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The flight of *Archaeopteryx*

Abstract The origin of avian flight is often equated with the phylogeny, ecology, and flying ability of the primitive Jurassic bird, *Archaeopteryx*. Debate persists about whether it was a terrestrial cursor or a tree dweller. Despite broad acceptance of its arboreal life style from anatomical, phylogenetic, and ecological evidence, a new version of the cursorial model was proposed recently asserting that a running *Archaeopteryx* could take off from the ground using thrust and sustain flight in the air. However, *Archaeopteryx* lacked both the powerful flight muscles and complex wing movements necessary for ground takeoff. Here we describe a flight simulation model, which suggests that for *Archaeopteryx*, takeoff from a perch would have been more efficient and cost-effective than from the ground. *Archaeopteryx* may have made short flights between trees, utilizing a novel method of phugoid gliding.

Introduction

The flight capabilities of *Archaeopteryx* have been debated for more than a century, ranging from preflight to powered flight modes. Ostrom (1979) has argued that *Archaeopteryx* was a terrestrial, flightless cursor, and its wing feathers were possibly used as insect traps. However, its encephalized brain with large cerebellum (Chatterjee 1997), the asymmetric vanes in its primary feathers (Feduccia and Tordoff 1979), a robust furcula for the origin of pectoralis muscle (Olson and Feduccia 1979), and the acute angle of the scapulocoracoid articulation (Feduccia 1996) suggest that *Archaeopteryx* could fly. The consensus is that it could glide and make flapping

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flights down from trees, but that it was incapable of taking off from the ground (Chatterjee 1997; Feduccia and Tordoff 1979; Olson and Feduccia 1979; Bock 1986; Rayner 1991; Poore et al. 1997; Vasquez 1994; Yalden 1985; Norberg 1990). Its lack of a supracoracoideus (SC) pulley, the primary elevator of the wing, would prevent *Archaeopteryx* from executing humeral rotation on the glenoid during the upstroke, a condition necessary for cursorial takeoff (Poore et al. 1997). The wrist of *Archaeopteryx* lacks the interlocking system to execute rapid wing beats during ground takeoff (Vasquez 1994).

In spite of these biological limitations, Burgers and Chiappe (1999) proposed a new model claiming that *Archaeopteryx* could indeed take off from the ground from a running start, using its wings as a primary thrust generator. In this report, we estimate the flight performance of *Archaeopteryx* using a flight simulation method and evaluate which kind of strategy would have been more energy-saving for *Archaeopteryx*: ground takeoff or "tree" takeoff.

Methodology

The aerodynamic theory on which flight simulation programs are based is an adaptation of the well-known momentum stream tube model often used for approximate calculation of helicopter performance (Templin 2000). A cylindrical stream tube of air with a diameter comparable with the wing span (b), initially approaching the animal at the flight speed (V), is assumed to pass through the wing system, where its direction and speed may be changed in reaction to the average wing aerodynamic forces. The stream tube momentum change, in flow speed and direction, is related to the aerodynamic thrust (or drag) and lift of the animal. Similarly, the change in kinetic energy flow in the stream tube is related to the propulsive power. We used the following two computer programs to estimate the flight performance of *Archaeopteryx*.

ANFLTPWR (animal flight power) is a program that computes the maximum continuous (aerobic) mechanical

power *available* for flight (from empirical data relating to animal mass), as well as the power *required* for steady level flight (usually a U-shaped curve in terms of flight speed, except for the smallest insects). Calculation of parasite and friction drag takes into account the wide range of Reynolds numbers in flight at all scales and speeds. Inputs to this program include speed, air density, and animal parameters, such as mass (M); wing span (b); and root chord in relation to a reference body length l, (where l is defined to be proportional to $M^{1/3}$); and the Oswald span efficiency (e) in hovering and at high speed, which are merged at intermediate speeds as a function of a power coefficient based on air density, speed, power, and span. The main output is the required power for equilibrium flight. Additional outputs include values of body and wing Reynolds numbers, the span efficiency e, the wake deflection angle required for equilibrium, and the so-called energy cost of transport.

ANFLTSIM (animal flight simulation) is a flight simulator program that computes the flight path of a winged animal in a vertical plane as a function of time in steady or unsteady flight. Inputs are similar to those of ANFLTPWR, except that power and wake deflection angle are control inputs, corresponding to throttle and control column movement in an aircraft. Flight begins from initial values of time, height, horizontal position, speed, and path angle. Takeoff from the ground is an option. Output quantities (speed, location, angle, etc.) are seen as a scrolling 9-column table on the screen at small time increments (usually 0.05 s). Since this scrolling is too rapid for continuous operator control, computation pauses after any specified number of time steps to await changes in power, wake angle, or aerobrake extension. Wake deflection angle, in addition to being under periodic operator control, is continuously modulated by the action of an adjustable-gain pitch damper subroutine, which suppresses the tendency toward long-period "phugoid" undulations (for example following the initial plunge after a low speed launch from a perch). The pitch damper imitates the ability of flying animals to control and stabilize their flight. Another built-in subroutine monitors aerodynamic lift and reduces power or wake angle if specified maximum lift coefficient limits are exceeded.

Biological limitations of *Archaeopteryx*

Taking off from the ground is a complex performance that combines three independent movements: dorsoventral flapping about the gleno-humeral joint, a rotation of the wing about its long axis, and a complex wrist movement to shorten the wing during the upstroke while locking the manus during the downstroke (Rayner 1991). The bird must beat its wings more vigorously to obtain the extra lift it needs. For this reason, most birds prefer to launch from a high place, such as a tree or cliff, to secure the necessary lift at less cost.

Archaeopteryx appears to lack both the powerful flight muscles and complex wing movements associated with ground takeoff. For example, *Archaeopteryx* could not position its wing high in an upstroke position, since it lacked a modern avian supracoracoideus (SC) pulley, the primary elevator of the wing (Poore et al. 1997). Perhaps it could raise its wing with the deltoideus muscle to some extent (Jenkins 1993), but not enough to generate appreciable thrust and lift in the following downstroke. Its glenoid faces directly laterally, indicating a limited elevation of the wing above a horizontal position (Martin 1991; Jenkins 1993). However, in modern birds the glenoid faces dorsolaterally, permitting the wing to orient in a fully vertical position during the upstroke, thus allowing a high-amplitude wing beat. With limited upstroke, *Archaeopteryx* would not be able to execute the powerful downstroke necessary for generating sufficient thrust during ground takeoff. The pectoral girdle is built in the fashion of a dromaeosaur, where the coracoids are not solid, strut-like braces. This indicates a relatively weak specialization for downstroke.

The wingbeat frequency is greatly enhanced in living birds by the SC pulley, imparting a high-velocity rotation about the longitudinal axis of the humerus which, in turn, augments supination of the distal wing. Lacking a modern avian SC pulley, *Archaeopteryx* could not rotate the humerus in this fashion, which would restrict its ability to flap its wings rapidly, an action necessary during slow flight, takeoff, and landing (Feduccia 1993). Takeoff from the ground would be further hampered because of its heavy wing loading. Flapping is powered by the flight muscles, which are relatively weak and short in *Archaeopteryx*. Its flight muscles comprise only 9% of the body mass (Speakman 1993), which is considerably less than the average 25% of the body mass found in modern birds (Greenewalt 1962).

Wrist movement also plays a critical role during flight. The wrist of *Archaeopteryx* is primitively designed in the grade of dromaeosaurs, but lacks the sophistication and complex articulation of modern birds necessary to withstand the powerful compression of flapping flight (Vasquez 1994). Its radiale and ulnare are small and ovoid, and it lacks a V-shaped and complex ulnare that functions as a bony stop. Conversely, the opposing ulna lacks the ventral articular ridge that limits the supination of the manus in the upstroke; its carpometacarpus is unfused; and its metacarpal III and ulnare do not form an interlocking system to prevent hyperpronating of the manus during the downstroke. The wrist of *Archaeopteryx* was not appropriately designed for sophisticated ground takeoff (Vasquez 1994).

Cursorial model

Archaeopteryx certainly spent some time on ground, as attested by its long and erect leg, but lack of fusion and rigidity in the critical region of the pelvis, sacrum, tibiotarsus, and tarsometatarsus indicates that it was not specialized for running like modern ground birds. Recently, Burgers and Chiappe (1999) have proposed a

Table 1 Comparison of running takeoffs of *Archaeopteryx* with its takeoffs from a perch

Takeoff from ground					Takeoff from perch		
Mass M (kg)	Distance to liftoff (m)	Liftoff speed (ms⁻¹)	Liftoff time (sec)	Climb angle (°)	Energy to liftoff (J)	Energy to level flight (J)	Minimum perch height (m)
0.2	13.4	7.6	2.75	6.2	8.2	7.1	5.5
0.4	28.1	8.6	4.7	2.9	24.0	13.3	7.9
0.6	47.3	9.1	7.0	1.4	48.1	19.0	9.5

new model claiming that *Archaeopteryx* could indeed take off from the ground from a running start, using its wings as a primary thrust generator. As the animal began running, it started flapping in such a fashion that it gained considerable velocity from the wing thrust, allowing it to take off from the ground. They proposed that the generation of thrust, not lift, was crucial during the ground takeoff. However, it is not clear from their argument how *Archaeopteryx*, lacking a modern avian SC pulley, could generate enough thrust to get airborne before it had reached full flying speed. Moreover, they use the loon (*Gavia* sp.), which lifts off from the water's surface, as a modern analog for the ground-effect mechanism of *Archaeopteryx*. The purpose of this paper is to evaluate which kind of strategy would have been more energy-saving for *Archaeopteryx*: ground takeoff or tree takeoff.

To test this cursorial model (Burgers and Chiappe 1999), we selected three size groups of *Archaeopteryx* (M=0.2, 0.4, and 0.6 kg), representing the Eichstätt, London (Yalden 1984), and Solnhofen (Wellnhofer 1992) specimens, respectively, and their corresponding takeoff energies are listed in Table 1. Takeoffs were computed using a flight simulator adapted from helicopter stream tube momentum theory (Templin 2000). This indicates that most flight performance items depend almost entirely on two parameters: mass (M) and wing span (b) (Fig. 1A). During the ground run (Fig. 1B) it is assumed that gradually increasing vertical lift is produced; as soon as $V_{liftoff}$ is reached, sufficient lift is generated for the animal to become airborne. There is a brief leg push at the beginning, and generated aerodynamic lift is slowly increased throughout the ground run. For the "leg work" we assume an 0.6-s push to 3 m s⁻¹ speed. Although our methodology is quite different from the model of Burgers and Chiappe (1999), our results concur with their estimated time and speed for the small individual. However, they assumed a mass of *Archaeopteryx* corresponding to the smallest individual known (M=0.2 kg), and did not specify the takeoff distance. We have incorporated variable mass data into our analysis. For example, the ground run was 13.4 m for M=0.2 kg and takeoff speed was 7.63 m s⁻¹, expending ground-run energy of 8.2 J followed by a shallow climb. For M=0.6 kg, the animal had to run 47.3 m (half of the length of a football field) for 7.0 s, expending 48.1 J, before it could take off (Table 1). Figure 1B shows results from ground-run simulations for three specimens of

Archaeopteryx. These curves indicate that *Archaeopteryx* should have been capable of a running takeoff, albeit awkwardly, because the power available was greater than the minimum power required for level flight (Fig. 1C). The heavier the animal, the further it must run during takeoff, and the climb angle after liftoff becomes progressively more shallow. It seems that mechanically the cursorial takeoff model could just work, but biomechanically it is highly unlikely because rapid wing beats were not possible during a ground takeoff (Poore et al. 1997; Vasquez 1994).

Arboreal model

Both anatomy and phylogeny strongly suggest that *Archaeopteryx* was an arboreal bird. The morphology (Yalden 1985) and curvature (Feduccia 1993) of the manual claw of *Archaeopteryx* are similar to those of a climbing bird such as a woodpecker. *Archaeopteryx* may have climbed efficiently with its forelimb claws and swivel wrist joints, similar to the style of a young hoatzin (Chatterjee 1997). There is further evidence for its climbing adaptation; in fingers I and II, the penultimate phalanx is longer than its proximal neighbor, a condition also present in hoatzins. The lengthening of the penultimate phalanx would increase the diameter of the available grasp between the opposing fingers, I and II. This would facilitate grasping broad tree trunks during climbing. The recent discovery of a series of small-feathered dromaeosaurs from the Early Cretaceous of China indicates that the direct ancestors of *Archaeopteryx* were arboreal and that flight originated from "trees down" (Xu et al. 2000).

Assuming that *Archaeopteryx* was a tree-dweller (Chatterjee 1997; Feduccia and Tordoff 1979; Olson and Feduccia 1979; Bock 1986; Rayner 1991; Poore et al. 1997; Vasquez 1994; Yalden 1984, 1985; Norberg 1990; Feduccia 1993), let us calculate the energy required for arboreal takeoff for three values of mass (0.2, 0.4, and 0.6 kg) (see Table 1). We have computed the flight paths using the 'animal flight simulation program' ANFLTSIM (Templin 2000). The lack of a SC pulley is no hindrance to gliding launches from a perch, since speed is rapidly built up during the initial glide. Figure 1D shows glide-path simulations of *Archaeopteryx*, all taking off at maximum continuous power from a perch at V_0=2 m s⁻¹ horizontally, and then pulling up at maximum continuous
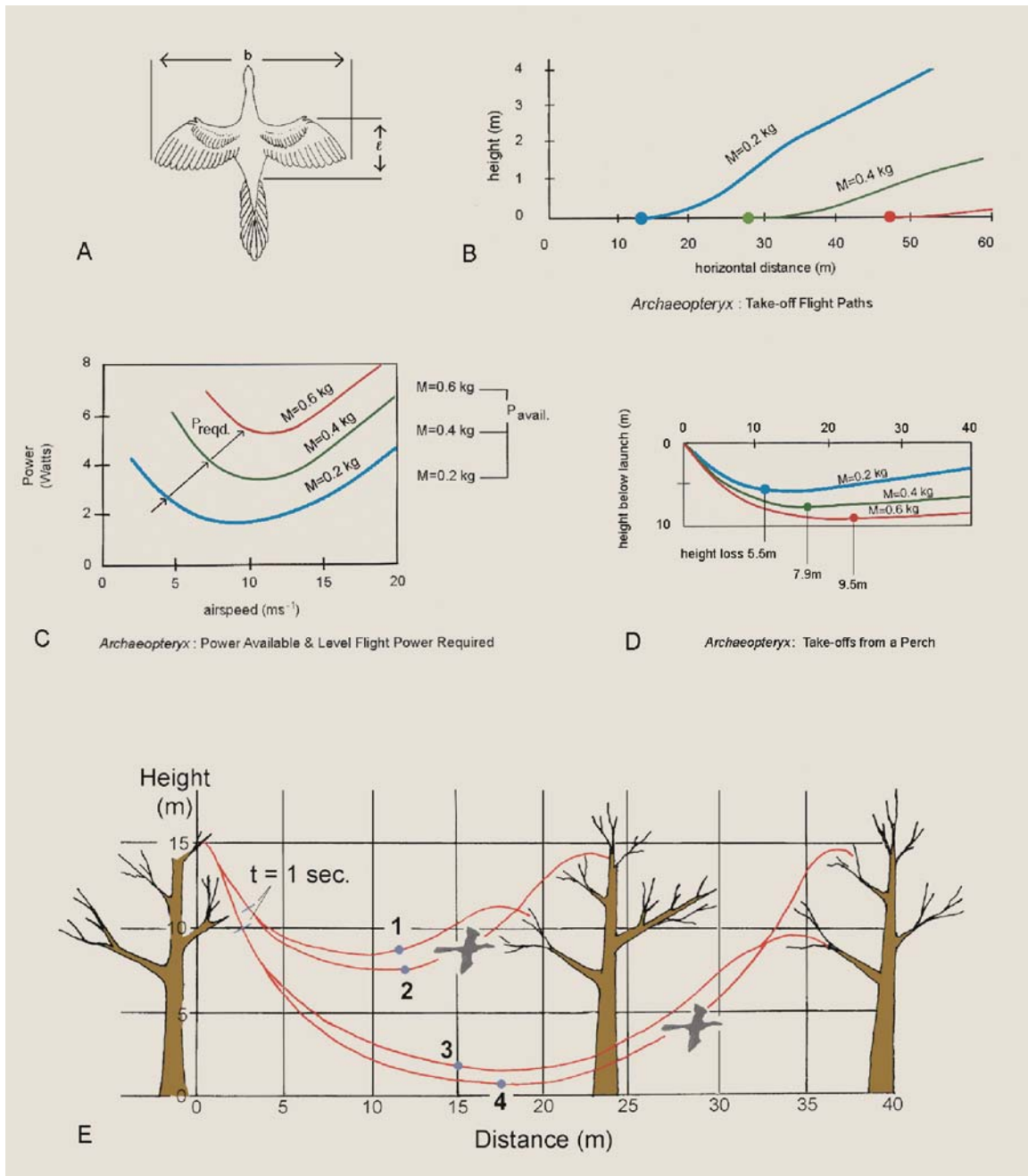
Fig. 1. A-E

power. Not surprisingly, the heaviest birds lose the most height, but at M=0.2 kg this loss is about 5.5 m. The pitch damper was used to suppress a subsequent wave motion. The height losses were used to define the minimum safe heights for "trees-down" launching. The energy required for a "tree" takeoff for varying masses of *Archaeopteryx* is listed in Table 1. For example, the energy required for a smaller individual (M=0.2 kg) in arboreal takeoff is only 7.1 J after 1.9 s. For larger animals, the cost/benefit ratio becomes apparent in the arboreal mode. Our flight

simulator study suggests that *Archaeopteryx* was capable of powered flights when launching from a height (<10 m), even with no headwind. When compared with the ground takeoff model, the energy expended in takeoff by an arboreal *Archaeopteryx* is more cost-effective.

The separate analysis of the two models strongly suggests that proper comparison should be done between two birds of the same size, one of which is a ground bird that does running takeoffs, and the other a perching bird that launches into flight from the trees. This arboreal bird can level off with minimum height loss. The same is not true for a ground-launched flight, and thus the arboreal model requires less energy to attain flight than the cursorial. Along these lines, for an adult specimen of

Fig. 1 A Two principal parameters for flight aerodynamics in *Archaeopteryx*, wing span (*b*) and body length (*l*). **B** Cursorial takeoff of *Archaeopteryx* (note expansion of vertical scale). Takeoff paths for *M*=0.2 (used by Burgers and Chiappe (1999) for the Eichstätt specimen (Yalden 1984), 0.4 and 0.6 kg based on our estimates for the London and Solnhofen (Wellnhofer 1992) specimens using Yalden's (1984) allometric equation. For *M*=0.2 kg, the wing span was set at 0.55 m and maximum continuous power at 3.4 W, varying as $M^{1/3}$ and $M^{2/3}$, respectively. Air density was set at the standard sea-level value of 1.225 kg/m^3. Flight is controlled by variation of power and momentum wake deflection angle (Ø) which controls aerodynamic lift. The wake angle was set to give takeoff speeds (listed in Table 1) safely above the minimum steady level speeds. The estimates of ground-run distance and energy expended shown in Table 1 may be underestimated, since no allowance was made for net thrust reductions due to limited wing flapping at low speed or to ground resistance. **C** Level flight power. Estimated continuous available power and power required for steady level flight. This suggests that although flight from ground takeoff is possible, power margins and climb angles (Table 1) are small at the highest weight. **D** Flight paths of *Archaeopteryx* for *M*=0.2, 0.4, and 0.6 kg taking off horizontally from a perch at 2 m s^{-1}, then pulling up at a maximum continuous power (3.42, 5.43, and 7.11 W, respectively). The simulator's pitch damper imitates automatic use of wings and tail in suppressing large-amplitude undulations which would follow the initial steep descent if left uncontrolled, until equilibrium climb is established. *Archaeopteryx* probably needed a ~6 to 10 m perch height for safe takeoff with no wind, depending on the animal's weight. Various tall trees, such as conifers, ginkgos, and cycads, were available to *Archaeopteryx* (Barthel et al. 1990), and its feet were adapted to perching. Arboreal takeoffs save significant energy (Table 1), especially for the largest individuals. **E** Phugoid gliding paths of *Archaeopteryx* at *M*=0.2 kg, launching from a height of 15 m with launch speed 2 m s^{-1} (horizontal). Curve 1 shows an unpowered glide at relatively high lift coefficient (C_L ≈1.13). One wave length later, about 18 m from launch, height passes through a maximum of 11.5 m (a loss of 3.5 m from launch). No pitch damping was used, in order to encourage the height recovery as much as possible. Curve 2 is the same initial glide up to 1 s after launch, when speed has increased to 8.4 m s^{-1}. Flapping flight is at maximum continuous power (3.42 W), and continues for a further 2.5 s. A final short ascending glide puts the trajectory over the treetop at nearly original height, with speed reduced to 3.3 m s^{-1}. The horizontal distance covered is 22.3 m for an average horizontal component of speed of 5.95 m s^{-1}. The energy expended during 2.5 s of powered flight is 3.42×2.5=8.55 J. Curve 3 is another unpowered phugoid, at half the lift coefficient assumed in curve 1. Consequently the height loss is considerably greater, but the horizontal distance covered is increased. The height recovery at the phugoid peak is less than for curve 1. Curve 4 corresponds to curve 2, but with 3.42 W of flapping wing power on for a duration of 3.5 s. The energy expended is 12 J, and full height is recovered with a final minimum speed of 2.7 m s^{-1}

Fig. 2 Three-dimensional mount of the London *Archaeopteryx* skeleton (cast) illustrating an arboreal takeoff from a ginkgo branch. Note that the feet were adapted for perching on branches. The cast was provided by Larry D. Martin; it was modified and mounted by Kyle McQuilkin and photographed by Bill Mueller

such as cycads, ginkgoes, seed ferns, and conifers in the central European islands where *Archaeopteryx* lived (Barthel et al. 1990). These trees may have provided places to perch and launch, as well as a trunk to climb (Fig. 2).

Phugoid gliding

Archaeopteryx may have innovated a novel method of gliding between trees to save energy. Flying squirrels travel through a forest by climbing the trunks of trees and gliding between trunks (Norberg 1990). When crows take off from a tree, they do not seem to use excess power; they lose height at first and then swoop up to swing between two perches. This occurs whenever any winged object (aircraft, model glider, or flying animal) finds itself in a non-equilibrium situation, such as when launched without sufficient wing lift to balance weight (Feduccia 1993). The result is an initial loss of height at an increasing speed. Lift increases as speed squares (if controls are not moved) and the subsequent motion is an undulation, known as phugoid oscillation, with potential and kinetic energy being periodically exchanged (Templin 2000; see Fig. 1E). In gliding flight, the motion is eventually damped to a steady glide and, in fact, the rate of damping is inversely proportional to the lift/drag (L/D)

Archaeopteryx (*M*=0.6 kg), the energy for ground takeoff is 48.1 J, whereas for the same bird the energy for an arboreal takeoff is only 19.0 J (about 40% of the ground value). It appears from our analysis that arboreal takeoff saves considerable energy compared with the cursorial mode, especially when the bird is large. An adult *Archaeopteryx* probably needed a certain height (~10 m) from which to launch itself safely in still air. A headwind would also have helped. There were tall trees (>10 m)
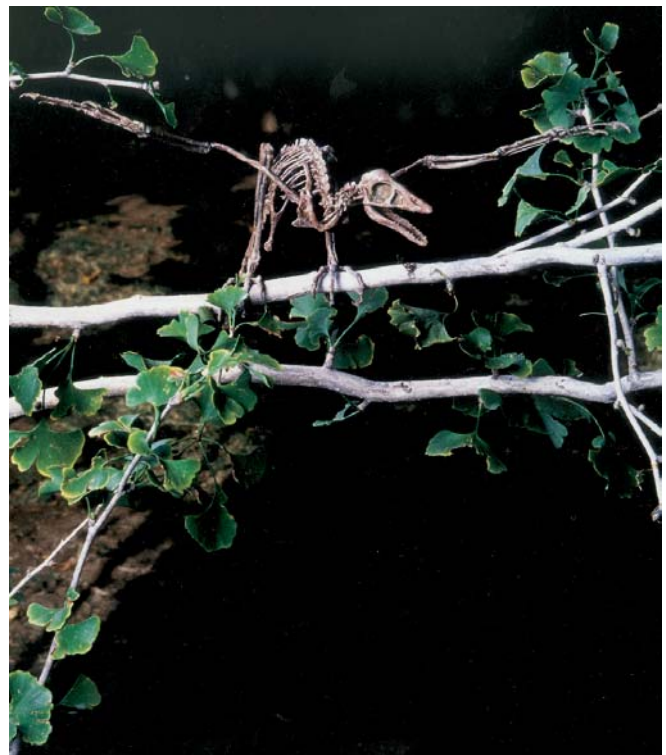
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ratio. Objects with high L/D configuration, such as modern aircraft, have low phugoid damping, but because the period of motion is proportional to speed, control is not difficult. *Archaeopteryx* probably used a similar strategy to move from tree to tree, using phugoid gliding without expending much energy.

In Fig. 1E, we show four glide paths of *Archaeopteryx* computed from ANFLTSIM with a launch speed of 2 m sec^{-1} (horizontal) from an arbitrary height of 15 m. The mass was fixed at 0.2 kg (representing the Eichstätt specimen) and the wing span was 0.545 m. No pitch damping was used, in order to encourage the height recovery as much as possible. Curves 1 and 3 show unpowered phugoid oscillations of *Archaeopteryx*, whereas curves 2 and 4 are with 3.42 W of flapping power (the estimated maximum available continuous power), beginning 1 s after jump-off when air speed is high enough to lift the wings during the upstroke without muscular effort. These curves show how *Archaeopteryx* could travel from treetop to treetop without expending much muscular energy (Fig. 2).

References

Barthel KW, Swinburne NHM, Conway Morris S (1990) Solnhofen: a study in mesozoic palaeontology. Cambridge University Press, Cambridge

Bock WJ (1986) The arboreal origin of avian flight. Mem Cal Acad Sci 8:57–72

Burgers P, Chiappe LM (1999) The wing of Archaeopteryx as a primary thrust generator. Nature 399:60–62

Chatterjee S (1997) The rise of birds. Johns Hopkins University Press, Baltimore

Feduccia A (1993) Evidence from claw geometry indicating arboreal habits of Archaeopteryx. Science 259:790–793

Feduccia A (1996) The origin and evolution of birds. Yale University Press, New Haven

Feduccia A, Tordoff HB (1979). Feathers of Archaeopteryx: asymmetric vanes indicate aerodynamic function. Science 203:1021–1022

Greenewalt CH (1962) Dimensional relationships for flying animals. Smithson Misc Collect 144:1–46

Jenkins FA (1993) The evolution of the avian shoulder joint. Am J Sci 293A:253–267

Martin LD (1991) Mesozoic birds and the origin of birds. In: Schultze HP, Traeub L (eds) Origin of the higher groups of tetrapods. Camstock, Ithaca, pp 485–540

Norberg UM (1990) Vertebrate flight. Springer, Berlin Heidelberg New York

Olson SL, Feduccia A (1979) Flight capability and the pectoral girdle of Archaeopteryx . Nature 278:247–248

Ostrom JH (1979) Bird flight: how did it begin? Am Sci 67:46–58

Poore SO, Sanchez-Haiman A, Goslow GE Jr (1997) Wing upstroke and the evolution of flapping flight. Nature 387:799–802

Rayner JMV (1991) Avian flight and the problem of Archaeopteryx. In: Rayner JMV, Wootton RJ (eds) Biomechanics in evolution. Cambridge University Press, Cambridge, pp 183–212

Speakman JR (1993) Flight capabilities of Archaeopteryx Evolution 47:336–340

Templin RJ (2000) The spectrum of animal flight: insects to pterosaurs. Prog Aero Sci 36:393–436

Vasquez RJ (1994) Functional osteology of avian wrist and evolution of flapping flight. J Morphol 211:259–268

Wellnhofer P (1992) A new specimen of Archaeopteryx from the Solnhofen limestone. Nat Hist Mus Los Angeles County Sci Ser 34:3–24

Xu X, Zhou Z, Wang X (2000) The smallest known non-avian theropod dinosaur. Nature 408:705–708

Yalden DW (1984) What size was Archaeopteryx? Zool J Linn Soc 82:177–188

Yalden DW (1985) Forelimb function in Archaeopteryx. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P (eds) The beginnings of birds. Freunde Jura-Museum, Eichstätt, pp 91–97