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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 [1,2,3,4,5,6]. 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 [2,3,4,5,6,11]. Proponents of the arboreal model consider *Archaeopteryx* to have been a tree climber, but evidence in support of this is weak at best [1,12,13,14]. 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 beats [15] *Archaeopteryx's* pectoral musculature was apparently sufficient for flapping[16]. This conclusion is also supported by the lateral orientation of its glenoid facet[17] and the passive pronation-supination of its hand, as inferred from its wrist morphology [18]. 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 birds [20].

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.

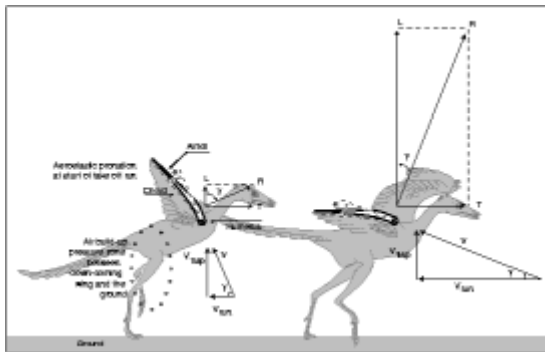


Figure 1 Vectorial representation (not to scale) of thrust generation and aeroelastic response at low running speeds (bold symbols represent vectors).

[Full legend](#)

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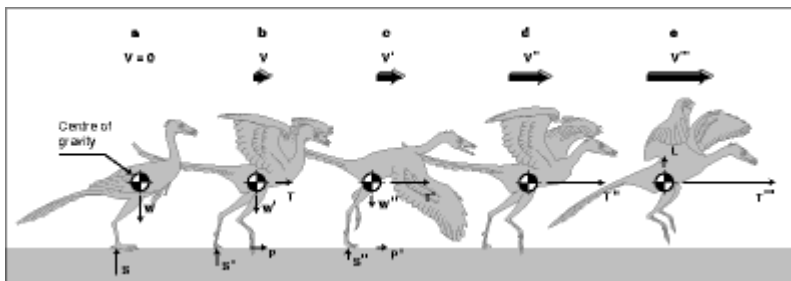


Figure 2 Net forces on *Archaeopteryx* throughout its modelled take-off run.

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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 run [8]. 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 times[21], 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 flight [22], 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 demands [2] 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 wings [24]. 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 [24,26], wing-generated thrust evolved before useful lift. Using this thrust and its ensuing residual lift, the flightless 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 [18,16] and Yalden [27]; our mathematical model agrees with those used in take-off studies of large extant birds [20]. 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 $V_f = f_s^\phi b y$, 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 y 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 \mathbf{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 $V_{\text{flap}}/V_{\text{run}}$. The resultant aerodynamic force vector generated by the wing is calculated by $\mathbf{R} = (0.5)^\rho \mathbf{V}^2 \text{CL} S p$ where ρ is the air density, \mathbf{V} is the velocity, CL is the lift coefficient (2), S is the wing area (0.0479 m^2), 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 of starting vortices on the upper side

of the wing favouring pressure gradients, enhanced leading edge vortex lift, ground effect, and lift hysteresis [28]. 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 \mathbf{T} and residual lift \mathbf{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.

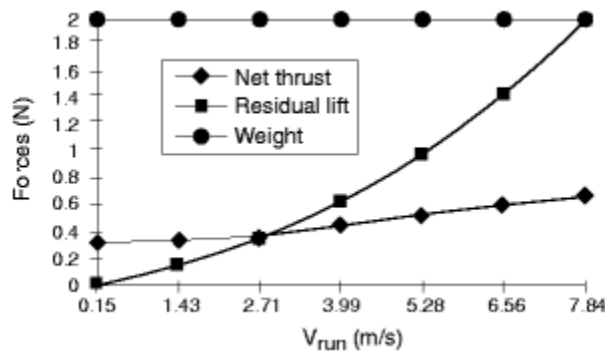


Figure 3 Progression of residual lift and net thrust throughout the modelled take-off run of *Archaeopteryx*.

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[High resolution image and legend \(8k\)](#)

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