NATURE'S AIRCRAFT:
Power-to-Mass, Morphing, and How Birds Use Half a Wing

Kenneth P. Dial, Ph.D.
Flight Laboratory, Division of Biological Sciences, University of Montana, Missoula, MT, 59812, U.S.A., kdial@mso.umt.edu
U.M. Flight Lab website: http://biology.umt.edu/flightlab/

Introduction

Most birds possess an array of locomotor features that permit extraordinary maneuverability, rapid acceleration and deceleration, and efficient long-distance travel. This broad range of flight capabilities should be as inspiring to aeronautical engineers and pilots today as it was for the first innovators of human flight. In fact, issues related to form and function continue to be of interest to both biologists and aeronautical engineers whose focus is to elucidate underlying principles of flight performance. For example, why are the vast majority of birds relatively small (<150 g; <0.33 lbs) and why do the largest flying birds all converge on a mass of about 12 kg (~25 lbs)? In other words, why are there no birds the size of cows or elephants? Is there a shared relationship of power-to-mass among birds and aircraft? Since human flight was inspired by animal flight, perhaps we should clarify both the origin of animal flight and the form-function principles of aircraft and animal flight. A long-standing problem within biological circles is an adequate explanation of the transitional adaptive stages of the avian wing during the evolution of flapping flight from their dinosaur ancestors. That is, how does one explain the function of a developing wing or half a wing? Here I describe how some birds employ their flapping wings in ways previously unappreciated by altering their wing excursion in order to create negative lift that pushes the animal against inclined surfaces.

In this paper, I briefly discuss recent research advances in: (1) measuring power-to-mass ratios and its influence on animal behavior, (2) how birds dynamically change shape or "morph" in flight, and (3) how some birds employ wing-assisted incline running (WAIR) and turn their wings into negative thrust generating devices. This last section relates to the novel use of flapping proto-wings and addresses the evolution of flight in birds. Arguably, all of these issues have potential applications to future aviation and robotic technology

Power-to-Mass Ratios:

Birds span over five orders of magnitude in body size; living species range from the 5 g Cuban Bee Hummingbird (*Mellisuga helenae*) to the African Ostrich (*Struthio camelus*), which exceeds 150 kg. Although numerous studies have recognized the importance of body size to physiology (Calder, 1984; Schmidt-Nielsen, 1984; Brown and West 2000), ecology (McMahon and Bonner, 1983; Peters, 1983; Brown and West, 2000), and aspects of life history (Roff, 1992), minimal attention has been directed toward empirical testing of allometric correlates of locomotor performance (acceleration, deceleration, maneuverability, and range of flight speeds). Maneuvering and linear acceleration are functions of mass-specific power (Warrick, 1998) transferred to lift and thrust; however, measuring the relationship between body mass and mechanical power output remains a challenge. Over the past decade, researchers from several animal locomotion labs have been tackling this problem by surgically implanting sonomicrometry (piezo-electric crystals that provide an instantaneous measure of muscle length change) and strain gauge technology (to record the force and bending moments created by the main flight muscle) in order to determine mechanical work-loops for individual wing beats (Biewener et al., 1998; Dial et al., 1997; Tobalske et al., 2003). By surgically implanting these and other miniature biomechanical recording devices, plus employing other macro-recording devices (e.g., force transducers, accelerometers, force plates, etc), we are understanding magnitude and timing of skeletal muscles, the animals actuators, that generate forces to propel these organisms through their environment.

In addition to measuring mechanical work, the significance of the adverse scaling of lift and power output must also be resolved if we are to clearly understand the mechanisms underlying the basic relationship of body size and locomotor performance (Marden, 1994; Ellington, 1991; Askew et al., 2001). By quantifying locomotor performance of animals (as we currently do for aircraft and automobiles), I predict we will uncover important and novel strategies of organismal design that will in turn inspire future aeronautical engineers in the development of superior aircraft.

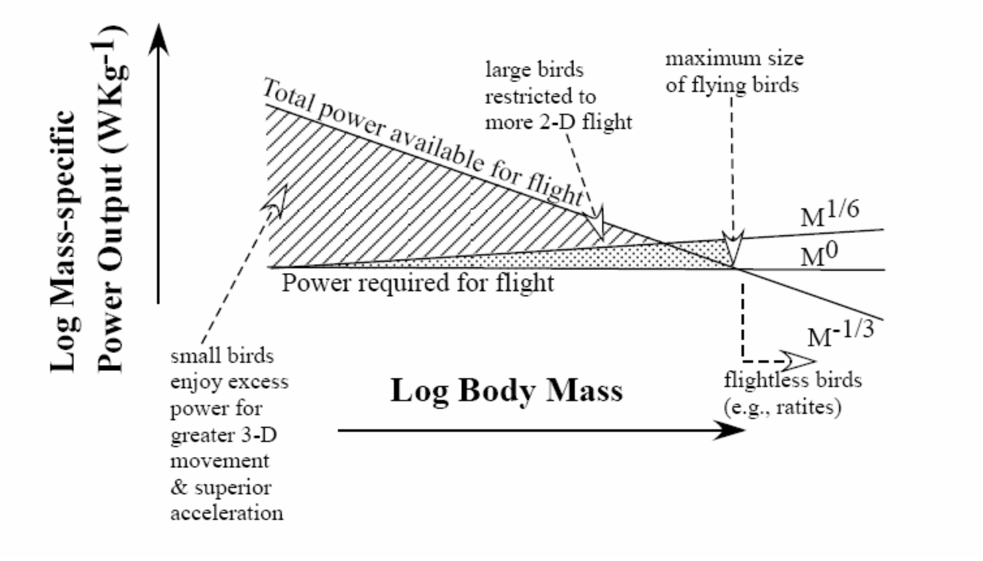

Figure 1. Theoretical relationship of body size, power required, and mechanical power available among birds. Since the cycle duration of oscillating structures varies positively with length (e.g., beating wings or clock pendulums), mechanical power output available appears to scale to approximately -1/3 body mass. Therefore, smaller organisms possess relatively greater power output compared to their larger relatives and thus enjoy superior acceleration, deceleration, and use of 3-D space (from Dial, 2003a).

How an animal exploits its three-dimensional environment is largely based on the relationship between its mass, the properties of its locomotor machinery (e.g. muscle investment and fiber types), and the density of the medium in which they travel (Fig. 1). Despite differences in flight morphology, the largest masses attained by all extant flying birds converge on approximately 12 kg (Mute Swan [*Cygnus olor*], Kori Bustard [*Ardeotis kori*], Wandering Albatross [*Diomedea exulans*], Wild Turkey [*Meleagris gallopavo*], and Andean Condor [*Vultur gryphus*]). This upper mass figure for flying birds should not be considered coincidental (Pennycuick 1969, 1985). Mechanical power required is influenced by mechanical factors (fluid viscosity, body mass, wing shape, etc) and is predicted to scale nearly independent of body mass (M^0) (or slightly positive $M^{1/6}$), but available power is influenced by muscle factors (cross-sectional area, contraction frequency, strain rates, etc.) and scales negatively to the 1/3 body mass ($M^{-1/3}$) (Marden 1994, Ellington 1991) (Fig. 1). There is a similar relationship for piston-driven, propeller aircraft (ranging in size of a scale-model aircraft, to a Cessna 210 and up to a DC-3) with respect to RPM, power, displacement and engine mass (McMahon and Bonner, 1983). For birds, the point at which the power slopes intersect appears to match the region of the upper-mass limit (12-14 kg) (Fig 1).

Most people (including the majority of biologists) do not appreciate that available locomotor power (supplied by skeletal muscle contraction) is responsible for much of what we consider to be the “behavior” of an animal. For example, in large birds there is limited power-available in excess of power required for basic level flapping flight, which likely limits their flight performance. At the other end of the spectrum, smaller animals as a rule enjoy excess power output (beyond that required for level flight), which translates into superior flight performance. Therefore, most small species inhabit more three-dimensional space and enjoy greater accelerative performance than their larger relatives. Ironically, this makes hummingbirds, normally considered delicate and curious, powerful and bold fliers. On the other hand, large eagles, normally thought of as fearless killers, are relatively slow and shy. I argue that variability in power-to-mass ratio (i.e. high wing-beat frequency and muscle force generation) among animals in general is a primary determinant of historic and current biodiversity (Dial, 2003a), because species with superior locomotor performance in time and space are able to unlock numerous ecological and evolutionary opportunities and survive to see tomorrow.

Just as smaller aircraft with high power-to-mass ratios (e.g., F-16, F-18, F-22) are capable of spectacular aerial performance (maneuverability, horizontal and vertical acceleration) compared with larger transport aircraft (e.g., C-5, C-141, KC-10), so do smaller birds enjoy superior flight performance compared to their larger relatives. This has had enormous impact on the predator-prey arms-race that has driven biological diversity over the millennia. As we come to quantify the mechanical power output of diverse species of birds and compare such numbers with their flight performance we will come to understand biological diversity and community structure from a new perspective. Why some birds inhabit cluttered forested areas while others specialize on open grasslands will undoubtedly be tied to an animal’s ability to escape predation or pursue prey. This has enormous ramifications in understanding conservation and biological diversity.

Morphing

The degree to which birds are capable of dynamically morphing during flight is remarkable. During takeoff, flying level over a range of speeds, or maneuvering through dense vegetation birds are capable of dramatically changing shape and area of their flight surfaces. They assume a fusiform, or bullet-shaped, posture one moment and then transform into a broad-surfaced glider milliseconds later. This morphing may enable birds to minimize their metabolic costs as they transition through different speeds and during diverse flight modes. However, considerably more research in this area is required if we are to provide a suitable explanation to the consequences of changing shape. Unlike fixed-winged aircraft, birds are inherently unstable and do not automatically assume a fixed posture in flight. This is most obvious when a hunter shoots a bird from the sky and the wounded animal instantly tumbles uncontrollably back to earth. Healthy, flapping birds possess an extraordinarily complex central computer (their central nervous system) that controls the position of all body parts, especially their rapidly moving flight surfaces (wings and tail). At the same time they are capable of stabilizing their head, and thus eyes, in all modes of flight (takeoff, landing, maneuvering, etc.) (Warrick et al., 2002)

Classic aerodynamic theory based on fixed-winged aircraft predicts that mechanical power should vary according to a U-shaped curve as a function of forward velocity. As a result of morphing, the relationship between mechanical power output and forward velocity in bird flight has been and continues to be a controversial subject bearing upon the comparative physiology and ecology of locomotion. Earlier work on the black-billed magpie (*Pica pica*) suggests that the mechanical power curve is relatively flat over a considerable range of intermediate velocities (Dial et al., 1997). The explanation of a flat curve comes from the fact that birds escape being a fixed-shaped and modify their wing presentation to minimize costs while maximizing performance.

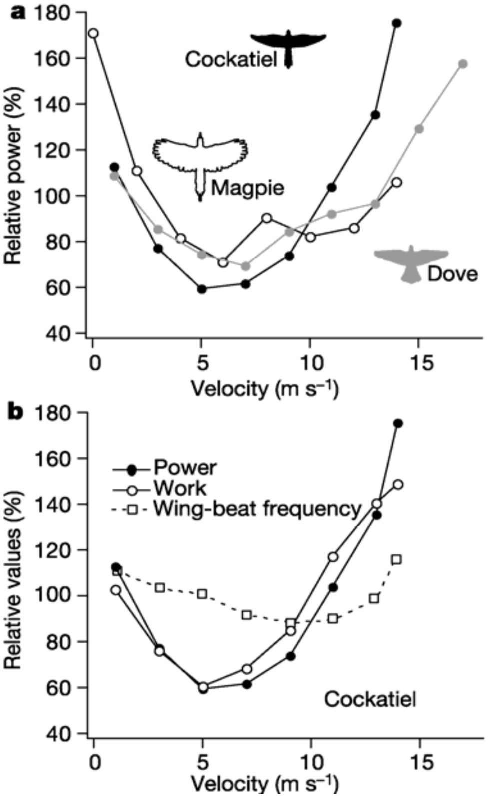

Figure 2. a. Relative pectoralis power of flight velocity for 3 species of birds. b. Mean relative pectoralis power, work and WBF in cockatiels. (from Tobalske et al., 2003)

In a recent study conducted at Harvard University, we (Tobalske, et al., 2003) integrated biomechanical recordings obtained from within the flying animal (i.e., *in vivo*) with quasi-steady aerodynamic models (Rayner 1979, Norberg 1990, Askew et al. 2001). Pectoralis (primary flight muscle) force was integrated over length change to determine *in vivo* levels of mechanical work during flight at different speeds. Pectoralis power output varied significantly with flight speed in both species (repeated-measures analysis of variance, $P \leq 0.002$; Figs. 2a, b). Our results suggest that the shape and magnitude of the power curve are different among species. The power curve for the cockatiel was acutely concave, while the curve for the dove was intermediate in shape, and exhibited higher mass-specific power output at most speeds. These findings complement data previously reported for magpies that exhibited a flat power curve. Our hypothesis poses that differences in morphology, wing kinematics, overall style of flight, and potential morphing ability have major effects upon the magnitude and shape of a species' power curve. Perhaps with the development of computer-aided control devices, future aircraft may be designed with similar dynamic morphing capabilities in order to more efficiently and effectively perform diverse flight tasks.

Recent work completed by my PhD student, Matt Bundle, will provide the best data to date that bridge our understanding of the changes in metabolic cost over a range of speeds with corresponding kinematic morphing (Bundle, PhD thesis in prep). In addition, Bundle will compare these data to simultaneously acquired mechanical power costs over these same speeds. For the first time someone will address with real (compared to theoretical) data regarding muscle efficiency (mechanical vs. metabolic power) in avian flight.

Wing-Assisted Incline Running (WAIR):

Bird wings can act like spoilers on a race car:

Birds exploit three-dimensional environments whether they are cruising within aerial, aquatic or upon terrestrial media. Most studies of avian locomotion have appropriately focused on horizontal movement, for example, flapping or gliding flight within a wind tunnel (e.g., Tucker, 1968; Nachtigall et al., 1986; Tobalske and Dial, 1997; Tobalske et al., 2003; Rosen and Hedenstrom, 2001; Park et al., 2001; Pennycuick et al., 2000; Ward et al., 2001) and walking or running upon a treadmill (Heglund et al. 1982; Taylor et al., 1982; Kram and Taylor, 1991; Gatesy and Biewener, 1991) or over ground (Roberts and Scales, 2002). Recent investigations into the growth of baby birds and their development into adult fliers led us to discover a new type of locomotion called "wing assisted incline running" (WAIR) (Dial, 2003b, Bundle and Dial, 2003). During WAIR, birds simultaneously employ their legs and wings in order to flap-run up obstacles (e.g., rocks, trees, cliffs). Their flapping wings function as spoilers on a race car, to enhance hindlimb traction. This permits birds to stick to the ground as they

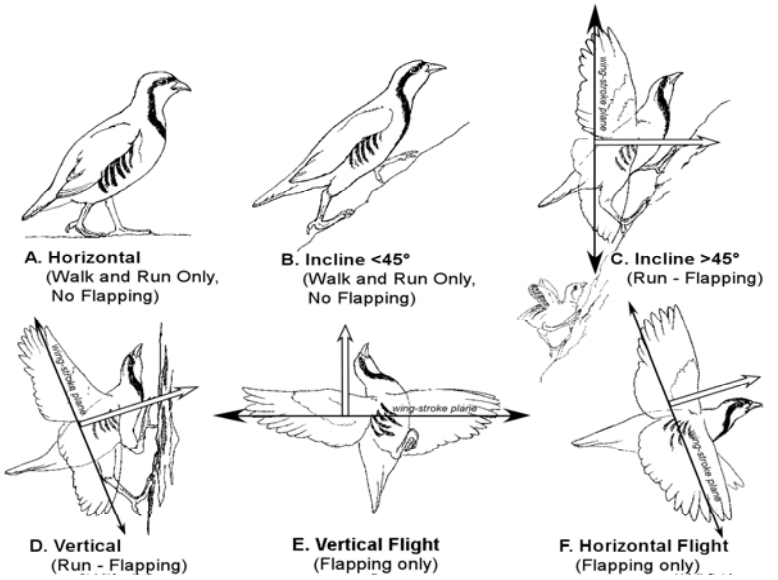

Figure 3. Various postures of ground birds during running, flap-running (WAIR) and flight (from Dial, 2003b).

employ WAIR up steep, inclined substrates; permitting even baby birds with wings unfit for aerial locomotion to achieve elevated refuges.

This may not sound very impressive until the reader is informed that WAIR permits a bipedal animal (like a chicken) to run vertically up an obstacle, such as a tree trunk or the face of a cliff. Even more significant, the flapping wings do not need to be fully-developed flight-capable wings since developing chicks with "half a wing" use their flapping forearms to assist their running legs as they reach a safe refuge. WAIR was previously unrecognized because it is performed during brief, explosive bouts and requires high-speed movie film (>100 Hz) to visualize the simultaneous orchestration of their legs and wings. The discovery of WAIR is opening new avenues of research, particularly exploration into the ontogeny of locomotion and the evolution of bird flight.

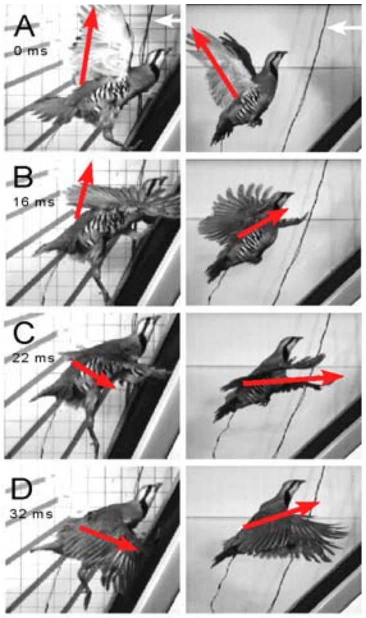

Figure 4. Birds are capable of changing their wing-stroke plane angle in order to direct aerodynamic forces (arrows in C). Left panel (A-D): Chukar flap-running on a tilted treadmill where wing-stroke orientation is from head to tail; acting to push the animal against the substrate in order to increase hindlimb traction. Right panel (A-D): Bird in aerial flight where wing- stroke is oriented from belly to back) creating aerodynamic forces that move the animal along its flight path. Red arrows represent the magnitude and direction of instantaneous, whole-body accelerations obtained from accelerometers attached to the animal's back (from Bundle & Dial, 2003).

We now understand that: (1) flapping wings can be used in previously unappreciated ways (e.g., creating negative lift), (2) both incipient and fully-developed wings act to enhance the hindlimb's ability to generate propulsive forces, and (3) WAIR illustrates how living animals undergoing growth and development might shed light on the fossil record of those dinosaurs ancestral to living birds. Finally, WAIR may provide a new model for aeronautical and robotic engineers involved in designing miniature air vehicles (MAVs) or other robots. Since only a fraction of the energy and wing surface required of flight are needed to perform WAIR, rapidly beating wings may have applications to future aircraft, MAVs, and robots in ways not currently appreciated.

The Future

Continued technological advances in biomechanical and motion recording equipment (e.g., high-speed light and x-ray digital video, animation software, and miniature bioelectrical devices) is permitting unprecedented visualization and quantification of the internal and external structures of moving animals. Future studies in flight behavior, physiology, and mechanics will provide novel and functional models for aeronautical engineers involved in developing future aircraft (e.g., micro-air vehicles, general and military aircraft). I believe there is a legitimate rationale for aeronautical engineers and biologists to jointly study animal locomotion in efforts to create new aircraft and better understand flight design and strategies of inherently unstable aircraft. For instance, understanding "morphing" and its application to aviation is self-evident—by maximizing utility and minimizing energy consumption future aircraft will offer applications far exceeding those aircraft in use today. Also, maneuvering flight at near zero flight speeds remains an area of considerable interest to those involved in designing combat and low-flying aircraft. Birds are unparalleled in their ability to dramatically and rapidly modify wing surfaces as they deal with complex, cluttered, and densely packed environments. Perhaps by studying the maneuvering strategies of birds we will come to appreciate alternative approaches to designing combat and low-altitude flying aircraft. Finally, since birds use their wings in ways we did not appreciate just several years ago, there may be novel application of airfoils in aircraft that we have not yet considered. I believe collaborative opportunities are numerous and will lead to exciting new technologies.

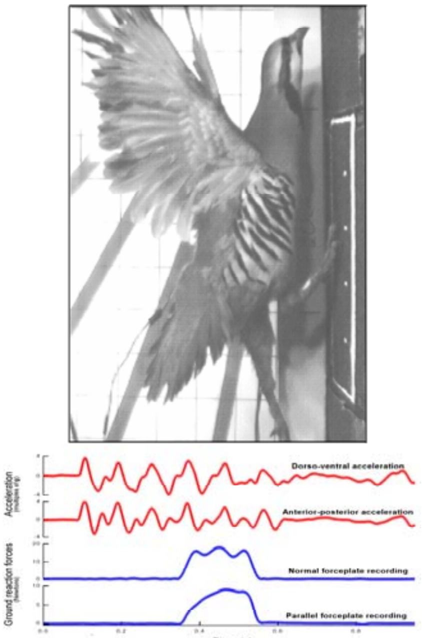

Figure 5. Chukar flap-running upon a vertical runway and harnessed with two accelerometers (recordings in red) and stepping upon a force plate (recordings in blue) (from Bundle and Dial, 2003)

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