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From baby birds to feathered dinosaurs: incipient wings and the evolution of flight

Ashley M. Heers, Kenneth P. Dial, and Bret W. Tobalske

Abstract.—Reconstructing the tree of life requires deciphering major evolutionary transformations and the functional capacities of fossils with “transitional” morphologies. Some of the most iconic, well-studied fossils with transitional features are theropod dinosaurs, whose skeletons and feathered forelimbs record the origin and evolution of bird flight. However, in spite of over a century of discussion, the functions of forelimb feathers during the evolution of flight remain enigmatic. Both aerodynamic and non-aerodynamic roles have been proposed, but few of the form-function relationships assumed by these scenarios have been tested. Here, we use the developing wings of a typical extant ground bird (Chukar Partridge) as possible analogues/homologues of historical wing forms to provide the first empirical evaluation of aerodynamic potential in flapping theropod “protowings.” Immature ground birds with underdeveloped, rudimentary wings generate useful aerodynamic forces for a variety of locomotor tasks. Feather development in these birds resembles feather evolution in theropod dinosaurs, and reveals a predictable relationship between wing morphology and aerodynamic performance that can be used to infer performance in extinct theropods. By spinning an ontogenetic series of spread-wing preparations on a rotating propeller apparatus across a range of flow conditions and measuring aerodynamic force, we explored how changes in wing size, feather structure, and angular velocity might have affected aerodynamic performance in dinosaurs choosing to flap their incipient wings. At slow angular velocities, wings produced aerodynamic forces similar in magnitude to those produced by immature birds during behaviors like wing-assisted incline running. At fast angular velocities, wings produced forces sufficient to support body weight during flight. These findings provide a quantitative, biologically relevant bracket for theropod performance and suggest that protowings could have provided useful aerodynamic function early in maniraptoran history, with improvements in aerodynamic performance attending the evolution of larger wings, more effective feather morphologies, and faster angular velocities.

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Introduction

Reconstructing the function(s) of forelimb feathers in theropod dinosaurs is key to understanding the origin and evolution of birds and bird flight. Since the discovery of *Archaeopteryx* in 1861, a number of feathered theropods have been described, particularly from China (Norell and Xu 2005; Xu 2006). These fossils demonstrate that both feathers and winglike structures were present in non-avian dinosaurs, in arrangements that initially differed from those of extant flight-capable adult birds and that became more similar to the extant condition throughout theropod evolution (Prum and Brush 2002; Norell and Xu 2005; Xu and Guo 2009; Heers and Dial

2012). Available evidence indicates that feathers debuted in basal theropods as filamentous or downlike “protofeathers” (although filamentous homologues of feathers may have arisen earlier) (Norell and Xu 2005; Zheng et al. 2009; Clarke 2013). Downlike feathers were often complemented in maniraptorans by pennaceous (vaned) feathers, which first appeared as “fans” on the distal tail and as small “protowings” with symmetrically vaned feathers on the distal forelimb. Pennaceous feathers became more widely distributed and more asymmetric in many paravians, particularly in avialans, forming larger and more birdlike wings (here, the pennaceous forelimb feathers of extinct theropods are collectively

referred to as “protowings” or “wings,” not to imply an aerodynamic function but merely to indicate degree of resemblance to the wings of extant birds). Interpreting this protowing-to-wing progression is central to reconstructing the evolutionary acquisition of bird flight.

However, the functions of protowings remain enigmatic. Many skeletal features associated with powered flight in extant adult birds (e.g., robust pectoral girdle, channelized wrist) are conspicuously absent in non-avian theropods and basal avialans (Ostrom 1976; Vazquez 1992; Heers and Dial 2012). In addition, the incipient wings of extinct theropods and the wings of extant flight-capable adult birds differ substantially in relative size and feather morphology; flapping velocity also presumably differs because adult birds, but not non-avian theropods and basal avialans, have large ossified keels for the attachment of powerful flight muscles (Prum and Brush 2002; Norell and Xu 2005; Makovicky and Zanno 2011; Wang et al. 2011). It is often assumed that such differences would have precluded early winged theropods from producing the aerodynamic forces necessary for powered (flapping) flight. For example, asymmetric primary feathers with thick rachises and tightly interlocking barbules are thought to help stabilize primary feathers against oncoming airflow (Norberg 1985), prevent excessive deformation (Nudds and Dyke 2010), and reduce feather permeability (Muller and Patone 1998), whereas large wings and a large keel (with large flight muscles) are thought to be necessary for a fast and effective flight stroke. Extinct theropods with incipient wings lacked most or all of these hallmarks of advanced flight capacity: basal maniraptorans (e.g., *Caudipteryx*) and some basal paravians (e.g., *Anchiornis*) had relatively symmetric and potentially more permeable feathers (Prum and Brush 2002; Xu and Guo 2009), and even avialans like *Archaeopteryx* and *Confusiusornis* had relatively thin rachises compared to extant adult birds (Nudds and Dyke 2010). Non-avian theropods and basal avialans are thus often assumed to have used their feathered forelimbs for non-aerodynamic purposes (such as display) and/or non-powered gliding (Heers and Dial 2012: Table 1).

Our understanding of the functional relationships between wing and feather morphology and aerodynamic performance is very limited, however. Several studies, for example, highlight how many of the assumptions underlying traditional views (e.g., Feduccia and Tordoff 1979; Speakman and Thomson 1994, 1995) of feather function are not well understood and are incongruent with a growing body of empirical evidence from live animals. For instance, it has recently been suggested that symmetric feathers would have been useful during drag-based aerial behaviors (Garner et al. 1999) or gliding (Dyke et al. 2013), and that paravians like *Anchiornis* and *Archaeopteryx* had layered wing feathers that might have compensated for the “weak” rachises of individual feathers (Longrich et al. 2012). Recent and ongoing work with extant animals shows that juvenile birds with small muscles and dinosaur-like protowings and skeletons (Heers and Dial 2012: Fig. 2) negotiate complex environments through flapping behaviors such as wing-assisted incline running (WAIR), “steaming” across the surface of water, and slowing aerial descents (Dial 2003; Dial et al. 2006; Jackson et al. 2009; Dial and Jackson 2011; Dial and Carrier 2012). Though not yet capable of level flight, these juveniles generate small amounts of aerodynamic force that improve locomotor performance and increase throughout ontogeny, culminating in full flight capacity (Dial 2003; Tobalske and Dial 2007; Heers et al. 2011). Recent analyses of both extant and extinct theropods thus call into question many assumptions about feather evolution. Though we often assume that protowings were not used by extinct theropods for flapping locomotion, developing birds demonstrate that incipient flight structures *are* aerodynamically functional, for a variety of flapping locomotor behaviors.

Flapping locomotor behaviors like WAIR and steaming are widespread across extant birds (Tinamiformes, Anserogalliformes, Apodiformes, Columbiformes, Procellariiformes, Strigiformes, Passeriformes [<http://www.youtube.com/user/UMflightlab>; Dial 2011]) and appear to be crucially important to juveniles with incipient wings. These behav-

TABLE 1. Body masses, effective forelimb lengths, feather morphologies and chukar models used to evaluate the aerodynamic potential of theropod protowings. *Stage i* is phylogenetically most basal and *stage iii* is most derived, with some overlap between stages (for example, some deinonychosaurs are *stage ii* and some are *stage iii*). Theropod masses and forelimb lengths based on published estimates and measurements (Burgers and Chiappe 1999; Seebacher 2001; Holtz 2007; Therrien and Henderson 2007; Turner et al. 2007; Erickson et al. 2009; Xu et al. 2009) (Supplementary Table 1).

Stage (Fig. 1)	Theropod examples	Body mass (kg)	Effective forelimb length (cm)	Morphology of remige feathers (if present)	Ontogenetic stage used for modeling
<i>Stage i</i>	Basal maniraptorans <i>Caudipteryx</i> , <i>Similicaudipteryx</i> STM22-6 <i>Sinosauropteryx</i> ,* <i>Similicaudipteryx</i> STM4-1	6 0.55–3.5	14–22 10	~Symmetric, relatively short feathers, more pronounced on distal forelimb	8, 10 dph
<i>Stage ii</i>	Basal paravians No examples, yet <i>Anchiornis</i>	0.7–1 0.1–0.3	22 10–14	~Symmetric to weakly asymmetric feathers	10, 20 dph
<i>Stage iii</i>	Basal paravians, basal avialans <i>Microaptor</i> , <i>Jeholornis</i> <i>Archaeopteryx</i> (e.g., Eichstatt, Munich)	0.7–1 0.1–0.3	22 10–14	Asymmetric, relatively long feathers	20, 49 dph

* Here, we follow (Makovicky and Zanno 2011) and consider compsognathids to be basal maniraptorans. Note that *Sinosauropteryx* does not have pennaceous forelimb feathers (at least not preserved), and is listed only to provide an example of body size.

iors involve the cooperative (simultaneous) use of wings and legs, and thereby act as a developmental bridge between leg-based terrestrial (or aquatic) locomotion and wing-based aerial locomotion. For example, immature, flight-incapable ground birds rely on WAIR to ascend steep slopes and reach refugia. Aerodynamic performance improves throughout ontogeny and allows developing birds to flap-run up progressively steeper slopes and eventually fly (Dial 2003; Tobalske and Dial 2007; Heers et al. 2011). By using their forelimbs and hind limbs cooperatively, juvenile ground birds thus supplement their incipient wings with their legs until the wings can fully support body weight during flight. Similarly, flight-incapable ducklings engage their legs and developing wings cooperatively to paddle rapidly across water and escape from terrestrial predators (steaming) (Livezey and Humphrey 1983; Aigeldinger and Fish 1995; Dial and Carrier 2012). Immature, “branching” owls sometimes flap their developing wings to “walk” up tree trunks and reach the safety of elevated branches (Marks et al. 1999; Marks 1982, 1986), and peachicks (*Pavo cristatus*) and young partridges (*Alectoris chukar*) improve jumping performance by flapping their wings and reducing deceleration with small amounts of aerodynamic force (Heers and Dial 2013). Even flight-capable birds, and birds that become highly leg-dependent (e.g., brush turkeys [*Alectura lathami*] or flightless (some steamer ducks [*Tachyeres*]) as adults, engage their wings and legs cooperatively to locomote (Livezey and Humphrey 1986; Dial and Jackson 2011). Wing-leg cooperation is therefore common and widespread among birds, and facilitates the transition from obligately bipedal juvenile to flight-capable adult in species with a diverse array of wing-leg morphologies and life-history strategies. Protowings capable of producing even small amounts of force enhance leg performance (incline-running, jumping, swimming), with incremental improvements in aerodynamic performance allowing juveniles to flap-run up steeper slopes, jump higher, and eventually fly.

Given that extant juvenile birds begin producing aerodynamic forces with very

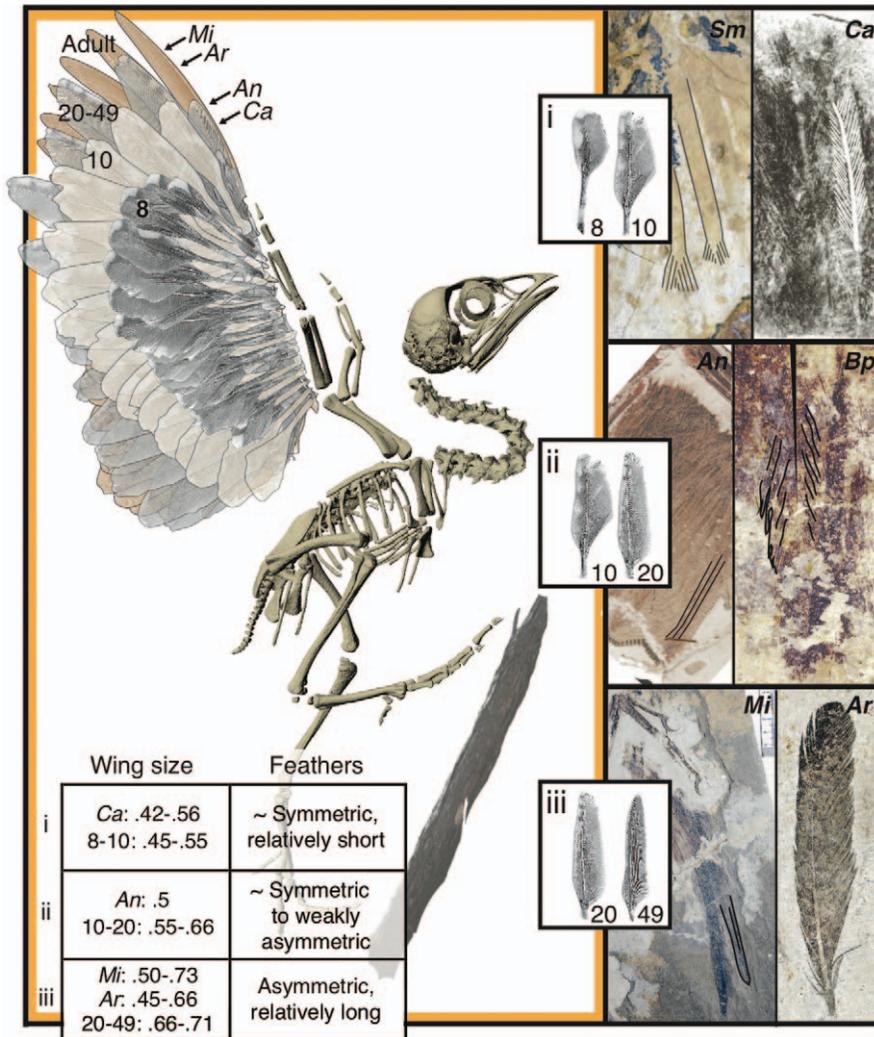


FIGURE 1. Incipient wings in the theropod-avian lineage. Ontogenetic trajectories in wing size and feather structure bear many similarities to evolutionary trajectories observed among theropod dinosaurs. Younger birds and more basal maniraptorans tend to have small wings with relatively symmetric primaries, whereas older birds and more derived maniraptorans tend to have larger wings with more asymmetric primaries. The feathers of younger birds also are more “open” and more transmissive than those of older counterparts (Heers et al. 2011; Dial et al. 2012), as hypothesized for early feathered theropods (Prum and Brush 2002). Left column: skeleton of 8-day-old chukar with wings of 8-day, 10-day, 20-day, and adult chukar attached and scaled to 8-day forelimb length; scaled wing lengths of extinct theropods indicated by arrows (Hu et al. 2009; Wang et al. 2011); “wing size” defined as length of distal primary divided by forelimb length (Wang et al. 2011). Right column, stages of feather ontogeny and evolution (Table 1), with chukar primary feathers shown in boxes and fossilized feathers on right: (stage i) 8–10-day chukar and basal maniraptorans with ~symmetric feathers; (stage ii) 10–20-day chukar and basal paravians with ~symmetric to weakly asymmetric primary feathers; (stage iii) 20–49-day chukar, basal paravians, and basal avialans with asymmetric primary feathers. Stage i is ontogenetically youngest and phylogenetically most basal, and stage iii is ontogenetically oldest and phylogenetically most derived, although overlap between stages occurs. *Sm*, *Similicaudipteryx*; *Ca*, *Caudipteryx*; *An*, *Anchiornis*; *Bp*, *BPM 1 3–13*; *Mi*, *Microaptor*; *Ar*, *Archaeopteryx*. Images of theropods from Zhou and Wang (2000), Norell et al. (2002), Xu et al. (2003, 2010), Hu et al. (2009), and Carney et al. (2012).

rudimentary flight apparatuses, protowings of extinct theropods similarly might have been aerodynamically functional. In many (most?) bird species, ontogenetic improvements in

locomotor capacity are attended by changes in feather and skeletal morphology that resemble feather and skeletal evolution in theropod dinosaurs (Dial et al. 2006; Heers et

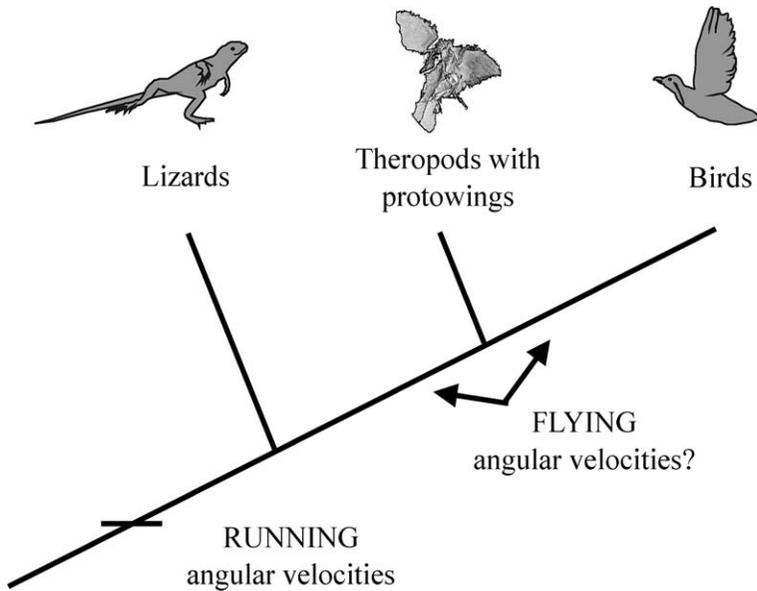


FIGURE 2. Phylogenetic bracket for estimating forelimb angular velocities in extinct theropod dinosaurs. Potential angular flapping velocities achieved by dinosaurs with protowings can be phylogenetically bracketed by assuming that theropod dinosaurs could have swung their forelimbs at least as fast as extant birds and lizards swing their limbs while running (Ω_{\min}), and at most as fast as extant birds flap their wings while flying (Ω_{\max}). Theropod images adapted from Christiansen and Bonde (2004) and Dial et al. (2008).

al. 2011; Heers and Dial 2012). Although the fossil record is complex, and extinct species undoubtedly utilized a variety of locomotor strategies with both gain and loss of aerodynamic function (e.g., reduced plumage in *Eosinopteryx* [Godefroit et al. 2013]), protowing-to-wing developmental transitions mirror the protowing-to-wing evolutionary transition in many ways (Fig. 1). For example, both younger birds (6 days post-hatching, dph) and more basal coelurosaurs (e.g., *Beipiaosaurus*, *Similicaudipteryx* STM4-1) often have distally branched forelimb feathers, whereas older birds and more derived coelurosaurs tend to have more unfurled and relatively symmetrically (8, 10 dph; e.g., *Caudipteryx*) or asymmetrically (49 dph; e.g., *Archaeopteryx*, *Microraptor*) vaned feathers (Ji et al. 1998; Xu et al. 1999; Xu et al. 2003; Dial et al. 2006; Xu et al. 2010). In addition, juvenile birds have more flexible, more transmissive (permeable) feather vanes than older birds (Heers et al. 2011; Dial et al. 2012). Developmental and fossil evidence suggests that the earliest forms of pennaceous feathers in theropod dinosaurs lacked barbicels and possibly barbules (Prum

1999; Prum and Brush 2002). This would indicate that, like immature birds, the pennaceous feathers of more basal coelurosaurs were less coherent and more transmissive than the pennaceous feathers of more derived coelurosaurs. Finally, in immature birds and in extinct theropod dinosaurs, the first pennaceous forelimb feathers to develop or evolve seem to be most pronounced on the distal forelimb (Garner et al. 1999; Dial et al. 2006; Xu and Guo 2009; Xu et al. 2010; Heers and Dial 2012). More proximally positioned pennaceous feathers appear in older birds and more derived dinosaurs. Thus, there are many similarities between ontogenetic and evolutionary trajectories in feather shape, structural integrity, and positioning along the forelimb. Immature birds engage in flapping locomotor behaviors at all of these stages of feather development, suggesting that extinct theropods might have used their feathered forelimbs similarly.

Immature birds are certainly not identical to extinct theropods—no extant bird, for example, has a long tail, and juvenile bird feathers are probably more asymmetric than the

feathers of some extinct maniraptorans. However, immature birds are far more similar to early winged theropods than adult birds are, and they are the only living vertebrates that can be observed transitioning from an obligately bipedal to flight-capable state. Developing birds with dinosaur-like anatomies bridge this transition by using their legs and incipient wings cooperatively (Dial 2003; Dial et al. 2006; Jackson et al. 2009; Dial and Jackson 2011; Dial and Carrier 2012; Heers and Dial 2012), and wing-leg cooperation may have similarly facilitated the evolutionary acquisition of flight. This is not to say that ontogeny strictly recapitulates phylogeny in a linear sense, as once proposed (Haeckel 1866). However, similarities between ontogenetic and evolutionary trajectories are fairly common (Mayr 1963; Gould 1977; Heers and Dial 2012) and even expected, because evolution is a process that modifies ontogeny—either by adding new characters or adjusting existing characters at various developmental stages (Gilbert and Epel 2009). Developing juveniles reveal how transitional, morphing anatomies function, and in this respect, the developmental acquisition of flight capacity in extant birds can help elucidate the evolutionary acquisition of flight capacity among extinct theropods—by demonstrating the ecological utility of dinosaur-like, incipient flight structures.

Here, we use the developing wings of a typical extant ground bird (Chukar Partridge [*Alectoris chukar*]) as possible analogues/homologues of historical wing forms to provide the first empirical evaluation of aerodynamic potential in flapping protowings of extinct theropods. To investigate how evolutionary trends in feather morphology, wing size, and flapping velocity might have influenced lift and drag production in dinosaurs choosing to flap their incipient wings, we spun an ontogenetic series of spread-wing preparations on a rotating propeller apparatus across a range of flow conditions, and measured aerodynamic force production. To the best of our knowledge, the modeling described here represents the first analysis to empirically explore flapping aerodynamics of the protowinging-to-wing transition among extinct theropods. This analysis is the continuation of a

study documenting the ontogeny of aerodynamic force production in extant chukars (Heers et al. 2011): here, we build upon previous work by using a developmental series of chukar protowings to model and explicitly quantify aerodynamic potential of fossil protowings. Although wing morphology is highly diverse among both living adult birds and extinct theropods, extant species with very differently shaped wings experience developmental trajectories in feather structure that are similar to each other and to evolutionary trajectories among theropod dinosaurs (Heers et al. 2011; Dial et al. 2012). Exploring functional morphology in chukar partridges thus provides a useful starting point for elucidating relationships between form, function, and behavior during protowinging-to-wing transitions.

Materials and Methods

To estimate lift and drag production for protowings and wings of extinct theropods, we used a $4 \times 3 \times 2$ factorial design with two replicates per treatment. Aerodynamic forces were measured for four wing morphologies (8, 10, 20, 49 dph) resembling basal to derived maniraptoran wings. We used younger chukar wings to model more basal maniraptorans, and older chukar wings to model more derived maniraptorans (stages i-iii in Fig. 1; Table 1). Wings were removed from deceased animals at the glenoid, dried in mid-downstroke posture, and then spun like a helicopter blade on a propeller force plate apparatus, which imitates the mid-downstroke phase of birds flapping at low advance ratios (high flapping velocity and low translational velocity, as during WAIR or takeoff) (Usherwood 2009). Each wing was spun at a range of Reynolds numbers (Re) (flow conditions, proportional to wing size and velocity), to mimic extinct theropods with three different wing sizes (forelimb lengths of 10, 14, 22 cm) flapping at slow (Ω_{\min}) and fast (Ω_{\max}) angular velocities. The wings used in this study are the same wings described by Heers et al. (2011), removed from deceased animals that were raised at the Field Research Station at Fort Missoula in Missoula, Montana, following protocols approved by the University of

Montana Institutional Animal Care and Use Committee; for full details on animal husbandry, wing preparation, and the construction of the propeller force plate apparatus, see Heers et al. (2011).

Reynolds number (Re) is used to define the flow conditions experienced by an organism or object:

$$Re = \frac{\rho lv}{\mu}, \quad (1)$$

where ρ is air density, l is mean wing chord length (average width of the wing, measured perpendicular to the leading edge), v is wing-tip velocity (tangential velocity of the wing tip, calculated as the product of wing length [m] and angular velocity [rad/s; rate of angular displacement]), and μ is dynamic viscosity (resistance to flow). Wings with identical structural properties flapping at identical Re will experience the same flow conditions at a given angle of attack. Thus, even though extinct theropods were often much larger than juvenile birds, and might have flapped their wings much more slowly (because they might have lacked large flight muscles and/or neural circuitry), coefficients of lift and drag calculated for an extant juvenile protowings spinning at an extinct theropod Re can be used to estimate lift and drag production for the extinct theropod (under the assumption that juvenile protowings are structurally similar to extinct theropod protowings; see *Introduction*). To evaluate an extinct theropod's potential capacity for generating aerodynamic forces, we therefore (1) estimated a range of Re that theropod protowings/wings might have experienced while flapping, (2) used a force plate and propeller apparatus to spin similar-looking chukar protowings/wings at those Re and measure coefficients of lift and drag (C_L , C_D), and (3) used published body mass estimates to estimate lift and drag as a percentage of body weight for extinct theropods with pennaceous forelimb feathers. We did not attempt to model animals with only downlike feathers (e.g., *Sinosauropteryx* [Chen et al. 1998]), immature animals with feathers that might still have been growing (i.e., *Similicaudipteryx*

STM4-1 [Xu et al. 2010]), or animals with secondary reductions in plumage (e.g., *Eosinopteryx* [Godefroit et al. 2013]), because the aim of this analysis was to explore the evolutionary acquisition (not loss) of flight.

Part 1: Estimating Re to Scale for Differences in Wing Size and Flapping Velocity

Because Re is proportional to the product of mean wing chord length and wing tip velocity (eq. 1), we estimated Re for flapping forelimbs of extinct theropods by estimating their mean wing chord lengths (l) and angular velocities (Ω ; proportional to tip velocity).

Mean Wing Chord Length (l).—We used theropod-to-chukar scaling factors to approximate mean wing chord lengths for protowings and wings of extinct theropods. First, we calculated summed “effective” lengths of the humerus, radius (ulna if data on radius unavailable), second metacarpal, and phalanges II-1 through II-2 in mid-downstroke posture for each bird wing (8, 10, 20, 49 dph) and for various basal maniraptorans, basal paravians, and basal avialans (Supplementary Table 1, Supplementary Fig. 1; here, we refer to the three theropod digits as I, II, and III). Effective forelimb lengths in extinct coelurosaurs ranged from 4 to 33 cm, with most lengths falling close to 10, 14, or 22 cm. We thus chose lengths of 10, 14, and 22 cm for analysis, to bracket the range of lengths observed in fossils. Although we cannot know the exact posture in which extinct theropods would have held their forelimbs (and hence the exact effective lengths and orientations), the aim of this project was not to estimate aerodynamic performance of specific fossilized theropods, but rather to determine how evolutionary changes in wing size and feather structure generally might have influenced aerodynamic performance. Wing length and posture clearly affect aerodynamic performance, but by using chukar wings to model a range of limb lengths, feather morphologies, and body masses, and by measuring aerodynamic performance at multiple angles of attack (see Part 2 below), we hoped to account for some of the variation in posture and anatomy and to realistically bracket the aerodynamic

performance that theropods might have achieved at a given phylogenetic stage.

Next, we computed scaling factors as the ratio of theropod-to-chukar effective bone lengths. We chose bone lengths to calculate scaling factors rather than wing or chord lengths because of the difficulty in measuring wing and chord lengths for fossils, whose wings are often folded or positioned at odd angles. Using theropod-to-chukar bone scaling factors and mean chord lengths of the four chukar age classes, we then estimated mean chord lengths (l) for theropod protowings with each type of feather morphology (8, 10, 20, 49 dph) and bone length (10, 14, 22 cm), using the following equation:

$$\frac{\text{Theropod effective bone length}}{\text{Chukar effective bone length}} = \frac{\text{Theropod chord length } (l)}{\text{Chukar chord length}}. \quad (2)$$

Given that wing size and shape are highly variable in both extant and extinct taxa, the analysis presented here best applies to theropods with relatively short, low-aspect-ratio wings. However, using chukar wings to model the wings of extinct theropods with similar feather morphologies is a logical starting point, because developing chukar wings are similar in shape and proportion to the incipient wings of many extinct theropods (Supplementary Box 1).

Flapping Velocities.—Potential flapping velocities achieved by extinct theropods with pennaceous forelimb feathers can be phylogenetically bracketed (Witmer 1995) by assuming that theropods could have swung their forelimbs at least as fast as extant birds and lizards swing their limbs while running (Ω_{\min}), and at most as fast as extant birds flap their wings while flying (Ω_{\max}) (Fig. 2).

1. Minimum angular velocities (Ω_{\min}). From previously published data on maximal running speeds in birds and lizards (Supplementary Table 2, Supplementary Fig. 2), we estimated the relationship between limb length and running angular velocity for extant lizards and birds as

$$\log_{10}(\text{running angular velocity, } \Omega_{\min}) = -0.60 \left(\log_{10}(\text{effective leg length}) \right) + 0.60, \quad (3)$$

where

$$\text{Running angular velocity } (\Omega_{\min}, \text{rad/s}) = \frac{\text{Leg tip velocity}}{\text{Effective leg length}}, \quad (4)$$

and

$$\text{Leg tip velocity (m/s)} = \frac{\text{Stride length}}{\text{Swing duration}} - \text{running velocity}. \quad (5)$$

Minimum angular velocities for theropod protowings were estimated using equation (3) by substituting theropod wing length for bird/lizard effective leg length. These values were then used to calculate minimum protowing tip velocities (v_{\min}):

$$v_{\min} = \text{Minimum wing tip velocity (m/s)} = (\text{wing length})(\Omega_{\min}), \quad (6)$$

where theropod wing lengths were estimated for theropod forelimbs with each type of feather morphology (8, 10, 20, 49 dph) and each bone length (10, 14, 22 cm), using the equation:

$$\frac{\text{Theropod effective bone length}}{\text{Chukar effective bone length}} = \frac{\text{Theropod wing length}}{\text{Chukar wing length}}. \quad (7)$$

2. Maximum angular velocities (Ω_{\max}). From previously published data on flying angular velocities in birds during takeoff (Supplementary Table 3, Supplementary Fig. 3), the relationship between wing length and wing angular velocity was estimated as

$$\log_{10}(\text{flying angular velocity, } \Omega_{\max}) = -0.54 \left(\log_{10}(\text{wing length}) \right) + 1.45. \quad (8)$$

Maximum protowing angular velocities were estimated using equation (8) by substituting theropod wing length (eq. 7) for bird wing length. These values were then used to

calculate maximum protowing tip velocities (v_{\max}):

$$v_{\max} = \text{Maximum wing tip velocity(m/s)} \\ = (\text{wing length})(\Omega_{\max}). \quad (9)$$

Part 2: Using a Force Plate and Propeller Apparatus to Measure Lift and Drag

Using the mean chord lengths and minimum and maximum velocities described above, we computed Re representing 10, 14, and 22 cm effective bone lengths swinging at minimum (Ω_{\min}) and maximum (Ω_{\max}) angular velocities (Supplementary Table 4), for a total of 24 feather morphology–bone length–angular velocity combinations. To measure aerodynamic force production at minimum angular velocities (Ω_{\min}), we followed the methods of Usherwood and Ellington (Usherwood and Ellington 2002) and spun each wing on a propeller force plate apparatus, at angles of attack of 15°, 30°, 45°, and 60° (Supplementary Movie 1; for full details on this procedure refer to Heers et al. [2011], and for a sketch of the experimental setup, see Crandell and Tobalske [2011]). Vertical and horizontal aerodynamic forces generated by the spinning wings were converted into coefficients of lift (C_L) and drag (C_D):

$$C_V = \frac{2F_V}{\rho\Omega^2S_2}, \quad (10)$$

$$C_H = \frac{2Q}{\rho\Omega^2S_3}, \quad (11)$$

$$C_L = (C_V\cos\varepsilon + C_H\sin\varepsilon)\left(\frac{1}{\cos\varepsilon}\right)^2, \quad (12)$$

and

$$C_D = (C_H\cos\varepsilon - C_V\sin\varepsilon)\left(\frac{1}{\cos\varepsilon}\right)^2, \quad (13)$$

where C_V is the coefficient of vertical force, C_H is the coefficient of horizontal force, F_V is vertical force measured by the force plate (N), Q is torque (Nm) about the z-axis, ρ is air density at Missoula, Montana (1.07 kg/m^3), Ω is angular velocity of the spinning chukar wing (rad/s), S_2 is the second moment of area

of the chukar wing (m^4), S_3 is the third moment of area of the chukar wing (m^5), and ε is the downwash angle; induced downwash velocity was modeled assuming a Rankine-Froude momentum jet and a triangular distribution for local induced downwash along the wing (see Usherwood and Ellington 2002). Lift and drag coefficients were then used to estimate lift and drag production by theropod protowings (see Part 3 below). For maximum angular velocities (Ω_{\max}), coefficients of lift and drag were recorded at Re based on in vivo kinematic measurements on chukars (Heers et al. 2011), under the assumption that these coefficients would be representative of wings moving at flying angular velocities regardless of scaling.

Part 3: Estimating Lift and Drag as a Percentage of Body Weight for Extinct Theropods with Pennaceous Forelimb Feathers

We used coefficients of lift and drag to estimate lift and drag production by theropod protowings using a blade element model:

$$\text{Resultant force(N)} \\ = 0.5\rho C_R \int_{r=0}^{r=R} \left((\Omega r)^2 + V_T^2 \right) c dr, \quad (14)$$

where ρ is air density at Missoula (1.07 kg/m^3), C_R is the resultant coefficient ($C_R = (C_L^2 + C_D^2)^{0.5}$) at a 45° angle of attack (in vivo angle of attack at mid-downstroke in chukars [Jackson et al. 2009; Heers et al. 2011]), R is theropod wing length (m), Ω is angular velocity (rad/s), V_T is translational velocity (m/s), and c is mean chord length (m). Translational velocities were conservatively set at 1.5 m/s for all theropods. During WAIR there is no clear relationship between body size and velocity, but both juvenile and adult chukars (Jackson et al. 2009) and peafowl (Heers and Dial 2013)—weighing between 100 g and 5 kg and spanning the range of estimated weights for theropods (Table 1)—can flap-run at least at 1.5 m/s. Birds in this size range move more rapidly when running on horizontal surfaces, jumping into the air, or using their wings to take off (Supplementary Fig. 4), and so 1.5 m/s is a conservative

translational velocity irrespective of behavior. Angular velocities (Ω) and translational velocities (V_T) were also conservatively modeled as perpendicular to one another, and summed to obtain the net wing velocity ($V_{\text{net}} = [(\Omega r)^2 + V_T^2]^{0.5}$). Resultant forces were multiplied by two (to account for both wings), then expressed as a percentage of body weight by dividing by published estimates of theropod body weights (Table 1).

Because propeller models mimic only forces produced at mid-downstroke, each force estimate for extinct theropods was standardized by the average resultant force (as a percentage of body weight) of two adult chukar wings spinning at flying angular velocities (Ω_{max}). Thus a force of 100% body weight suggests that a theropod could have fully supported body weight during flight. A force of ~6–8% body weight suggests that a theropod could have engaged in WAIR, because the resultant force produced by 6–8-day-old chukars during WAIR is ~6–8% of the force produced by adult chukars during flight (based on *in vivo* measurements [Tobalske and Dial 2007] and on the force plate measurements described here).

Following standardization, all force estimates for maximum (but not minimum) angular velocities were reduced by 20% to account for the additional flight musculature that was not considered in calculations of body mass, and that would presumably be necessary to oscillate wings at high speed (our goal was to estimate the *maximal* flight performance possible—as if extinct theropods were capable of oscillating their forelimbs like extant birds—which presumably would require extant-like values of muscle mass). Forelimb muscle mass varies widely across extant species (Hartman 1961), but is not necessarily dictated by size. Chukars (~500 g) and peafowl (~4–5 kg, approaching the upper limit of sizes considered here), for example, are both capable of rapid burst takeoffs and both have pectoral muscle (pectoralis + supracoracoideus) masses that are 20–21% of their body mass (Heers and Dial 2013). Galliforms are known for their rapid wingbeat frequencies and powerful burst flight, so a theropod with pectoral muscles of

20% body mass should have been capable of high wingbeat frequencies. Finally, the smallest body sizes (100 g with a 14-cm forelimb, 700 g with a 22-cm forelimb) were eliminated from calculations at maximum angular velocities (Ω_{max}) because such small animals probably could not have oscillated 14- or 22-cm forelimbs at such high speeds, given that a 49-dph chukar with an 11.2-cm forelimb weighs ~250 g. For a sample calculation, see Supplementary Box 2.

Results

Aerodynamic performance improves during protowing-to-wing transitions, by increasing aerodynamic force production and lift-to-drag ratios ($r_s = 1$ for peak C_L and peak C_L/C_D vs. age [Heers et al. 2011]) (Fig. 3A,B). At all combinations of bone size and angular velocity (all *Re* categories), older wings with stiffer, more structurally coherent (less transmissive), and more asymmetric primary feathers produce larger aerodynamic force coefficients than younger protowings with more flexible, more transmissive, and weakly asymmetric or symmetric feathers (i.e., older wings [representing the wings of more derived coelurosaurs] have greater aerodynamic performance than younger wings [representing the wings of more basal coelurosaurs]; *stage iii* > *stage ii* > *stage i*) (Supplementary Figs. 5, 6). At all combinations of bone size and feather morphology, fast angular velocities (Ω_{max}) yield higher aerodynamic forces than slow angular velocities (Ω_{min}) (because force \propto velocity²). However, when aerodynamic forces (lift, drag) are normalized for wing size and velocity (and expressed as C_L , C_D), there appears to be a slight tendency for younger (i.e., more basal) protowings to perform best at slower tip velocities, and older (i.e., more derived) wings to perform best at faster tip velocities (tip velocity = product of angular velocity and wing length; $r_s = 1$ for age vs. tip velocity at which peak C_R and peak C_L/C_D occur) (Fig. 3C,D).

Chukar wing models and published estimates of forelimb lengths and body masses for theropod dinosaurs (Table 1, Supplementary Table 1) suggest that weight-specific aerodynamic force production would have increased

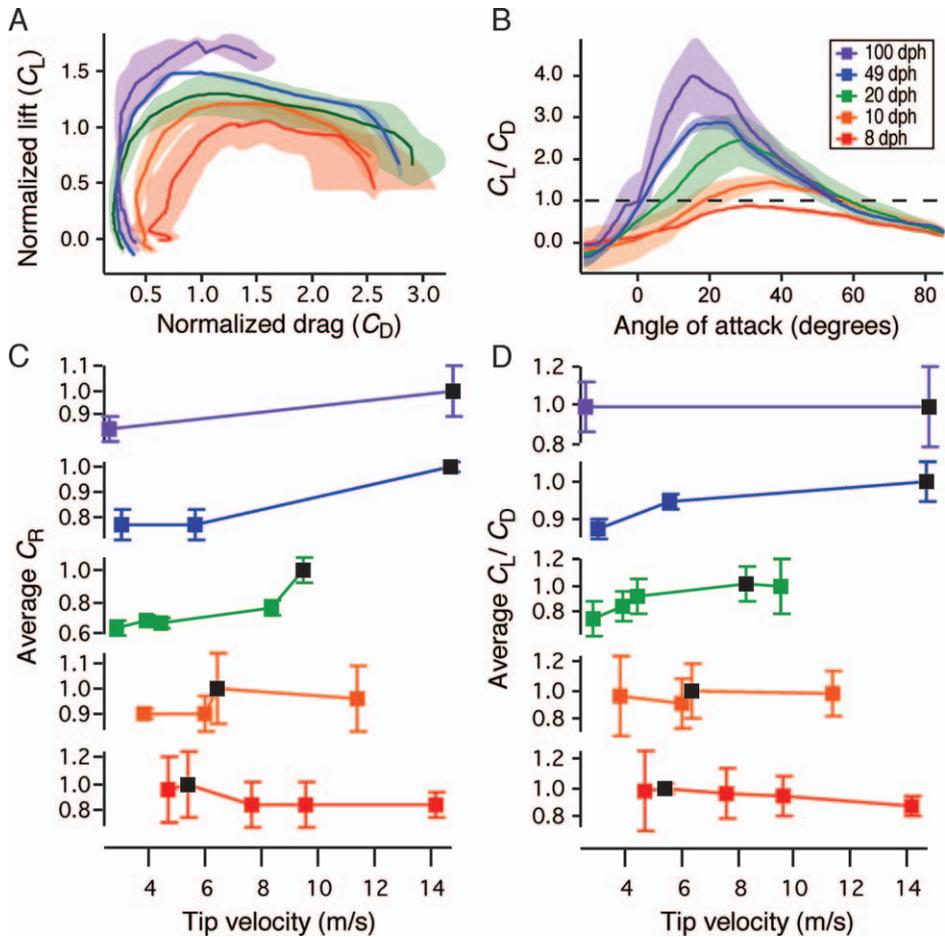


FIGURE 3. Protowing-to-wing transitions in aerodynamic performance. Protowing-to-wing transitions in extant chukar improve aerodynamic performance by increasing aerodynamic force production (A) and lift-to-drag ratios (B), with the protowings of younger birds tending to perform best at slow tip velocities and the wings of older birds performing best at fast tip velocities (C, D). A and B are based on in vivo angular velocities; similar trends hold across a range of angular and tip velocities (Supplementary Figs. 5, 6). Coefficient of lift (C_L), coefficient of drag (C_D), and resultant coefficient (C_R [vector sum of C_L and C_D]) all normalized by wing size and velocity. C_R (panel C) and C_L/C_D (panel D) are averaged over angles of attack of 15–60° and standardized by values at in vivo velocities, with peak values indicated by black squares; standard errors shown as clouds around lines or bars above and below points. If viewed in black-and-white, older wings are always located above younger wings. A and B modified from Heers et al. (2011).

during maniraptoran evolution (Fig. 4). At slow angular velocities (Ω_{\min}), aerodynamic force estimates range from <1% body weight in *stage i* basal maniraptorans with small wings and relatively symmetric feathers, to ~2–12% body weight in *stage ii* basal paravians with larger wings and symmetric or weakly asymmetric feathers, to ~3–15% body weight in *stage iii* basal paravians and basal avialans with asymmetric feathers. At fast angular velocities (Ω_{\max}), aerodynamic forces range from ~2–13% body weight in *stage i*

basal maniraptorans, to ~34–100% body weight in *stage ii* basal paravians, to ~48–100% body weight in *stage iii* basal paravians and basal avialans. For example, our calculations suggest that a theropod like the Eichstatt *Archaeopteryx* (*stage iii* feather morphology, ~10 cm effective forelimb length [calculated from fossilized material; Supplementary Table 1], ~19–20 cm wing length [wings of chukars 20–49 dph scaled to 10 cm limb length; Supplementary Table 4]) could have flapped its protowings at least at ~10–11 rad/s (Ω_{\min} ;

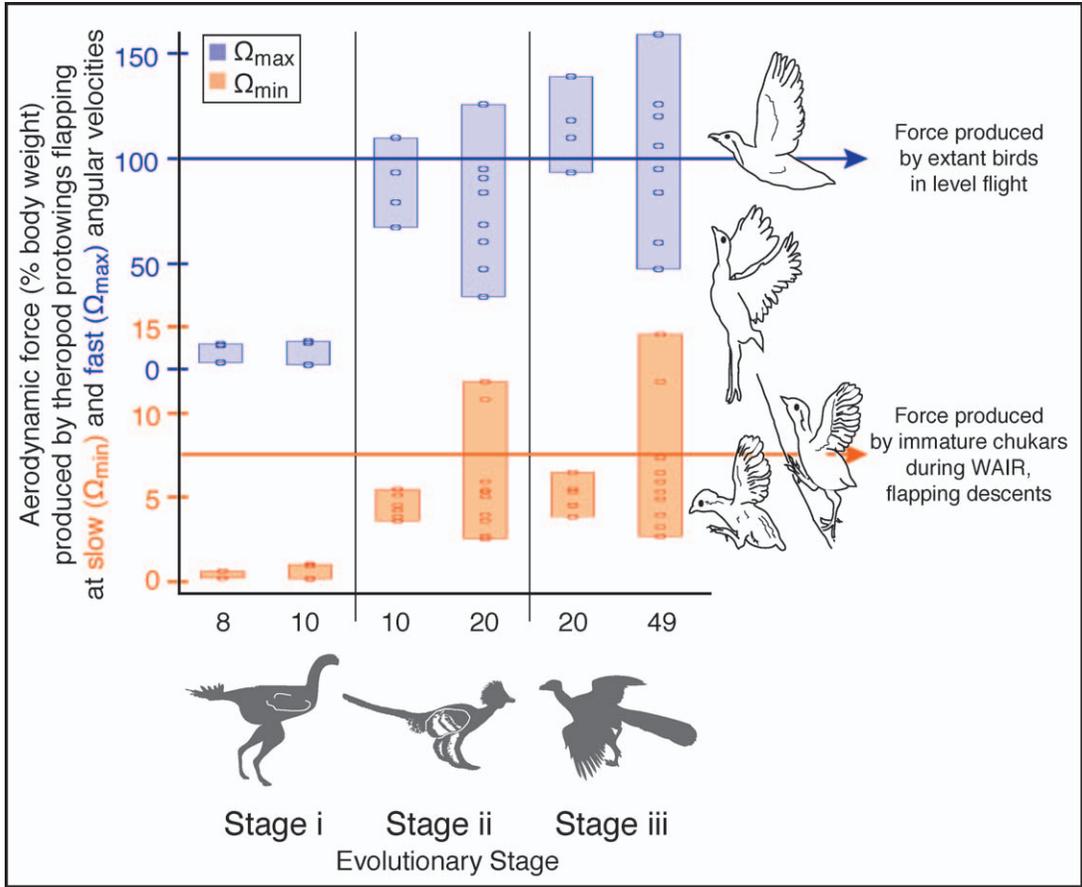


FIGURE 4. Potential aerodynamic utility of incipient wings during theropod evolution. Aerodynamic force, as a percentage of body weight, increases with increasing angular velocity (blue vs. orange), and with changes in feather structure and increases in relative wing size (evolutionary stages *i-iii*, as illustrated in Fig. 1 and defined in Table 1). At slow angular velocities (Ω_{\min} ; orange, lower bars) and small body sizes, aerodynamic forces produced by basal paravians and basal avialans (stages *ii, iii*) are similar in magnitude to those produced by immature chukars during WAIR and flapping descents (orange line). At fast angular velocities (Ω_{\max} ; blue, upper bars), aerodynamic forces produced by basal maniraptorans (stage *i*) are sufficient for behaviors like WAIR, whereas aerodynamic forces produced by basal paravians and basal avialans (stages *ii, iii*) are sufficient to support body weight (blue line). Ovals within bars represent estimates of aerodynamic forces produced by fossilized theropods flapping their protowings at slow or fast angular velocities; each oval represents a hypothetical combination of feather morphology (8, 10, 20, or 49 days), limb length (10, 14, or 22 cm; calculated from fossilized material), and body mass (based on published estimates), with bars bracketing the range of values produced by theropods at a given phylogenetic stage (see Table 1 for list of combinations). Note that ovals best represent theropods with effective forelimb lengths close to 10, 14, or 22 cm, but that any winged theropod with an effective forelimb length between 10 and 22 cm (and no secondary reductions in plumage) should fall within the bars. Lines with arrows indicate aerodynamic force produced by 6–8-day old chukars during WAIR (orange) (Tobalske and Dial 2007; Heers et al. 2011) or by older chukars during flight (blue). Numbers above fossils (8, 10, 20, 49) refer to age of chukar wings used to model theropod wings. Images of chukars based on high-speed video or adapted after Dial et al. (2008). Images of fossils, left to right: *Caudipteryx*, *Anchiornis*, and *Archaeopteryx*, modified after AMNH diorama (artist Denis Finnin), Li et al. (2010), and Chiappe (2007), respectively.

eq. 3), and at most at $\sim 67\text{--}70$ rad/s (Ω_{\max} ; eq. 8), resulting in a minimum Re of $\sim 8000\text{--}9000$ and a maximum Re of $\sim 51,000\text{--}57,000$. Spinning 20- and 49-dph chukar wings with *Archaeopteryx*-like stage *iii* feather morphologies at the minimum Re and a 45° angle of attack yields a C_L of 0.87–1.02 (eq. 12), a C_D of

0.49–0.75 (eq. 13), and a resultant force of 0.053–0.065 N (two wings, eq. 14). Assuming a body mass of 100 g (Erickson et al. 2009)—which is comparable to that of juvenile peafowl with similarly sized wings (Heers and Dial 2013)—gives a resultant force of $\sim 5\text{--}7\%$ body weight (Supplementary Tables 4 and

5, Supplementary Box 2). This range is very similar in magnitude to the aerodynamic forces produced by immature chukars during WAIR, controlled flapping descents, and jump-flapping up to elevated perches ($\sim 6\text{--}8\%$ body weight in birds 6–8 dph; orange line in Fig. 4) (Tobalske and Dial 2007; Jackson et al. 2009; Heers et al. 2011), suggesting that *Archaeopteryx*-like theropods would have been capable of comparable behaviors. By similar reasoning, at maximum angular velocities ($\sim 67\text{--}70$ rad/s, Ω_{\max}), *Archaeopteryx*-like theropods would have produced forces sufficient to support their body weight during flight ($\geq 100\%$ body weight).

Discussion

Our findings, in conjunction with work on developing birds, suggest that flapping protowings could have provided useful aerodynamic function early in the history of Maniraptora, with improvements in aerodynamic performance attending the evolution of larger wings, more effective feather morphologies, and faster flapping velocities. Though feathered forelimbs serve many functions in extant birds, and were probably used for a variety of purposes before being exapted for powered flight (e.g., insulation [Norell and Xu 2005], display [Xu and Guo 2009; Dimond et al. 2011], and/or balance [Fowler et al. 2011]), our results indicate that forelimb feathers also could have functioned aerodynamically for flapping locomotor behaviors like WAIR. Our experiments indicate that at slow angular velocities (Ω_{\min}), maniraptorans with *stage ii* and *stage iii* feather morphologies could have produced aerodynamic forces sufficient for flap-running up slopes, jumping and flapping up to elevated surfaces, and slowing aerial descents (Fig. 4, orange line). At fast angular velocities (Ω_{\max}), all maniraptorans (*stages i–iii*) would have been capable of WAIR, flap-jumps and controlled aerial descents, and maniraptorans with *stage ii* and *stage iii* feather morphologies would have been able to support their body weight during flight as well (Fig. 4, blue line). Our ontogenetic models using *Re* to account for variation in size and to bracket potential flapping velocities (Fig. 2) thus indicate that protowings could have

functioned aerodynamically relatively early in maniraptoran history, with evolutionary changes in feather structure, relative wing size, and flapping velocity dramatically improving aerodynamic performance.

Feather Structure

Feather morphology changes considerably during bird ontogeny and theropod evolution. In chukars, flight feathers begin to emerge at ~ 6 days post-hatching, in the form of protowings that enable chicks to produce aerodynamic forces and flap-run up slopes or slow aerial descents. Protowings with flexible, transmissive, and relatively symmetric feathers therefore provide useful aerodynamic function early in chukar ontogeny. In species examined thus far, developmental changes in feather structure that are similar to changes occurring during theropod evolution are correlated with increases in aerodynamic force production and higher lift-to-drag ratios (Dial et al. 2006; Tobalske and Dial 2007; Heers et al. 2011; Dial et al. 2012; Heers and Dial 2012) (Fig. 3A,B), most likely due to increases in flexural stiffness and feather asymmetry, and/or decreases in wing and feather transmissivity. Asymmetric primary feathers with thick rachises and tightly interlocking barbules may improve performance by stabilizing primary feathers against oncoming airflow (Norberg 1985), preventing excessive deformation (Nudds and Dyke 2010), reducing feather permeability (Muller and Patone 1998; Heers et al. 2011; Dial et al. 2012), and/or influencing three-dimensional wing morphing. Improved performance cannot be explained by ontogenetic changes in static wing shape (aspect ratio, camber), wing size, or flapping velocity (Heers et al. 2011; Dial et al. 2012). For example, by 49 dph, chukars have grown all of their flight feathers (primaries, secondaries, coverts) and differ from adults only with respect to feather structure and the relative lengths of the two distal-most primaries (Supplementary Fig. 7). Given that adult wings produce more aerodynamic force and more lift per unit drag than 49-dph wings (Fig. 3), even when standardized for wing size and velocity, feather structure must play an important role in aerodynamic force produc-

tion—though even symmetric, flexible, and transmissive pennaceous feathers are aerodynamically useful.

In short, protowings are immediately functional in extant birds, and potentially in extinct theropods. Developmental changes in feather morphology and attending improvements in aerodynamic performance suggest that comparable evolutionary changes in feather structure might similarly have improved aerodynamic performance among extinct theropods. According to our experiments, at slow angular velocities (Ω_{\min}), maniraptorans with *stage ii* and *stage iii* feather morphologies could have produced aerodynamic forces sufficient for WAIR and similar behaviors (Fig. 4, orange line); at fast angular velocities (Ω_{\max}), all maniraptorans (*stages i–iii*) would have been capable of WAIR-like behaviors, and maniraptorans with *stage ii* and *stage iii* feather morphologies would have been able to engage in flight as well (Fig. 4, blue line).

Flapping Velocity

Irrespective of feather morphology, all wings produce more aerodynamic force at higher angular velocities (force \propto velocity²). However, when aerodynamic force is standardized for wing size and flapping velocity (C_L , C_D), wings seem to perform better at in vivo velocities, with the wings of older birds tending to perform best at higher velocities and the wings of younger birds tending to perform best at lower velocities (Fig. 3C,D). This pattern may suggest that the incipient wings of younger birds and more basal maniraptorans are(were) tuned to flapping at lower tip velocities, and that the wings of older birds and more derived maniraptorans are(were) tuned to flapping at higher tip velocities. Such aeroelastic “tuning” is consistent with ontogenetic and evolutionary increases in wing length and in keel size (Wang et al. 2011; Heers and Dial 2012)—for a given angular velocity, increasing wing length increases wing tip velocity (as observed in chukars that do not change Ω much during development [Jackson et al. 2009; Heers et al. 2011]), whereas increasing keel size is presumably associated with increases in pectoral

muscle mass and the ability to achieve higher flapping velocities. Feather morphology and wing kinematics thus may be developmentally and evolutionarily tuned or coupled (see Shyy et al. 2010).

Also irrespective of feather morphology, all wings produce aerodynamic force at slow angular velocities (Ω_{\min}). Developing birds demonstrate that even small amounts of aerodynamic force (<10% body weight) improve locomotor performance during behaviors like WAIR, controlled flapping descent, or jumping and flapping to elevated perches (Dial 2003; Tobalske and Dial 2007; Jackson et al. 2009; Heers et al. 2011; Heers and Dial 2013). Thus, extinct theropods that were not capable of flapping rapidly (Fig. 4, orange bars), or of producing a fully birdlike wing stroke (with high stroke amplitudes or channelized kinematics), might still have benefited from flapping their feathered forelimbs and producing some aerodynamic force. Fast angular velocities and “birdlike” wing strokes may not be prerequisites for locomotor behaviors requiring little aerodynamic force, such as controlled flapping descent and WAIR or jumping.

Relative Wing Size

Published estimates of forelimb lengths and body masses for theropod dinosaurs (Table 1, Supplementary Table 1) indicate that relative wing size, and hence the potential to produce useful aerodynamic forces, increased during maniraptoran evolution. At slow angular velocities (Ω_{\min}), aerodynamic force estimates range from \sim 1% to \sim 15% body weight, with more derived maniraptorans tending to produce larger forces (*stage iii* > *stage ii* > *stage i*; Fig. 4, orange bars). At fast angular velocities (Ω_{\max}), aerodynamic force estimates range from \sim 2% to 100% body weight, with larger forces again being produced by more derived maniraptorans (blue bars). Immature chukars can flap-run up steep inclines ($>65^\circ$), jump and flap up to low perches, and slow aerial descents by producing aerodynamic forces that are less than 10% of their body weight (\sim 6–8% body weight for birds 6–8 dph during WAIR [Tobalske and Dial 2007]), indicating that small theropods with *stage ii* or *stage iii*

feather morphologies may have achieved similar behaviors, even when flapping slowly. Basal paravians and basal avialans capable of flapping more rapidly might have been able to generate forces sufficient to support body weight for level flight.

Although maniraptorans with *stage i* feathers seemingly had wings that were too small to generate much aerodynamic force relative to adult mass at slow angular velocities (Ω_{\min} ; Fig. 4, orange bars), it is plausible that juveniles of even large-bodied theropods might have benefited from flapping their feathered forelimbs (Dial and Jackson 2011). Owing to a paucity of data, this study could not consider extinct juveniles. However, many theropod species required several years to reach adult mass (Padian et al. 2001; Erickson et al. 2004). If wings developed early, as in many precocial ground birds, then immature individuals might have been able to generate useful aerodynamic forces prior to outgrowing their wings as adults. Brush turkeys (Dial and Jackson 2011) and peafowl (Heers and Dial 2013), for example, have relatively larger wings and greater wing performance as juveniles. Similarly, *Velociraptor* (Turner et al. 2007b) and other maniraptorans that were relatively large and flight-incapable as adults may have had aerodynamically functional wings as juveniles. Although we often focus on adult stages, selection on aerodynamic capacity might have originally occurred among juveniles, and only later among adults that did not attain large body size.

Wing-Leg Cooperation

An important theme that has emerged from work with extant developing birds is that even small amounts of aerodynamic force improve locomotor performance, particularly during behaviors involving the cooperative use of wings and legs. Wing-leg cooperation enhances locomotor performance throughout ontogeny, bridging obligately bipedal and flight-capable developmental stages by allowing juveniles to transition from (1) leg-based terrestrial (or aquatic) locomotion, to (2) wing- and leg-based locomotion on inclined (or aquatic) substrates, to (3) wing-based aerial locomotion (Dial et al. in press). Behaviors like

WAIR, steaming, or jumping and flapping to elevated surfaces are ubiquitous across extant birds and crucial to immature birds with incipient wings (Dial 2011), leading to the hypothesis that wing-leg cooperation might also have served as an evolutionary bridge between leg- and wing-based locomotion.

This hypothesis is consistent with the fossil record. With some extant exceptions (e.g., Apodiformes), hind limbs have always been a conspicuous part of theropod anatomy and thus probably played an important role during the evolutionary acquisition of flight. In some coelurosaurs, hind limb input may have occurred in the form of ground reaction forces during WAIR (Dial 2003) and/or launching and landing (Earls 2003; Heers and Dial 2013). In other coelurosaurs—the “four-winged” paravians—hind limbs may have also generated aerodynamic forces (e.g., Xu et al. 2003). Extinct species undoubtedly utilized a variety of locomotor strategies and engaged their fore- and hind limbs for many purposes, including non-locomotor behaviors such as feeding or signaling. In all cases, however, the hind limbs probably facilitated wing-based locomotion, playing a crucial role in coelurosaurs with protowings and potentially becoming less important as larger and more robust flight apparatuses evolved (see Dial 2003; Xu and Zhang 2005; Heers and Dial 2012; Zheng et al. 2013).

Conclusions

Collectively, our findings suggest that “protowings” may have provided useful aerodynamic function early in the history of maniraptoran theropods, particularly among small or immature individuals. Improvements in aerodynamic performance would have occurred as (1) changes in feather structure increased force production and lift-to-drag ratios, (2) reductions in body mass and increases in wing size increased relative wing size, and (3) increases in flight musculature allowed for faster flapping velocities. Extant juvenile birds demonstrate that incipient wings *can* function aerodynamically, especially when wings are supplemented by legs during behaviors like jumping and flapping to elevated surfaces or WAIR (Tobalske and Dial 2007;

Heers et al. 2011; Heers and Dial 2013). Given that developing birds rely on small muscles and dinosaur-like protowings and skeletons (Heers and Dial 2012) to bridge the developmental transition from obligately bipedal juvenile to flight-capable adult, such behaviors may have been similarly important to theropods during the evolutionary acquisition of flight. By using a protowing-to-wing developmental transition to model the protowing-to-wing evolutionary transition among theropod dinosaurs, and aerodynamic theory to account for differences in size and potential flapping velocity, this study provides the first experimental evidence to suggest that feathered dinosaurs choosing to flap their incipient wings would have been capable of producing useful aerodynamic forces, similar in magnitude to those produced by immature birds using their wings and legs cooperatively or flapping to slow aerial descents. Protowings are aerodynamically functional, and incremental changes in form, function, and behavior that facilitate the development of flight among extant birds may have similarly facilitated the evolution of flight among extinct theropods.

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