluid mechanics variables like Reynolds number.

The third measure, $S(j\omega)$ or S(jk), is a turbulence sensitivity transfer function, and is used to examine the frequency (or wavenumber) dependence of sensitivity. It is obtained from the Fourier magnitudes of the force or torque, and velocity, for example:

$$\|S_{f_y,u_y}(j\omega)\| \equiv \frac{\|F_y(j\omega)\|}{\|U_y(j\omega)\|}$$
(E.4)

$$\|S_{f_y,u_y}(jk)\| \equiv \frac{\|F_y(jk)\|}{\|U_y(jk)\|}$$
(E.5)

$$\|S_{\tau_z, u_y}(jk)\| \equiv \frac{\|T_z(jk)\|}{\|U_y(jk)\|}$$
(E.6)

The last two examples above use the wavenumber (spatial frequency) k for the frequency domain and will allow us to examine changes in sensitivity due to shape.

E.2 Describing the turbulence

As a quick review of turbulence, I identify the Reynolds number of interest for this flow as the same scaling uses by Davidson (2004):

$$Re = \frac{ul}{\nu} \tag{E.7}$$

where u is the typical fluctuating velocity of large eddies, l is the size scale of large eddies, and $\nu = 15 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ for air. Here the large eddies are assumed to be comparable to the size of the initiating cylinder in the experiment.
The calculations of chapter 4 also require a model spectrum. Again I adopt the same definitions as (Davidson, 2004) for velocity correlation function:

$$Q_{ij} = \langle u'_i(\mathbf{x})u'_j(\mathbf{x} + \mathbf{r})\rangle \tag{E.8}$$

and for energy spectrum:

$$E(k) = \frac{2}{\pi} \int_0^\infty R(r)kr\sin krdr$$
(E.9)

$$R(r) = \int_0^\infty E(k) \frac{\sin kr}{kr} dk$$
(E.10)

The properties of the energy spectrum are that $E(k) \ge 0$, for eddies of size r; that E(k) peaks around $k \sim \pi/r$, and:

$$\frac{1}{2}\langle \mathbf{u}^2 \rangle = \int_0^\infty E(k) do \qquad (E.11)$$

Strictly speaking, since the energy function is nonlinear, eddies at a given size (say r) will contribute broadly to the energy spectrum. However, we'll treat the force they generate as linear and see how bad it is.

The last piece necessary for chapter 4 is a model spectrum (Davidson, 2004), obtained partially from scaling arguments and partially from empirical results:

$$E(k) = \hat{k}^4 (1 + \hat{k}^2)^{-17/6} \exp\left[-\hat{k} \operatorname{Re}^{-3/4}\right], \hat{k} = kl$$
(E.12)

The slopes here reflect the slopes of the measurements of velocity via ultrasonic anemometer and via microphone in chapter 4.

E.3 Simulating turbulence

The turbulence sensitivity estimate proceed by simulating some turbulence generated by the model spectrum. First, a vector of magnitudes is constructed, where here the square root reflects the relationship between velocity and energy:

$$|U(jk)| = u' (E(k))^{\frac{1}{2}}$$
(E.13)

Let the phase ϕ be random, uniformly distributed on the interval $[0, 2\pi)$.

u is given by the inverse Fourier transform, however since we will be implementing this using discrete Fourier transform there is some normalization that needs to be done.

$$u = ifft(U) \tag{E.14}$$

We want Parseval's Theorem to hold, so

$$\int_{-\infty}^{\infty} |u(x)|^2 dx = \int_{-\infty}^{\infty} |U(k)|^2 do$$
 (E.15)

or

$$x_s \sum |u[n]|^2 = \frac{k_s}{N} \sum |U[k]|^2$$
 (E.16)

or

$$\frac{1}{N}\sum |u[n]|^2 = \frac{k_s^2}{N^2}\sum |U[k]|^2$$
(E.17)

or

$$\operatorname{var}(u) = \frac{k_s^2}{N^2} \sum |U[k]|^2$$
 (E.18)

is a scaling/normalization that must be applied to the simulated velocities.

E.4 Shapes as spatial filters

To treat the shapes as spatial filters, I refer to (Siebert, 1985) to adapt concepts from signal processing to the turbulence problem at hand. First, consider the side force generated by a distribution of side velocity impinging on a flat rectangular plate. The resulting force could be modeled by scaling, shifting, and summing the velocity (squared) values, in other words, a convolution of a filter h(r) with a stationary random variable $u^2(r)$. In the wavenumber (frequency) domain, this is simple to deal with using Fourier transforms applied to E(k):

$$F = \int_{L} 0.5\rho u^2 (r-\xi) Cw d\xi \tag{E.19}$$

to first order and ignoring viscous effects and assuming $C \sim 1$ for bluff bodies.

Recasting as a filter:

$$h(r) = \begin{cases} L^{-1} & |r| < L/2\\ 0 & \text{otherwise} \end{cases}$$
(E.20)

$$H(k) = \frac{1}{2\pi}\operatorname{sinc}(\frac{kl}{2}) \tag{E.21}$$

In other words, convolution in time becomes multiplication in the frequency domain (Siebert, 1985). For torque, remember that the filter kernel includes a term to multiply each differential force contribution by the moment arm:

$$T = \int_{L} 0.5\rho u^2 (r-\xi)C\xi w d\xi \qquad (E.22)$$

also to first order and ignoring viscous effects and assuming $C \sim 1$ for bluff bodies. Recall that multiplication by x in the spatial domain is similar to taking a derivative in the wavenumber (frequency) domain gives a predicted shape for the torque (spectral) transfer function.

$$H_t(k) = \frac{d}{dk} \frac{1}{2\pi} \operatorname{sinc}(\frac{kl}{2})$$
(E.23)

which becomes like an enveloped cosine wave with suppressed low frequency terms compared to the force (spectral) transfer function.

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