

A fundamental avian wing-stroke provides a new perspective on the evolution of flight

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The evolution of avian flight remains one of biology's major controversies, with a long history of functional interpretations of fossil forms given as evidence for either an arboreal or cursorial origin of flight. Despite repeated emphasis on the 'wing-stroke' as a necessary avenue of investigation for addressing the evolution of flight¹⁻⁴, no empirical data exist on wing-stroke dynamics in an experimental evolutionary context. Here we present the first comparison of wing-stroke kinematics of the primary locomotor modes (descending flight and incline flap-running) that lead to level-flapping flight in juvenile ground birds throughout development (Fig. 1). We offer results that are contrary both to popular perception and inferences from other studies⁵⁻⁷. Starting shortly after hatching and continuing through adulthood, ground birds use a wing-stroke confined to a narrow range of less than 20°, when referenced to gravity, that directs aerodynamic forces about 40°

above horizontal, permitting a 180° range in the direction of travel. Based on our results, we put forth an ontogenetic-transitional wing hypothesis that posits that the incremental adaptive stages leading to the evolution of avian flight correspond behaviourally and morphologically to transitional stages observed in ontogenetic forms.

Just as evolutionary developmental biology is providing remarkable advances in our understanding of the history of organismal diversity and construction of body plans, we propose that explorations of the ontogeny of post-natal behaviour and morphology among extant taxa provide insight into ecological and evolutionary locomotor transitional stages. With this perspective, we studied the locomotor development of hatchling to adult chukars (*Alectoris chukar*), a common ground bird. Here we focus on two critical variables that define the orientation of the resultant aerodynamic vector

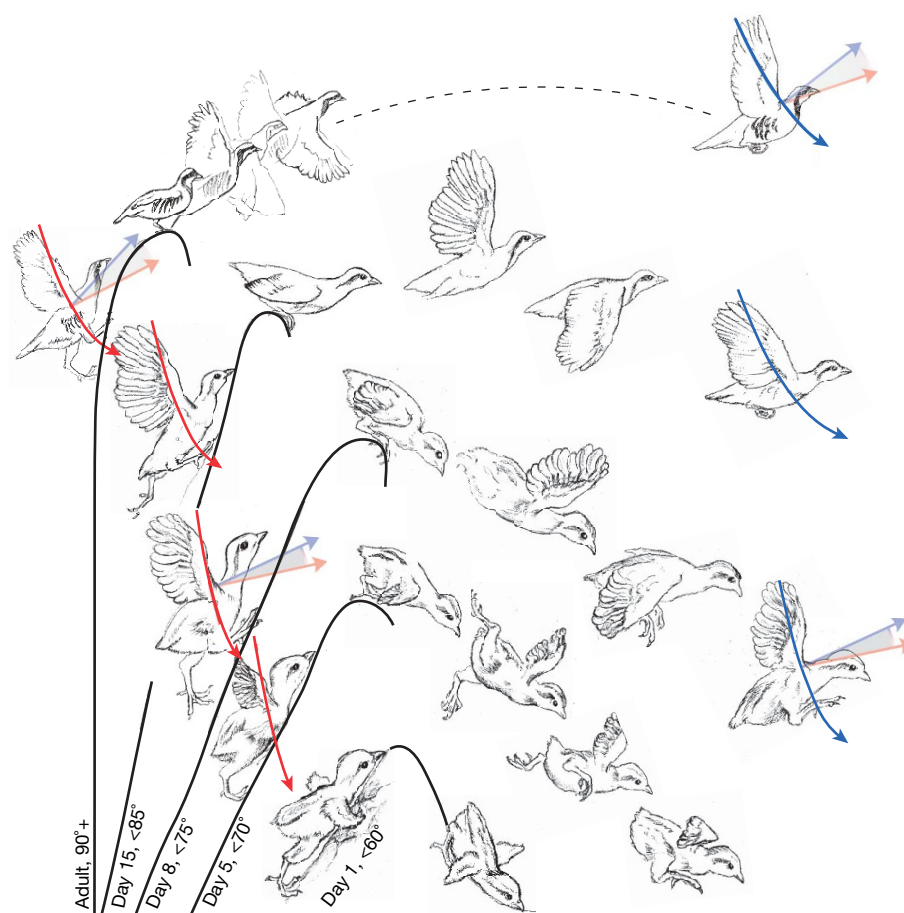


Figure 1 | Locomotor development during ontogeny in the chukar partridge from hatching to adulthood. Our data suggest a default or basal wing-stroke is used by young and adults and may exist in all birds (Supplementary Videos). The fundamental wing-stroke described herein is used days after hatching and during all ages and over multiple behaviours (that is, flap-running, descending and level flight) and is the foundation of our new ontogenetic-transitional wing hypothesis. At hatching, chicks can ascend inclines as steep as 60° by crawling on all four limbs. From day 8 through adulthood, birds use a consistently orientated stroke-plane angle over all substrate inclines during wing-assisted incline running (red arcs) as well as during descending and level flight (blue arcs). Estimated force orientations from this conserved wing-stroke are limited to a narrow wedge (see Fig. 3b).

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during flapping: (1) stroke-plane angle (SPA, the angle of the plane swept out by the wing in downstroke); and (2) angle of attack (AOA, the angle of the wing-plane). To provide a rigorous experimental investigation, we compare three-dimensional (3D) kinematics during level flapping flight (the definitive stage of aerial locomotor capacity in avian evolution) with the primary locomotor behaviours involving forelimb use that precede level flight in developing ground birds, (1) flap-descending flight and (2) flap running (also called wing-assisted incline running, WAIR^{8–11}), over a wide-range of inclines. These experimental conditions and ontogenetic stages represent a broad continuum of wing morphologies and locomotor behaviours that are exhibited by birds.

Analysing our data from the traditional vertebral frame of reference (that is, relative to the body axis, Supplementary Fig. 1), we expected and found that in all age classes, the vertebral SPA transitioned (greater than 30°) from a relatively anterior–posterior orientation during incline flap-running (WAIR), through dorso-ventral, to a slightly posterior–anterior orientation in flight (Figs 2a and 3a). Consequently, the vertebral AOA (the amount of pronation or supination of the wing with respect to the body) at the midpoint of downstroke shifted at least 45° from strongly pronated in WAIR to nearly parallel to the vertebral axis in flight (Table 1). The SPA and AOA results could be interpreted *prima facie* as aerodynamic forces acting in different directions (that is, ventrally in WAIR, dorso-anteriorly in flight) and support the observation that birds substantially change their wing-stroke when executing different behaviours. Coincidentally, most historical reconstructions of the origin of the wing-stroke and avian flight (for review, see refs 12 and 13) rely on

the vertebral axis to describe forelimb transitional stages over evolutionary time, which has impeded the development of alternative hypotheses.

Our results led us to consider alternative frames of reference¹⁴ that allow an evaluation of the function of flapping wings (whether proto- or flight-capable wings), to generate aerodynamic forces primarily to overcome gravitational forces and thus offer weight support. Therefore, we examined kinematics in two external frames of reference (global and gravitational, Supplementary Fig. 1 and Supplementary Methods). Briefly, the global frame of reference allows evaluation of aerodynamic force orientation whereas the gravitational frame of reference allows an evaluation of wing kinematics relative to gravity while accounting for the movement of the bird's body. Here we unexpectedly found SPA and AOA to be remarkably similar among vastly different locomotor behaviours (Figs 2b, c and 3, Table 1 and Supplementary Video 1). Despite the disparate orientations of travel, the estimated orientation of aerodynamic force (orthogonal to the global SPA) fell within a narrow wedge (19°, Fig. 3b). Juveniles began to exhibit a wing-stroke similar to the adults in SPA and AOA around 8 days post-hatching (Table 1, Supplementary Fig. 2 and Supplementary Videos 2 and 3). This constricted range of aerodynamic force orientation and AOA (Fig. 3c) allows a wide range of locomotor activities in juveniles and adults (Fig. 1) and strongly suggests a stereotypic or fundamental wing-stroke that we hypothesize to be functionally aligned to gravity.

This fundamental wing-stroke does not appear to be unique to the chukars or ground birds studied here. Numerous high-speed video observations by our laboratory of more than 20 avian species

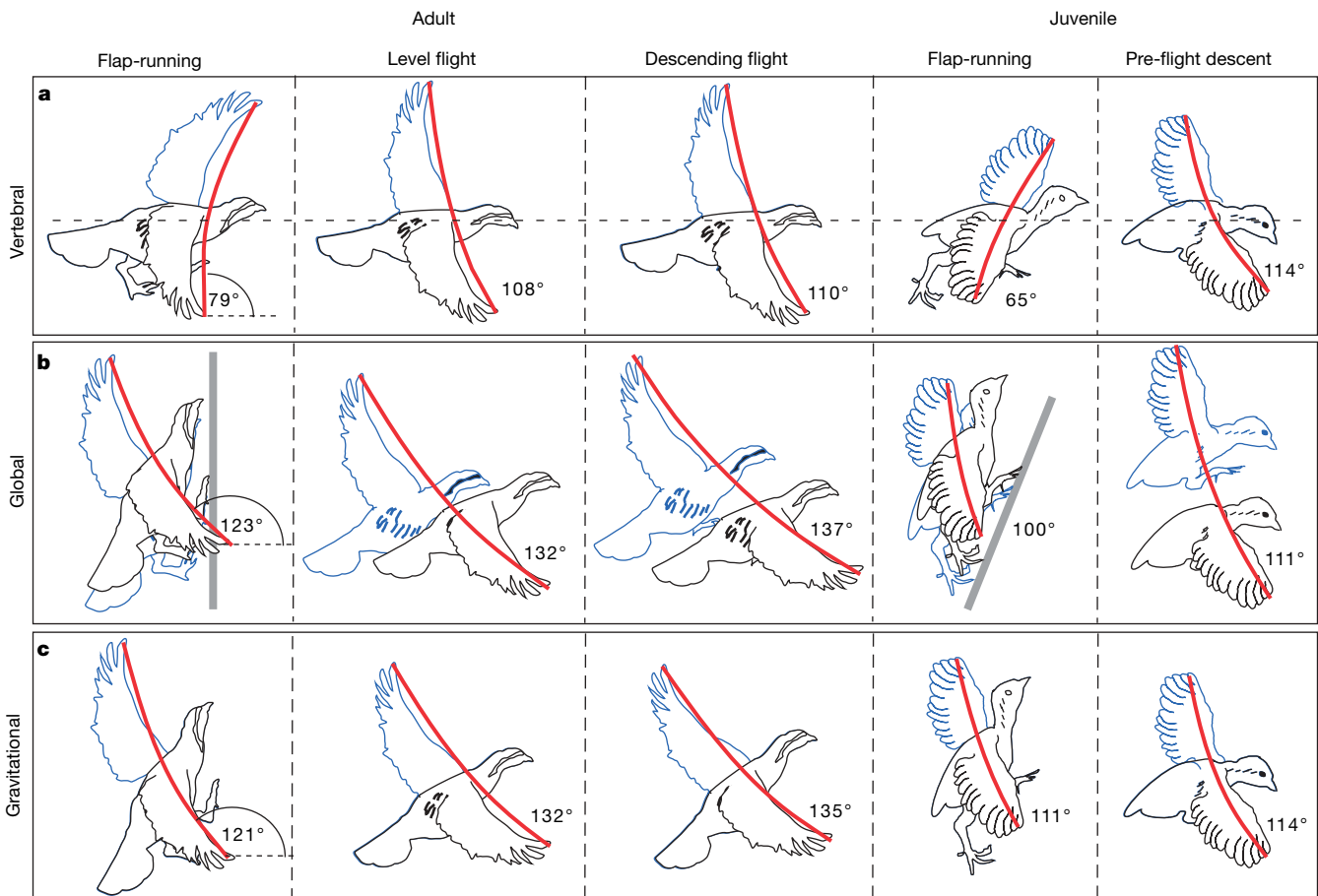


Figure 2 | Average stroke-plane angle among locomotor styles in three frames of reference. Blue and black outlines represent the positions of the bird and wing at the start and end of downstroke, respectively. **a**, In the vertebral space, the mean wing-stroke plane angle shifts more than 30° from a more antero-posterior orientation during flap-running to dorso-ventrally

in flight, implying different wing-strokes are used to execute different locomotor modes. The wing-stroke path is consistently oriented, however, in both the **(b)** global and **(c)** gravitational coordinate spaces over diverse locomotor behaviours, illustrating a simplified wing-stroke that is multi-functional. Data for juveniles are presented from 8- to 10-day olds.

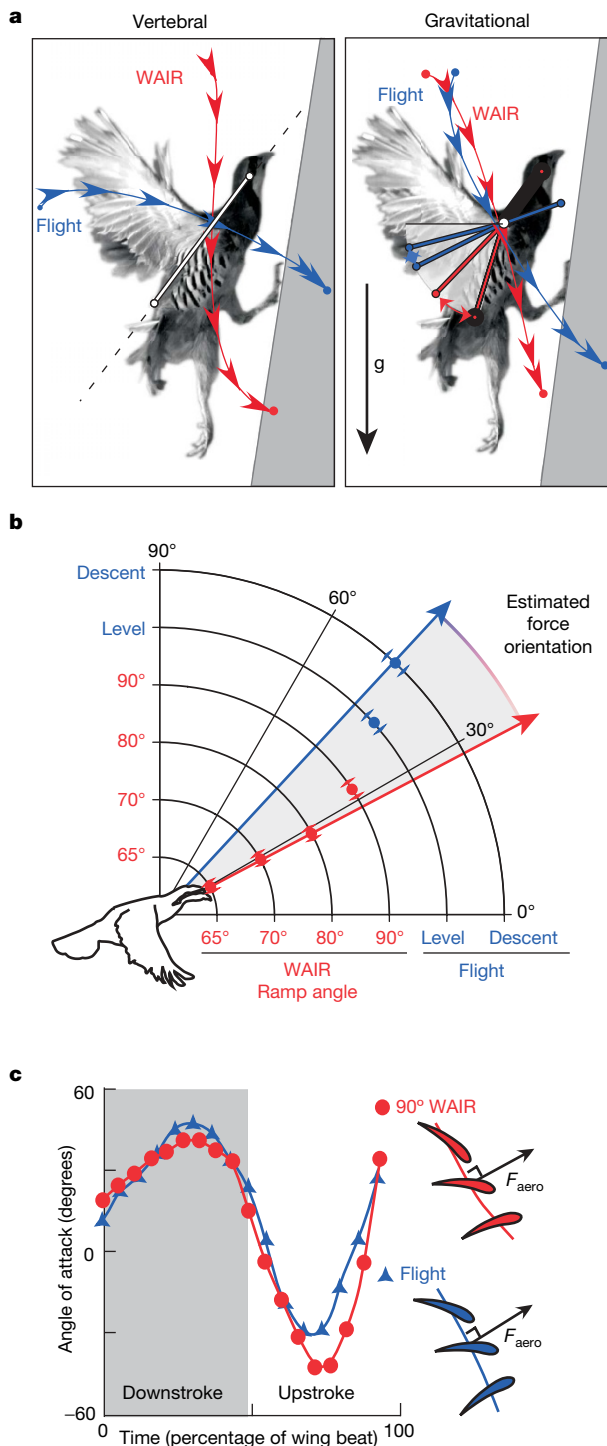


Figure 3 | Comparison of wing-stroke plane angle, estimated force orientation and angle of attack among locomotor styles. **a**, When wing-stroke plane angles are viewed side-by-side in both the vertebral and gravitational frames of reference, the wing-stroke is nearly invariant relative to gravity whereas the body axis re-oriens among different modes of locomotion. Red lines represent the wing-tip trace in WAIR (flap-running) and blue lines represent the wing-tip trace in level flight. **b**, Wing-strokes are estimated to produce similar aerodynamic forces oriented about 40° above the horizon during WAIR, level flight and descending flight. Error bars are s.e.m. **c**, Representative traces of AOA through a wing-beat for an animal flap-running vertically (red) and in horizontal flight (blue) demonstrate the similarities of AOA among behaviours. The similarities are further clarified by examining wing cross-sections and mean global stroke-planes in the first, middle and last thirds of downstroke. Here, the orientation of the aerodynamic force (F_{aero}) is estimated from the middle third.

(ranging from basal, for example Tinamiformes, to derived, for example Passeriformes; Supplementary Video 4) demonstrate that most taxa are capable of similar body axis to wing-stroke postures (during WAIR and free flight). This suggests that the fundamental wing-stroke we describe is plesiomorphic and elementary to understanding critical elements of avian locomotion, and perhaps its evolution.

We propose that this fundamental wing-stroke provides sufficient locomotor capacity for many basal taxa (for example, Tinamiformes, Galliformes, Anseriformes¹⁵) that have relatively fixed flight speeds and narrow flight styles. The range of locomotor behaviours exhibited by basal birds is accomplished by adjusting power output (estimated here from WBF and stroke amplitude; Table 1) consistent with changes in locomotor demand while slinging the body to optimal positions around the stroke-plane. Analogously, helicopters accomplish a wide range of locomotor capacity within a similarly restricted wedge of rotor plane angles by modifying power output and slinging the body of the aircraft around beneath the rotor-plane. Derived taxa (for example, Falconiformes, Columbiformes, Psittaciformes, Passeriformes) are expected to use this fundamental wing-stroke yet are capable of modifying wing excursion to allow advanced forms of aerial locomotion (for example, an array of flight speeds, which makes them more tractable for variable-speed wind-tunnel studies, more precise landings and superior manoeuvrability^{16,17}). Yet its existence in basal taxa also provides a key inference for the evolution of flight.

The general impression (including those of the authors, originally) that birds change their wing-stroke to execute different locomotor behaviours stems from casual observation of birds in the field and is reinforced by inferences generated by quantitative kinematic studies of derived taxa during flapping flight in variable-speed wind tunnels working in the vertebral frame of reference^{5–7}. Such studies accurately delineate changes in wing-stroke and body angle as birds match air speeds. In this study we allowed the birds to choose their preferred locomotor speed, as they do in natural settings and in contrast to wind-tunnel flight, we did so over a range of flapping behaviours, and we used multiple frames of reference. This alternative approach demonstrated that basal birds exhibit a relatively fixed wing-stroke and alter power to achieve differing locomotor behaviours.

The fact that this relatively fixed wing-stroke is expressed at several days post-hatching (Supplementary Fig. 2) raises the question, what function does it serve before the fledgling can achieve level flight? We now know that very young birds possessing only partly developed wings are able to produce significant and functional aerodynamic forces (even with their symmetrically constructed feathers^{10,11}, contrary to published comments^{18–23}); these forces assist them in climbing to an elevated refuge¹¹ and when they descend to a lower substrate resulting in a lower impact speed²⁴. Thus, the wing-stroke and a proto-wing have a function early in life to negotiate immediately 3D terrestrial habitats and ultimately the aerial environment. If extant flight-incapable bipeds are able to enjoy incremental aerodynamic contributions from flapping developing wings, we argue that proto-bird ancestors lacking flight-capable forelimbs may also have done so (Fig. 1).

Based on our results, we put forth an ontogenetic-transitional wing (OTW) hypothesis for the origin of flight. The hypothesis posits that the transitional stages leading to the evolution of avian flight correspond both behaviourally and morphologically to the transitional stages observed in ontogenetic forms. Specifically, from flightless hatchlings to flight-capable juveniles, many ground birds express a 'transitional wing' during development that is representative of evolutionary transitional forms. Our experimental observations reveal that birds move their 'proto-wings', and their fully developed wings, through a stereotypic or fundamental kinematic pathway so that they may flap-run over obstacles^{8–11}, control descending flight²⁴ and ultimately perform level flapping flight (Fig. 1). The OTW hypothesis provides a simple adaptive argument for the evolution of flight

Table 1 | Summary statistics for key three-dimensional kinematic variables

Kinematic variable	WAIR					F‡	Level flight		Descending flight		F§
	65°		70°	80°	90°		Adult	Juvenile	F§		
	Adult	Juvenile									
N (wing beats)	15	13	11	18	18	10	24	5			
Body angle (deg.)†	55 (3)	43 (2)	58 (2)	66 (2)	65 (4)	2.99**	47 (7)	47 (4)	−28 (12)	6.63*	
Wing beat frequency (Hz)	17.2 (0.5)	19.3 (1.0)	18.0 (0.8)	19.3 (0.1)	19.9 (0.2)	10.27**	22.7 (0.1)	20.2 (0.2)	28.6 (2)	122.01**	
Stroke amplitude (deg.)	136 (3)	144 (7)	149 (6)	151 (4)	149 (3)	3.20*	127 (7)	118 (5)	111 (23)	13.28*	
Angle of attack (deg.)	35 (1)	50 (6)	34 (2)	27 (2)	28 (2)	3.98*	30 (2)	33 (1)	42 (14)	0.01	
Stroke-plane angle (deg.)											
Vertebral	82 (3)	65.4 (4)	78 (2)	78 (2)	79 (3)	0.50	108 (2)	110 (2)	104 (7)	48.70**	
Global	120 (1)	94 (3)	119 (2)	118 (2)	123 (2)	1.45	132 (2)	137 (2)	105 (13)	12.34*	
Gravitational	118 (1)	91 (3)	116 (2)	116 (2)	121 (2)	2.29	132 (2)	135 (5)	94 (9)	13.23*	

* $P < 0.05$; ** $P < 0.001$. †All data presented as mean (s.e.m.). ‡Repeated-measures analysis of variance, factor: ramp angle (adult data). §Repeated-measures analysis of variance, factor: 90° ramp versus level flight (adult data).

and can be tested and observed in extant fledglings. This hypothesis differs from other published accounts in that it is flap-based (in contrast to requiring a gliding precursor), involves an aerodynamically functional proto-wing¹¹, incorporates both the simultaneous and independent use of legs and wings^{8–10} and assumes that a fundamental wing-stroke (described herein) was established for aerodynamic function early in the bipedal ancestry leading to birds. Such an evolutionary pathway provides a parsimonious explanation for numerous non-avian theropod morphologies (for example, semi-lunate carpal, delto-pectoral crest, furcula, proto-wings, symmetrically vaned feathers, long bipedal hindlimbs, etc.) that have not been discussed in a synthetic context.

The unequivocal morphological changes in the shoulder during the evolution of birds^{25,26} are compatible with the OTW hypothesis. The shoulder joint (glenoid) is thought to have evolved from a primitive ventro-lateral orientation allowing a cranial–caudal excursion (as observed in theropod ancestors) to the derived dorso-lateral orientation allowing a dorso-ventral excursion (among extant flying birds)²⁶. Jenkins²⁶ suggested the 90° rotation of the glenoid's excursion axis relative to the body was to accommodate the derived wing-stroke angle of extant birds. We agree with the character states Jenkins eloquently describes and offer a novel perspective about the process underlying the evolutionary sequence. We suggest the orientation of the shoulder joint remained relatively fixed in 3D space (in the global and gravitational frames of reference) over evolutionary time. This allowed the body axis to rotate, up to 90°, resulting in the observed character states of the shoulder (in the vertebral frame of reference), described above. Living ground birds exhibit a slinging of the torso about the shoulder (Fig. 3a). We suggest this same feature allowed proto-birds to use a functional wing-stroke (even with proto-wings) aligned to gravity which assisted their hindlimbs as they scaled increasingly pitched obstacles, allowed controlled flapping descent and powered rudimentary flight in the transitional stages leading to level flapping flight (Fig. 1). In other words, the gravity-based wing-stroke did not come about through a long series of migrational stages of the forelimb (from ventro-lateral to lateral to dorso-lateral): rather, the primitive wing-stroke started in a similar orientation as we see it today in hatchlings using their proto-wings.

Perhaps we can cut the Gordian knot created by the false dichotomy⁴ of the highly charged, but unresolved, cursorial–arboreal debate. The OTW hypothesis embraces salient features of both the arboreal and cursorial hypotheses yet clearly differs from both. For example, arboreal hypotheses assume a gliding form was prerequisite to flapping flight because half a wing would have no function, and that the flap-stroke appears too complex and thus relegated to the derived condition. However, this line of reasoning is inconsistent with observations of all extant forms. For example, gliding and soaring are essentially absent in the most basal avian clades (that is, Tinamiformes, Galloanserae¹⁵) as well as in early ontogenetic stages of all birds: these forms flap their forelimbs. We propose gliding to be the derived condition within Aves because it is mostly confined to

adult-sized individuals of non-basal taxa. A serious flaw with the assumption of a gliding precursor transitioning towards flapping is the fact that not a single species, among hundreds of living non-avian vertebrate gliders, flaps their webbed appendages to generate powered thrust or lift. Commonly held assumptions within the cursorial school about the plausible function of proto-wings are inconsistent with the ontogenetic biology of extant forms; for example, no extant species uses its wings to run faster, to secure prey or run–glide.

Locomotor abilities of extinct taxa, such as the recently discovered fossil forms possessing what is assumed to be 'half a wing'^{27,28} and long cursorial legs²⁹, might be better understood if we evaluate how proto-wings and hindlimbs function during ontogeny in extant taxa^{8,10}. Our experimental observations show that proto-wings moving through a stereotypic and conserved wing-stroke have immediate aerodynamic function, and that transitioning to powered flapping flight is limited by the relative size of the wing and muscle power, rather than development of a complex repertoire of wing-beat kinematics.

METHODS SUMMARY

We used four internally synchronized high-speed digital video cameras (250 Hz, 1250 s^{−1}) to record chukars every two days, beginning one day after hatching through to adulthood, while they passed through a 3D calibrated volume. We quantified 12 kinematic variables (wing beat frequency, duty factor, body and wing velocities, wing angular velocity, body angle, stroke amplitude, stroke plane angle, angle of attack, dynamic wing loading, dynamic wing length and actuator disc loading) in 3D space to characterize body and wing dynamics (Supplementary Fig. 1). Ten points on the right wing and body were marked with reflective tape, digitized and analysed by direct linear transformation in Ariel Performance Analysis Software (Ariel Dynamics, Inc.). Computations of vectors, planes and angles were performed in a custom program within IGOR Pro (WaveMetrics, Inc.).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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- Gauthier, J. A. & Padian, K. in *The Beginnings of Birds: Proc. Int. Archaeopteryx Conf., Eichstatt 1984* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 185–197 (Freunde des Jura-Museums, Eichstatt, West Germany, 1985).
- Padian, K. The origins and aerodynamics of flight in extinct vertebrates. *Paleontology* **28**, 413–433 (1985).
- Padian, K. & Chiappe, L. M. The origin of birds and their flight. *Sci. Am.* **278**, 38–47 (1998).
- Padian, K. in *New Perspectives on the Origin and Early Evolution of Birds. Proc. Int. Symp. in Honor of J. H. Ostrom* (eds Gauthier, J. A. & Gall, L. F.) 255–272 (Special Publication of the Peabody Museum of Natural History, New Haven, 2001).
- Tobalske, B. W. & Dial, K. P. Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *J. Exp. Biol.* **199**, 263–280 (1996).
- Hedrick, T. L., Tobalske, B. W. & Biewener, A. A. Estimates of circulation and gait change based on a three-dimensional kinetic analysis of flights in cockatiels (*Nymphicus hollandicus*) and ringed turtle-doves (*Streptopelia risoria*). *J. Exp. Biol.* **205**, 1389–1409 (2002).

7. Park, K. J., Rosén, M. & Hedenström, A. Flight kinematics of the barn swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel. *J. Exp. Biol.* **204**, 2741–2750 (2001).
8. Dial, K. P. Wing-assisted incline running and the evolution of flight. *Science* **299**, 402–404 (2003).
9. Bundle, M. W. & Dial, K. P. Mechanics of wing-assisted incline running (WAIR). *J. Exp. Biol.* **206**, 4553–4564 (2003).
10. Dial, K. P., Randall, R. J. & Dial, T. R. What use is half a wing in the ecology and evolution of birds? *Bioscience* **56**, 437–445 (2006).
11. Tobalske, B. W. & Dial, K. P. Aerodynamics of wing-assisted incline running in birds. *J. Exp. Biol.* **210**, 1742–1751 (2007).
12. Chiappe, L. M. *Glorified Dinosaurs: The Origin and Early Evolution of Birds* (Wiley, New York, 2007).
13. Witmer, L. M. in *Mesozoic Birds: Above the Heads of Dinosaurs* (eds Witmer, L. M. & Chiappe, L. M.) 3–30 (Univ. California Press, Berkeley, 2002).
14. Gatesy, S. M. & Baier, D. B. The origin of the avian flight stroke: a kinematic and kinetic perspective. *Paleobiology* **31**, 382–399 (2005).
15. Sibley, C. G. & Ahlquist, J. E. *Phylogeny and Classification of Birds, a Study in Molecular Evolution* (Yale Univ. Press, New Haven, 1990).
16. Warrick, D. R. & Dial, K. P. Kinematic, aerodynamic and anatomical mechanisms in the slow, maneuvering flight of pigeons. *J. Exp. Biol.* **201**, 655–672 (1998).
17. Hedrick, T. L. & Biewener, A. A. Low speed maneuvering flight of the rose-breasted cockatoo (*Eolophus roseicapillus*) I. Kinematic and neuromuscular control of turning. *J. Exp. Biol.* **210**, 1897–1911 (2007).
18. Feduccia, A. & Tordoff, H. B. Feather of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. *Science* **203**, 1021–1022 (1979).
19. Norberg, U. M. in *The Beginnings of Birds: Proc. Int. Archaeopteryx Conf., Eichstatt 1984* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 293–302 (Freunde des Jura-Museums, Eichstatt, West Germany, 1985).
20. Norberg, R. A. in *The Beginnings of Birds: Proc. Int. Archaeopteryx Conf., Eichstatt 1984* (eds Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 303–318 (Freunde des Jura-Museums, Eichstatt, West Germany, 1985).
21. Speakman, J. R. & Thomson, S. C. Feather asymmetry in *Archaeopteryx*. *Nature* **374**, 221–222 (1995).
22. Garner, J. P., Taylor, G. K. & Thomas, A. L. R. On the origins of birds: the sequence of character acquisition in the evolution of avian flight. *Proc. R. Soc. Lond. B* **266**, 1259–1266 (1999).
23. Paul, G. S. *Dinosaurs of the Air* (Johns Hopkins Univ. Press, Baltimore, 2002).
24. Segre, P. & Dial, K. P. Half a wing in motion: the ontogeny and wing kinematics of WAIR in chukars. *Int. Comp. Biol.* **45**, 1191 P2.48 (2006).
25. Ostrom, J. H. Some hypothetical anatomical stages in the evolution of avian flight. *Smithson. Contr. Paleobiol.* **27**, 1–21 (1976).
26. Jenkins, F. A. The evolution of the avian shoulder joint. *Am. J. Sci.* **293**, 253–267 (1993).
27. Xu, X. *et al.* Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**, 680–684 (2004).
28. Padian, K. & Dial, K. P. Origin of flight: could ‘four-winged’ dinosaurs fly? *Nature* **438**, E3 (2005).
29. Jones, T. D., Farlow, J. O., Ruben, A., Henderson, D. H. & Hillenius, W. J. Cursoriality in bipedal archosaurs. *Nature* **406**, 716–718 (2000).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Animal care and training. The chukar partridge (*Alectoris chukar*) is a ground bird that preferentially uses WAIR over flight to reach elevated refuges when threatened^{8–10}. Chukars (592 ± 24 g, mean \pm s.e.m.) were obtained from a commercial breeder, housed in outdoor aviaries at the Fort Missoula Research Station of the University of Montana, and given food and water *ad libitum*. For the ontogenetic series, eggs were obtained from a commercial breeder and incubated indoors until hatching. Chicks were left in the incubator up to 24 hours after hatching, then removed to an indoor climate controlled room at Fort Missoula Research Station with food and water *ad libitum*. All the experimental procedures were approved by the University of Montana Institutional Animal Care and Use Committee (IACUC: protocol #016-03KDDBS-010104).

Three adults were trained to run to an elevated perch by an inclined (65° , 70° , 80° and 90°) ramp covered with coarse sandpaper (36 grit). The training served to familiarize the birds with the experimental environment so that they maintained a consistent level of performance and fitness, even though chukars perform WAIR without training. The trained birds plus four other birds were used to study horizontal and descending flight, which was induced by stimulating the birds to fly from a raised perch down a large flight corridor or to the floor, requiring no training.

The chicks, starting the day after hatching, were encouraged to climb a small ramp set at 65° to reach a group of cohorts housed in a box at the top of the ramp. This natural inclination to rejoin a group, and an innate ability to climb ramps, eliminated any need for training. Similarly, a lone chick placed upon an elevated perch (1 m) readily launched itself to the ground to rejoin a group of chicks sitting on a thick foam pad below.

Data acquisition and analyses. Bouts of flapping locomotion were recorded by using four internally synchronized high-speed digital video cameras (250 frames per second, shutter 1250^{-1} s, two Redlake Motionscope PCI, Redlake MASD and two Troubleshooter HR, Fastec Imaging). The body and one wing of each bird was marked using 25 mm^2 (adults) or 9 mm^2 (chicks) tabs of reflective tape (3M, part no. 8850) on the head, the rump (on the midline between the acetabula), at the shoulder, the wrist, the longest primary (wing tip), the fourth primary, the first secondary and the longest tertial. The rump marker was used to estimate the movement of the centre of mass, and the rump and shoulder markers were used to define the vertebral axis of the bird.

The recordings were digitized in Ariel Performance Analysis System software (Ariel Dynamics Inc.), which uses a direct linear transformation to convert the two-dimensional videos into a three-dimensional volume. We calibrated the filmed volume using a 24-point calibration frame (0.7 m^3) around the adult ramp, a 24-point frame (0.4 m^3) around the small ramp, and a 30-point frame (1.5 m^3) for the horizontal and descending flight trials. Coordinate values (x , y , z) of each marker were smoothed and velocity measurements calculated with a quintic spline in Ariel Performance Analysis System software. All values were then interpolated using the smoothing spline feature (smoothing factor = 0) in Igor Pro (version 6.0, Wavemetrics, Inc.) to allow for determination of values at exact times. We found less than 5% positional error in the digitizing and analysis techniques by filming a mock wing marked to simulate the size and shape of an adult chukar wing.

Three-dimensional vectors were created between pairs of neighbouring points at each point in time. We used three frames of reference, which differ in the placement of the origin and the orientation of the x and y axes, to calculate 3D coordinates: (1) the vertebral frame of reference: the x axis lies along rump-shoulder, the y axis points dorsally, the z axis points laterally, and the origin is fixed to the shoulder; (2) the gravitational frame of reference: the origin is fixed to the shoulder, but the y axis is parallel to gravity and the x axis is horizontal; (3) the global frame of reference: the y axis is parallel to gravity, the x axis is horizontal, and the origin is fixed in space (Supplementary Fig. 1).

We defined the kinematic start and end of downstroke by the interpolated turnaround times of the wrist. For each downstroke, we calculated numerous 3D kinematic variables throughout the wing beat in all three frames of reference. The vertebral stroke angle, gravitational stroke angle and global stroke angle describe the angle in the x - y plane (parasagittal to the bird) between the plane traced out by the wingtip and the x axis. Because the stroke angle is used to estimate the direction of aerodynamic force, the z components (transverse) of the left and right wings should cancel, and hence were ignored. All stroke angles presented here are calculated from 16% to 83% (the middle 67%) of the time of each downstroke. The actuator disc area for both wings is calculated as twice the area of the plane swept out by the leading edge of the target wing during the entire downstroke in the global frame; the actuator disc loading is the mass of the bird divided by the disc area. Stroke amplitude is defined as angle swept out by the leading edge from the start to the end of downstroke in the vertebral frame. Angular velocity is given as the average over the entire downstroke, calculated as the stroke amplitude divided by the duration of downstroke.

As with the wing movement, the plane of the wing is described in multiple frames of reference. The vertebral wing angle is defined as the angle between the plane of the wing and the plane containing the x axis and the leading edge. We also calculated the AOA, which is the angle between the plane of the wing and the incoming air velocity. The air velocity for a freely moving wing has two components: the absolute velocity of the wing, measured from the video; and the induced velocity about the wing. The highly unsteady nature of slow flight and flapping in WAIR prevented us from attempting an estimate of induced velocity, thus AOA is not a measure that can be used to estimate the absolute magnitude of aerodynamic forces. Vertebral wing angle and AOA are presented as the surface-area weighted average of the hand-wing and arm-wing wing angles.

The dynamic surface area of the right wing was calculated by using triplets of markers to divide the wing into four triangles; the dynamic wing loading is the bird's mass divided by double the area of the right wing.

Statistical analysis. We found no significant differences between kinematic variables of individual birds. Thus we present means and s.e.m. for each treatment (for example, ramp angles, level, descending flight) from all the wing beats pooled. To test the effects between treatments, we used a repeated-measures analysis of variance (Igor Pro, version 6.0, Wavemetrics, Inc.). Tests were run among all angles of WAIR, between level and descending flight, and between vertical WAIR and level and descending flight. In figures and text we refer to the treatment mean \pm s.e.m. among individuals.