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The wing of *Archaeopteryx* as a primary thrust generator

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Since the late 1800s, the debate on the origin of flight in birds has centred around two antagonistic theories: the arboreal (take-off from trees) and cursorial (take-off from running) models^{1–6}. Despite broad acceptance of the idea that birds evolved from bipedal and predominantly terrestrial maniraptoriform dinosaurs^{1,7}, the cursorial model of flight origins has been less successful than the arboreal model. Three issues have contributed to this lack of success: the gap between the estimated maximum running speed of *Archaeopteryx* (2 metres per second) and its estimated minimum flying speed (6 metres per second)⁸; the high energy demands of evolving flight against gravity^{2,3}; and the problem of explaining the origin of the 'flight' stroke in an earthbound organism^{3,4}. Here we analyse the take-off run of *Archaeopteryx* through lift-off from an aerodynamic perspective, and emphasize the importance of combining functional and aerodynamic considerations with those of phylogeny^{1,9,10}. Our calculations provide a solution to the 'velocity gap' problem and shed light on how a running *Archaeopteryx* (or its cursorial maniraptoriform ancestors) could have achieved the velocity necessary to become airborne by flapping feathered wings.

Although, as a flier, it probably represents a relatively late stage in the evolution of bird flight, *Archaeopteryx* plays a central role in the debates on the origins of flight^{2–6,11}. Proponents of the arboreal model consider *Archaeopteryx* to have been a tree climber, but evidence in support of this is weak at best^{1,12–14}. Despite lacking the pulley-like action of the supracoracoid muscle of modern birds, which probably limited its capacity for carrying out fast, high-

amplitude wing beats¹⁵, *Archaeopteryx*'s pectoral musculature was apparently sufficient for flapping¹⁶. This conclusion is also supported by the lateral orientation of its glenoid facet¹⁷ and the passive pronation-supination of its hand, as inferred from its wrist morphology¹⁸. Thus, *Archaeopteryx* appears to have been a predominantly terrestrial animal that, given the limited volume of its pectoral muscles and the relatively low amplitude of its wing beat, presumably had to run to take off^{9,19}, flapping its wings in a fashion similar to that of large extant birds²⁰.

Our aerodynamic model begins with *Archaeopteryx* initiating the take-off run with forward propulsion generated by its hindlimbs at the same time as it starts flapping its wings (Figs 1, 2). Calculations indicate that, during the take-off run, the initial hindlimb-supplied propulsion is gradually replaced by wing thrust (see Methods). Simultaneously, the lift generated by the wings—here called 'residual' as it does not exert work on the bird until lift-off—'unloads' the hindlimbs of the body weight (Fig. 2). This dual force migration (propulsion and body weight support) from the hindlimbs toward the wings has profound implications for the estimated maximum running speed of *Archaeopteryx*. Clearly, flapping increases the bird's running speed. As the residual lift due to flapping relieves the hindlimbs of body weight support, its running speed is further increased, which, in turn, increases the residual lift (which increases with the square of the running speed). At a certain point in the take-off run, the residual lift becomes greater than the bird's weight and so is converted to useful lift: *Archaeopteryx* takes off. At this point, lift becomes a force that exerts work on the bird. Wing thrust is now the sole source for generating the velocity necessary for sustained lift.

Previous calculations for the maximum running speed of *Archaeopteryx* assumed that its hindlimbs alone generated propulsive force and provided support for its full weight during the take-off run⁸. However, when the proposed upward force migrations are considered, *Archaeopteryx* can reach its estimated minimum flying speed (6 m s⁻¹ in ref. 8), 7.8 m s⁻¹ in our model) by means of the thrust and residual lift produced by its flapping wings. Our calculations indicate that, 3 s after beginning its take-off run, *Archaeopteryx* would have achieved a speed of 7.8 m s⁻¹. Extant lizards are known to have burst speeds which last for much longer times²¹, and there is no indication that *Archaeopteryx* was metabolically incapable of the same. Thus, the 'velocity gap' ceases to exist.

This study indicates that *Archaeopteryx*'s wings may have been an efficient aerodynamic thrust generator. Although lift generation has been the focal point of most aerodynamic discussions on the origin of flight²², the importance of thrust has often been underexplored. Thrust, however, must have played a fundamental role in the origin of flight. As shown in our calculations, thrust is the only force that exerts work on *Archaeopteryx* along its entire take-off run (residual lift does not exert any work). Thus, we regard thrust, and not lift, as the primordial force ultimately responsible for sustained flight. Because the direction of thrust is perpendicular to that of gravity, not against it, objections to the cursorial theory on the basis of strenuous energetic demands² may not be relevant.

Even though our study centres on *Archaeopteryx*, our conclusions can be applied equally to non-avian maniraptoriforms flapping their wings in a downstroke–upstroke fashion. It is likely that these dinosaurs had the ability to passively supinate and flex their forelimbs^{9,18} as well as to flap them within ranges comparable to those of *Archaeopteryx*^{9,23}. Some of them have even been found to possess fully fledged wings²⁴. Thus, the structures and functions necessary for wing-generated thrust were already present in the flightless ancestors of birds. Long, vaned feathers, like those of the non-avian theropods *Caudipteryx* and *Protarchaeopteryx*²⁴, and the 'flight' stroke evolved in the context of terrestrial thrust. As previously implied^{25,26}, wing-generated thrust evolved before useful lift. Using this thrust and its ensuing residual lift, the flightless

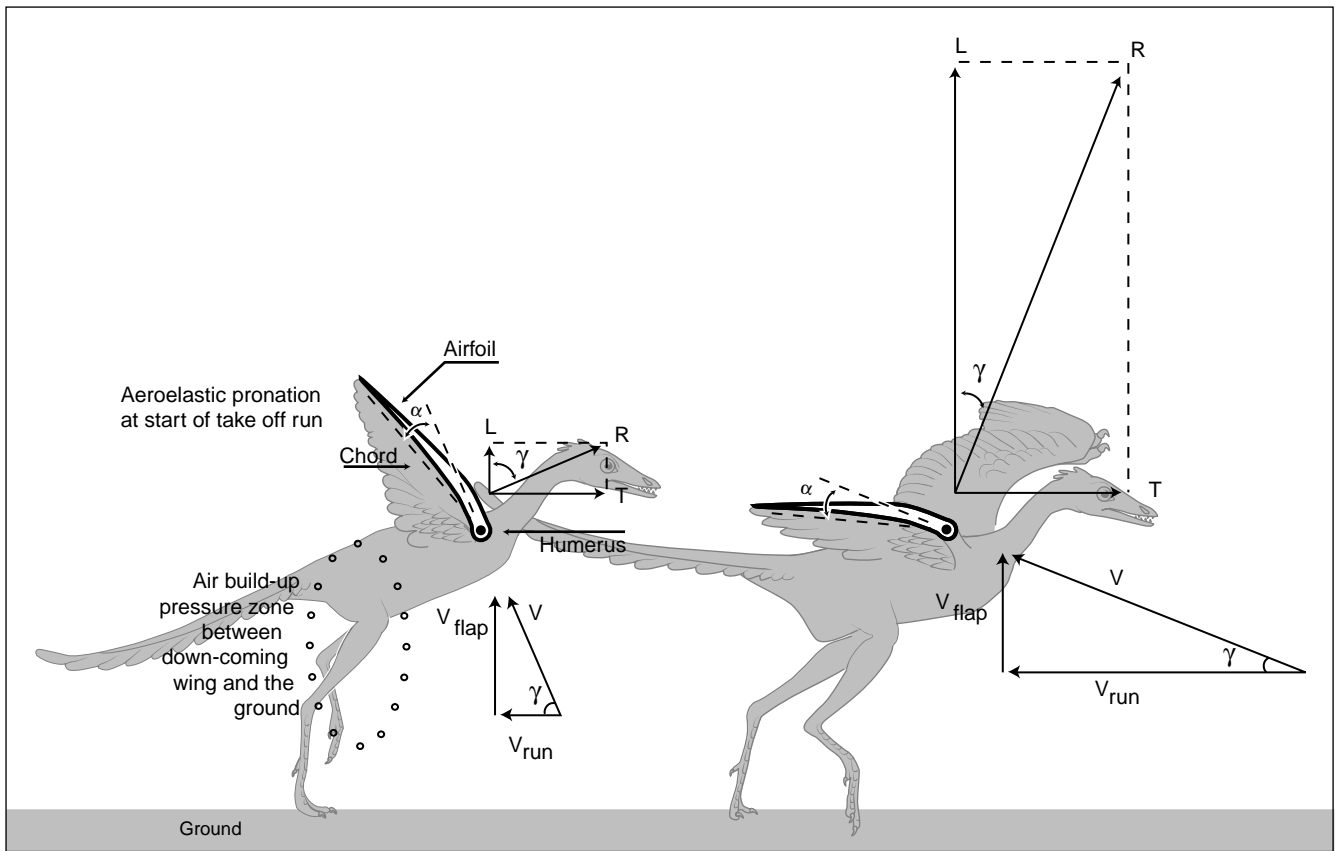


Figure 1 Vectorial representation (not to scale) of thrust generation and aeroelastic response at low running speeds (bold symbols represent vectors). While running at the speed V_{run} (left), *Archaeopteryx* flaps its wings downward with a velocity V_{flap} and encounters the upcoming flow V at a steep angle with the horizon (wing path angle γ). During the downstroke, the airfoil aligns itself to the upcoming airflow by rotating aeroelastically, trailing edge up, owing to the pressure build-up between the wing and the ground (elliptical dotted zone). This aeroelastic response is possible because the feathered wing of *Archaeopteryx*

is attached to the body only at the shoulder. This alignment is also expected as the result of wrist pronation along its semilunate carpal¹⁸. Thus, the wing meets the incoming airflow V at an angle α and generates R , an aerodynamic force perpendicular to V . The horizontal and vertical projections of R are thrust T and lift L , respectively. As the running speed increases (right), the aerodynamic resultant R increases its magnitude and rotates counterclockwise. This rotating is due not to an induced drag increase but to an increase in the thrust and lift components. All forces shown are aerodynamic forces, not net forces on the bird.

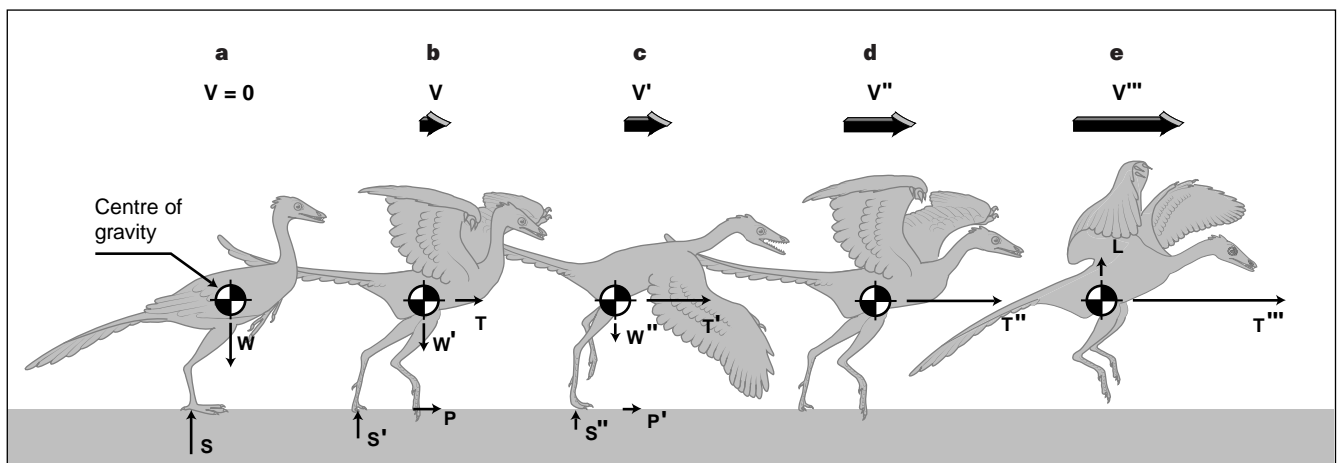


Figure 2 Net forces on *Archaeopteryx* throughout its modelled take-off run. The increasingly larger vectors (V to V''') depict the incremental velocity of *Archaeopteryx*. **a**, At standstill *Archaeopteryx* weighs W and the hindlimbs provide an equal and opposite force S to counteract it. **b**, At the beginning of the take-off run, *Archaeopteryx*'s hindlimbs produce a forward propulsion P , and when it starts to flap its wings these produce a thrust T . Owing to the generation of residual lift L , the hindlimbs need to supply a smaller upward force S' to counter the smaller net weight W' . This is called the 'vertical force migration'. **c**, During the take-off run, thrust T' gradually overtakes the propulsion P' (W'' and S'' decrease as a result of the vertical force migration). The migration of the forward force from

propulsion to thrust is called the 'horizontal force migration'. **d**, An instant before lift off, the horizontal force migration is completed and propulsion P' has disappeared. The only net force acting on the bird is thrust T'' . The vertical force migration is also completed, and the residual lift now equals weight. **e**, At lift-off, residual lift transitions into useful lift L . L , now a vertical net force, exerts work on the bird, lifting it up; this force translates into an ascensional velocity. Thrust T''' continues to exert work on the bird. 'Residual lift' refers to a lift force that does not act as a net force and that, as long as it is smaller than the bird's weight is unable to exert any vertical work on the bird. Since it is not a net force, residual lift is not depicted in **a-d**.

Table 1 Data for the curves of residual lift and net thrust in Fig. 3

	V_{run} (m s ⁻¹)	Net thrust (N)	Residual lift (N)	Weight (N)
Instant after standstill	0.15	0.32	0.013	1.96
	1.43	0.34	0.15	1.96
	2.71	0.37	0.34	1.96
Halfway through take-off run	3.99	0.45	0.61	1.96
	5.28	0.52	0.96	1.96
	6.56	0.60	1.41	1.96
At lift-off	7.84	0.66	1.96	1.96

Values for running velocity V_{run} , net thrust, residual lift and weight are given for an instant after standstill, half through the take-off run and at lift-off. Flapping frequency, 9.3 Hz. See Methods for equations.

ancestors of birds increased their cursorial velocity and ability to jump great heights.

Explanations of flight origins are conjectural and, as such, unlikely ever to be tested. The origin of bird flight from cursorial theropods is, however, not only the least conflicted hypothesis given the available phylogenetic and functional data but, as illustrated here, is also aerodynamically achievable. □

Methods

Our parameters for *Archaeopteryx* are those given by Rayner^{8,16} and Yalden²⁷; our mathematical model agrees with those used in take-off studies of large extant birds²⁰. In our model, an *Archaeopteryx* weighing 1.96 N (0.2 kg) runs and flaps its wings at 9.3 Hz. The wings accelerate uniformly downwards. The final vertical velocity of the wings (at the end of the downstroke) is calculated by $V_f = f_s \phi b v$, where f_s is the sum of wing strokes per second (18.6) (each cycle consisting of a downstroke and an upstroke), ϕ is the angle subtended by the wings during the downstroke (50°), b is the wingspan (0.58 m), and v is the span-wise wing station at which the vectorial calculations are performed (0.7 or 70% of semispan). The average flapping velocity of the wing V_{flap} is half the value of V_f . To calculate the relative air velocity across the airfoil V , the Pythagorean theorem is applied to add V_{run} and V_{flap} vectorially (Fig. 1). Throughout the calculations, V_{run} is considered to be an independent variable and ranges between 0.15 m s⁻¹ and 7.84 m s⁻¹ (take-off speed; headwinds would reduce this value) (Fig. 3; Table 1). The wing path angle γ is calculated by the arctangent of V_{flap}/V_{run} . The resultant aerodynamic force vector generated by the wing is calculated by $\mathbf{R} = (0.5)\rho V^2 CLS \mathbf{p}$ where ρ is the air density, V is the velocity, CL is the lift coefficient (2), S is the wing area (0.0479 m²), and p is an average factor that considers lift being generated only during the downstroke (0.5). The relatively high value for lift coefficient (for the low Reynolds number of the wing) adopted here may be due to the combined effects of the proximity

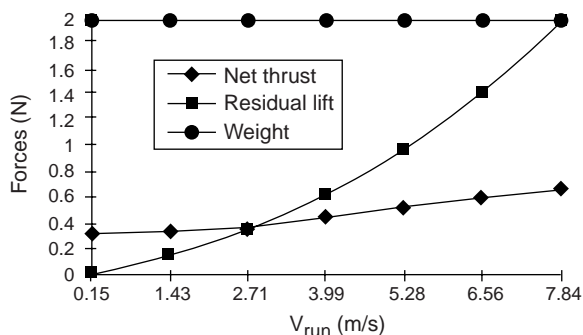


Figure 3 Progression of residual lift and net thrust throughout the modelled take-off run of *Archaeopteryx*. An instant after starting the take-off run, the thrust generated by flapping is 24 times higher than the residual lift (Table 1). Although for much of the take-off run the lift exerted on the bird is higher than thrust, thrust is the only force exerting work on the bird and increasing continuously the level of its kinetic energy. The cumulative power exerted by the thrust on the bird at a certain time during the take-off run can be calculated by the area under the thrust curve, from the beginning of the run until that time. At lift-off (the intersection of the residual lift and the weight curve), *Archaeopteryx* has reached the kinetic energy necessary for flight; residual lift cancels out weight. Residual lift becomes useful lift at lift-off.

of starting vortices on the upper side of the wing favouring pressure gradients, enhanced leading edge vortex lift, ground effect, and lift hysteresis²⁸. Given that vector \mathbf{R} is always perpendicular to the incoming flow \mathbf{V} , its inclination is also known (γ with respect to the horizontal). Thrust T and residual lift L are calculated by the horizontal and vertical projection of \mathbf{R} , respectively. The mathematical basis for the vertical force migration is that, during the take-off run, the sum of all vertical forces on the bird must be zero, because no vertical acceleration exists.

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Induction and organization of Ca²⁺ waves by enteric neural reflexes

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The motility of the gastrointestinal tract consists of local, non-propulsive mixing (pendular or segmental) and propulsive (peristaltic) movements^{1–5}. It is generally considered that mixing movements are produced by intrinsic pacemakers which generate rhythmic contractions^{4–6}, and peristalsis by intrinsic excitatory and inhibitory neural reflex pathways^{1–5,7,8}, but the relationship between mixing and peristalsis is poorly understood^{4–6}. Peristalsis is compromised in mice lacking interstitial cells of Cajal⁹, suggesting that these pacemaker cells^{10–14} may also be involved in neural reflexes. Here we show that mixing movements within long-