

The evolution of vertebrate flight

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Flight—defined as the ability to produce useful aerodynamic forces by flapping the wings—is one of the most striking adaptations in vertebrates. Its origin has been surrounded by considerable controversy, due in part to terminological inconsistencies, in part to phylogenetic uncertainty over the sister groups and relationships of birds, bats and pterosaurs, and in part to disagreement over the interpretation of the available fossil evidence and over the relative importance of morphological, mechanical and ecological specializations. Study of the correlation between functional morphology and mechanics in contemporary birds and bats, and in particular of the aerodynamics of flapping wings, clarifies the mechanical changes needed in the course of the evolution of flight. This strongly favours a gliding origin of tetrapod flight, and on mechanical and ecological grounds the alternative cursorial and fluttering hypotheses (neither of which is at present well-defined) may be discounted. The argument is particularly strong in bats, but weaker in birds owing to apparent inconsistencies with the fossil evidence. However, study of the fossils of the Jurassic theropod dinosaur *Archaeopteryx*, the sister-group of the stem-group proto-birds, supports this view. Its morphology indicates adaptation for flapping flight at the moderately high speeds which would be associated with gliding, but not for the slow speeds which would be required for incipient flight in a running cursor, where the wingbeat is aerodynamically and kinematically considerably more complex. Slow flight in birds and bats is a more derived condition, and vertebrate flapping flight apparently evolved through a gliding stage.

KEY WORDS:—Flight – evolution – birds – bats – pterosaurs – *Archaeopteryx* – flapping wings – pectoral girdle.

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INTRODUCTION

The appearance of a major adaptation such as flight in an animal group can have many consequences. Flight has become a dominant character in three vertebrate lineages. Its effects include the acquisition of significant morphological, physiological and behavioural specializations, and the ability to use ecological resources in new and varied ways. Its establishment has been accompanied by dramatic radiations and by the appearance of a diverse range of forms exploiting the new adaptation.

However, it is not only a novel ecological environment with which the newly-specialized animals must contend. The mechanical environment into which they evolve can be equally harsh, and can form a major constraint on the evolution of proto-fliers and their subsequent radiation. The physical demands on flying animals are great, and the influence of mechanical factors can be traced in many aspects of the biology of contemporary fliers. The most important constraint is the need to support the weight in the air and to flap the wings to obtain thrust, but flight also influences many other aspects of morphological and physiological adaptation. These same demands must have had yet greater importance in the early stages of flight evolution, for a proto-flier must contend with constraints reflecting its ancestors' mode of life as well as those of its newly acquired mobility. In this paper I use studies of the aerodynamics of modern fliers to model the initial appearance of flight and to explore the associated phylogenetic, morphological and behavioural developments.

BIRDS, BATS AND PTEROSAURS

Flight has appeared often in vertebrates (see, for example, Rayner, 1981; U. M. Norberg, 1985a; Padian, 1985), but many flying animals have been simple parachuters or gliders, making passive use of the lift or drag forces generated by static aerodynamic surfaces around the body or limbs. Although important as potential analogues to the precursors of true fliers, I do not consider these animals here. Rather, I am concerned with true flapping flight, which has arisen in only three groups of vertebrates, in stem-group reptiles (giving rise to pterosaurs), in dinosaurs (birds) and in mammals (bats). In each of these groups the specializations for flight share many similarities (Padian, 1985; fig. 1). The forelimbs are extended to form the supporting member for a wing. Specialized structures, unique to each of the groups, give the wing mechanical integrity without excessive weight or developmental cost. The bones and muscles of the pectoral girdles are enlarged and stiffened, and to maintain rigidity and lightness the wing articulation constrains the movements of the forelimb largely to those required in flight. The whole body has been lightened to save mass, and thereby to give the animal greater flexibility and to reduce the high energy demands of flight. The blood and respiratory systems and the flight musculature (at least in birds and bats) optimize transport of oxygen to the muscles and its subsequent conversion to mechanical work. The mechanical constraints imposed by flight are strong, and few other features of birds, bats and pterosaurs remain uninfluenced by it. It is vital to appreciate the demands of flight to understand modern fliers; it is even more important to consider them when studying the origins of flight.

Birds

Birds are the dominant group of vertebrate fliers, and their origin and relationships and the evolution of their flight have long been the subject of controversy (for reviews see Stephen (1979), and papers in Hecht, Ostrom, Viohl & Wellnhofer (1985) and Padian (1986); much of the palaeontological evidence cited in this paper is drawn from these sources). There is overwhelming evidence that birds evolved from small bipedal theropod dinosaurs during the Middle or Late Jurassic Period, probably 140–160 million years ago (Gauthier, 1986). The transformations in morphology and size from dinosaur to bird appear from the limited fossil evidence to have been fairly modest. But in the process birds acquired two features—the power of flight and the possession of feathers—which set them apart from other dinosaurs. The closest known relative of birds is *Deinonychus*, a predatory cursorial theropod some 2 m in length; other contemporary theropods such as *Compsognathus* were much smaller, and more comparable with the likely size of the first birds.

Birds share with other theropods light build, elongated forelimbs and a fully-erect bipedal stance: the feathered wing and other specialized features associated with flight are among the few characters which effectively distinguish the two groups. Some other features common to theropods and early birds (such as teeth) were lost at a later stage of avian evolution.

We know little of the first birds, and the limited fossil record and the apparent sister-group relationships may obscure the true avian origins. The question of size is important here: there are sound mechanical reasons (Pennycuick, 1986; Rayner, 1986) for expecting the first flying dinosaurs to be much smaller than *Deinonychus*. Yet, although size is a significant phylogenetic character in modern birds (for reasons probably related to flight), it is a relatively poor character for saurischian dinosaurs. We cannot be certain that the fossil record is sufficiently complete for systematic and morphological studies of theropods to give an accurate prediction of the hypothetical pro-avian; however, on the basis of the available evidence, the proavian was a small cursorial or semi-cursorial biped, with good running agility and predatory habits. We know nothing of its habitat.

Bats

The situation in bats is in many ways different from that in birds. The oldest fossil bat, *Icaronycteris index* from the Eocene of Wyoming (Jepsen, 1970; Padian, 1987), scarcely differs from modern Microchiroptera. There are no intermediates linking it to other fossil or extant mammals, but we can reasonably expect the sister groups of bats to be readily traceable within contemporary mammals.

Bats show considerable morphological homogeneity, and a narrow range of ecological adaptations compared to birds (Norberg & Rayner, 1987; Rayner, 1987). It has been proposed recently that bats are paraphyletic, with the Old World fruit bats or Megachiroptera descending from Primates via the Dermoptera, and the Microchiroptera from insectivores or edentates (Smith, 1976; Pettigrew, 1986); this debate remains unresolved. Whatever the outcome, it is clear from their morphological convergence that if the two chiropteran groups are separate the processes involved in their evolution will have been closely similar.

Bats differ from birds in many respects. They are mammals, so are hair-covered, viviparous, and have the complex musculature of the mammalian shoulder girdle rather than the simpler form of archosaurs (Fig. 1). The most obvious morphological feature of bats is the flight membrane, spanning both fore- and hind-limbs, and supported by greatly extended hand digits; this membrane is similar to the flight surface of gliding mammals. The other character distinguishing bats is the involvement of the legs and feet in the membrane; this has been a major constraining influence on the radiation of bats, restricting terrestrial movement to an awkward scurrying, imposing an inverted resting posture, and preventing the adoption of certain feeding niches (Rayner, 1981, 1986; Norberg & Rayner, 1987). But—as I discuss below—this flight morphology carries several implications for the mode of evolution of bats.

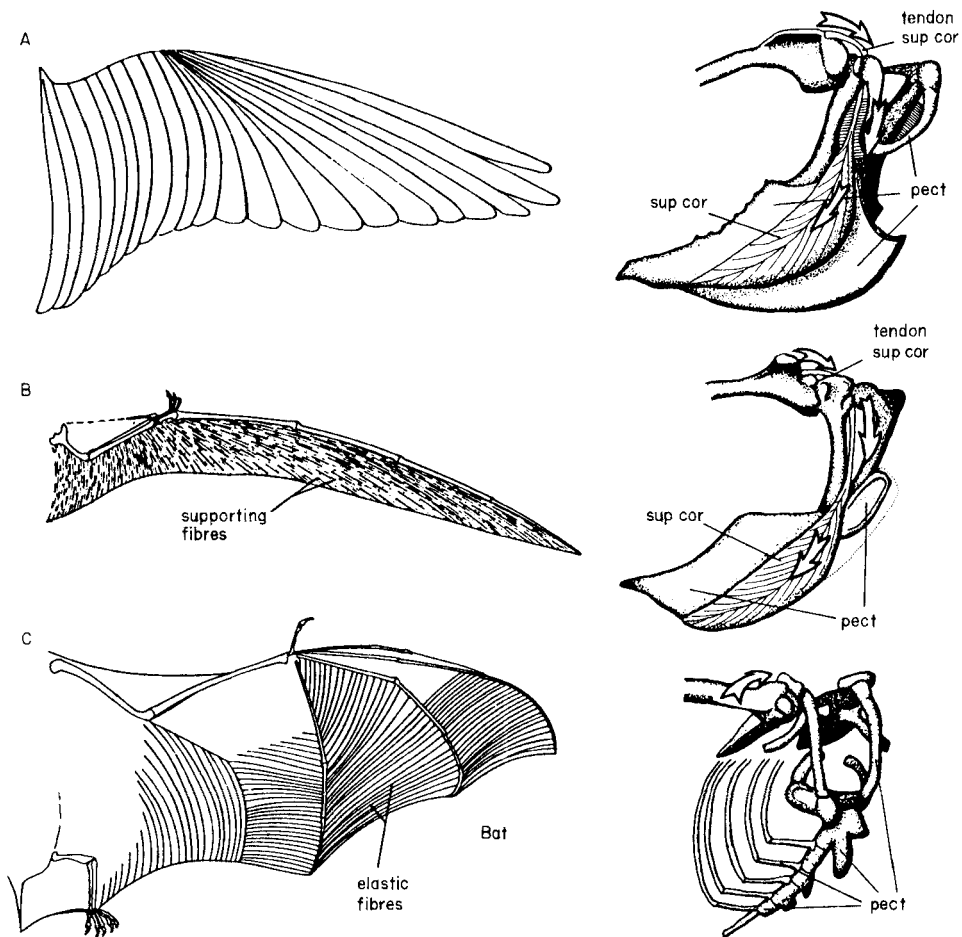


Figure 1. Morphology of the wing (left) and pectoral girdle (right) showing areas of attachment of pectoralis and supracoracoideus (not bats) muscles in vertebrate fliers. A, birds; B, pterosaurs; C, bats. In birds the wing surface is provided by feathers, and in pterosaurs by stiffening fibres; the bat wing is an elastic membrane spread between extended digits. In birds and pterosaurs the elevating moment is applied to the humerus by the supracoracoideus, which originates on the sternum and whose tendon passes over the humeral joint. (From Padian, 1983.)

Pterosaurs

The pterosaurs are the most enigmatic of the three groups. The problems of their interpretation have been discussed extensively by Padian (1983, in press), and will not be repeated in detail here. They centre on whether a pterosaur should be reconstructed as bat-like, with the wing formed by a membrane attached to an extended fourth digit and to the feet, or as bird-like, with a wing free of the hind limb and given structure by embedded stiffening fibres. The two reconstructions imply different stance, and probably different modes of life. Although historically the more favoured, there is no fossil evidence for the bat-like reconstruction. Moreover, the fully-erect stance of the bird-like model avoids the enormous problems in reconstructing a bat-like animal with suspended posture reaching the enormous size of some late Cretaceous pterosaurs. This debate cannot yet be fully resolved, although current opinion strongly favours the bird-like form. Until we know more of the fossil record of proto-pterosaurs the question of pterosaur flight evolution must remain open; it would, however, be natural to model the origin of flight in a bird-like pterosaur as being similar to that in birds.

FLAPPING FLIGHT AERODYNAMICS

I have defined flight in this paper by the ability to generate useful aerodynamic forces by the flapping wings. This implies that flying animals have sophisticated control and sensory performance, and a physiological system capable of delivering sufficient energy through contraction of the flight muscles. It also implies that the wings function as aerofoils. Space does not permit me to enlarge on flapping flight aerodynamics here, and I have discussed the following topics more fully elsewhere (Rayner, 1986, 1987, 1988).

With wings outstretched, a gliding animal obtains a *lift* force from its flight surface, which acts as an aerofoil. The cambered wing-section profile with rounded leading edge and smooth trailing edge accelerates air passing above it while decelerating air below, and thereby generates a pressure difference which is experienced by the animal as a lift force, transverse to the line of flight. There is also a *drag* force, representing the sum of friction on the body and wings, and the energetic cost of generating the wake vortex system which is responsible for lift. Since drag always retards the animal there is no possibility of obtaining a positive force along the line of flight while the wings remain rigid, and therefore to maintain lift, drag and weight in equilibrium a glider must lose height (or—for a limited period—speed). Generally lift is considerably greater than drag, and is of the same order of magnitude as the weight. Glide angle is therefore rather shallow in most animals.

Flapping fliers must also use aerofoil action to sustain and propel themselves. But the purpose of flapping the wings is not to balance weight—they can do that with lift alone—but to compensate for drag. If the animal is to attain steady level flight, the wingbeat must supplement the vertical weight-supporting component of lift with a horizontal positive thrust parallel to the line of flight. The only force which can be used for this is the aerofoil lift, and the wingbeat must be configured so that the mean lift is directed forwards and upwards. The animal can achieve this by generating the majority of force during the

downstroke, when the wings move forwards and downwards relative to the air; this is the dominant part of the wingbeat. The aerodynamic role of the upstroke proves to be more variable, and to depend in particular on flight speed.

Recent high-speed cinematography and flow visualization experiments (reviewed by Rayner, 1987, 1988) have clarified the process of force generation. This work has demonstrated that there are no substantial *aerodynamic* differences between flying birds and bats, and that in all flying animals the nature of the wingbeat changes significantly with speed. At low speed the upstroke is inactive and generates no useful aerodynamic force; in a complex movement the wing is closely furled, and the wingtip moves near to the body. At higher speeds the upstroke can generate useful aerodynamic force contributing to weight support, but—since the wing moves upwards relative to the air—also tending to retard the animal. The wing remains near-planar throughout, and deforms much less; in birds the wing-tip is swept back at the wrist through a small angle during the upstroke; in bats the arm wing is shortened slightly to produce the same effect, and the tip is not markedly swept. These experiments have allowed the development of a mathematical model of flapping flight (Rayner, 1986) by which mechanical power and wing root forces and moments can be estimated. This model predicts the observed change in upstroke function with speed.

These conclusions have many consequences for flight evolution. The difference in wingbeat with speed is particularly important. The low speed wingbeat requires complex deformation of the wing surface, primarily to minimize wing inertia. The wingbeat amplitude and frequency are both higher than in the much simpler cruising flight wingbeat. The vortex ring wake at low speeds with its periodic variation in vortex strength or circulation is more complex than the continuous wake with constant circulation of high speeds. All of these factors argue that the low speed configuration is in evolutionary terms the more derived, and strongly imply that relatively high speeds would have been more appropriate for the first appearance of flapping (this argument is explored in more detail below). The conclusion is reinforced by the patterns of roll moments applied by the pectoralis muscle at the wing-root at different flight speeds (Fig. 2). At high speeds the moment changes only slightly through the wingbeat, and is always positive so that only a depressor muscle is required. At low speeds the moment varies substantially, and is negative for much of the latter part of the downstroke and early upstroke. Active muscle action is required to elevate the wing, and aerodynamic force generation during the upstroke is inefficient. Again, slow flight is the more derived condition.

FLIGHT EVOLUTION HYPOTHESES

I have discussed some of the major mechanical demands imposed by flight; these are so substantial that the selective pressures encouraging flight evolution must have been very significant. Moreover, flight is an important phylogenetic character in its own right: so far as birds can be distinguished from other dinosaurs, and bats from other mammals, it is by features associated with flight.

Not surprisingly, many hypotheses have been advanced for the appearance of flight in vertebrates. Some do not attempt to address the mechanical problems, but explain the appearance of wings and feathers by behavioural factors such as display and fighting (Cowen & Lipps, 1982), heron-like aquatic foraging

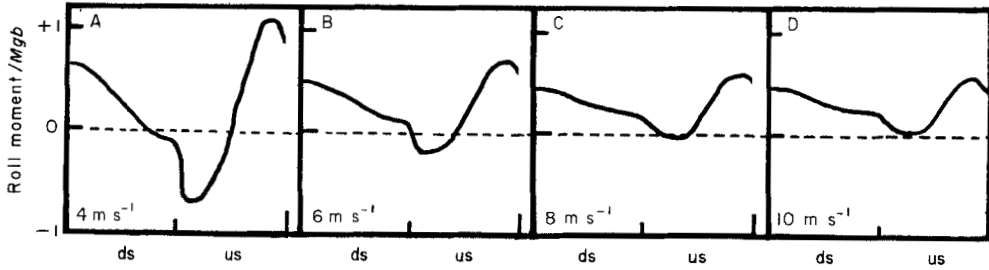


Figure 2. Roll moments at the wingroot in flapping flight at different speeds for kestrel *Falco tinnunculus*. The pattern is similar for other birds. Only the dorso-ventral moment in a vertical plane normal to the flight path is shown, normalized with respect to Mgb , the product of weight and wing semi-span. Negative moment implies muscle action (by the supracoracoideus) is required to elevate the wing. A–D increasing flight speeds from 4 to 10 m s^{-1} ; cruising flight speed is around 8 m s^{-1} . In each part the first half of the horizontal axis indicates the downstroke (ds), the second half the upstroke (us). At cruising speeds the moment varies only weakly, and is always positive. At low speeds the moment becomes negative during part of the upstroke, and it is inefficient to use the upstroke for force generation. From Rayner, in 1988.

(Thulborn & Hamley, 1985), thermoregulation (Regal, 1975, 1985) or water-repellance (Dyck, 1985). Some hypotheses are far-fetched, others more convincing, but few can be discounted. They may suggest behavioural correlates or precursors of flight, but are irrelevant to this discussion since they do not address the major question of how an animal might have evolved a flapping wing capable of generating useful aerodynamic forces. It is this which distinguishes birds, bats and pterosaurs from their non-flying relatives.

Three models attack this problem. Each has its adherents, and each has been the butt of valid (and often invalid) criticisms. Space does not permit a full review of the arguments here, but I have considered the models and their advantages and disadvantages elsewhere (Rayner, 1985a, b, 1986; see also U. M. Norberg, 1985b). Similar arguments, driven by similar mechanical constraints, characterize the debate over insect flight evolution (Wootton & Ellington, in press).

The gliding model

The oldest of the models was proposed first by Darwin (1859), who argued that bats evolved through a gliding stage, and that proto-bats were not dissimilar to contemporary gliding squirrels. (The colugo (*Cynocephalus*, Dermoptera), a relatively large glider from South-East Asia, is a close relative of at least some bats; J. D. Pettigrew, pers. comm.) Very similar phrases were later used by March (1880) in advancing the gliding model for birds. Many authors have since accepted this idea, and its implications have been considered in great detail (see, for example, Bock, 1986). Its predominant feature is that proto-flappers used gravity to power their flights, probably within vegetation, but perhaps among rocks and cliffs, and began flapping to provide thrust to elongate the glide. The animals' use of gravity justifies the intuitive attraction of this model, especially to the biomechanicist, but it has yet to win complete acceptance.

The gliding hypothesis is often referred to as the 'arboreal' model. Animals often live or move in trees, and many are able to climb; trees are a ready source of potential energy with which to start a glide. Moreover, virtually all contemporary tetrapod gliders are associated with trees. However, this nomenclature has been the source of one of the main objections to the gliding model as applied to birds. There have been few cogent objections to its validity in bats, since trees, and arboreal habit in mammals, were widespread in the Eocene. The morphology of bats—particularly the quadrupedal support of the flight membrane—and their relationship to other arboreal and gliding mammals support this view. In the Jurassic, at least in the relevant geographical areas, the presence of trees for a proto-bird is unlikely; moreover, theropods do not show specialized features for climbing. I therefore prefer to use the term 'gliding' to describe the model to divorce it from reliance on the presence of trees, and to emphasize its mechanical rather than ecological correlates.

The cursorial model

The most widely voiced alternative to gliding is the so-called 'cursorial' model. This envisages the proto-flier as a running biped (the difficulty of running effectively excludes it from applying to bats), making short jumps from the ground. These jumps become extended, the wings are used for balance and propulsion, and the animal begins to fly. The hypothesis originated with Williston (1879) but was clearly expressed first by Nopsca (1907, 1923). With growing understanding of flight mechanics it fell into disfavour since gliding has intuitive advantages; moreover it is apparently impossible to provide thrust with the legs while gaining any height while jumping from the ground. Above all, what has been most lacking from the argument as originally presented has been a clear selective pressure favouring the appearance of flight in a cursor.

Realization of the bipedal cursorial habits of theropods and their relationship to birds forced reconsideration of the role of running in bird flight evolution. Onstrom (1974, 1979) proposed that catching flying insects while running and jumping could favour the development of wings functioning like tennis rackets (Fig. 3); moreover, the wingstroke needed to trap a flying insect would be similar to the arm movements of *Deinonychus*, and was claimed to be similar to the flight stroke of a bird (see also Padian, 1985). More recently, Caple, Balda & Willis (1983) proposed that stability while running, perhaps at high speed while escaping a predator, is a better pressure for wing enhancement. Both of these are cogent models for the appearance of wings in a cursor, and both are consistent with the apparent terrestrial habits of proto-birds. But both are implausible, in part because of the absence of contemporary analogues, but mainly because neither sensibly addresses the question of *why* the wings should be flapped, and how the imprecise forms of wing waving needed for predation or stability should have developed into true flapping. The cursorial model as generally understood is only a first step towards flight evolution, and cannot directly be compared with the more completely formulated gliding model.

Fluttering proto-flappers

A third alternative proposal is more elusive to mechanical formulation. The 'fluttering' model proposes that flight began with animals beating their wings

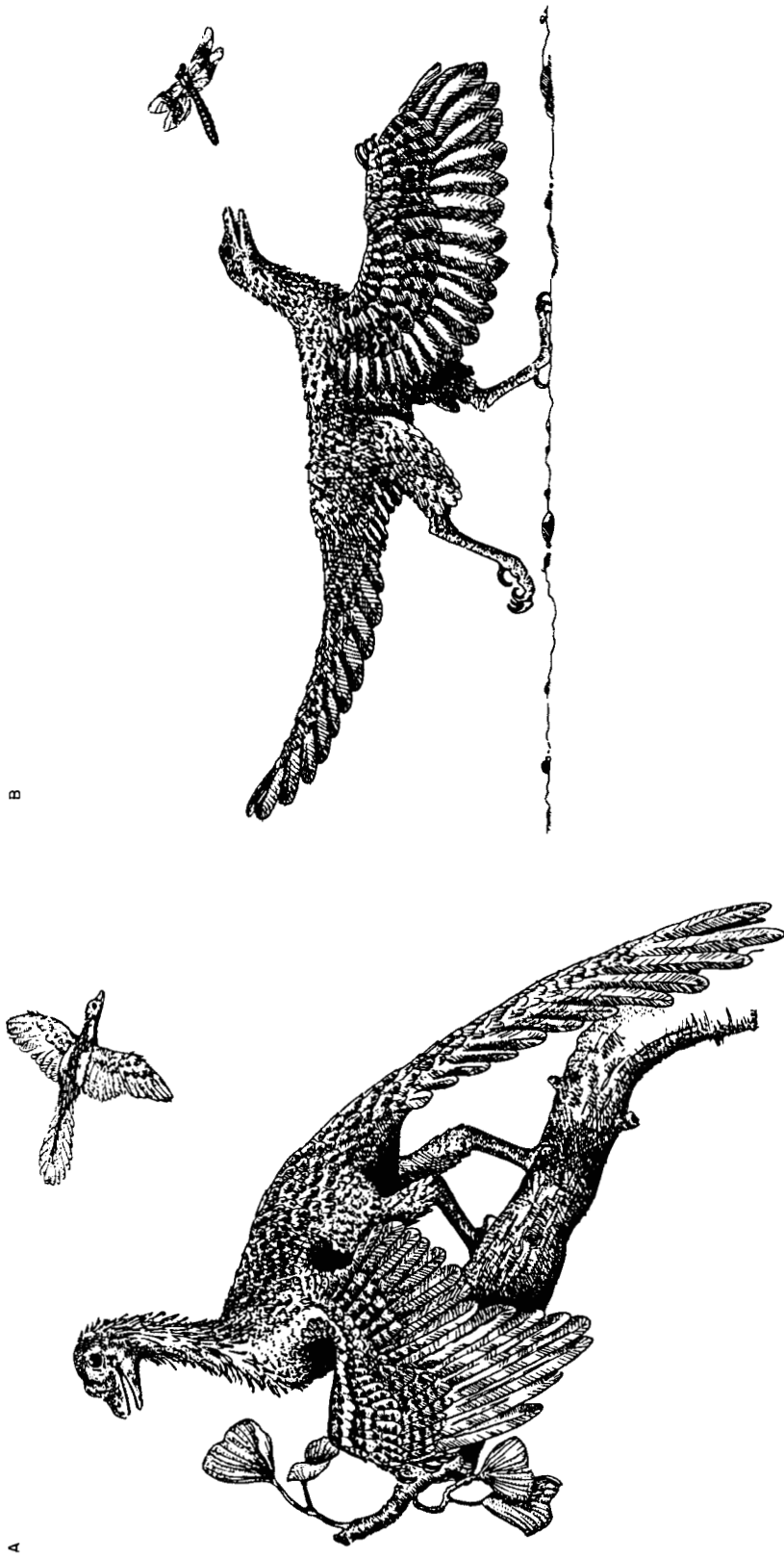


Figure 3. The cursorial and gliding models of flight evolution illustrated for the first bird *Archaeopteryx*. A, Gliding, showing the possible stance of an arboreal animal using the forelimb claws for support; and B, the cursorial model, illustrated by Ostrom's (1974) running insect-gatherer. (Drawings by Nicola Hector.)

erratically, and finding that useful aerodynamic forces could be generated; flight would thus have evolved rapidly, almost by saltation. The fluttering scenario has been advanced most commonly for bats (Jepsen, 1970; Pirlot, 1977; Caple *et al.*, 1983). The main pressure for this model has come from unfounded objections to the gliding model, often arising from misunderstanding of flapping flight mechanics (e.g. Balda, Caple & Willis, 1985). The first 'flights' of a fluttering proto-flapper would have been at low speeds, where the energetic demands of flight are at their most extreme (Clark, 1977), and the wingbeat cycle is at its most complex. The fluttering model fails because it takes no account of the extreme morphological, physiological and behavioural specializations required for flight. I therefore do not consider it further.

THE GLIDING AND CURSORIAL MODELS

To resolve the problem of flight evolution a mechanical model should therefore compare the gliding and cursorial hypotheses. The sequence of appearance of adaptations for flight must be consistent with phylogeny, at least as far as it is known. Further, biomechanical and physiological developments as flight improves must be gradual and morphologically consistent, and intermediate forms must be viable in some sense. It is impossible to say much of the physiology of the hypothetical proto-fliers. Biomechanical evidence based on the performance of different structures can however give a valuable guide to the relative likelihood of the two models.

Biomechanical analysis relies on estimation of quantities such as energy rates, speeds and forces in the muscles and limb segments. These data can be used in two ways: first, they may form the basis for comparison with what an animal of the assumed design might have been able to achieve; and second, they allow the results of similar assumptions for the two models to be considered side-by-side. The first programme has the very real difficulty that it demands accurate knowledge of the dimensions of a hypothetical proto-flier and of the mechanical properties of its tissues; any absolute predictions may therefore be unreliable. The second approach can be more informative: the relative values for the two models should give a fair comparison of the alternatives. In this discussion I consider only the step from the presence of a wing generating static aerodynamic forces to the flapping of that wing. As I have argued above, it is this which distinguishes flight, and is therefore the prime characteristic of birds, bats and pterosaurs. I assume that the wing already possesses the main features of its structure, namely the membrane of bats and the feathers of birds. The methods and conclusions are summarized here, and the detailed arguments are given elsewhere (Rayner, 1985a, b, 1986). The first stage in the analysis is to consider the requirements of the two models.

The gliding model

Climbing

The first essential for a glider is the ability to gain height. Glides are driven by gravity, and the animal must descend. I assume that the proto-flier had access to a suitable habitat, and had the ability (morphological and physiological) to climb. Climbing performance gives a reasonable estimate of the forces and

energy rates it might be able to generate, especially since—whether it is bipedal or quadrupedal—the main forces in climbing are associated with the fore-limbs. For instance, if it were to hang in a suspended position, say against a tree trunk, with its limbs at an angle of 45° to the vertical, the animal would have to impose a static moment of $0.36 Mgb$ at the humeral joint, where M is body mass, g the gravitational acceleration, and b the length of one forelimb. Squirrels and the colugo commonly hang in this posture (Scholey, 1986), as do some climbing birds. In active climbing a somewhat greater moment would be needed, perhaps approaching twice this value. The energy rates in climbing are hard to estimate without knowing climbing speed, but will certainly exceed the rate of gain of potential energy.

Gliding

The glides of extant gliders (squirrels (Petauristinae), *Draco*, etc.) consist of an initial leap followed by a drop to gain speed before a sustained steady glide. Presumably the proto-flier would have been similar. Glide speed depends on the area of the flight surface: slowing the glide reduces the risk of accident, and there is pressure to increase wing area. Height loss is related to drag, which depends in part on the shape of the wing. With constant area, a longer and more elongated wing gives a shallower glide. The lift generated by the membranes is responsible for support of weight, and a static moment is required at the humeral joint to maintain the wing in position; I have estimated this moment as $0.23 Mgb$, where b is now the wing semi-span. This value is less than that in hanging and vertical climbing. A climbing animal therefore already has the muscular capacity to hold its wing outstretched in gliding. The acquisition of gliding by a climber is simple if the animal can develop a flight surface, and this has happened many times in vertebrates. The main advantages of gliding are that it is energetically economical and relatively fast: a gliding squirrel might travel at up to 15 m s^{-1} (Scholey, 1986), while its running speed on level ground is unlikely to exceed 2 m s^{-1} . In a suitable habitat climbing and gliding is an efficient means of locomotion: the energy for transport is expended in climbing rather than running, but the time expended in climbing is outweighed by the high speeds of gliding (Rayner, 1986; Scholey, 1986).

Flapping

A glider must lose height as potential energy is expended against drag. By flapping the wings the animal can generate thrust, and, provided there is no significant reduction in weight support (which would imply either downwards acceleration or faster flight), even a small thrust will reduce the glide angle and increase the distance travelled. I have used the geometry of the wake vortex in flapping flight in a fully developed flapper flying at the normal glide speed to predict the effect of incipient flapping (Rayner, 1986). Small, low amplitude wingbeats enhance drag or reduce weight support, but wingbeats greater than about 25° can generate useful thrust while still balancing weight. The increment in forces at the wing root are relatively modest, and mainly reflect wing inertia rather than additional thrust and drag (Fig. 2). The peak positive roll moments at high speeds remain comparable to those in climbing. The energy required for flight is also not excessive: a 27 g proto-bat climbing a tree at 0.7 m s^{-1} would require a minimum of 0.18 W mechanical energy; a noctule bat of the same

mass requires 0.2 W in steady level flight at its cruising speed of around 6 m s^{-1} (Rayner, 1986).

The cursorial model

The cursorial model is less straightforward to analyse since existing hypotheses fail to predict the mechanical environment in which the flight stroke first appeared. The problem of getting off the ground is compounded by the apparent change of action of selection forces from favouring the hind-limbs for speed and agility in a cursor, to the fore-limbs as the animal begins to fly. Did the proto-flier have to transport different muscles for the two modes? Both climbers and gliders use the fore-limb muscles in locomotion, and are not affected by this problem.

To make it comparable with the gliding model, I envisage a situation in which the cursor makes the best possible use of its hind-limbs to fly: it jumps from the ground, while still running, to gain height. Its initial flaps can then take place while descending, and like the gliding model are assisted by gravity. This comparison favours the cursorial model: any alternative working *against* gravity would increase the mechanical and energetic demands of incipient flight and make the model relatively less attractive in comparison with the gliding model.

Running

The mechanics of running in bipedal birds, mammals and lizards are well understood. Without using the forelimbs the animals have good agility, and can move at relatively high speeds up to 2 m s^{-1} ; the energy rates required at higher speeds are extreme, and can be sustained only for brief periods.

Jumping and flying

If it is to jump before initiating flying, a running proto-flier must use some of the energy available from its hind limbs to leave the ground. At maximum exertion this must be associated with some degradation of running performance, and I have calculated that for a biped of mass 0.2 kg and typical theropod morphology the drop in running speed associated with the jump is of the order of 30–40% (Rayner, 1985b). For a likely running speed of 2 m s^{-1} this implies very low gliding or flying speeds. The animal would be unable to extend its jumps significantly by flapping to obtain thrust since the energy demanded would be considerable. Moreover acceleration to higher and more efficient flight speeds takes time, and would not be permitted by its short leaps.

This strategy of running, jumping and gliding is energetically attractive in that cost of transport at maximum aerobic exertion is slightly below that for continuous running. However, it is evidently too slow to favour flying. A biped *could* get sufficiently off the ground to glide briefly, and it *could* save energy by so doing. It *could* benefit further by flapping. But it has insufficient energy to reach speeds at which flapping is mechanically straightforward, and the costs of flight at these low speeds are so high that the demands on the forelimb musculature become extreme. It seems that mechanically the cursorial gliding model could just work; but practically it is highly unlikely.

The models compared

The separate analysis of the two models strongly suggests gliding is an essential precursor of the appearance of flapping flight. However, as the absolute estimates may not be correct, comparison of the two models under similar assumptions should give a clearer indication. To do this I assume that the purpose of movement is for transport, and that the animal will choose to move in such a way that it minimizes the cost of transport, that is the energy to transport unit mass through unit distance. This ignores other possible—but less readily quantified—benefits such as escape from predation or access to new microhabitats. We then compare two situations:

(1) An animal climbs a tree or other height, then glides to the next tree, then gradually begins flapping small wings. As the wings and the wingbeat develop, so the thrust generated increases until the flight path is level.

(2) A running biped makes small jumps from the ground, simultaneously flapping its wings to extend the jumps. As the wings develop, the thrust increases and the jumps become longer.

The assumptions involved are detailed elsewhere (Rayner, 1985a, b, 1986).

Cost of transport in gliding

Climbing and gliding is the typical locomotory mode of gliding squirrels, and reduces cost of transport considerably compared to running (Scholey, 1986: fig. 4). This form of gliding is adaptively successful even if the wings are not flapped, and becomes more attractive if the wings enlarge (although long non-flapping wings may be a liability in a cluttered habitat). Adding flaps as the wings develop gives a greater advantage, with a continuous and gradual reduction in cost of transport to as little as 20% of the climbing and gliding value. Provided the animal can take advantage of the reduced cost (by travelling further to forage, for instance) there is strong feedback encouraging development of the wings and other flight organs (Fig. 4). Moreover, if the contribution to fitness is inversely proportional to cost, feedback is stronger in the early stages of wing development.

Cost of transport for a cursor

By comparison, the cost savings for running and jumping are initially very small, and the cost for running is rather higher than for climbing and gliding. The end result, assuming progression to a fully adapted flier, must be the same as for the gliding model, so the total reduction in cost is considerably greater than for the climber (Fig. 4). Feedback from the new adaptation is weak in the initial stages, and only becomes significant in the later stages when wings and flight are fully developed, and the cost reduction can be attributed more to radiation than initial evolution of flight. The initial cost saving is unlikely to outweigh the developmental and other costs of enhancing the fore-limbs for flapping while remaining a viable running biped. Given the simultaneous problems of attaining sufficient speed and sufficiently long jumps, it is unlikely that a cursorial runner could have begun to fly. Comparison of the two models therefore strongly implies that on mechanical grounds a gliding origin of flapping flight in both birds and bats is considerably more probable.

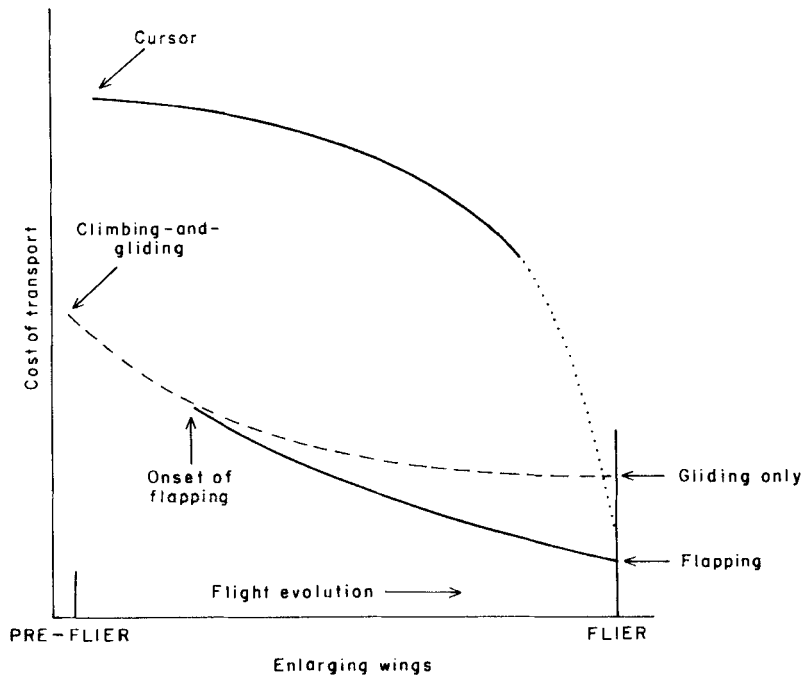


Figure 4. The cost of transport changes as wings enlarge and lengthen for the gliding (lower curves) and cursorial (upper curve) models. Calculation for gliding model explained by Rayner (1985a, 1986, for bats; 1985c, for birds); cursorial model after Rayner (1985b). The graphs are non-dimensional, but the qualitative predictions are relevant for climbers or cursors between about 20 g and 0.5 kg in mass, and there is little relative difference between the two options with size. Flapping with the short, broad wings of a passive glider is disadvantageous, but thereafter flapping brings considerable advantage, reducing total cost of transport by as much as 80%. For the cursorial model the initial energy saving is small; only as flapping flight becomes fully developed is there a significant reduction in cost; the final part of the curve (.....) is notional and has not been modelled in detail.

ARCHAEOPTERYX AND THE ORIGIN OF BIRD FLIGHT

So far I have deliberately omitted mention of some of the most significant evidence for the flight evolution problem, at least as it applies to birds. Five fossils of *Archaeopteryx lithographica*, a small theropod dinosaur, have been discovered in the Jurassic of Solenhofen in Bavaria. *Archaeopteryx* is distinguished from other theropods by its possession of feathers and of other bird-like features which indicate its ability to fly. Although it is unlikely that *Archaeopteryx* itself is a direct avian ancestor, there is little doubt that it is a sister group to the stem-group birds (Gauthier, 1986) and therefore gives the best indication of the morphology of the pro-avian. Because of this intermediate dinosaur-bird status these fossils have been invested with considerable importance, but authors have been undecided on how this evidence should be interpreted. In this paper I have developed a hypothetical mechanical argument showing that a gliding ancestry for flight is inescapable. This argument can be further supported—for birds at least—by study of the skeletons of *Archaeopteryx*.

Archaeopteryx shares apparently cursorial morphology with other theropods; there are no conventional arboreal features. Its small size (mass 0.2–0.4 kg,

comparable to that of a pigeon, *Columba livia*; Yalden, 1985) indicates reasonable agility and locomotor flexibility, and from the osteological evidence climbing cannot be ruled out. Yalden (1985) has demonstrated that the morphology of its fore- and hind-limb claws are similar to those of arboreal birds and mammals, but these claws are also characteristic of larger, related but terrestrial theropods.

In the context of flight evolution the most obvious question about *Archaeopteryx* is whether it could flap its wings, and if so in what way. Here there is some—albeit inconclusive—anatomical evidence. The pectoral girdle morphology is similar to that of non-flying theropods; the coracoids are not the solid strut-like braces of modern birds; some specimens have a furcula, but all lack a calcified (or preserved) sternum (Ostrom, 1974). These features suggest relatively weak specialization for flapping. In modern birds the sternum is the main origin for the *M. supracoracoideus* which elevates the wing, and is also the origin of some fibres of the much larger *M. pectoralis* which depresses the wing (Olson & Feduccia, 1979). The majority of *pectoralis* fibres originate below the humeral joint and produce a positive vertical or roll moment to the humerus (cf. Fig. 2); fibres from the sternum below and behind the joint pronate the wing during the downstroke by applying an additional pitching moment. The sternum may be absent through poor preservation, or may have been cartilaginous, but even without it the animal may have flown well. Bats do not have functional sterna, although of course their pectoral anatomy is very different from that of birds (Fig. 1). Most theropods also lack calcified sterna (Ostrom, 1976). Without a sternum *Archaeopteryx* might well have been able to depress the wing, but is unlikely to have been able to pronate it. However, extreme pronation is required only in slow flight, where it is used to control the varying circulation associated with the vortex ring gait; in fast flight the wingbeat is primarily dorso-ventral, and the wing remains near planar (above). This implies that *Archaeopteryx* was unable to fly slowly, and that the keeled sternum is a derived character associated with the later development of slow flight.

More definite evidence is provided by the upstroke musculature. In birds and pterosaurs (Fig. 1) the wing elevator is the *supracoracoideus*, lying deep under the *pectoralis*, and attaching to the dorsal side of the humerus through a cavity within the humeral joint (the *foramen triosseum*). *Archaeopteryx* did not possess this arrangement (Ostrom, 1974, 1976). It may have used other muscles to elevate the wing, but if this is the case what pressures favoured the later migration of one muscle to form the *supracoracoideus*? More likely, *Archaeopteryx* flew in such a way that it never needed active muscle action to elevate the wing. Figure 2 showed the predicted wingroot bending moments for a kestrel at different flight speeds; the patterns are broadly similar for all birds and bats. At normal cruising speeds (7–9 m s⁻¹ for these data) the depressor moment is always positive, and the wing is elevated in the upstroke by aerodynamic forces. Only at low speeds is an elevator muscle required. Again, it appears that *Archaeopteryx* had poor slow-flight performance.

The wing skeleton also indicates poor slow-flight performance. The semi-lunate carpal forming the wrist articulation is shared by theropods such as *Deinonychus* (Ostrom, 1974; Padian, 1985). This would appear to prevent distortion of the wing out of its plane during the upstroke, but would permit

sweeping of the wingtip during the upstroke in fast flight, as in most modern birds (above). This flexure pre-adapts a gliding theropod proto-bird for flapping when combined with dorso-ventral movement of the humerus: such a wingbeat generates thrust simply, without the complex twisting, folding and flexing of the wing needed in slow flight.

Without elevator muscles, as also without longitudinal pectoralis fibres originating from a sternum, *Archaeopteryx* could not have flown slowly. Fast or cruising flight is less strenuous than slow flight: the forces required from the pectoralis are less extreme, no elevator muscle is needed, mechanical energy demands are less, and the wingbeat geometry is simpler. There is no evidence that *Archaeopteryx* would have been unable to flap at reasonably high speeds, comparable to the speeds of a gliding proto-bird. This is much faster than the speeds that could be reached by a cursor without the aid of gravity, and flight at the running speeds of a cursor would require active muscular pronation and elevation of the wing. As I envisage it, *Archaeopteryx* was capable of incipient flapping at relatively high flight speeds, but would have been unable to fly slowly or to control its flight to any great extent (Rayner, 1985a, b, c). At a later stage in bird radiation the sternum and supracoracoideus would have evolved in response to pressures for slow flight and manoeuvrability. The apparent absence of adaptations reflecting a cursorial origin of flight in this oldest bird strongly implies a gliding origin for birds and their flight.

DISCUSSION

Although the gliding—or arboreal—model is evidently strongly indicated by applying flight mechanics to estimate performance and to reconstruct the muscle function and locomotion of *Archaeopteryx*, there remain real objections to it, particularly in birds. Climbing would be impossible without suitable habitat, and this conflicts with the apparent terrestrial environment of the time. Proto-fliers and their sister groups would be expected to show some morphological specialization if climbing was important to them, but *Archaeopteryx* and other small theropods may have been sufficiently small to show no specialized arboreal or scansorial features: tupaiids, for instance, show little evidence of their arboreality. Some writers have argued that since gliding is an adaptive plateau in extant mammals, gliders are unlikely to evolve further. The logic of this is false: gliding is an essential pre-adaptation for flapping, and it is precisely because gliding is adaptive in this way that there were animals in which flapping could evolve. Moreover, it is as illogical to argue that gliding proto-flappers should become extinct through competition with flappers as to claim that dinosaurs became extinct because one group of them evolved into birds.

Objections to the cursorial model are more specific: The most critical—as has long been appreciated—is the need to provide a vertical force *against* gravity at an early stage in flight evolution. For this reason speeds in running cannot approach those at which flight is energetically or morphologically efficient. The wingbeat cycle in slow flight, the associated muscular specializations and the wake aerodynamics are complex and more derived than in cruising flight. Moreover, no author has proposed a logical selective pressure explaining the morphological and mechanical developments necessary for a cursor to fly.

These conclusions are reinforced by comparison of the two models. Gliding gives more rapid returns in foraging radius, locomotion efficiency and behavioural flexibility; the contribution these make to fitness provides positive feedback as the wings develop and begin to flap. The sequence envisaged is consistent with mechanics and aerodynamics and with the ecology and morphology of the hypothetical proto-flier, and moreover with the pectoral girdle and wings of *Archaeopteryx*. I have no doubt that bats evolved through gliding: on balance I consider this by far the more likely model for birds.

But these arguments are founded entirely on locomotion mechanics. I have used transport energetics as a basis for the models, presuming an animal evolves to move in the most economic way compatible with its design. But locomotion strategies may also be dictated by other factors. Gliding is used by foraging lizards (such as the genus *Draco*) and by arboreal birds (R. Å. Norberg, 1981, 1983) to increase manoeuvrability around a habitat. Access to otherwise unavailable food resources might select for flapping; even so, for mechanical reasons a gliding pathway to flapping is still inevitable. Escape from predation is a further possibility, but its relation to selection is hard to quantify: an incipient flight adaptation might render an animal more vulnerable, and so be selected *against*. Time invested in movement may be more critical than energy, so selection would favour high flight speed; this also implies a gliding origin, and yet higher speeds are easily attained by reducing wing size. Unpredictability of movement pattern is one pressure which might be more favoured by the cursorial model; the energetic and other mechanical obstacles to the transformation to flapping still remain, and there is no obvious pressure to leave the ground which could have been sufficient to overcome these difficulties.

To complete the discussion, a further possibility should be considered. I have modelled the evolution of flying vertebrates as a gradual progression through adapted and adaptive levels. Some pre-adapt to following stages (as does gliding to flapping), and the sequence is driven by consistent, readily identified and realistic selective pressures. Intermediate stages might have been maladaptive compared to their precursors or successors, as long as they were not subject to significant predation or other pressures. It is of course possible that flight evolved rapidly (by saltation), so that no intermediates would have existed. (The apparent identification of *Archaeopteryx* as a sister group to the stem-group pro-avian may well discount this.) Or proto-flappers might have benefited from some remarkable environmental conditions in which selective pressures were sufficiently strong and mechanical constraints sufficiently weak that the comparison with aerodynamics of contemporary fliers is completely invalid. However, if flight did appear suddenly there is no mechanical—or evolutionary—problem to discuss. The first bird or bat would have had the same attributes as modern animals, and its success in flight would be mediated by much the same ecological pressures; questions of its evolution become untestable and meaningless.

In this survey I have not considered all the problems of flight evolution. I have ignored features such as the behavioural and ecological flexibility of an incipient flier, its likely predators, and the habitats it might have used. I have not considered the important role of control and stability. (Does *Archaeopteryx* have a long bony tail just because its ancestors did? Does the superficial similarity with magpies (*Pica*, Corvidae) indicate arboreal habit?) The

biomechanical approach cannot unequivocally resolve these points, any more than it can *prove* that proto-fliers had to be gliders. Its value lies in showing that some possibilities—such as the fluttering model—are untenable, and that some are *more likely* than others. The arguments are convincing, but as in all evolutionary debates the central difficulty lies not only in assembling the evidence, but also in assessing its worth, particularly when predictions or interpretations conflict. Mechanical arguments would be devalued if they predicted the most likely behaviour or morphology of a proto-flier to be phylogenetically or developmentally untenable. But in this case they do not do this: evidence from aerodynamics and flight mechanics is reinforced by the interpretation of *Archaeopteryx* that this approach implies, and strongly predicts a gliding origin of flight in all groups of vertebrates.

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