
1 Flight

Muscle powered flight requires a high metabolic rate and a very efficient respiratory system. Constable (1990)

1.1 Energetic Cost of Flight

Defined as capacity to produce lift, accelerate, and maneuver at various speeds, powered flight is an elite form of locomotion. It has compelled incomparable structural specializations and refinements and striking functional integration of practically all the organs and organ systems, especially the gastrointestinal, cardiovascular, respiratory, muscular, and nervous systems. Exerting substantial metabolic, mechanical, and aerodynamic demands, flight adaptively evolved in response to particular selective pressures in order to meet specific survival needs. To morphologists and physiologists, in many ways volant animals offer exceptional an opportunity in determination and understanding of the upper limits of biological design and performance of vertebrates.

A novel mode of locomotion, flight sets birds well apart from other vertebrates. Historically, humans have coveted ability to fly since the first moment that the cave person looked up into the sky and observed birds soaring effortlessly. In the Greek mythology, some 3500 years ago, using fake wings of which the feathers were affixed to their arms with bee's wax, Daedalus and his son Icarus escaped from King Mino's island prison dungeons (Fig. 1). Unfortunately, as the story goes, with youthful daring, Icarus disregarding his father's wise counsel flew too close to the sun, the wax melted, the 'wings' disintegrated, and he fell to his death. Without the relentless provocation and attestation presented by birds that gravity could be overcome, it would have taken much longer before human beings thought of flight as a feasible form of locomotion. In his 1505 treatise entitled '*On bird flight*', Leonardo da Vinci, who strongly believed that human beings would never learn to fly until they thoroughly understood the secrets of bird flight, wrote: "*I remember that in my*

earliest childhood, I once dreamed that a vulture flew towards me, opened my mouth and stroked it a number of times with its feathers, so that I could talk about wings for the rest of my life". For understandable, though not defensible reasons, the physiology and to some extent the morphology of the human being is the conventional reference point against which other animals are compared and measured. From this anthropocentric position, factual errors have resulted from direct extrapolation of the mammalian functional morphology to that of birds and other animals. Failing to appreciate nature's remarkable resourcefulness of conceiving different solutions to various selective pressures, a great deal of time and immense resources have been wasted pursuing costly, unproductive inquiries. For example, on strong belief that all that was needed to fly (just like in the case of the mythological angels, dragons, and the 'flying' horse Pegasus) was to strap on 'wings' and flap, fatalities after jumping from heights using various contraptions (including a raincoat!) are well documented in the recent past. It took time and great frustration before the fact that humans were never built to fly at long last sank in. Literally going back to the drawing boards, it was ultimately realized that active flight would never be achieved by directly emulating birds but rather by alternatively engineering flying machines. Such designs had to be formulated on the universal laws of nature that apply to all moving objects, including birds.



Fig. 1. A fourteenth century illustration showing the mythical flight of Daedalus and Icarus from King Mino's prison island. From an anonymous nineteenth century wood carving

Paying back a well-deserved tribute to their ‘feathered instructors’, Orville Wright (of the Wright brothers) wrote: “*Learning the secret of flight from a bird was a good deal like learning the secret of magic from a magician. After you once know the trick, you see things that you didn’t notice when you didn’t know exactly what to look for*”. Despite the great advances that have now been achieved in the field of avionics, materials and technology needed to construct machines that can fly efficiently using flapping deformable wings are still in the offing.

An underlying principle in biology is that manifestation of exclusivity, e.g. in structure and/or function, offers important insight into the opportunistic paths that evolution has taken. Obliging many constraints on structure, flight is the single most important factor that has decreed the form and function of birds. As they got bigger, it necessitated more energy for birds to fly. At odds with what would be expected, doubling-up body mass does not result in a doubling-up of the energy needed to fly at minimum speeds but rather by an increase by a higher factor of 2.25. Realization of certain intricate adaptive traits like volancy entails certain trade-offs and compromises. For flight in birds, these changes included the following: (a) aerodynamic streamlining of the body, (b) total commitment of the forelimbs (wings) to flight, (c) development of a long flexible neck to perform the activities previously executed by the wings (forelimbs), and (d) inevitably with development of a long neck a long trachea. A long trachea precipitated respiratory limitations regarding air flow resistance and large dead-space volume. To offset the restrictions, birds developed a wider trachea (about three times larger than that of a mammal of equivalent body mass) and a slower respiratory rate.

The exacting demands that flight compelled on birds (the entire class of Aves) obligated greater uniformity in their external morphology than has been possible in single orders of fishes, amphibians, and reptiles (Marshall 1962, p 555). Yapp (1970, p. 40) observes that, in the entire population of birds, there is less variation in structure than in the 90 or so species of primates and 290 species of *Carnivora*. Even those birds that have lost capacity for flight, e.g. ostrich, cassowaries, rheas, emu, and kiwi, cannot be mistaken for any other vertebrate group! Paradoxically, while a harmonious external form exists, flight has imposed exceptional diversity in the internal, anatomical structural details of birds (King and King 1979, p 2). The features pertaining to the respiratory system are mentioned in this account. In some cases, they are of uncertain or no functional consequence. The benefits reaped by birds from capacity of flight were enormous. Capable of overcoming geographical obstacles, they occupied diverse ecological niches and habitats, consequently undergoing remarkable adaptive radiation that has culminated in about 9000 species (e.g. Morony et al. 1975; Gruson 1976). In contrast, the contemporary reptiles total about 6000 species (Bellairs and Attridge 1975, p. 17) whilst mammals (Yapp 1970, p. 40) and amphibians (Bellairs and Attridge 1975, p. 17) have fewer species. Bats, the only volant mammals, comprise some 800 species – in specific numerical diversity they are only exceeded by the order

Rodentia with 1660 species. Of all known mammalian species, one in five species is a bat! After the human being, *Myotis* (family: Vespertilionidae) is said to be the most widely spread naturally occurring mammalian genus on earth (Yalden and Morris 1975). Constituting about 75 % of the envisaged 5 to 50 million animal species (e.g. May 1992), both numerically and specifically, the insects (another volant taxon) are the most abundant (e.g. Wigglesworth 1972). The fact that birds and bats are the only existing vertebrates capable of powered flight clearly attests to the extreme selective pressure that the mode of locomotion imposes.

After evolving independently from reptiles much later than mammals (e.g. de Beer 1954; Ostrom 1975) and achieving endothermic homiothermy, birds reached metabolic scopes between resting and maximal rates of exercise or cold-induced thermogenesis that are 4 to 15 times higher than those of their progenitors at same body temperature (e.g. Lasiewski 1962). Moreover, among the endotherms, birds, especially the passerines, the most successive taxon with 5739 (over 60 % of the total number of extant avian species; e.g. Sibley and Alhquist 1990; Barker et al. 2004), operate at a relatively higher body temperature of 40–42 °C compared with the lower one (38 °C) of mammals (e.g. Lasiewski and Dawson 1967; Aschoff and Pohl 1970). A significant metabolic barrier separates ectothermic from endothermic animals and volant from nonvolant ones. The evolution of flight in birds is thus unmistakably associated with development of an exceptionally efficient respiratory system. Whether by default or by design, the lung-air sac system appears to have been the optimal solution to the metabolic needs of birds. Since bats, a taxon with a characteristic mammalian lung (e.g. Maina 1985, 1986) but a highly refined one (e.g. Maina et al. 1982; Maina and King 1984; Maina et al. 1991), fly as well as birds (e.g. Norberg 1990), it is patently clear that the design of the avian respiratory system is not a prerequisite for flight.

The grace and majesty with which birds in particular fly are extremely deceptive of the severe constraints that had to be surmounted to achieve and maintain flight. In practically all active vertebrate groups, locomotion exerts the highest demands on the respiratory system (e.g. Banzett et al. 1992). Skeletal muscle accounts for 96 % of a flying animal's total oxygen consumption (VO_{2c}) during flight (Thomas and Suthers 1972; Thomas et al. 1984). The need to lower the cost of transport may have been the foremost selective pressure that compelled the evolution of flight (Scholey 1986). During migration or while foraging, compared with other vertebrates, birds and bats travel over longer distances at faster speeds (Fenton et al. 1985).

Active flight is innately a highly energetically demanding form of locomotion (Ellington 1999; Nudds and Bryant 2000; Tobalske et al. 2003). The mass-specific aerobic capacities of flying birds and bats are 2.5 to 3 times greater than those of mammals of the same body mass running fast on the ground (e.g. Thomas 1987). During continuous flight, e.g., bats increase their VO_{2c} by a factor of 20–30 (e.g. Thomas and Suthers 1972) and, in turbulent air or when ascending, a bird can increase VO_{2c} for brief periods by the same

magnitude (Tucker 1970). At an ambient temperature of 20 °C, a 12-g bat, *Myotis velifer*, amazingly increases VO_{2c} 130 times that at rest (Riedesel and Williams 1976). A budgerigar, *Melopsittacus undulatus*, in level flight, i.e. at its most economical speed, increases its VO_{2c} 13 times its standard metabolic rate (MR), a value that is about 1.5 times that of a similar sized mouse, *Mus musculus*, running hard on a tread mill (e.g. Tucker 1968). In the pigeon, *Columba livia*, when running on the ground, VO_{2c} is 27.4 ml.min⁻¹ and, during flight at a speed of 10 m s⁻¹, VO_{2c} is 77.8 ml min⁻¹, a factorial difference of 3 (e.g. Grubb 1982). In the herring gull, *Larus argentatus*, during flight, the MR is twice the resting value while, in the grey-headed albatross, *Diomedea chrysostoma*, the rate is about three times the predictable basal one (e.g. Costa and Prince 1987).

Flight has only been realized by two phyla, namely the Chordata and the Arthropoda. Chronologically, volancy was achieved by the insects about 350 million years ago (mya; e.g. Wigglesworth 1972), the now extinct pterodactyls some 220 mya (e.g. Bramwell 1971), in birds around 150 mya (e.g. de Beer 1954), and bats 50 mya (e.g. Yalden and Morris 1975). *Archeopteryx lithographica* of the Upper Jurassic and *Icaronycteris index* of the Eocene are respectively the oldest bird and bat. The variety of animals wrongly said to 'fly', e.g. the freshwater butterfly-fish, *Pantodon buchholzii*, of the West African rivers, the parachuting frog of Borneo, *Rhacophorus dulitensis*, the flying snakes of the jungles of Borneo, *Chrysopelea* sp., the flying squirrel, *Glaucomys volans*, of North America, the flying lemur, *Cyanocephalus volans*, and the East Indian gliding lizard, *Draco volans*, are strictly acrobatic passive gliders or parachutists that use modifications of certain parts of their body to delay a fall by using drag and lift. Such animals have not had to grapple with the daunting aerodynamic and metabolic imperatives for active flight.

While costly in terms of absolute demands for energy, powered flight is an exceptionally efficient form of locomotion. At high speed, the distance covered per unit energy expended is much less than that incurred during most other kinds of locomotion (e.g. Schmidt-Nielsen 1972; Rayner 1981). In the bat species *Phyllostomus hastatus* and *Pteropus gouldii*, e.g., the energy needed to cover a given distance is respectively between one-sixth and one-quarter of that required by similarly sized, nonflying mammals (Thomas 1975). At their optimal speeds, the minimum cost of flying for a 380-g bird is about 30 % of the energetic cost of a 380 g nonvolant mammalian runner (e.g. Hainsworth 1981). On the whole, birds have a larger daily physical activity, i.e. field MR, than mammals (King 1974). A 380 g bird spends about 74 % more energy daily than a 380-g mammal (Powell 1983). Further to achieving a more economical mode of foraging, animals that accomplished flight reaped extra advantages from it. They were able to: (1) inhabit a less crowded and almost limitless ecological niche, (2) escape from ground predation, and (3) experience unimpeded geographical dispersal, allowing extensive adaptive radiation that culminated in remarkable speciation. By the end of Eocene (about 35 mya), e.g., 26 of the modern 27 avian orders were well established, a process

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