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The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents

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Background. Powered flight is implicated as a major driver for the success of birds. Here we examine the effectiveness of three hypothesized pathways for the evolution of the flight stroke, the forelimb motion that powers aerial locomotion, in a terrestrial setting across a range of stem and basal avians: flap running, Wing Assisted Incline Running (WAIR), and wing-assisted leaping. **Methods.** Using biomechanical mathematical models based on known aerodynamic principals and in vivo experiments and ground trothed using extant avians we seek to test if an incipient flight stroke may have contributed sufficient force to permit flap running, WAIR, or leaping takeoff along the phylogenetic lineage from Coelurosauria to birds. **Results.** None of these behaviours were found to meet the biomechancial threshold requirements before Paraves. Neither was there a continuous trend of refinement for any of these biomechanical performances across phylogeny nor a signal of universal applicability near the origin of birds. None of these flap-based locomotory models appear to have been a major influence on pre-flight character acquisition such as pennaceous feathers, suggesting non-locomotory behaviours, and less stringent locomotory behaviours such as balancing and braking, played a role in the evolution of the maniraptoran wing and nascent flight stroke. We find no support for widespread prevalence of WAIR in non-avian theropods, but can't reject its presence in large winged, small-bodied taxa like *Microraptor* and *Archaeopteryx*. **Discussion**. Using our first principles approach we find that "near flight" locomotor behaviors are most sensitive to wing area, and that non-locomotory related selection regimes likely expanded wing area well before WAIR and other such behaviors were possible in derived avians. These results suggest that investigations of the drivers for wing expansion and feather elongation in theropods need not be intrinsically linked to locomotory adaptations, and this separation is critical for our understanding of the origin of powered flight and avian evolution.

The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents

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INTRODUCTION

Evolution of powered flight in vertebrates was a key innovation that spurred the evolutionary success of birds, bats, and pterosaurs (Sears et al. 2006; Butler et al. 2009; Benson and Choiniere 2013). Of the three radiations, the theropod to bird transition has garnered the most interest and scholarship due to the higher quality of the fossil record documenting the origin and refinement of their flight including: the evolution of feathers, reduced body size, an avian-like physiology and respiration, elongate forelimbs, and modifications of the pectoral and forelimb musculoskeletal system (Baier et al. 2007; Codd et al. 2008; Dececchi and Larsson 2009, 2013; Makovicky and Zanno 2011; Benson and Choiniere 2013; Brusatte et al. 2014; Xu et al. 2014). Despite the wealth of fossil evidence documenting this transition, optimizing the evolution of perhaps the most key biomechanical innovation, the flight stroke that permitted aerial locomotion, remains elusive.

The flight stroke of extant birds traces a complex ellipsoidal path that is controlled by derived muscle origins and insertions and modified shoulder, elbow, and wrist joints and ligaments (Gatesy and Baier 2005). Many antecedent functions of the flight stroke have been proposed. These include a raptorial function of the forelimbs for fast prey capture (Ostrom 1974), behavioural precursors such as courtship, balance, or warning displays (Fowler et al. 2011; Foth et al. 2014), as well as locomotory functions (Caple et al. 1983; Dial 2003; Chatterjee and Templin 2007).

Powered flight differs from gliding flight in that it uses active flapping to generate thrust. Some models of the origin of avian flight propose antecedents living in trees and deriving the flight stroke from a parachuting or gliding stage (Chatterjee and Templin

2004; Alexander et al. 2010; Dyke et al. 2013) based primarily on the observation that many modern arboreal tetrapods perform similar behaviors (Dudley et al. 2007; Evangelista et al. 2014). Yet nearly all stem avians have hindlimb morphologies that compare most closely to extant cursorial tetrapods (Dececchi and Larsson 2011) and a multivariate analysis of limb element lengths recovered the earliest birds as most similar to extant terrestrial foragers (Bell and Chiappe 2011; Mitchell and Makovicky 2014). The only theropod taxa that may diverge from this are Scansoriopterygidae, a clade known from four small, fragmentary specimens, but presenting intriguing and radically divergent morphologies from other maniraptoran theropods. Notably, when preserved, they possess large pedal and manual phalangeal indices, a reduced curial index, a reduced hindlimb length, and reduced limb integument not seen in avian antecedents, including paravians (Glen and Bennett 2007; Bell and Chiappe 2011; Dececchi and Larsson 2011; Dececchi et al. 2012). One scansoriopterygid may even possess a skin patagium that may have functioned as an airfoil (Xu et al. 2015). These putative gliding structures are extremely divergent from other theropods and likely represent a convergent pathway to becoming volant.

Of all the models for the origin of the flight stroke from a terrestrial life history two major categories exist: those that have locomotory functional aspect are flap running (Burgers and Chiappe 1999), wing assisted incline running or WAIR (Dial 2003), and vertical leaping (Caple et al. 1983). Behaviors in the second category are non-locomotory behaviors, such as balancing during prey capture (Fowler et al. 2011) and braking during high-speed turns (Schaller 2008). The three stringent locomotory behaviours (WAIR, flap running and vertical leaping) are variations on a proto-flight stroke assisting in force generation to increase ground and launch velocities (Burgers and Chiappe 1999) or to assist in ascending steep inclines to facilitate escape into trees (Dial 2003). All three are present throughout much of extant bird diversity and have been areas of research into the possible pathways for the origins of powered flight.

WAIR is a behaviour observed primarily as a means of predator escape, especially in pre-flight capable juveniles (Tobalske and Dial 2007; Dial et al. 2008; Jackson et al. 2009; Heers and Dial 2012; Heers et al. 2014). This has been suggested to provide a series of functional and morphological stages using immature age classes of extant individuals as proxies for transitional evolutionary stages from basal coelurosaurs to volant birds (Dial et al. 2006; Heers and Dial 2012). At the earliest juvenile stages (0-5 days post hatching [dph] and < 20 g), Chukars either crawl or asymmetrically flap their wings to produce forces of approximately 6% of their body weight (Jackson et al. 2009; Heers et al. 2011; 2014) to ascend inclines of less than 65^{o}, slightly greater than the level that they can ascend using their legs alone (55-60^{o}) (Dial and Bundle 2003; Dial et al.2006). At these low angles, the primary locomotory forces are generated from the hindlimbs but this changes when higher angles are attempted (Bundle and Dial 2003). To ascend angles of greater than 70^{o}, juvenile and older individuals must produce forces equaling a minimum of 50% of their body weight (Dial and Jackson 2010). Larger birds with masses greater than 0.8 kg struggle to WAIR at this level (Dial and Jackson 2010). Low angle WAIR has been hypothesized to be present throughout Coelurosauria and steep angle WAIR minimally at Paraves (Dial 2003, Heers et al. 2012, 2014).

Vertical leaping (both from the ground and perches) begins as an effectively ballistic process in flying animals, initiated by the hindlimbs in birds (Heppner and Anderson 1985; Bonser and Rayner 1996; Earls 2000; Tobalske et al. 2004), bats (Schutt et al. 1997; Gardiner and Nudds 2011), and insects (Nachtigall and Wilson 1967; Nachtigall 1968, 1978; Schouest et al. 1986; Trimarchi and Schneiderman 1995; Dudley 2002). Immediately after the ballistic phase is initiated, the wings are engaged for the climb out phase of launch. Leaping takeoffs are common among medium to small-bodied birds (Provini et al. 2012) but are also present in many larger birds including Turkeys (Tobalske and Dial 2000), Peafowl (Askew 2014), Tinamou (Silveria et al.) and herons, storks, eagles, and vultures (pers. obs.), and has been proposed as a model for the origin of flight in birds (Caple et al. 1983). The largest living flying birds, Kori bustards, are documented to use a very short run before launch (Prozesky, 1970), though large captive specimens have demonstrated a true leaping takeoff, as well (pers. obs. MBH). Flap-running is used in some extant birds, especially semi aquatic species, to accelerate to takeoff speeds whether starting from a water or land launch (though mostly associated with compliant surfaces, e.g. water – see Earls, 2000).

Here we present biomechanical models to test when and if a flight stroke may have contributed to flap running, WAIR, or leaping takeoff along the phylogenetic lineage from Coelurosauria to birds and if these models coincide with the evolution of pennaceous feathers and musculoskeletal adaptations for flight. Our goal is to take evolutionary narratives about pathways to flight origins and evaluate them using quantitative, mechanical models derived from living birds. Although feathery integument is likely to have been a synapomorphy for all dinosaurs and perhaps even all ornithodirans (Godefroit et al. 2014) but see (Barrett et al. 2015), the evolution of pennaceous forelimb and hindlimb feathers has been hypothesized to have aided locomotion (Burgers and Chiappe 1999; Xu et al. 2003; Dial 2006; Heers et al. 2011). Thus we set up a testing regime to determine if non-avian theropods could produce biomechanical values that fit within the realms of those measured in modern animals exhibiting these behaviors, and if is there a decoupling of the timing of the success in these behaviours from the origin of previous proposed flight related traits.

MATERIALS AND METHODS

Due to uncertainty regarding soft tissues in fossil organisms, some variables were treated as constants in the taxa modeled and based on values for extant birds. These include feather material properties and arrangements and muscle power. [illegible]ng these values provided conservative estimates in the sense that they would yield more capable performances for taxa that may lie near biomechanical thresholds. Wing feather arrangements for some fossils appear to be similar to modern birds (Elzanowski 2002; Xu et al. 2003; Foth et al. 2014) though for some taxa this has been disputed (Xu et al. 2010b; Longrich et al. 2012). Fore- and hindlimb force generations were estimated using powers calculated from a 10% and 30% proportion of body mass, respectively. These values are within the range previous estimated for non-avian maniraptorans (Allen et al. 2013), whose estimates do not include the M. caudofemoralis for the pelvic limb and the M. pectoralis for the pectoral limb.

A greater challenge is muscle mass and power output. [illegible]ant birds have extremely large wing muscles, as a proportion to their bodyweight (Marden 1987). The mass of m. pectoralis for birds ranges between 10-20% of total body mass (Greenewalt 1975; Askew et al. 2001), and total flight muscle fractions for birds can reach 40% (Hartman 1961; Greenewalt 1962). This is significantly larger than that estimated in non-avian theropods or early birds. For example, *Archaeopteryx*'s pectoral muscles are estimated at only 0.5% of its body mass (Bock 2013) with the entire forelimb (including bone and all other tissues) at 11-14% (A[illegible]n et al. 2013).

Yet power and muscle mass may not be the main determinant for the use of wings as locomotory structures. Jackson et al. (2011) estimated that pigeons, with approximately 20% of their body mass as pectoralis muscles, only used approximately 10% of their mass-specific power for low angle WAIR. Further, it has been suggested that the ability to produce aerodynamic lift force, not power output, determines flight ability ([illegible]den 1987). As we have assumed extant bird power productions and metabolic capacities for short "burst" activities for non-avian theropods and early birds, though paravian and early avian metabolism was not as advanced a[illegible]odern birds, it was likely sufficient to perform short term, high effort activities (Erickson et al. 2009). Regardless, as our methodology uses wing-beat frequency in conjunction with body size and wing arc measures to generate a lift production value, we are not dependent on either theory (power or lift force) to produce meaningful results.

Taxonomic sampling

Forty-five specimens representing twenty-four non-avian theropod taxa and five avian taxa were examined. Non-avian theropod specimens ranged in mass from approximately 60 g to 18 kg (Table 1, Table S1). Of these, twenty-eight are from specimens accounting for twelve non-avian theropod taxa with preserved feather material, the rest are from closely related taxa that are inferred to be feathered and were included to broaden the scope of the maniraptorans represented. We a priori excluded the tyrannosaurids *Yutyrannus*, because of its large size (estimated mass ~1400 kg), and *Dilong*, due to its incompletely preserved forelimb. Multiple individuals were included for *Anchiornis*, *Similicaudipteryx*, *Caudipteryx*, *Microraptor*, *Sinosauropteryx*, *Mei*, *Archaeopteryx*, *Jeholornis*, and *Sapeornis* to represent different size classes and ontogenetic stages. Different stages in ontogeny may have different life history strategies (Parsons and Parsons 2015). Too address the possibility of WAIR in juvenile but not adult members of Pennaraptora, three late stage embryos: MOR 246-1 *Troodon formosus* per Varricchio et al. (2002), MPC-D100/971 *Citipati osmolskea* and MPC-D100/1018 *Oviraptor incertae sedis* per Yu et al. (2013) were included in this analysis. These specimens are incomplete, but forelimb lengths could be estimated based on the fact that the humerus / forelimb ratio in non-avian and basal avian theropods does not change significantly across ontogeny (Table S2). We used the value of ~43% MOR 246-1 based on the ratios seen in other Troodontids (range between 39-45%) based on *Mei*, *Jinfengopteryx*, *Anchiornis*, *Aurornis*, *Sinovenator*, *Sinornithoides* and *Xiaotingia*. For MPC-D100/971 and MPC-D100/1018 we used 41% based on *Citipati*. For all late stage embryos we reconstructed wing area as if they possessed wings with pennaceous feathering proportional to that seen in adults. This is likely an overestimation, as hatchling and young juveniles in other non-avian theropods do not show pennaceous development to the extent of adults (Xu et al. 2009, Zelenitszky et al. 2012).

Mass estimations for non-avian theropods were based on values for femur length (Christiansen and Fariña 2004) except for *Yixianosaurus*, which has no preserved hindlimbs, for whom upper and lower mass estimate boundaries were taken from Dececchi et al. (2012). For birds, two mass estimates were generated from the regressions derived from extant birds of (Liu et al. 2012; Field et al. 2013). We used humerus length equations as these showed high correlation values and were easily computable for all specimens. Nodal values were calculated based on a modified version of the phylogeny in Dececchi and Larsson 2013 (Data S1).

Wing dimensions

Wing length was calculated based on the length of the humerus, ulna, metacarpal II, and the longest primary feather length, arranged in a straight line. Metacarpal length was used instead of total manus length as the longest primaries attach to the metacarpals and distal forelimb in paravians (Savile 1957; Elzanowski 2002; Xu et al. 2010a; Foth et al. 2014). This gives values similar to those previously reported for maximal straight-line length of the wing in *Archaeopteryx*, differing by less than 1% (Yalden 1971). Wing area was estimated using a chord value 65% of maximum primary length based on the differences between the longest primary feather and the shortest, distal primary in *Archaeopteryx* (Elzanowski 2000; Foth et al. 2014) and *Caudipteryx* (Qiang et al. 1998). This estimate produces a greater wing area than calculated by Yalden (1971) for *Archaeopteryx* (115%, with similar overestimations for *Microraptor* sp. based on the estimates from Chatterjee and Templin (2007) (138%) or Alexander et al. (2010) (109%).and *Zhenyuanlong (105%)* calculated by Liu and Brussatte (2015). We treat these as upper estimates of wing area. These values are overestimates as they ignore the natural flexed position that the limbs take during locomotion. We used this value for our primary analysis as it gives highest possible values for all our force production data and thus the maximum likelihood of success in achieving the minimum threshold values indicating the possible presence of a behavior in said taxon. For taxa without primary feathers preserved (Table 1), we estimated their length based on either other members of the same genus or closely related taxa and assuming congruent lengths. We estimated body width using furcular widths (Table S3). This represents an addition of between 10-15% to the value of the non-avian theropod skeletal arm span with feathers adding another 40+% in modern bird wings (Nudds et al. 2007) and proportionally more in many non avian theropods (Table 1). Wing span was set 2.1 times wing length to assure we did not underestimate the potential wingspan in non-avian taxa.

Model construction

To test WAIR, flap running, and vertical leaping we used equations based on extant bird flight work of Burgers and Chiappe (1999) and Pennycuick (2008) to estimate force production in a similar context to what is examined here. This relatively simple model was chosen as it is easier to update with new paleobiological information and allowed us to see directly the result of varying the input data to see how varying models of theropod functional limitations shape the results. To test the accuracy of our model, we compared our body weight support results to published data for Chukar partridges during WAIR across the three ontogenetic stages, Pigeon data during WAIR, and birds during takeoff (Table 2). Our values are within the range seen in published data for all three stages of WAIR development and show values greater than 1.0 for all birds undertaking leaping takeoff. As our simple model accurately matches real world experimentally derived values of extant taxa, we believe it a suitable starting point to derive comparative force production data for fossil avian and non-avian theropods.

Creation of Benchmarks

As WAIR ability is not uniform across ontogeny and seems to be linked to force production (Dial et al. 2012), we created two bench markers of proportion of body mass supported for taxa to reach. Values between 0.06-0.49 body weight (bw) are classified as level 1 WAIR, which corresponds to the earliest stages of ontogeny and sub vertical ascents of less than 65^0 (Jackson et la. 2009) with greater than 50% contribution to external vertical work generated by the hindlimbs (Bundle and Dial 2003). 0.5 bw and greater denote level 2 WAIR, equivalent to more mature Stage II and III individuals which are capable of high angle to vertical ascents and whose forelimbs become more prominent in force production (Bundle and Dial 2003). Although we understand these are semi-artificial cut offs, they were chosen to represent real world recorded minima and thus should be considered minimal levels achieved before reconstructions of WAIR are accepted.

Coefficient of lift (Specific lift)

We examined potential performance during the wing-driven phase of flap-running, WAIR, and leaping takeoff in our analyses. As a result, all three of the behaviors are subject to constraints of lift production efficiency. The production of lift relative to planform area, speed, and fluid density is summarized as the coefficient of lift.

During WAIR analysis, a coefficient of lift (CL) of 1.0 was used. This corresponds to a value estimated during WAIR use in juvenile Chukars (10 dph) (Heers et al. 2014) but greater than that in the earlier ontogenetic stages (Heers et al. 2011). We choose this value as this age class has been proposed to be analogous to derived maniraptoran theropod capabilities such as *Anchiornis* and *Microraptor* and this Cl is achievable by all ontogenetic stages beyond 5 dph (Heers et al. 2014). For leaping takeoff we choose a CL of 1.5, which corresponds to the minimal values estimated in adult Chukars during high angle WAIR (Heers et al. 2011) and below the 1.64 calculated for the pigeon during takeoff (Usherwood 2009). For flap running we used the equations of Burgers and Chiappe (1999) with the following modifications: we ran permutations for all three downstroke angles and reduced the CL to 1.2 from 2. We choose to make the CL closer to that estimated during late stage Chukar WAIR attempts (Heers et al. 2011) as WAIR is simply a specific use case of flap running on a highly angled substrate. s value is achievable by Chuckars older than 20 dph (Heers et al. 2014). Using the CL of non-volant and juvenile Chukar both produces minimal values for these behaviours and more closely simulates the expected outputs in non-avian theropods before powered flight.

During low advance ratio wing-driven behaviors (launch, landing, WAIR, etc), the coefficient of drag can be quite large. In young Chukars, the coefficient of drag can be near the coefficient of lift, thereby potentially providing a significant component of weight support during controlled descent or significantly affecting reaction forces during WAIR (Heers et al., 2011). To confirm that using pure CL as our specific fluid force coefficient was an accurate approach (instead of the total fluid resultant with both CL and CD), we compared predicted reaction forces and weight support to values measured *in vivo* and reported in the literature. Because a close match was found across multiple size classes, we assume for the remainder of the calculations that reaction forces during WAIR are not greatly affected by a high coefficient of drag (though we note that for controlled descent or burst climb out, behaviors we did not investigate, high CD is likely a critical component).

Wing beat frequency

Wing beat frequencies scale negatively to body mass in steady flight (Greenewalt 1975; Pennycuick 2008) and takeoff (Askew et al. 2001; Jackson 2009) across species in extant birds. Wingbeat frequencies during takeoff are similar to those during WAIR (Tobalske and Dial 2007). For this study we used the maximum takeoff regressions from Jackson (2009) for all birds in his sample (ALL in Supplemental Tables), and for only ground foraging birds (GF), we also added Galliformes takeoff data from Askew et al. (2001) to Jackson’s dataset to produce a third regression equation (MOD). For the MOD dataset we incorporated a phylogenetic correction using PDAP v 1.15 (Midford et al. 2010), with branch lengths based on divergence times derived from the chronograms of Jetz et al. (Jetz et al. 2012) (Data S2).

Wing range of motion

Abduction of the forelimb beyond 90° from the ventral vertical plane was not possible in most non-avian theropods (Senter 2006a,b; Turner et al. 2012). The glenoid fossa faces ventrolaterally in these taxa and only shifted to a more lateral configuration at Paraves (Makovicky and Zanno 2011; Turner et al. 2012). The glenoid continued to translate upward until reaching the dorsolaterally facing position of most extant birds at the phylogenetic level of *Jeholornis* and *Sapeornis* (Zhou and Zhang 2003a,b).

Extant birds have extensive shoulder abductive ranges. For example, during WAIR, the abductive flap angle of juvenile Chukars ranges from 90 degrees at stage I to greater than 143° at stage II (Jackson et al. 2009) and images show that in all cases, the forelimb ascends to a vertical or slightly beyond position (see Tobalske and Dial 2007 figs 4,6; Jackson et al. 2009 Fig. 1).

Given the abduction limitations of the non-avian theropod glenoid, we chose flap angles of 50°, 70° and 90° to encapsulate the range of values expected across Theropoda and ran them for all taxa. For avians more derived than *Archaeopteryx,* we included a fourth value, 143° as their shoulder girdle allowed for flap angles similar to extant birds. 90° is likely unattainable for all non-avian theropods due to the constraints of the substrate angle and shoulder morphology since the humerus cannot exceed the dorsal rim of the glenoid which is aligned with the plane of the vertebral column. It was included to create an upper bracket on possible support values.

Velocities used for the different analyses were based on those of extant birds. For WAIR it was assigned 1.5 m/s based on the speed of adult birds (Tobalske and Dial 2007). This is higher than achieved for the early, pre-flight capable ontogenetic stages (0.6 m/s), and thus acts as a fair upper velocity bound, though it is likely beyond the capabilities of non-avian theropods with less developed wings. For leaping we calculated three values, height gain if wing thrust was added to that generated by the hindlimbs, vertical distance increase given the increased take off velocity due to flapping and takeoff potential from a standing jump. Calculating height and distance gain was done through a modification of existing equations used to model pterosaur launch (Witton and Habib 2010) to account for the bipedal nature of non-avian theropods (see Supplementary Information for these equations). To compensate for the effects of body size, a scalar is introduced to ensure the pre-loading values would be 2.4, a conservative value well within the range seen in extant tetrapods (Biewener 2003). For leaping takeoff we choose two different takeoff speeds (3.8 and 4.1 m/s) based on extant avians (Earls 2000; Tobalske et al. 2004). Higher values for leaping have been recorded in some mammals (Günther et al. 1991) and after several wing beats in birds (Berg and Biewener 2010), thus these values may not represent the maximal possible values for small theropods. For flap running we chose a start value of 2 m/s., which corresponds to the value used in Burgers and Chiappe (1999). This speed is well within the range of sprint speeds of many lizards (Huey 1982; Christian and Garland 1996; Irschick and Jayne 1999) and small mammals (Iriarte-Díaz 2002), whereas many terrestrial birds can sustain this speed for over thirty minutes (Gatesy and Biewener 1991; Gatesy 1999). These values are likely well below the maximum sprint speed of these taxa (Sellers and Manning 2007) but allowed us to determine if there was significant increase in speed using the wing generated thrust alone.

We excluded the potential drag and damage caused by hindlimb feathers of some paravians through contact with the substrate. At low hindlimb angles used during the ascent of inclined surfaces (see the metatarsus during WAIR from Jackson et al. 2009 Figure 1) the distal limb feathers would have contacted the surface and caused frictional drag, which would have reduced performance and damaged the feathers (Dececchi and Larsson 2011). Although these variables may have evolved throughout the transition, treating them as constants provided a “best case scenario” for non-avian theropods constraining the upper limits for when these behaviours were possible.

Wing contribution to leaping

Three additional estimates for wing contributions to a vertical leaping were made. The first estimates the extension to the maximum vertical height on a leap through the thrust generated by flapping alone. [illegible]s calculation assumed the maximum wing output occurred at the top of the leap arch, and that the forces generated were directed vertically. This was done through a modification of the terrestrial launch methodology of Witton and Habib ([illegible]0, see Data S3) to accommodate bipedal theropod models with and without wing generated thrust. The difference between the maximum height gained with wing generated thrust was presented as a percentage increase (see Data S3, 4 for more detailed description of the equations used and a sample calculation spreadsheet).

The second was done to see the maximum horizontal distance extension done through flapping alone. This was done by taking the speed at take off, generated by the equation above at both 30 and 45^0 which corresponds both to the theoretical best angle for a projectile and one which more closely resembles the angle of take off measured in human and lizard leapers (Toro et al. 2004; Linthorne et al. 2005, Wakai and Linthorne. 2005). In both cases our models were treated as if there was no difference in takeoff and landing height, thus making the calculation of jump distance

$$D_{jump}=(v^2 \sin 2\Theta)/g$$

Where v equals the takeoff velocity and Θ the angle of takeoff.

Vertical take offs were deemed possible when body weight (bw) support values were equal to or greater than 1.0 using the speed and lift parameters mentioned above.

RESULTS

Wing loading

Increase in WAIR ability broadly corresponds to decreased wing loading in Chukars (Heers and Dial 2015), something noted in other galliform birds (Dial et al. 2011). Thus wing loading values may offer a rough comparison between non-avian theropod specimens and Chukars of a similar body mass. Among non-avian theropods, wing loading values ranged from less than 5 kg/m^2 (*Microraptor*) to over 1000 kg/m^2 (*Sinosauropteryx*). Of the thirty-four non-avian specimens included, only eight, representing five genera (all are deinonychosaurs) showed loading values less than that seen in day old Chukars, the highest values recorded across ontogeny. Day old Chukar chicks could only surmount inclines of less then 48^0, still performed asynchronous wing beats, and the wings made prolonged contacts with the substrate (Jackson et al. 2009, Heers and Dial 2015). No non-paravian showed values less than the 165% measured at 1-3 dph Chukars, with most pennaraptorans at values 2-8 times that seen at even the highest Chukar chick loadings (Figure 2). Focusing on the embryonic and early ontogenetic stage specimens in our analysis, to test whether WAIR was possible at early ages and lost through ontogeny, we recovered loading values again significantly higher than the highest values seen during Chukar ontogeny, with values 126%-234% those of day old chicks. For comparison, the hatchling size *Similicaudipteryx* specimen (STM 4-1) had a body mass estimated at approximately 63g, similar to a 17dph Chukar chick (stage II), but wing loading values 5.8 times higher due to it having a wing area only the size of a six dph chick. This suggests that none of the non-paravian theropods could perform even the lowest levels of WAIR, even disregarding their limited range of motion and flapping frequency. None of the avian taxa, under either mass reconstruction, showed loading values above 7.5 kg/m^{2,} which corresponds to approximately 11 dph (stage II) Chukar chicks, approximately the time where fledgling begins (Harper et al. 1958; audabon .org, Christian 1996).

WAIR

Nine of thirty-four specimens of non-avian theropods reached the level 1 WAIR cutoff (0.06 bw) minimally once across all permutations using a speed value of 1.5 m/s and 8 at speed of 0.6vm/s. Again, all are deinonychosaurs. Three specimens (the larger *Similicaudipteryx* specimen, and the smaller mass estimates for *Yixianosaurus* and

Yulong) approach the WAIR level 1 criteria, but none yield values higher than 0.05 bw, and this only under the MOD reconstruction at the highest abduction angle. All specimens of *Microraptor* and the smaller specimens of *Anchiornis* and *Eosinopteryx* yielded bodyweight support values above 0.06 bw across all permutations at 1.5 m/s whereas at 0.6 m/s only the smaller *Anchiornis* and *Microraptor gui* specimens achieve this. Within non-avian theropods using a 90^0 flap angle at 1.5m/s, only a single specimen of *Microraptor gui* (BMNHC PH881) has body weight support values reaching the 0.5 bw cutoffs for WAIR level 2, though the larger specimen (IVPP V 13352) comes close under the MOD reconstruction (Figure 1, Table S4-6). 50^0 all non-avians and *Archaeopteryx* failed to reach values higher than 0.33 bw with only *M. gui* and the smaller *Anchiornis* reaching 0.1 bw.

In birds, the different mass estimation methods produced significantly different values, with specimen's body weight support values differing by between 36% (*Eoconfuciusornis*) and almost 400% in the Eichstatt specimen of *Archaeopteryx*. All basal avians show the capability of level 1 WAIR at all flap frequencie mass estimates and angles used here, with no avians showing values below 0.1 bw under any permutation. In *Archaeopteryx*, there is no clear trend in WAIR capability and allometry. At the higher flap angle and lower mass, all avians show the capability for level 2 WAIR (>0.5 bw). All more derived birds y l body weight support values well in excess of 1 at 143^{o} a $90\,^{o}$ under both body mass estimates, except for *Sapeornis* that only exceeds this threshold using the lower mass estimate. Of note, the values recovered for more derived avians are significantly higher than those observed in experimental data

(Tobalske and Dial 2007) or calculated using extant measurements (Table 2, Table S7) and well above the 1.0 threshold for take off. This suggests that these taxa could have performed this behavior at lower wing beat frequencies, body velocities and flap angles than the values used here, as seen in some extant birds (Jackson et al. 2011), or that physiology and power production differed between extant and basal birds (Erickson et al. 2009, O'connor and Zhou 2015), or a combination of both. If the latter is correct, it suggests our measurements for non-avian theropods overestimate the power production potential in these taxa, and thus overestimate their WAIR capabilities.

Flap running

Among non-avian theropods, flap running peaked in effectiveness within small-bodied paravians (Figures 2, 3, Table S8). With a 90^0 flap angle, the smaller *Anchiornis* specimen and *Microraptor gui* were the only non-avian taxa to show increases greater than 1.0 m/s under all permutations (71-79% and 75-208% performance increases, respectively), although only *Microraptor* achieved speeds capable of flight. More realistic 50^0 flap angles yielded only a 23-27% and 26-65% performance increase for these taxa. Among non-paravian members of Pennaraptora, no taxon exceeded an increase of 17% (*Similicaudipteryx*) and at abduction angles below 90^0 only the larger *Similicaudipteryx* and the lighter mass estimated *Yixianosaurus* specimens yielded velocity increases reaching 10%. Although some paravians had high levels of increased speed, *Mahakala, Mei, Jinfengopteryx, Xiaotingia, Tianyuraptor*, and *Sinovenator* showed increases of less 17% under all permutations, with many showing values in the single digits. At 50^0 only *Microraptor* sp. *Changyuraptor*, *Eosinopteryx* and *Anchiornis* showed a greater than 10% increase. All specimens of *Archaeopteryx* showed speed increases similar to or greater than those seen in *Microraptor* and *Anchiornis* though there is no clear pattern relating body size to speed, as the largest (London) and smallest (Eichstatt) specimens yielded similar values (Table S8). Only *Microraptor* and all specimens of *Archaeopteryx* showed the ability to achieve takeoff velocities by this method alone (Table S8).

Leaping

The use of forelimbs during jumping was divided into three discrete analyses, one examining the potential of the wings to increase maximum jump height, one to examine distance gained horizontally, and finally to see if the wings could generate enough force to take off from a standing start as seen in extant birds.

Vertical

No non-paravian gained more than 8% additional height with flapping using the highest flap angles, and most gained less than 3% (Figure 3, Table S9). Using more reasonable flap angles of 50^0, none exceeded 4%. Within paravians, several taxa generated greater than 10% height increases, including *Anchiornis*, *Microraptor*, *Eosinopteryx*, *Changyuraptor*, *Aurornis* and all *Archaeopteryx specimens* (Table S9). Despite this most troodontids, both the “short armed” Jehol Dromaeosaurs, *Mahakala* and *Sinornithosaurus* showed values more similar to non-paravians, between 1-8.5% increase in height. Of interest, the “four winged” taxa used here (*Anchiornis*, *Microraptor*, and *Changyuraptor)* yielded increased height gains on the order of 16-64%, with *Microraptor gui* specimens showing values in excess of 50% (Figure 3, Table

S9). Even under the lowest flap angle settings, both specimens of *M. gui* showed leaping height increases of greater than 30%, almost four times the value for the non-paravians under any setting, and *Changyuraptor* and *Microraptor hanqingi s*howed values of approximately 20%, which is greater than twice the highest value seen in any non-paravian. All *Archaeopteryx* specimens showed height gains greater than 30% under all mass permutations, with the lighter estimates for the Berlin, Thermopolis and 11th specimen exceeding 190% non-flapping height values. Interestingly the only specimen that did not reach the 50% height gain under any permutation is the Eichstatt specimen, the smallest in our analysis, whose range between 134-148% gain is similar to what is seen in the larger microraptorine specimens (excluding *Sinornithosaurus*).

Horizontal

Similar to vertical leaping, there was a marked disparity between distance gained in the “four winged” paravian taxa and all others (Table S10). Only one non-paravian, under the highest setting at the 45^0 takeoff angle showed distance increases of 5% or greater (*Similicaudipteryx* STM-22). Among paravians *Microraptor*, *Changyuraptor*, the smaller *Anchiornis* and all species of *Archaeopteryx* show leaping values greater than 20% non-flapping horizontal distance at the 45^0 take off, though this drops to 15% at 30^0.

Vertical takeoff

Among non-avians, only *Microraptor gui* achieved body weight supports greater than 1 under any flap angle or flapping frequency permutation under the two avian derived take off speeds assessed. No non-paravian showed values greater than 0.15

bw under these conditions (Tables S11-13). Outside of *Microraptor, Changyuraptor* and the smaller specimen of *Anchiornis*, deinonychosaurians did not have values beyond 0.5 bw under either speed or any flap frequency permutation. In avians at the lower body weight estimate, all taxa showed values greater than 1 bw at the high end of their flapping angle range. At the higher mass estimates, multiple specimens of *Archaeopteryx* showed levels below 1 bw, with the lowest values seen in the Eichstatt and London specimens (Tables S11-13). Many extant avians use launch speeds of 1.5 m/s (Earls 2000, Berg and Biewener 2010). At that takeoff speed, Cretaceous avians still achieved values in excess of 1 bw, with the exception of the larger mass estimates of *Sapeornis (*Tables S4-6). At the higher speed of 5.1 m/s, achievable by strong leapers, beyond *Microraptor* the only other non-avian theropods to achieve greater than 1 bw support was the smaller specimen of *Anchiornis* under a single flap rate permutation at 90^0 flap angle.

DISCUSSION

A major challenge of attempting to create models that examine evolutionary transitions is that of efficiency versus effectiveness. Evolved traits may need to only function at some basic level, rather than contribute high degrees of functional adaptation. Thus an argument against our use of thresholds, such as a 6% body weight support as the minimum for WAIR, is that smaller values, such as 5% or even 1%, may still provide selective advantages for individuals. Although this line of thought is defensible, we suggest a challenge to this. The first is that these low values are not testable in the sense that there are not physically defined thresholds to when they may or may not function. Without these parameters to test, any discussion becomes a story-telling scenario. In addition, we have used liberal parameters in reconstructing extinct taxa based on output values measured in modern, derived avians. Given that non-avian theropods have additional functional restrictions based on the relative lack of derived musculoskeletal and integumentary morphologies present in extant birds that have evolved over the subsequent 130 million years since the minimal origin of powered flight, the claim that paravians would be able to perform functions at levels below that seen in extant taxa without these restrictions is difficult to defend. For example, flapping frequency and flap angle have large effects on the resulting body weight support values and using avian take off values are likely significant over estimations for values obtainable in most if not all the taxa sampled here. Our use of a velocity of 1.5 m/s is based on the speed of adult Chukars, whose WAIR ability is much greater than proposed of any non-avian taxa examined here. Using juvenile values (0.6 m/s of stage I) reduces the bw support values by approximately one third. Additionally, by using coefficient of lift values of 1, which is higher than is seen in a 20 dph Chukar at 45-degree angle of attack (stage II per Jackson et al. 2009), we are likely highly positively biasing the results. Thus we argue that due to our relaxed constraints and the significantly higher wing loadings to that seen in any stage of Chukar development (even the asymmetrical crawling stage of 1-3d ph from Jackson et al. 2009), the taxa sampled here that did not reach the 0.06 bw threshold derived from in vivo experiments or meet the wing loading values seen in the earliest stages of ontogeny should not be considered WAIR capable. Although we do not have in vivo derived values to compare with leaping and flap running estimates, proposing that small incremental increases measured only under unnaturally lenient conditions indicate support for a behavior is not parsimonious

For all behaviours tested here there is a sharp contrast in performance levels between a small number of paravian taxa (*Microraptor, Anchiornis, Changyuraptor, Aurornis and Eosinopteryx*) and all other non-avian taxa. This discrepancy is marked not only because it does not correlate to the origin of pennaceous feathers at pennaraptora but it also does not include all members of Paraves within the high performing category. Multiple small bodied and basal members of both deinonychosaurian subgroups, such as *Mahakala, Xiaotingia, Jinfengopteryx, Mei, Sinovenator and Sinornithosaurus*, show little evidence of benefit from flapping assisted locomotion. As these taxa are similar in size to the paravians that do show potential benefits, the argument that this loss is a byproduct of allometry is not possible. Allometric loss of performance is possible though in the larger, feathered dromaeosaurs like *Velociraptor* (~15 kg, Turner et al. 2007) or *Dakotaraptor* (~350 kg, Depalma et al. 2015). As our measurements for the small paravian wing areas are based either on preserved feather length (*Sinornithosaurus*) or on long feathered close relatives (*Anchiornis* for *Xiaotingia*, *Jinfengopteryx*, *Mei*, *Sinovenator* and *Microraptor* for *Mahakala*) our values for them are likely overestimates and suggests that locomotion was not a major driver for forelimb evolution, even among small sized paravians.

Flap Running

There are question as to whether a flap running model is particularly efficient for any taxa. One immediate set of constraints relates to performance of the hind limb under a potential flap-running model. The thrust production model we used assumes the hindlimb and forelimb propulsion potentials were simply additive. However, in reality the hindlimb performance must have some maximum output that is likely to be exceeded if the forelimbs produce significant additional propulsive force. Thus at high wing-produced thrust production, the hindlimbs likely cannot move fast enough to accommodate the faster speeds. Under such conditions, an animal would pitch forward and fall.

We also assume that most of the lift produced by the wings during flap-running could be oriented as thrust. The proportion of force that can be oriented as thrust is, however, constrained by wing kinematics, particularly the amount of spanwise twist that the wing can undergo during the flight stroke (Iosilevskii 2014). Thus our thrust proportions for theropods may be unrealistically high, overestimating the speed generated.

Additionally, downstroke lift production not reoriented as thrust would necessarily act to displace some weight. Although this is important and necessary in flight, it would reduce hindlimb performance during flap-running by reducing the normal force acting through the feet. A similar phenomena occurs during high angled WAIR (Bundle and Dial 2003). Finally, the production of lift during flap-running, regardless of orientation relative to travel, would generate significant amounts of drag (including profile drag, pressure drag, and induced drag). Given these potential performance constraints, it is questionable whether flap-running would be as effective a locomotion mode as our data suggests, even for taxa like *Microraptor*.

WAIR

The finding that not a single non-paravian reaches the 6% bw threshold for level 1 WAIR challenges the proposal that WAIR offers a behavioural pathway for basal maniraptorans (Dial 2006, Heers et al. 2011, 2014). The few cases that approach these values (*Similicaudipteryx*, *Yulong*, and *Yixianosaurus*) are only achieved under wing angle and wing beat permutations that are unrealistic given their pectoral musculoskeletal structures (Baier et al. 2007; Turner et al. 2012). MOD derived wing beat values for the larger *Similicaudipteryx* (6), *Yixianosaurus* (7-8), *Yulong* (10) are greater than or equal to those of smaller extant birds such as the Magpie (9.2), Crow (6.6) and Raven (6.1) (Jackson 2009) and are so elevated due to the inclusion in that dataset of galliform birds, which are short burst specialists with shortened wings, large pectoralis and supracoracoideus muscle masses and muscle fiber adaptations to maximize their flight style (Askew and Marsh 2001; Tobalske et al. 2003). These specialized muscles are adapted to allow wing beat frequencies beyond those of other birds at a similar body mass (Tobalske and Dial 2000, 2007; Jackson 2009; Jackson et al. 2009) thus inflating our wing beat estimates. Wing beat frequencies were likely much lower in non-avian theropods than in modern birds during takeoff, which is higher than during level flight (Dial 1992, Berg and Biewener 2013), given the relatively small size of their wing musculature and plesiomorphic musculoskeletal anatomy (Jasinoski et al. 2006; Allen et al. 2013; Baier et al. 2007; Bock 2013; Burch 2014).

In none of our nine permutations did values indicating level 1 WAIR performances become unambiguously optimized at Paraves (Data S1). Given the liberal application of constraints coupled with the low values seen in most paravians that do shown positive scores, indicates that tightening these constraints (such as reducing flapping frequency, body velocity, or wing area, or a combination of the three) would likely exclude marginally performing taxa like *Aurornis* and *Eosinopteryx* from even this threshold. Given the low values seen in the former and reduced flapping ability in the latter (Godefroit et al. 2013) it is likely that only *Anchiornis*, *Microraptor* and *Changyuraptor* among non-avian theropods would even have the potential to use this behavior. Including other factors, such as symmetrical feathers and plesiomorphic pectoral girdle morphology would likely have limited the prevalence of this trait further. This does not make a strong case that this behavior was present ancestrally in Paravians, yet alone that it coincided with pennaceous feather evolution and elongation (present at Pennaraptora) or other flight related adaptations. If so, this suggests a minimum of two origins for the use of flap-based locomotion with the presently accepted phylogenetic hypotheses; once within microraptorines, and once in Aves. This is not completely surprising as other traits related to flight, such as an alula, elongated coracoid, and a broad, ossified sternum, are also independently derived in *Microraptor* and basal avians that are more derived than *Sapeornis*, suggesting convergence evolution in early powered flight (Zheng et al. 2014).

To compare our results, the WAIR and leaping takeoff analyses were rerun using previously published values for *Archaeopteryx* (Yalden 1984), *Microraptor* (Chatterjee and Templin 2007; Alexander et al. 2010), *Caudipteryx* and *Protarchaeopteryx* (Nudds and Dyke 2009). In all cases, WAIR values were similar, often below, values calculated in our analysis (Table S14). Non-paravians yielded WAIR values near 0 and take off speeds were required to be greater than 46 m/s. *Microraptor* specimens showed takeoff velocities between 4.1 - 6.6 m/s, values achievable either by running or leaping methods and similar to those estimated in our original analysis.

Locomotory pathways to flight: necessity or red herring?

One of potential arguments for why a locomotory pathway is required for the evolution of flight related characters is that the muscle hypertrophy in the pectoral girdle present in extant flying birds would be unlikely to have evolved passively if display or stability flapping methods drove the origin of large wings. Although it is undeniable that extant avians have proportionally and significantly more wing musculature than non-avian theropods, the minimum level needed to achieve a ground-based takeoff is unknown. There are several volant birds with flight muscle ratios (flight muscle mass proportion of total mass) below 16% (Marden 1987). Juvenile Chukars that fledge less than two weeks after hatching (Harper et al. 1958; audabon.org, Christiansen 1970, 1996) and peafowl that fledge one to two weeks (Fowler 2011), also have ratios below this value. Recent estimates for *Microraptor* yield values within this range (Allen et al. 2013).

In juvenile galliforms, the proportional total forelimb muscle mass is 40-60% of adult values (Heers et al. 2015). Yet because of the proportionally larger wing area's wing loading values are between also significantly less (40-51% in Chukars, 25-35% in Peafowl) suggesting that larger enough wing area could compensate for the reduced muscle mass. Given that all fossil avians as well as *Microraptor* have similar wing loading values to fledging aged Chukar (10-15 dph) as well as adult Chukars and Peafowl (Heers et al. 2015), we suggest that even with reduced muscle masses (though within the range of juvenile galliforms and some birds) and power output they would be capable of ground based take off due to their large wing size. Given the lack of features indicating significant hypertrophy in pectoral musculature in the earliest fliers, such as a lack of a sternal plate (Zheng et al. 2014) and the delayed presence of a keel until Ornithothoraces (O'Connor et al. 2015) suggests powered flight originated before pronounced muscle hypertrophy. Thus the pathway to large pectoral muscles is one that occurred within Aves, not before, and arguments on pathways to muscle hypertrophy need not be invoked when discussing the origins of flight.

Our first principles modeling approach, which accurately predicts WAIR values for Chukar chicks, supports the postulate that for these "near flight" behaviors, wing area is the major determinant of function rather than power. Selective regimes expanded wing area before it would provide any locomotory benefit such as display, egg shielding, braking, or balance, must be sought in order to understand the drivers for a major pre-requisite for the flight stroke: reduced wing loading. This presents several possibilities as to the origin of the flight stroke itself, once we have divorced it from the early expansion of the wing and the origin of pennaceous feathers within minimally

Maniraptora. The first is that after expansion into the wing-loading region where wing based locomotory regimes are possible, there was co-evolution in early avians for several traits such as musculoskeletal adaptations for forelimb mobility and high wing beat frequencies and integumentary adaptations for feather length and rigidity. The other is that wing area expanded into the range that would allow these behaviours first and than wing frequency, flap angle, and power generation evolved either independently or in tandem to allow wing based locomotion to be achieved. The first precludes WAIR, flap running or jumping from having a major role in pre-flight taxa, whereas the second could be interpreted to accommodate WAIR as still an evolutionarily important pathway. Our data indicates that even in the second scenario, WAIR would be restricted in its functional presence to, at the earliest, small-bodied Paraves or more likely the base of Aves; well after previous suggestions (Heers and Dial 2012).

Energetics and WAIR

A possible restriction on WAIR that has yet to be fully explored is the energetic demands in its use. Short flights are energetically extremely costly with empirical measurements of 12.5 - 29 times basal metabolic rate (Nudds and Bryant 2000; Hambly et al. 2004). Much of this is due to the expenditures of take off (Nudds and Bryant 2000). The cost for WAIR across birds has not been fully documented, though reduced power input from the pectoralis compared to flight has been observed in the pigeon (Jackson et al. 2011b). If this means significantly less total energy expenditure compared to takeoff is unknown (Jackson et al. 2011b) as the hindlimbs contribute between 37-98% of the total work done (Bundle and Dial 2003). Also, this reduced pectoralis power output coincides with reduced wing beat frequency and amplitude, something not observed in WAIR performed in galliforms, whose values are similar to that of burst takeoff (Askew et al. 2001; Tobalaske and Dial 2007; Jackson et al. 2009). As these factors are linked to increased muscle activation (Robertson and Biewener 2012), this suggests that energetic costs in Chukars are likely high, especially when the contribution of the hindlimbs is factored in.

The reduced power outputs needed in pigeons for WAIR may be due to their proportionally larger wings, which produce higher body weight support values even at these reduced wing beat values (Table 2). Non-avian theropods had proportionally even smaller wings, suggesting that wing based locomotory behaviours, if possible, would have been significantly more costly than in many extant taxa and again that wing size, not muscle mass, may be the most significant variable.

This poses the problem of why, if it is energetically costly, did WAIR evolve in the first place? A simple answer may be though early avians had forelimbs capable of grasping, the vast majority of later taxa did not. Although there is no evidence for arboreal or scansorial adaptations in non-avian theropods, apart for Scansoriopterygidae, (Dececchi and Larsson 2011), climbing may have been possible in basal avians such as *Sapeornis* and *Jeholornis* for predator avoidance. These taxa are suggested to have been primarily terrestrial feeders (Bell and Chiappe 2011; Dececchi and Larsson 2011; Mitchell and Makovicky 2014) but do show the reduced relative hindlimb length and reversed hallux typically present in taxa that can perch (Zhou and Zhang 2003a,b). Critically, they also possessed forelimbs with clawed and functionally independent manual digits capable of grasping. This may have been sufficient to occasionally ascend inclines providing a predictable means of escape that is less energetically costly than takeoff. Though climbing up inclined surfaces is often energetically more expensive than running horizontally (Taylor et al. 1972; Wunder and Morrison 1974), the costs are not extreme at the small sizes estimated for early birds (Hanna and Schmitt 2011).

Ontogenetic versus phylogenetic signals

The findings that all non-paravian theropods and most deinonychosaurians were incapable of using WAIR, raises the question of when along the lineage could WAIR have evolved and under what selective context? As our data shows there is no evidence of WAIR in non-paravian theropods, this challenges the hypothesis that modern bird ontogeny recapitulates the pathway to the origin of flight. Although it is tempting to suppose that behaviours young extant birds undertake offers insight into the origins of flight, they do not present plesiomorphic morphologies. Although they begin with somewhat reduced forelimb muscle masses and feathering, the musculoskeletal morphology is still comparable with adult extant fliers. Even chicken embryos at only half gestation develop a broad sternum with a robust midline keel (Hall and Herring 1990). The oblique acrocoracohumeral ligament orientation and triosseal canal that is unique to advanced fliers is also present in embryos long before hatching. Interestingly, paralysis of chick embryos greatly reduces sternal development to the point of a loss of much of the sternal plate and absence of a sternal keel (Hall and Herring 1990). This suggests that activation of the powerful, hypertrophied pectoral musculature is necessary for the development of the derived avian sternum, and in turn, that no non-avian theropod had this musculature.

Modified flapping behaviors are present in other birds that can’t fly, such as steaming in pre-fledgling ducklings (Aigeldinger and Fish 1995), begging and signaling in altricial chicks (Rydén and Bengtsson 1980; Glassey and Forbes 2002; Ngoenjun et al. 2009), and social displays and thermoregulation in Ostriches (Bolwig 1973; Mushi et al. 2008). This indicates that even in the most basal lineage of extant avians, the ancestral flight stroke has been modified by juvenile and non-volant individuals to preform other tasks. Even late stage avian embryos and wingless hatchlings perform coordinated flapping motions on their own and when stimulated (Hamburger and Oppenheim 1967; Provine 1979, 1981a,b, 1982) showing that the neurological pathway for flapping motion is active and functioning before hatching in precocial birds (Provine 1979). These embryonically established neural controls are thus available to the earliest hatchlings. Absence of a keeled sternum in stem avians implies that these embryonic rhythmic pectoral contractions were also absent, and thus those chicks may not have had the coordinated flapping behaviours extant chicks do.

Although ontogenetic trajectors are relatively linear, with regards to a species, phylogenetic trajectories are not. The WAIRing capabilities of extant birds may be a direct result of their advanced powered flight adaptations rather than a precursor for it. Because the factors that facilitate WAIR are the same as those that permit flight (increased wing area, muscle resources, and flapping arc), WAIR may be more of a spandrel that extant birds have capitalized on rather than a selective pathway. Thus we propose instead that juvenile birds exapted the flight stroke for use as an escape technique before they were capable of takeoff and flight, and this derived escape response was only possible once the complex flight adaptations of derived birds evolved.

Ground takeoff in *Microraptor* and *Archaeopteryx*

Although no thrust based locomotory method succeeded in providing an adequate evolutionary pathway with an obvious evolutionary trend that surpassed biophysical thresholds, some taxa did. Notably *Microraptor gui* and *Archaeopteryx* showed significant results in all three methods. Interestingly, both taxa were estimated to have had the potential for ground based take off at either sprint speeds and leaping take off values (Tables S8, 11-13). Given the effects of flap running's thrust generation (though see potential limitations below), take off speeds can be achieved with a starting velocity well within the range of similar sized extant tetrapods. Even a sprint speed, without wing assistance, of 7 m/s is not unrealistic given greater speeds are obtained by the Roadrunner (Lockwood 2010), Red legged Seriemas (Abourachid et al. 2005), multiple small mammals (Iriarte-Díaz 2002), and some lizards (Huey 1982; Clemente et al. 2009).

Living birds that launch by running are overwhelmingly aquatic or semi-aquatic taxa, suggesting that running takeoff is mostly an adaptation to compliant surfaces. (Earls 2000). Other birds utilize a leaping takeoff to initiate flight with high instantaneous speeds during leaping (Biewener 2003), easily matches the values used here. The required speed values for takeoff we calculated could be lowered if we assumed a coefficient of lift above 1.5, similar to the seen during take off in extant birds

(Usherwood 2009) or if we reduced our mass estimates. *Microraptor* has an elongated hindlimb, especially when compared to basal birds of similar snout-vent length (Dececchi and Larsson 2013) which would not only increase its top speed, as leg length is related to stride length and speed (Garland and Janis 1993; Hoyt et al. 2000), but also likely leads to an overestimation of body mass (Dececchi and Larsson 2013). If we reduce the mass of *Microraptor gui* (IVPP V 13352) to that of a similar sized *Archaeopteryx* specimen (Solnhofen) we get a mass estimate of between 0.4-0.6 kg, or between 42-67 % of the value used here for IVPP V 13352. This is similar to differences we see between mass estimates of femur length and 3D models for LVH 0026 (Tables S1,14). Using 0.6 kg for *Microraptor* values of greater that 1.0 bw are achieved at speeds of 3.8 m/s, and even less if Cl values closer to extant birds of 1.64 are used. This suggests that at reasonable speeds, even with a coefficient of lift below that of extant birds, *Microraptor* was likely capable of ground based take off. Also during leaping take off, the horizontal velocity of birds increases rapidly after the first few strokes (Berg and Biewener 2010). Therefore, effective flight strokes coupled with a strong ability to jump would supply ample velocity to help achieve vertical takeoff.

Although no single locomotory behaviour tested here surpasses minimal thresholds for high incline running or powered flight, a flight stroke in stem avians may have had performance benefits to biomechanical scenarios that are more difficult to test. Specifically, feathered forelimbs, coupled with a nascent flight stroke, may have contributed subtle, but evolutionarily advantageous performance benefits to high speed maneuvering and braking and balancing during prey capture. Even slight performance enhancements to vertical and horizontal leaping may have had highly positive adaptive effects. Enhancements of even a few percent may had tremendous advantages to these predators, particularly if we compare the small margins of performance differences of extant predator-prey interactions.

CONCLUSION

All models tested here suggest that that the feathered forelimbs of all non-paravian theropods and most non-avian theropods were not capable of surpassing the minimal physical thresholds of powered flight and WAIR. The origin of pennaceous feathers was not tied to a dramatic locomotory shift in these early non-avian theropods. Non-paravian taxa such as *Caudipteryx*, *Similicaudipteryx*, and *Yixianosaurus* have forelimb feathers greater than 100 mm in length, and similar sized feathers are suspected to have been found on larger oviraptorosaurs (Paul 2002), Hop and Orsen2004), large dromaeosaurs (Depalma et al. 2015) and even ornithomimids (Zelenitsky et al. 2012; van der Reest et al. 2016). These structures represent a significant energetic investment for structures that we estimate to have had minimal locomotory benefits. Moreover, the symmetry of the vanes of the pennaceous feathers in these taxa would make the feathers aeroelastically unstable, further constraining their use in a locomotor context (even the pennaceous feathers of microraptorines may have been somewhat unstable during aerial locomotion, with vane asymmetries below the critical values for functional aeroelastic flutter reduction (Feo et al. 2015)). These taxa also possessed large tail feathers that were likely used for display (Pittman et al. 2013; Persons et al. 2014) and feather melanin based pigmentation likely coincides with the origin of pennaceous feathers (Li et al. 2010, 2014). This suggests other non-locomotory functions such as display or brooding were likely significant evolutionary driver for pennaceous feather growth (Hopp and Orsen 2004; Zelenitsky et al. 2012).

The mosaic evolution of flight related characters and the episodic pattern of thrust driven locomotion that reaches minimal thresholds across Maniraptora suggests the evolution of the flight stroke was not continuous in this clade, nor driven by a single overall driver. If different behavioural traits or locomotory functions without clear thresholds were driving the evolution of feather elongation in different lineages compared to other “pre-flight” characters, one may not expect their concordance in all members of the clade. This would explain the non-uniform distribution of traits such as the elongated forelimbs with well-developed feathers (Dececchi and Larsson 2013; Godefroit et al. 2013; Foth et al. 2014), laterally facing glenoid (Gao et al. 2012), and an ossified sternum for rigid muscle attachment (Zheng et al. 2014).

Although it is beyond the scope of this paper to speculate on which driver or combination of drivers led to feather elongation and forelimb musculoskeletal evolution for powered flight, we suggest that future research not focus on any single event or “pathway” to attempt to explain pre-avian evolution of characters later exapted into the flight apparatus. Given the long branch lengths, the time between the Paravian-avian split and the appearance of the Jehol microraptorines is approximately 40 million years, estimated from the oldest known paravian *Anchiornis* (161 Ma) and *Microraptor* (120 Ma) (Xu et al. 2000; Xu et al. 2009). Within this vast time span, a single, or a single continuous locomotory based evolutionary driver is unlikely. Moreover, it seems unparsimonious to argue that refining flapping based locomotion was central to the evolution of maniraptorans, such that it required major anatomical and physiological changes to improve it in Paraves, when no non-paravian exhibited any refinements of these morphologies and inferred behavioral performances over the 100+ million year duration of these lineages.

Although the selective pressures for each of these pathways is [illegible]known, what is apparent is it that pennaceous feathers and other critical characters related to the evolution of powered flight were not originally adapted for significantly different locomotion. It is also clear that WAIR was not a major driver for the evolution for much of Maniraptora or even Paraves. These findings reshape how we view the origins of birds and the evolution of different maniraptoran clades and refocus our investigations to look at taxa not as steps of a ladder towards the origin of flight, but as organisms adapting to the unique demands of their immediate behavioural and ecological surroundings.

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Table 1(on next page)

Table 1

Fossil taxa examined in this study. Taxa in bold were specimens without preserved forelimb remegies for whom feather lengths were estimated based on closely related taxa or other members of the same genus. For these taxa @ based on other *Archaeopteryx* specimens, # denotes estimates based on *Microraptor gui*, * based on *Anchiornis*, $ based on *Caudipteryx*. For *Jianchangosaurus* we based our estimate on the longest preserved body feather traces, this is defensible as this clade is not know to have pennaceous remegies (Foth et al. 2014) and in other maniraptorans without remegies the integument on the distal cervicals are similar in size, if not longer, than those on the forelimbs (Currie and Chen 2001).CF indicates mass estimated based on Christiansen and Farina 2004, Liu indicates avian mass estimates based on Liu et al. 2014, Fe for avian mass estimates based on Field et al. 2013 See text for discussion of body mass calculations and wing beat frequencies.

Taxa	Reference	wing length (m)	span (m)	mass (kg) CF	mass (kg) Liu	mass (kg) FE	Wing Area (m^2)	Wing loading N/M2
Anchiornis	Li et al. 2010	0.16	0.33	0.09	-	-	0.01	70
Anchiornis	Sullivan et al. 2010	0.24	0.50	0.38	-	-	0.03	146
Archaeopteryx	Foth et al. 2014	**0.31**	**0.65**	-	**0.24**	-	**0.06**	38
Archaeopteryx	Foth et al. 2014	0.31	0.65	-	-	0.36	0.06	57
Archaeopteryx	Mayr et al. 2007	**0.29**	**0.61**	-	**0.23**	-	**0.06**	38
Archaeopteryx	Mayr et al. 2007	0.29	0.61	-	-	0.32	0.06	55
Archaeopteryx	Elzanowski 2002	**0.33**	**0.69**	-	**0.31**	-	**0.07**	45
Archaeopteryx	Elzanowski 2002	0.33	0.69	-	-	0.48	0.07	70
Archaeopteryx	Mayr et al. 2007, Nudds and Dyke 2010	**0.26**	**0.55**	-	**0.18**	-	**0.05**	38
Archaeopteryx	Mayr et al. 2007, Nudds and Dyke 2010	0.26	0.55	-	-	0.25	0.05	53
Archaeopteryx	Mayr et al. 2007	**0.27**	**0.57**	-	**0.19**	-	**0.05**	36
Archaeopteryx	Mayr et al. 2007	0.27	0.57	-	-	0.27	0.05	51
Archaeopteryx	Mayr et al. 2007	**0.19**	**0.39**	-	**0.11**	-	**0.02**	47
Archaeopteryx	Mayr et al. 2007	0.19	0.39	-	-	0.14	0.02	60
Aurornis*	Godefroit et al. 2013	0.22	0.47	0.38	-	-	0.02	160
Caudipteryx	Zhou and Wang 2000	0.35	0.72	5.52	-	-	0.09	631
Caudipteryx	Sullivan et al. 2010	0.28	0.58	3.77	-	-	0.04	863
Changyuraptor #	Han et al. 2014	0.68	1.42	5.64	-	-	0.43	130
Citipati MPC-D100/971	Lu et al. 2013	0.11	0.22	0.05			0.00	397
Confuciusornis	Chiappe et al. 1999	**0.32**	**0.67**	-	**0.14**	-	**0.09**	15
Confuciusornis	Chiappe et al. 1999	0.32	0.67	-	-	0.19	0.09	20
Eoconfuciusornis	Sullivan et al. 2010	**0.22**	**0.46**	-	**0.09**	-	**0.04**	24
Eoconfuciusornis	Sullivan et al. 2010	0.22	0.46	-	-	0.12	0.04	30
Eosinopteryx	Godefroit et al. 2013	0.16	0.33	0.14	-	-	0.01	111
Jeholornis	Ji et al. 2003	**0.41**	**0.86**	-	**0.34**	-	**0.12**	29
Jeholornis	Ji et al. 2003	0.41	0.86	-	-	0.54	0.12	45
Jeholornis*	Zhou and Zhang 2002	**0.55**	**1.15**	-	**0.60**	-	**0.21**	28
Jeholornis*	Zhou and Zhang 2002	0.55	1.15	-	-	1.05	0.21	49
Jianchangosaurus	Pu et al. 2013	0.40	0.83	14.70	-	-	0.03	5018
Jinfengopteryx*	Ji et al. 2005	0.17	0.37	0.46	-	-	0.01	317
Mahakala#	Turner et al. 2011	0.20	0.42	0.67	-	-	0.03	229
Mei long*	Gao et al. 2012	0.12	0.26	0.36	-	-	0.01	505
Mei long*	Xu and Norell 2004	0.15	0.31	0.73	-	-	0.01	714
Microrpator	Li et al. 2012	0.24	0.50	0.17	-	-	0.04	46
Microrpator	Xu et al. 2003, Sullivan et al. 2010	0.41	0.86	0.88	-	-	0.12	69
Microraptor hanqingi#	Gong et al. 2012	0.47	0.98	2.05	-	-	0.18	110
Oviraptor incertae	Lu et al. 2013	0.09	0.19	0.03			0.00	305

sedis MPC-D100/1018								
Protoarchaeopteryx	Ji and Ji 1997	0.26	0.54	2.58	-	-	0.02	1445
Sapeornis	Pu et al. 2013	**0.44**	**0.92**	-	**0.51**	-	**0.12**	43
Sapeornis	Pu et al. 2013	0.44	0.92	-	-	0.88	0.12	74
Sapeornis*	Zhou and Zhang 2003	**0.57**	**1.21**	-	**0.80**	-	**0.20**	40
Sapeornis*	Zhou and Zhang 2003	0.57	1.21	-	-	1.49	0.20	74
Similicaudipteryx	Xu et al. 2009, Dececchi and Larsson 2013	0.40	0.84	4.23	-	-	0.12	345
Similicaudipteryx	Xu et al. 2009, Dececchi and Larsson 2013	0.07	0.15	0.06	-	-	0.00	372
Sinocalliopteryx	Sullivan et al. 2010	0.37	0.77	18.43	-	-	0.05	3596
Sinornithodes	Russell and Dong 1993							
Sinornithosaurus	Ji et al. 2001	0.26	0.54	1.94	-	-	0.02	1032
Sinornithosaurus	Sullivan et al. 2010	0.19	0.41	0.29	-	-	0.01	229
Sinosauropteryx	Currie and Chen 2001	0.10	0.20	0.88	-	-	0.00	4755
Sinosauropteryx	Currie and Chen 2001	0.05	0.09	0.19	-	-	0.00	11910
Sinovenator*	Benson and Choiniere 2012	0.24	0.50	2.44	-	-	0.03	919
Tianyuraptor	Chan et al. 2013, Dececchi and Larsson 2013	0.39	0.82	13.36	-	-	0.06	2272
Troodon Embryo MOR 246-1	Varricchio et al. 2002	0.08	0.16	0.05			0.00	214
Xiaotingia*	Xu et al. 2011	0.24	0.50	0.82	-	-	0.03	305
Yixianosaurus	Dececchi et al. 2012	0.29	0.61	1.30	-	-	0.04	323
Yixianosaurus	Dececchi et al. 2012	0.29	0.61	1.89	-	-	0.04	470
Yulong%	Lu et al. 2013	0.18	0.38	0.50	-	-	0.02	280
Zhenyuanlong	Lu and Brussatte. 2015	0.58	1.22	11.99	-	-	0.23	515

Table 2(on next page)

Table 2

Results of equations for calculating forces produced during WAIR and takeoff. using data from extant avians. For Chukars body mass, wing area and body velocity are based on Tobalske and Dial 2007, Flapping frequency and angle are based on Jackson et al. 2009. Coefficient of lift values (Cl) ed on Heers et al. 2011. For pigeons WAIR all data based on Jackson et al. 2011 except for wing area, which is taken from pigeons Crandall and Toblaske (2011) from pigeons with similar mass and wing length. For avian takeoff values are based on Tobalske and Dial 2000 and Askew et al. 2001.

Taxon	Stage	Body Mass (kg)	Wing Area (m^2)	flap angle (rad)	hz	m/s	BW	BW	BW	BW
							Cl=1.0	CL=1.2	CL=1.5	CL=1.6
Chukar	I	0.024	0.0036	1.57	22	0.60	0.06	0.08	-	-
Chukar	II	0.222	0.0297	2.5	18.7	1.20	0.85	1.02	-	-
Chukar	III	0.605	0.0499	2.16	18.7	1.50	0.65	0.78	0.97	1.02
Pigeon	WAIR 65^0	0.42-0.47	0.067	1.57	6.2-6.7	1.50	0.21-0.26	0.25-0.31	0.31-0.39	0.33-0.41
Pigeon	WAIR 85^0	0.42-0.47	0.067	1.57	7.3-7.7	1.50	0.28-0.31	.034-0.37	0.42-0.46	0.45-0.49
Northern Bobwhite	Take off	0.199	0.02428	2.44	19.9	3.25	-	-	-	1.25
Chukar	Take off	0.4915	0.04832	2.64	16.1	2.87	-	-	-	1.62
Ring Necked Pheasant	Take off	0.9434	0.10015	2.64	11	2.34	-	-	-	1.37
Turkey	Take off	5.275	0.34531	2.79	7.6	2.32	-	-	-	1.26
blue Breasted Quail	Take off	0.0436	0.00977	2.44	23.2	4.81	-	-	-	2.42
Harris Hawk	Take off	0.92	0.119	2.60	5.8	4.13	-	-	-	2.07
Pigeon	Take off	0.307	0.03516	2.48	9.1	2.62	-	-	-	1.19

Figure 1(on next page)

Figure 1

Mapping of highest body weight support (bw) value for fossil taxa compared to the ontogenetic trajectory of WAIR. Only 1 taxa, *Archaeopteryx* (red star) succeeds in type II (high angle) WAIR, *Microraptor* (blue star) and *Anchiornis* (purple star) succeed in low angle (type I) WAIR. while all other taxa (*Sinosauropteryx*- orange circle, *Similcaudipteryx*-yellow circle, *Mei long*-green circle) do not reach the minimal level seen for any stage of WAIR. WAIR in Chuckars modified from Jackson et al. 2009, silhouettes from phylopic images by B. McFeteers, T.M. Keesey, M. Martynuick.

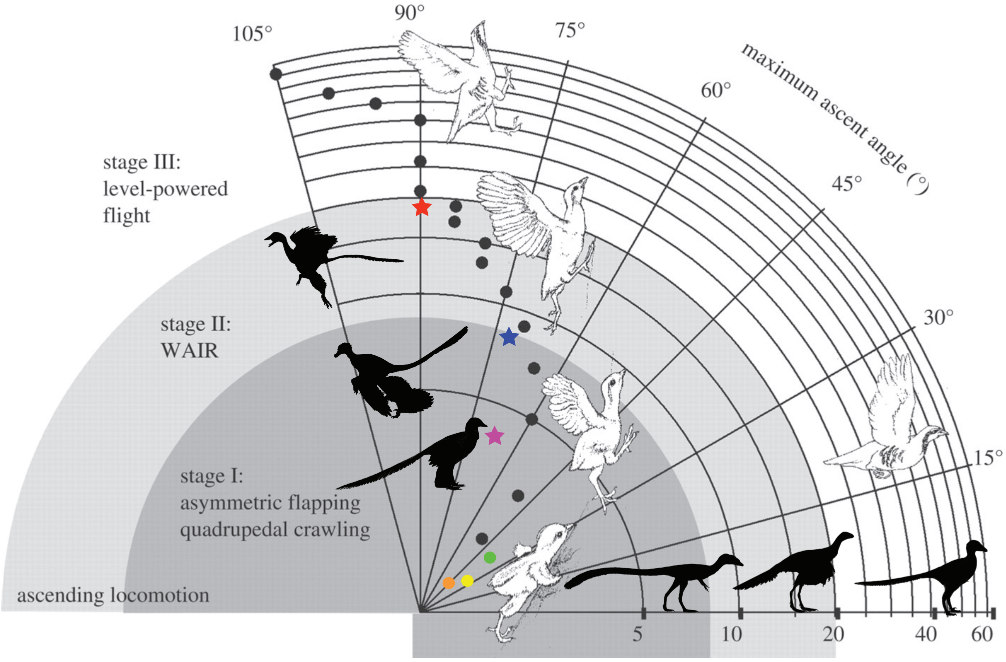

105°
90°
75°
60°
45°
30°
15°
maximum ascent angle (°)
stage III:
level-powered
flight
stage II:
WAIR
stage I:
asymmetric flapping
quadrupedal crawling
ascending locomotion
5
10
20
40
60

Figure 2(on next page)

Figure 2

Wing loading values in non-avian theropods, each open circle denotes the value per specimen for taxa with multiple specimens included in analysis. Note that only a minority of paravian specimens lines denoting Chukar values which corresponds to the when WAIR begins (3 dph) and when fledging occurs (10 dph).

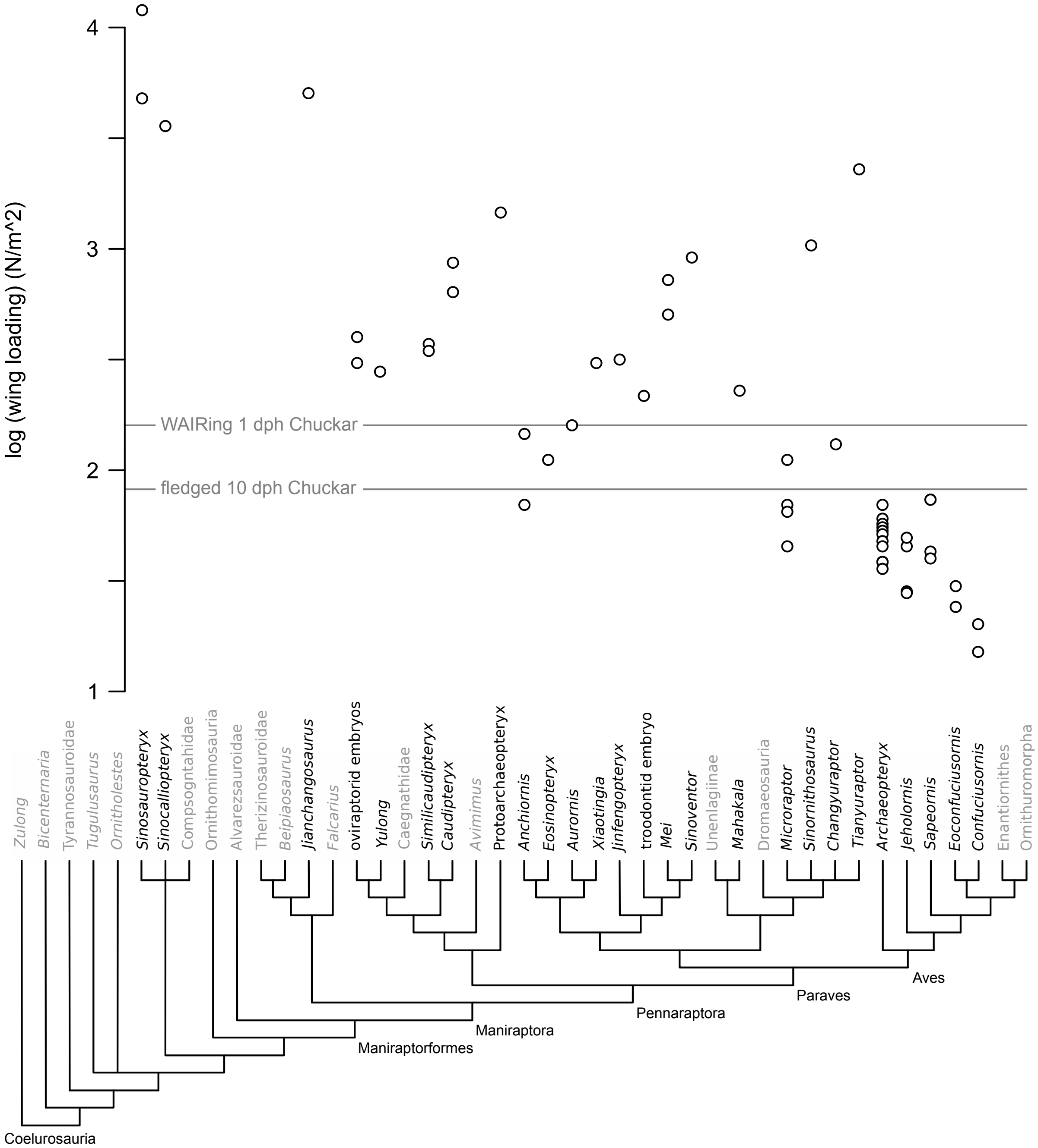
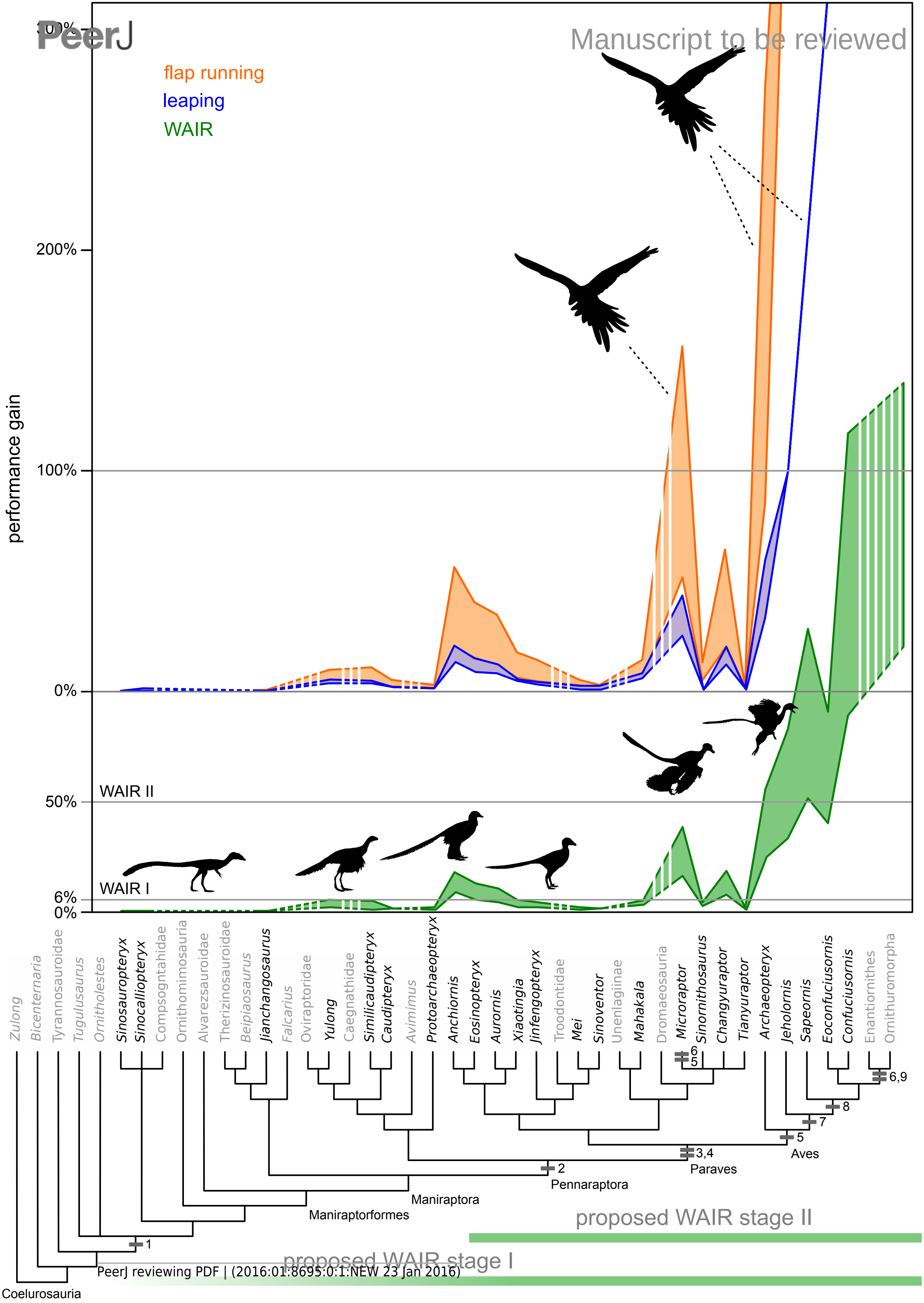

log (wing loading) (N/m^2)
1
2
3
4
WAIRing 1 dph Chuckar
fledged 10 dph Chuckar
Zulong
Bicenternaria
Tyrannosauroidae
Tugulusaurus
Ornitholestes
Sinosauropteryx
Sinocalliopteryx
Compsogntahidae
Ornithomimosauria
Alvarezsauroidae
Therizinosauroidae
Beipiaosaurus
Jianchangosaurus
Falcarius
oviraptorid embryos
Yulong
Caegnathidae
Similicaudipteryx
Caudipteryx
Avimimus
Protoarchaeopteryx
Anchiornis
Eosinopteryx
Aurornis
Xiaotingia
Jinfengopteryx
troodontid embryo
Mei
Sinoventor
Unenlagiinae
Mahakala
Dromaeosauria
Microraptor
Sinornithosaurus
Changyuraptor
Tianyuraptor
Archaeopteryx
Jeholornis
Sapeornis
Eoconfuciusornis
Confuciusornis
Enantiornithes
Ornithuromorpha
Aves
Paraves
Pennaraptora
Maniraptora
Maniraptorformes
Coelurosauria

Figure 3(on next page)

Figure 3

Evolution of flight stroke performance. Proposed evolutionary ranges of WAIR stages I and II (Dial 2003, Heers et al. 2012, 2014) are mapped under the phylogeny. Flight-stroke specific characters are mapped onto the phylogeny: 1, forelimb integument; 2, pennaceous feathers on forelimb; L-shaped scapulocoracoid; 4, laterally facing glenoid; 5, asymmetrical remigies; 6, alula; 7, incipient ligament-based shoulder stabilization; 8, dorsolaterally facing glenoid; 9, full ligament-based shoulder stabilization. Graph displays estimated percentage values for performance gains for each taxon (when present, multiple specimens are averaged). The bottom coloured lines denote 50^0 wing angles and upper coloured lines 90^0.


flap running
leaping
WAIR
performance gain
200%
100%
0%
50%
6%
0%
WAIR II
WAIR I
Zulong
Bicenternaria
Tyrannosauroidae
Tugulusaurus
Ornitholestes
Sinosauropteryx
Sinocalliopteryx
Compsogntahidae
Ornithomimosauria
Alvarezsauroidae
Therizinosauroidae
Beipiaosaurus
Jianchangosaurus
Falcarius
Oviraptoridae
Yulong
Caegnathidae
Similicaudipteryx
Caudipteryx
Avimimus
Protoarchaeopteryx
Anchiornis
Eosinopteryx
Aurornis
Xiaotingia
Jinfengopteryx
Troodontidae
Mei
Sinoventor
Unenlagiinae
Mahakala
Dromaeosauria
Microraptor
Sinornithosaurus
Changyuraptor
Tianyuraptor
Archaeopteryx
Jeholornis
Sapeornis
Eoconfuciusornis
Confuciusornis
Enantiornithes
Ornithuromorpha
6
5
6,9
8
7
5
3,4
Aves
Paraves
2
Pennaraptora
Maniraptora
Maniraptorformes
1
Coelurosauria
proposed WAIR stage II
proposed WAIR stage I