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REVIEW

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## WHAT IT TAKES TO FLY: THE STRUCTURAL AND FUNCTIONAL RESPIRATORY REFINEMENTS IN BIRDS AND BATS

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### Summary

In absolute terms, flight is a highly energetically expensive form of locomotion. However, with respect to its cost per unit distance covered, powered flight is a very efficient mode of transport. Birds and bats are the only extant vertebrate taxa that have achieved flight. Phylogenetically different, they independently accomplished this elite mode of locomotion by employing diverse adaptive schemes and strategies. Integration of functional and structural parameters, a transaction that resulted in certain trade-offs and compromises, was used to overcome exacting constraints. Unique morphological, physiological and biochemical properties were initiated and refined to enhance the uptake, transfer and utilization of oxygen for high aerobic capacities. In bats, exquisite pulmonary structural parameters were combined with optimal haematological ones: a thin blood–gas barrier, a large pulmonary capillary blood volume and a remarkably extensive alveolar surface area in certain species developed in a remarkably large lung. These factors were augmented by, for example, exceptionally high venous haematocrits and haemoglobin concentrations. In birds, a particularly

large respiratory surface area and a remarkably thin blood–gas (tissue) barrier developed in a small, rigid lung; a highly efficient cross-current system was fabricated within the parabronchi. The development of flight in only four animal taxa (among all the animal groups that have ever evolved; i.e. insects, the now-extinct pterosaurs, birds and bats) provides evidence for the enormous biophysical and energetic constraints that have stymied volancy. Bats improved a fundamentally mammalian lung to procure the large amounts of oxygen needed for flight. The lung/air sac system of birds is not therefore a prescriptive morphology for flight: the essence of its design can be found in the evolution of the reptilian lung, the immediate progenitor stock from which birds arose. The attainment of flight is a classic paradigm of the remarkable adaptability inherent in organismal and organic biology for countering selective pressures by initiating elegant morphologies and physiologies.

Key words: bird, bat, lung, flight, oxygen consumption, blood, hypoxia, haematocrit.

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### Introduction

*‘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 did not notice when you did not know exactly what to look for’.*

Orville Wright

Evinced in the fact that the structural complexities and functional efficiencies of the gas exchangers parallel the phylogenetic levels of development, body size and life styles pursued (e.g. Maina, 1998a, 2000), respiration has been central to the evolution of animal life. In active animals, the capacity of increasing metabolic rates during locomotion places great demands on the respiratory system (e.g. Banzett et al., 1992; Bundle et al., 1999). Flapping (active=powered) flight is energetically a very costly form of locomotion (e.g. Tucker,

1972a; Berger and Hart, 1974; Carpenter, 1975; Thomas, 1975). In the Animal Kingdom, powered flight has evolved only in two phyla, namely the chordates and the arthropods. The insects, the now-extinct pterodactyls, birds and bats, chronologically in that order, are the only taxa that have ever evolved volancy: the insects (in their adult form) are the only volant invertebrates while, birds and bats are exclusively the only extant volant vertebrates. This clearly attests to the extreme selective pressure that flight compels. Nature places severe constraints on the evolution of highly refined biological processes and designs. Their fabrication entails accurate analysis of the costs involved against the benefits acquired. Transactions that entail trade-offs and compromises ensue. Animals that have adapted to life under extreme conditions or have attained unique life styles (e.g. flight) have always

intrigued biologists. In this regard, studies of flight with respect to its aerodynamic, physiological, morphological and biochemical prescriptions offer excellent paradigms for understanding the evolution of complex adaptations and for exploring the upper limits of natural designs and performances of organisms and organ systems. The realization of flight necessitated profound refinement, commitment and integration of virtually all organ systems and biological processes, especially the sensory, digestive, cardiovascular, locomotory and pulmonary systems, for a single activity.

Although both mammals and birds originated from cotylosaurian reptiles some 300 million years ago, the more recent progenitors of these two vertebrate groups diverged from this lineage at different times, with birds evolving from reptiles after mammals (e.g. de Beer, 1954; Ostrom, 1975; Pough et al., 1989). *Archeopteryx lithographica* of the Upper Jurassic (150 million years ago) is apparently the oldest well-known fossil bird (e.g. de Beer, 1954), and *Icaronycteris index* of the Eocene (50 million years ago), a specimen that morphologically resembles the modern Microchiroptera (Jepsen, 1970), is the oldest known fossil bat (Jepsen, 1970; Wimsatt, 1970; Yalden and Morris, 1975). The earlier dominance of the diurnal niche by the birds perhaps exerted a strong competitive pressure that relegated bats to their characteristic nocturnal lifestyle. Avoidance of predation or competition for food are the main plausible explanations for night flying (e.g. Moore, 2000).

On account of their different phylogenies and, hence, different genetic resources, to overcome common constraints, bats and birds utilized various schemes to meet individually the aerodynamic and energetic requirements of flapping flight. Substantial benefits accrued from the attainment of flight: volant animals occupied a less crowded and almost limitless ecological niche (the atmosphere), escaped from ground predation, adopted a more economical mode of foraging and, by overcoming geographical obstacles, underwent remarkable adaptive radiation and speciation. Constituting approximately 75% of the envisaged 5–50 million species (e.g. May, 1988, 1992), the insects are the most abundant animal taxon (e.g. Wigglesworth, 1972); there are as many as 9000 avian species (e.g. Molony et al., 1975; Gruson, 1976) and, of the 4200 mammalian species, 1000 (i.e. approximately 25%) are bats (Wimsatt, 1970; Yalden and Morris, 1975). After the human being, *Myotis* (Family: Vespertilionidae) is reported to be the most widely dispersed naturally occurring mammalian genus on Earth (Yalden and Morris, 1975). Despite their numerical abundance and wide geographical distribution, however, and perhaps because of their elusive nocturnal lifestyle, bats largely remain animals of curiosity, myth and even prejudice.

### Energetic demands for flight

The grace and the effortlessness with which birds, in particular, fly are highly deceptive of the severe constraints that were surmounted for flight. The energetic demands of flight are beyond those attainable by non-flying vertebrates (Tucker,

1972a,b; Berger and Hart, 1974; Carpenter, 1975; Thomas, 1975). Hence, a significant metabolic barrier must separate volant from non-volant vertebrates. After evolving independently from reptiles, birds and small mammals attained aerobic metabolic scopes between resting and maximal rates of exercise- or cold-induced thermogenesis that are 4–15 times those of their progenitors at the same body temperature (e.g. Bennett and Dawson, 1976; Bartholomew, 1982; Dawson and Dawson, 1982). Bats and birds increase their rate of oxygen uptake ( $\dot{V}_{O_2}$ ) from rest to flight by 10- to 20-fold (e.g. Thomas, 1987; Butler, 1991) and insects by 120- to 400-fold (e.g. Weis-Fogh, 1967). In level flight, i.e. at its most economical speed, a budgerigar (*Melopsittacus undulatus*) increases  $\dot{V}_{O_2}$  to 13 times that at its standard metabolic rate (Tucker, 1968b). This is approximately 1.5 times the  $\dot{V}_{O_2}$  of a similar-sized mouse running hard on an exercise wheel (Tucker, 1968a,b). In turbulent air or when ascending, a bird can increase its  $\dot{V}_{O_2}$  for brief periods by approximately 20- to 30-fold, whereas even a good human athlete can attain such an increase for only a few minutes (Tucker, 1970). The  $\dot{V}_{O_2}$  of the pigeon while running was estimated to be 27.4 ml min<sup>-1</sup> and while flying at a speed of 10 m s<sup>-1</sup> was 77.8 ml min<sup>-1</sup>, a factorial difference of 2.8 (Butler et al., 1977; Grubb, 1982). In the herring gull (*Larus argentatus*) during gliding flight, the metabolic rate is twice the resting value, while in the grey-headed albatross (*Diomedea chrysostoma*), the metabolic rate is approximately three times the predicted basal rate (e.g. Baudinette and Schmidt-Nielsen, 1974; Costa and Prince, 1987).

The mass-specific aerobic capacities of flying bats are essentially the same as those of birds in forward flapping flight but are 2.5–3 times those of running non-flying mammals of the same size (Thomas and Suthers, 1972; Carpenter, 1975; Thomas, 1987). Bats increase their  $\dot{V}_{O_2}$  during sustained flight by a factor of 20- to 30-fold (Bartholomew et al., 1964; Thomas and Suthers, 1972). *Myotis velifer* increases its  $\dot{V}_{O_2}$  by an astounding factor of 130 at an ambient temperature of 20 °C (Riedesel and Williams, 1976). The theoretical maximum aerobic power output estimates for birds of 200–250 W kg<sup>-1</sup> (Ruben, 1991) correspond to the highest value of the mass-specific power output that has been experimentally estimated from explosive flight performance (e.g. Pennycuick and Rezende, 1984; Marden, 1990).

Although expensive in its absolute demands for energy, compared with other forms of locomotion, e.g. swimming, running or walking, active flight is a more cost-effective form of locomotion. At fast speeds, the distance covered per unit of energy expended in flight is substantially less than for other forms of locomotion (Tucker, 1970; Thomas, 1975; Rayner, 1981; Schmidt-Nielsen, 1972, 1984). In the bat species *Phyllostomus hastatus* and *Pteropus gouldii*, respectively, the energy needed to move a given distance is only one-sixth and one-quarter of that used by the same-sized non-flying mammal to cover the same distance (Carpenter, 1975; Thomas, 1975). At their optimal speeds, the minimum cost of flying for a 380 g bird is approximately 30% of the energetic cost of an equivalent-sized mammalian runner (e.g. Hainsworth, 1981).

The need to reduce the cost of transport may have been the primary selective pressure that favoured the evolution of flight (Scholey, 1986).

Hovering, stationary flight relative to the surrounding air, where the downward air movements that support the mass of an animal are generated by the wing beats alone, is energetically the most expensive mode of flight (e.g. Epting, 1980; Rayner, 1982; Casey et al., 1985). The  $\dot{V}_{O_2}$  of a hovering bird is 2.5 times that in forward flapping flight. In hovering and forward-flying hummingbirds,  $\dot{V}_{O_2}$  ranges from 40 to 85 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (Pearson, 1950; Lasiewski, 1963a,b; Epting, 1980; Berger, 1985; Bartholomew and Lighton, 1986; Wells, 1993). These values are considerably higher than the  $\dot{V}_{O_{2max}}$  of a 7 g running pygmy mouse (15.7 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), a 1.1 kg kangaroo rat (10.6 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) and a 2.1 kg dog (9.5 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) (Seeherman et al., 1981).

Only a small number of birds and bats effectively hover. Hummingbirds typically do so more than 100 times per day (Krebs and Harvey, 1986). Each bout lasts for less than a minute, with 20% of the daylight hours being spent foraging (Diamond et al., 1986). The flight aerobic capacities of the small hummingbirds appear to constitute the upper limit of vertebrate mass-specific metabolic rate that is structurally and functionally tenable with efficient biological design of endothermic homeotherms. Among vertebrates, the flight muscles of the hummingbirds have the highest oxygen demand per unit tissue mass (e.g. Mathieu-Costello et al., 1992), and their maximum enzyme activities are, by general avian standards, exceptional (Suarez et al., 1986, 1991).

Regarding agility, the small species of bats show a greater scope for flight. They can even hover (Norberg, 1976b). Like certain birds that commonly use energy-saving modes of flight such as gliding and soaring (e.g. Baudinette and Schmidt-Nielsen, 1974; Norberg, 1985; Rayner, 1985), bats also do so to some extent. *Pipistrellus pipistrellus*, for example, adopts gliding flight for 13.4% of its flight time, the glides lasting for 0.1–0.3 s (Thomas et al., 1990a). On oceanic islands, some large diurnal megachiropteran bat species (e.g. flying foxes; *Pteropus* spp.) frequently use thermal- or slope-soaring during foraging flights to save energy (Norberg et al., 2000). The V-shaped flight arrangement commonly adopted by some birds, such as geese (e.g. Heppner, 1974; Hainsworth, 1987), is an energy-saving stratagem that allows birds, except the leader, to rest their wing tips on the rising vortex of air displaced by the wings of the bird in front (e.g. Lissaman and Shollenberger, 1970; Badgerow and Hainsworth, 1981; Hainsworth, 1988; Cutts and Speakman, 1994) and may facilitate long-distance flights at reduced energy cost. Bounding flight, as performed by certain small passerine birds, is another energy-saving mode of flight (Rayner, 1985).

The allometric modifications of flight performance in animals with increasing body mass indicate that certain physical laws govern animal design. Models based on theoretically and empirically derived data on features such as wingbeat kinematics, flight muscle physiology, bone strength and wing loading have been used to explain the progressive

decay of flight performance with increasing body mass (e.g. Pennycuick, 1968; Lighthill, 1977; Tucker, 1977; Weis-Fogh, 1977; Marden, 1994). Most insects, small birds and bats are able to perform different modes of flight at a wide range of speeds, while large birds, particularly those weighing more than 1 kg, are largely incapable of vertical take-off and have to taxi and thereafter fly only over short distances at low speeds. This is fundamentally because large animals generate less lift per unit muscle power: muscle-mass-specific lift, which ranges from 54 to 86 N kg<sup>-1</sup>, is approximately constant, while muscle-mass-specific power output scales positively with body mass (e.g. Marden, 1994). Recently acquired data on the energetics of short explosive flights suggest that, for a wide range of volant animals, flight performance is independent of body size (e.g. Chappell, 1982; Rayner, 1982; Casey et al., 1985; Marden, 1987, 1990; Ellington, 1991), the upper limit of aerobically sustainable mass-specific power output being approximately 100 W kg<sup>-1</sup> of flight muscle.

Aerodynamic theory predicts that the increase in an animal's mechanical power requirement for flight ( $P_{aero}$ , which is proportional to  $W^{1.185}$ , where  $W$  is body mass) rises more steeply with increasing body mass than does the capacity for metabolic power output ( $\dot{V}_{O_{2max}}$ , which is proportional to  $W^{0.7}$ ) in both flying birds and bats (Maina et al., 1991). As body mass increases, the upper limit of muscle power output capacity should constrain flight, imposing an upper body size limit that a flying animal can attain (Thompson, 1942; Marden, 1994). Continuous forward flapping flight is not common in birds weighing more than 4 kg (e.g. Rayner, 1981). In bats, the minimum power output in flight decreases markedly with body mass (Carpenter, 1986); predicting from his Fig. 8, which correlates the two variables, the power output for flight in a bat weighing 1.6 kg would be zero. It is interesting that the heaviest bats, the flying foxes (pteropotids), may weigh as much as 1.5 kg: limitations in the allometric scaling of the factors associated with the uptake and transfer of oxygen and the energetic requirements for flight with body mass must have prescribed the optimal size for volancy in bats. That there are no non-flying bats demonstrates the importance of flight for the survival of this taxon.

In the extant birds, the upper body mass limit for flight, which ranges from approximately 15 to 18 kg, occurs in birds such as the Californian condor (*Gymnogyps californianus*), the kori burstard (*Ardeotis kori*), the white pelican (*Pelecanus anocrotalus*) and the mute swan (*Cygnus olor*) (Thompson, 1942; Pennycuick, 1972; Ellington, 1991). The great burstard (*Otis tarda*) has, however, been said to reach a body mass of 21 kg (e.g. Martin, 1987). Other large now-extinct animals that were able to fly are the super-condor (*Teratornis incredibilis*) of the North American Pleistocene (said to have weighed in excess of 25 kg) and the giant *Argentavis magnificens* (thought to have weighed 120 kg) (e.g. Wetmore, 1960; Bramwell, 1971; Martin, 1987). In those early years, flight may have been possible in giant birds because of the lower level of gravity (e.g. Carey, 1976), the higher air density and the hyperoxic atmosphere (Graham et al., 1995; Kerr, 1999). Recent

computations of maximum power generation (e.g. Ruben, 1991; Ellington, 1991; Marden, 1994) indicate that, even under the present gravitational force of  $9.8 \text{ N kg}^{-1}$ , at least take-off and probably anaerobically powered short burst flights should have been possible in some of the ancient birds, even in the 250 kg dinosaur *Quetzalcoatlus northropi* (Paul, 1990, 1991)!

The multiplicity and synergy of the factors required to support the high aerobic metabolic rate of flight are probably nowhere more conspicuous than in the small energetic hummingbirds that have (i) very well-developed flight muscles (e.g. Greenewalt, 1975; Suarez et al., 1986, 1991; Mathieu-Costello et al., 1992), (ii) a rapid heart rate and wingbeat frequency (e.g. Lasiewski, 1962; Greenewalt, 1975), (iii) a large cardiac output (e.g. Johansen et al., 1979), (iv) a short whole-body circulatory time (Johansen, 1987), (v) a high blood oxygen capacity (e.g. Johansen et al., 1987), (vi) a high capillary surface area to flight muscle fibre number ratio (e.g. Lasiewski et al., 1965; Grinyer and George, 1969; Suarez et al., 1991; Mathieu-Costello et al., 1992) and (vii) highly refined pulmonary structural variables (Dubach, 1981; Duncker and Guntert, 1985a,b).

To support the enormous energetic demands, especially in flight, a hummingbird weighing 4–5 g ingests approximately 2 g of sucrose per day (Powers and Nagy, 1988). Before migration, the fat content of the body increases at a phenomenal rate of 10% of the body mass per day (Carpenter et al., 1983). To facilitate a high absorptive rate, the gastrointestinal system of the hummingbird has a large sucrase activity per unit of surface area (Martinez del Rio, 1990) and higher densities of intestinal glucose transporters than in any other vertebrate species known (Diamond et al., 1986; Karasov et al., 1986). During the premigratory period, the ruby-throated hummingbird accumulates approximately 0.15 g of triacylglycerols each day per gram body mass, a value that in a human would be equivalent to a weight gain of 10 kg per day (Hochachka, 1973). In bats, the intestines show distinct morphological adaptive features for efficient and rapid absorption of nutrients. In both frugivorous and insectivorous bats, the gastrointestinal system has a large absorptive surface area that is attained by prominent epithelial folding and microvillous amplifications (Makanya and Maina, 1994; Makanya et al., 1997).

### Flight speed, endurance and altitude

#### Birds

There are only a few species of birds in which flight speeds have been reliably determined. The swifts (Apodidae), the loons (Gaviidae) and the pigeons (Columbidae) reach speeds of between 90 and  $150 \text{ km h}^{-1}$ , while the peregrine falcon *Falco peregrinus* has been measured moving at a speed of  $205 \text{ km h}^{-1}$ , but can attain a speed of  $403 \text{ km h}^{-1}$  during a complete dive on a prey (e.g. Tucker, 1998). Although certain of the avian flight speeds may appear mediocre, when normalized to the number of body lengths covered per unit time, they are relatively fast. The small passeriform birds, e.g.

swifts, starlings and chaffinches, flying at a speed of  $40 \text{ km h}^{-1}$  cover approximately 100 body lengths  $\text{s}^{-1}$  (e.g. Kuethe, 1975) compared with only 5 body lengths  $\text{s}^{-1}$  in a highly athletic human and only 18 body lengths  $\text{s}^{-1}$  in the cheetah, the fastest land mammal (e.g. Hildebrand, 1961).

During its annual migration, the Arctic tern *Sterna paradisaea* flies from pole to pole (a return distance of approximately 35 000 km) between the breeding seasons (Berger, 1961; Salomonsen, 1967). The American golden plover *Pluvialis dominica* flies 3300 km nonstop from the Aleutian Islands to Hawaii in only 35 h (Johnston and McFarlane, 1967). The small 3 g ruby-throated hummingbird *Archilochus colubris*, amazingly, flies nonstop for nearly 1000 km across the Gulf of Mexico from the Eastern United States, a distance that may take approximately 20 h to cover (Lasiewski, 1962). Many passerine species are known to fly continuously for 50–60 h on the Europe-to-Africa trans-Saharan route (Berger, 1961). The swifts (Apodidae) fly continuously (day and night) (Lockley, 1970). The same applies to the wandering albatross *Diomedea exulans*, a champion flyer of the high seas (Jameson, 1958). The alpine chough *Pyrrhocorax graculus*, a bird that nests above an altitude of 6.5 km (Swan, 1961), faces hypoxia ( $P_{\text{O}_2}=9 \text{ kPa}$ ), low temperatures ( $-27^\circ\text{C}$ ) and a desiccating atmosphere.

Flocks of birds have been observed by radar at an altitude of 6–8.5 km (e.g. Richardson, 1976; Stewart, 1978; Elkins, 1983). The highest authenticated record of a flying bird is that of a Ruppell's griffon vulture *Gyps rueppellii*; a specimen was sucked into the engine of a jet aircraft at an altitude of 11.3 km (Laybourne, 1974). At that altitude, the barometric pressure is approximately 24 kPa (i.e. 20% of that at sea level), the  $P_{\text{O}_2}$  in the expired air is less than 5.3 kPa (closer to 2.7 kPa if hyperventilation brings the  $P_{\text{CO}_2}$  to approximately 0.67 kPa) and the ambient temperature is below  $-50^\circ\text{C}$  (Torre-Bueno, 1985). The ability of birds to survive, let alone to exercise, under the extreme conditions of high altitude is well beyond the reach of the non-flying mammals.

The most astounding high-altitude flight behaviour in birds is unquestionably that of the bar-headed goose *Anser indicus* during its annual trans-Himalayan migration from the wintering grounds on the Indian subcontinent to the breeding grounds around the great lakes in the South-Central regions of Asia (altitude 5.5 km) (Swan, 1970). The bird takes off from virtually sea level and flies nonstop across the Himalayan mountains, very quickly reaching an altitude of approximately 10 km over the summits of Mount Everest and Annapurna 1 (Swan, 1961, 1970; Black et al., 1978; Black and Tenney, 1980). The barometric pressure at these altitudes is approximately 31 kPa, and the  $P_{\text{O}_2}$  in dry air is 6.5 kPa (e.g. West, 1983). Presuming that during these excursions the goose maintains a constant body temperature of  $41^\circ\text{C}$  and that the inhaled air is warmed to that of the body (lung  $40^\circ\text{C}$ ), the  $P_{\text{O}_2}$  in the air reaching the air capillaries would barely exceed 4.9 kPa. Up to a simulated altitude of 6.1 km, resting *Anser indicus* maintains normal  $\dot{V}_{\text{O}_2}$  without hyperventilating and on 'ascending' to 11 km, where the concentration of

oxygen is only  $1.4 \text{ mmol l}^{-1}$ , the resting bird takes in an adequate amount of oxygen to necessitate only a minimal increase in the ventilatory rate (Black and Tenney, 1980). At  $39^\circ\text{C}$  and  $\text{pH } 7.4$ , *Anser indicus* has a much higher blood oxygen-affinity (lower  $P_{50}$ ;  $P_{50}=3.9 \text{ kPa}$ ) than the greylag goose *Anser anser* ( $P_{50}=5.3 \text{ kPa}$ ), a close relative that subsists at lower altitudes (Petschow et al., 1977; Black et al., 1978).

In the Himalayan goose *A. indicus* and the Andean goose *Cleophaga melanoptera*, where high blood oxygen-affinity is crucial for survival, amino acid residues  $\alpha$ -119 and  $\beta$ -55, which form  $\alpha_1\beta_1$  contact in human haemoglobin, respectively, are altered (Hiebl et al., 1987), a feature that appears to increase oxygen affinity (Weber et al., 1993). In *A. indicus*, proline is substituted by the shorter amino acid alanine, and in *Cleophaga melanoptera*, leucine is substituted by short-chained serine, resulting in the loss of a single intramolecular contact (Hiebl et al., 1987; Weber et al., 1993). The similarities in the strategies adopted by the Himalayan bar-headed and the Andean geese, i.e. two single-point amino acid mutations that alter intramolecular contact and enhance haemoglobin oxygen-affinity, in two geographically separated species is a case of convergent adaptive evolution at the molecular level.

Adaptively, during high-altitude flight, birds hyperventilate without risk of respiratory alkalosis and cerebral vasoconstriction from hypocapnia (e.g. Black and Tenney, 1980; Faraci and Fedde, 1986; Bernstein, 1987; Faraci, 1990). An increase of the ventilatory rate of approximately 78% at a simulated altitude of 6.1 km does not cause respiratory alkalosis in house sparrows *Passer domesticus* (e.g. Tucker, 1968a; Lutz and Schmidt-Nielsen, 1977). In some species, such as the pigeon and the bar-headed goose, the blood flow to the brain actually increases during hyperventilatory hypocapnia (Grubb et al., 1977). By reducing the  $P_{\text{O}_2}$  gradient between the arterial blood and the inhaled air (Shams and Scheid, 1987) and by evoking a Bohr effect, which raises the oxygen content of the blood (Grubb et al., 1979), the hyperventilatory response during high-altitude hypoxia enhances the oxygen-carrying capacity of the blood. In the human being, lowering the arterial  $P_{\text{CO}_2}$  to 1.3 kPa results in hypocapnic cerebral vasoconstriction, causing a reduction of approximately 50% in the blood flow to the brain (Wollman et al., 1968). Birds have been shown to tolerate an arterial  $P_{\text{CO}_2}$  of below 0.9 kPa (Faraci and Fedde, 1986; Shams and Scheid, 1987; Scheid, 1990). Fedde et al. (1989) observed that muscle blood supply and oxygen unloading from the muscle capillaries rather than ventilation or pulmonary gas transfers are the rate-limiting steps in the contraction of the flight muscles of the bar-headed goose under hypoxia. Extrapolating measurements made on human beings at the altitude of Mount Everest, Dejours (1982), West (1983) and Scheid (1985) estimated that, if the human alveolar lung was replaced with the avian parabronchial lung, for the same arterial blood gas levels, a human would be able to ascend 780 m higher.

## Bats

Regarding speed, distance and manoeuvrability, in their own right, bats are excellent fliers (e.g. Kranowski, 1964; Vaughan, 1966; Griffin, 1970; Norberg, 1976a,b; Fenton et al., 1985; Norberg and Rayner, 1987; Rayner, 1986). Speeds of  $16 \text{ km h}^{-1}$  in *Pipistrellus pipistrellus*,  $30\text{--}50 \text{ km h}^{-1}$  in *Myotis lucifugus*,  $40 \text{ km h}^{-1}$  in *Glossophaga soricina* and  $64 \text{ km h}^{-1}$  in *Eptesicus fuscus* have been measured (e.g. Hayward and Davis, 1964; Jones and Rayner, 1989; Winter, 1999). Migratory distances of approximately 1000 km have been reported in *Lasiurus borealis*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Nyctalus noctula* and *Tadarida brasiliensis* (Baker, 1978; Thomas, 1983). *Epomophorus wahlbergi* and *Scotophilus viridis* are known to cover distances of approximately 500 km in a night as they forage (Fenton et al., 1985). Among other factors, flight style and optimum speed in bats depend on choice of food, foraging behaviour and habitat selection (Norberg, 1981). The small bats show a greater scope for flight with regard to agility and can even hover momentarily (Norberg, 1976a,b). Compared with birds, which show remarkable disparities in flight capabilities, with certain species even being flightless, all bats fly to varying extents.

Although, compared with birds, bats are not known to fly at high altitudes, bats have been shown experimentally to be capable of tolerating extreme hypoxia. Resting *Pteropus poliocephalus* can withstand acute exposure to simulated altitudes from 0 to 11 km (Thomas et al., 1985). Because of the relatively poor insulation and presence of skeletal muscles (compared with the feathered wings of birds, which do not have significant muscles on the wing surface), excessive convective heat loss to the cold air may occur across the wings of a bat at the extremely low temperatures at high altitude. The wing muscles may be cooled to a critical temperature below which proper nervous coordination, necessary for efficient flight, is curtailed. Using isolated forearm muscles from a number of temperate-zone bats, Nelson et al. (1977) observed that the duration of contraction of forearm muscles at temperatures below  $8^\circ\text{C}$  was 5–10 times longer than that at  $32^\circ\text{C}$ . In *Myotis lucifugus*, at  $5^\circ\text{C}$ , breathing is arrhythmic in character, the apnoeic phases lasting for as long as 48 min (Hock, 1951). Some bats have, however, been reported to fly in ambient temperatures as low as  $-5^\circ\text{C}$  (O'Farrell and Bradley, 1977). Temperate-zone bats are known to hibernate or to migrate to warmer regions of the world during winter (Kulzer, 1965; Thomas et al., 1990b).

## The avian respiratory system

### Structural and functional adaptations

Among vertebrates, the avian respiratory system, the lung/air sac system, is exceptionally morphologically complex and remarkably efficient (e.g. Schmidt-Nielsen, 1975; Scheid, 1979; Maina, 1996, 1998a). The lungs are compact and virtually inexpandable (e.g. Jones et al., 1985) (Fig. 1A). They are continuously and unidirectionally ventilated by synchronized action of the air sacs (e.g. Scheid, 1979).

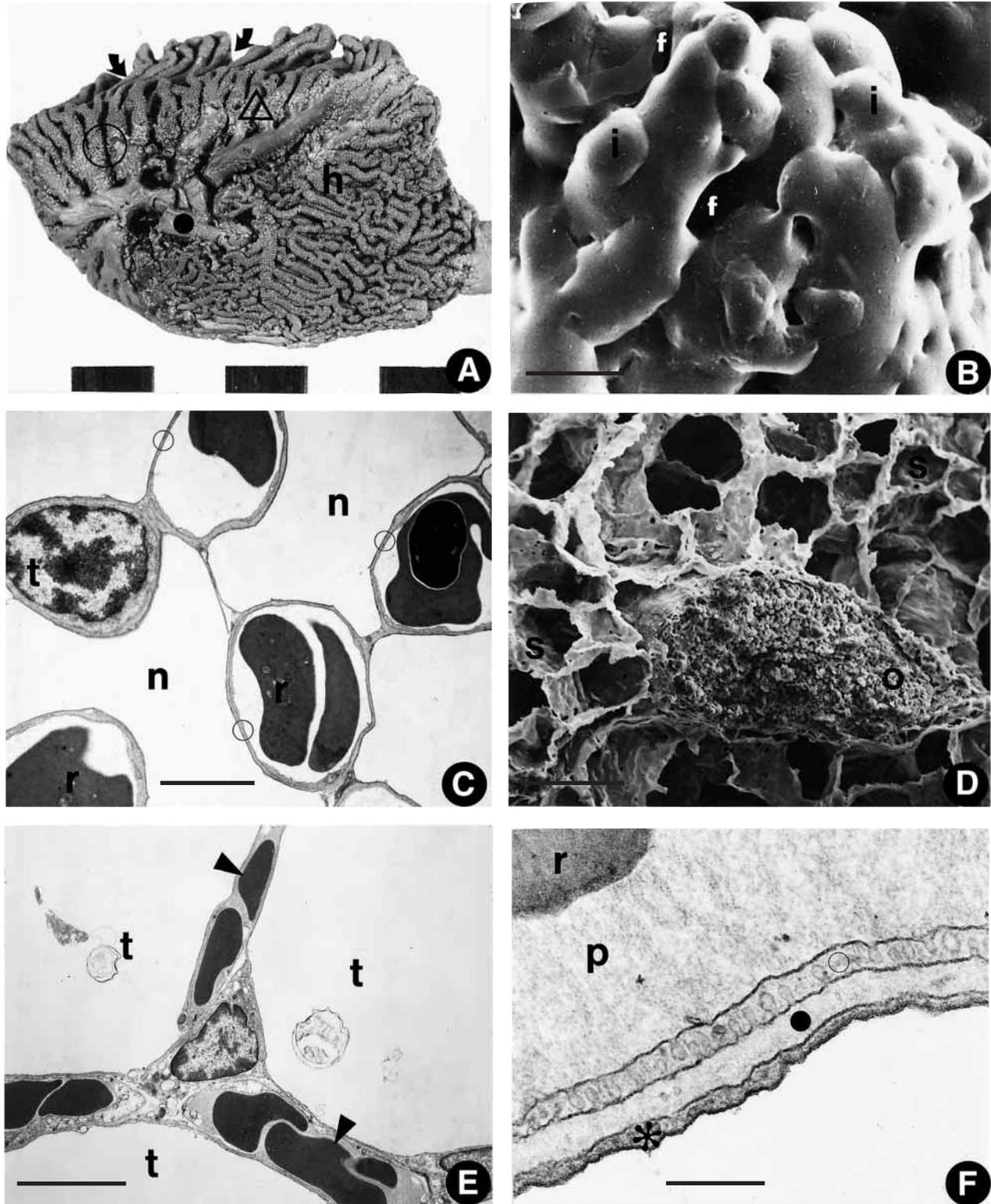


Fig. 1.

Although birds have relatively smaller lungs per unit body mass than non-flying mammals (Maina, 1989, 1993; Maina et al., 1989) (Fig. 2), their rigidity allows a substantially high respiratory surface area (Fig. 3) to be generated through intense partitioning of the parenchymal tissue. The

terminal gas-exchange components, the air capillaries, are anastomosing continuous tubules (Fig. 1B,C) and not spherical terminal units as is the case for the alveoli of the mammalian (bat) lung (Fig. 1D,E). In the 'fixed' (inexpansile) avian lung, surface tension is not a constraining factor to the ultimate

Fig. 1. (A) Cast of a lung of the domestic fowl *Gallus domesticus*. The avian lungs are compact and inexpandible. ○, medioventral secondary bronchi; △, mediadorsal secondary bronchi; ●, primary bronchi; h, parabronchi; curved arrows, costal sulci (impressions left by the ribs). Scale bar, 1 cm. (B) The tubular anastomosing air capillaries (i) of the avian lung, which interdigitate intimately with blood capillaries (f). Scale bar, 5  $\mu\text{m}$ . (C) A cross-sectional view of the air capillaries (n) and blood capillaries that contain the characteristically nucleated avian red blood cells (r). A thin blood-gas barrier (○) separates air and blood. t, a rare epithelial cell nucleus in the exchange tissue. Scale bar, 8  $\mu\text{m}$ . (D) Lung of the epauletted fruit bat *Epomophorus wahlbergi* showing alveoli (s) and a large blood vessel (O). Scale bar, 100  $\mu\text{m}$ . (E) A section of the bat lung showing alveoli (t) separated by interalveolar septa. Arrowheads, blood capillaries containing red blood cells. Scale bar, 50  $\mu\text{m}$ . (F) Blood-gas barrier of the bat lung: \*, epithelial cell; ●, basement membrane; ○, endothelial cell; p, blood plasma; r, red blood cell. Scale bar, 0.5  $\mu\text{m}$ .

diameter of the terminal gas-exchange components. The surface density of the blood-gas (tissue) barrier, i.e. the surface area per unit volume of parenchyma (a variable that denotes the relative degree of partitioning of the gas-exchange tissue and, hence, the relative sizes of the terminal gas-exchange components), is substantially greater in the avian lung than in the lungs of bats and those of the non-flying mammals (Fig. 4).

The values range from 172  $\text{mm}^2 \text{mm}^{-3}$  in the domestic fowl *Gallus domesticus* (Abdalla et al., 1982) to 389  $\text{mm}^2 \text{mm}^{-3}$  in the hummingbird *Colibri coruscans* (Dubach, 1981; Duncker and Guntert, 1985a,b) and the house sparrow *Passer domesticus* (Dubach, 1981; Maina, 1989; Maina et al., 1989). In mammals, the values are approximately one-tenth of those of birds (e.g. Gehr et al., 1981). The air capillaries (Figs 1B,C) of birds are only 3–10  $\mu\text{m}$  in diameter (Duncker, 1972; Maina, 1982) compared with the diameter of the smallest alveoli in a mammalian lung of approximately 30  $\mu\text{m}$  (reported for a bat lung; Tenney and Remmers, 1963). The total volume of blood in the bird lung constitutes as much as 36% of the lung volume, with 58–80% of it being in the blood capillaries (Duncker and Guntert, 1985a,b; Maina et al., 1989). The pulmonary capillary blood volume in birds is 2.5–3 times greater than that in the lung of a mammal of equivalent body mass, where only 20% of it is found in the alveolar blood capillaries (Weibel, 1963).

Birds range in body mass from the minute 1.6 g Cuban bee hummingbird *Calypte helenae* to the ostrich *Struthio camelus*, a flightless bird of the African savanna that may reach a body mass of 160 kg. Manifest respiratory structural/functional correlations that correspond with body size, life style and phylogeny occur in birds. The small energetic species show pulmonary morphometric specializations (e.g. Duncker and Guntert, 1985a,b; Maina, 1989; Maina et al., 1989). The

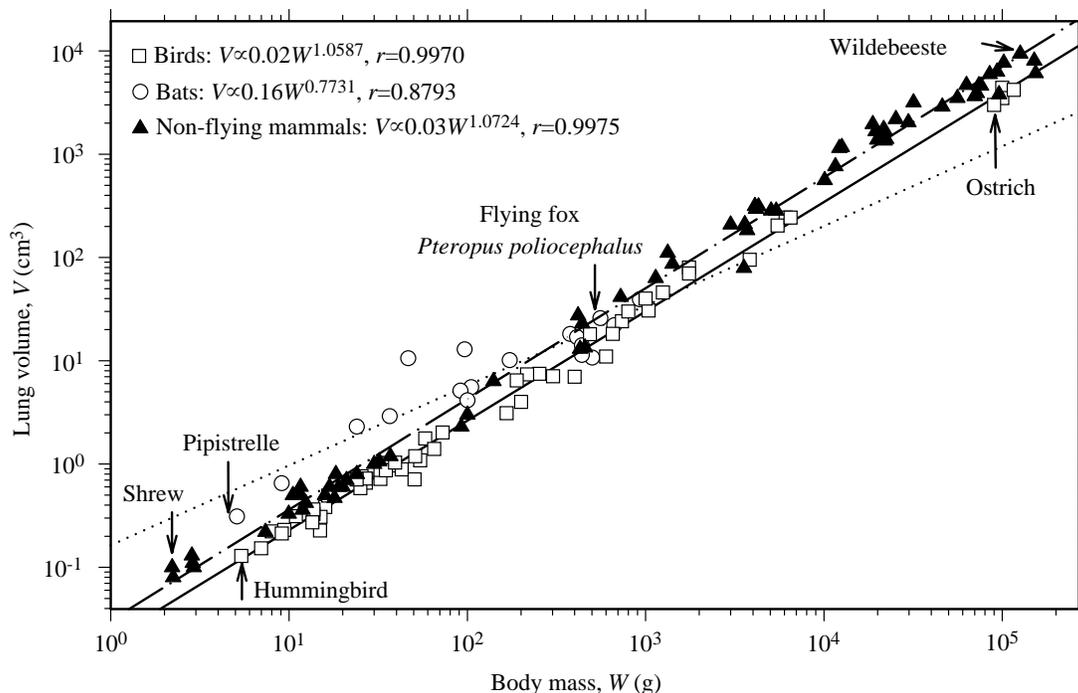


Fig. 2. Relationship between lung volume ( $V$ ) and body mass ( $W$ ) in bats, birds and non-flying mammals. Of the three groups of animals, bats have the largest lungs, followed by the non-flying mammals and birds. Data for the bats are given by Maina and King (1984) and Maina et al. (1991), for the birds by Maina (1989) and Maina et al. (1989) and for the non-flying mammals by Gehr et al. (1981). The regression lines for the three taxa are significantly different. The statistical analysis was carried out using an SAS program (STAT Guide for Personal Computers, Version 1.02, 1994: SAS Institute Inc., pp. 773–876, 941–948). The probability level of significance was set at 5%. The rationale for the statistical methods used in the analysis of the data and in comparisons of the regression lines of the pulmonary morphometric variables in birds, bats and the non-flying mammals are given in detail by Sprent (1969), and a critique of the approach was given by Maina et al. (1989, pp. 11, 45).

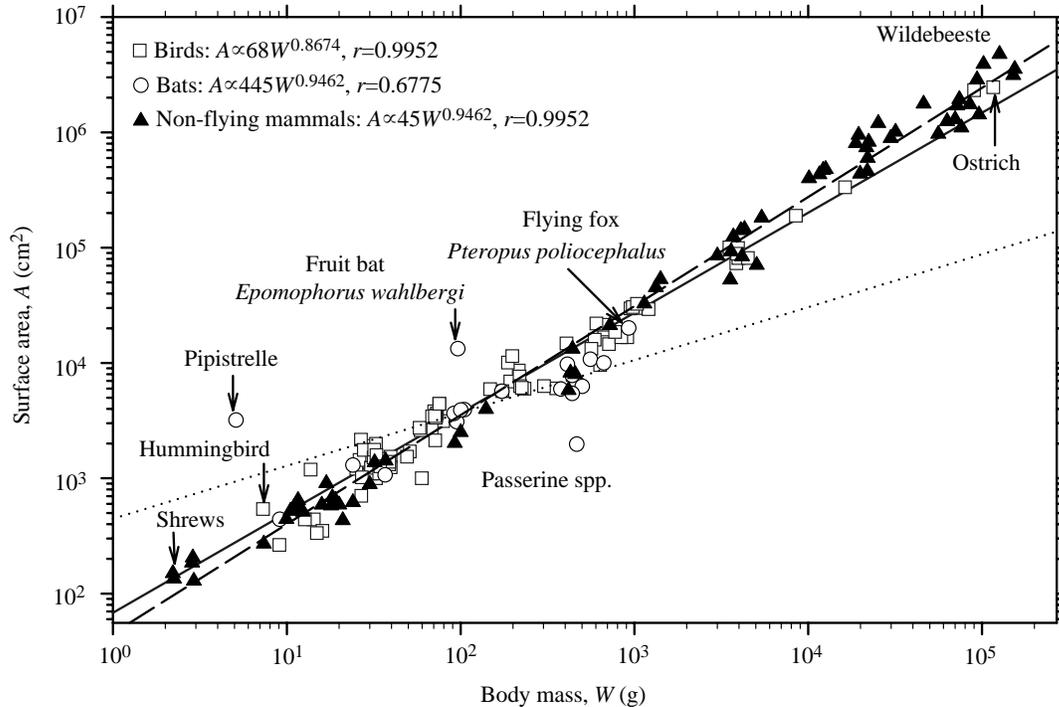


Fig. 3. Relationship between respiratory surface area ( $A$ ) and body mass ( $W$ ) for bats, birds and non-flying mammals. Certain species of bat (e.g. *Pipistrellus pipistrellus* and *Epomophorus wahlbergi*) have a greater respiratory surface area than those of the non-flying mammals and birds. Non-flying mammals with a body mass greater than 200 g have a greater respiratory surface area than birds with an equivalent range of body mass. The regression lines are significantly different ( $P < 0.05$ ). See Fig. 2 for sources of data and statistical analysis.

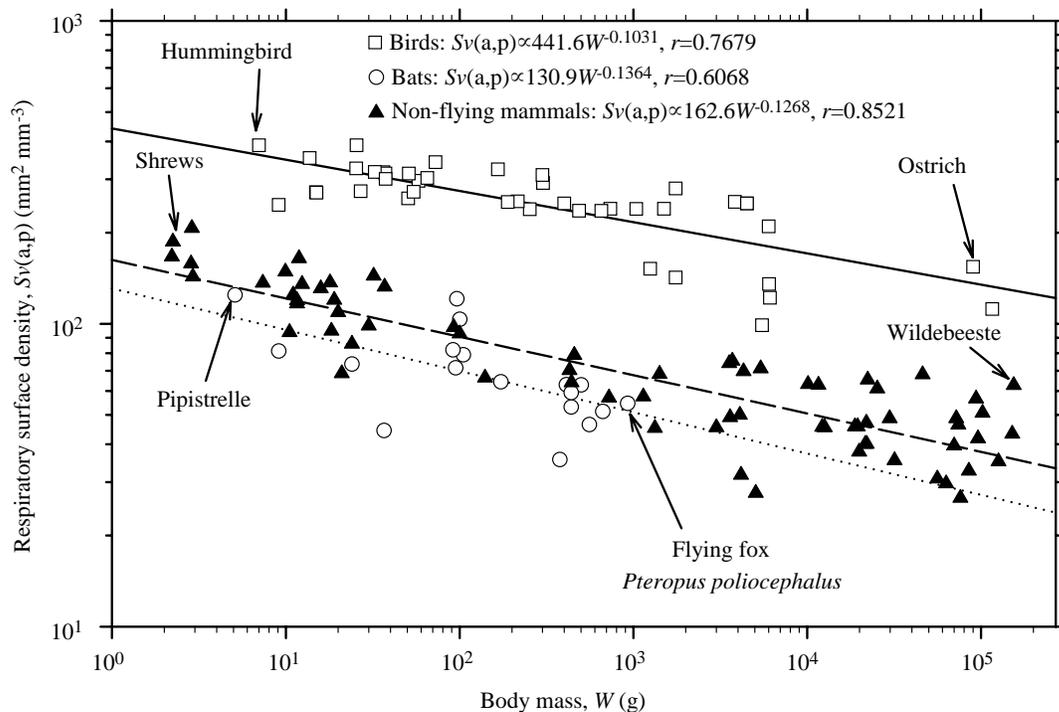


Fig. 4. Relationship between the surface density (respiratory area per unit volume of the parenchyma;  $Sv(a,p)$ ) and body mass ( $W$ ) for bats, birds and non-flying mammals. Birds have a significantly higher  $Sv(a,p)$  than non-flying mammals and bats.  $Sv(a,p)$  is an indicator of the intensity of subdivision of the parenchyma and, hence, the relative diameters of the terminal gas-exchange components. The air capillaries of birds are markedly smaller in diameter than the mammalian alveoli. It is difficult to account for the apparently relatively larger alveolar diameter in the bat lung compared with that of the non-flying mammals, as indicated by this plot. See Fig. 2 for sources of data and statistical analysis. The regression lines are significantly different ( $P < 0.05$ ).

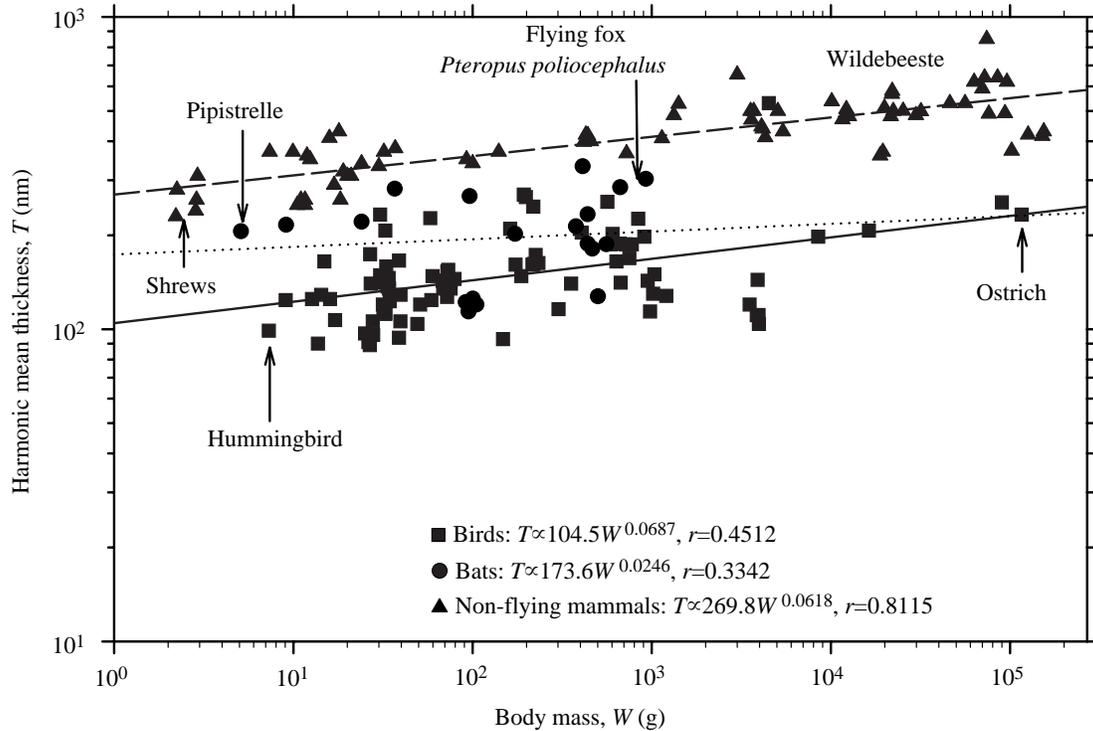


Fig. 5. Relationship between the harmonic mean thickness ( $T$ ) of the blood–gas barrier for bats, birds and non-flying mammals and body mass ( $W$ ). The small slope (scaling factor) of the regression lines in the three groups of animals shows that, in the three taxa, this variable is highly optimized. Birds have extremely thin barriers, while those of bats fall between those of birds and those of non-flying mammals. The regression lines are significantly different ( $P < 0.05$ ). See Fig. 2 for sources of data and statistical analysis.

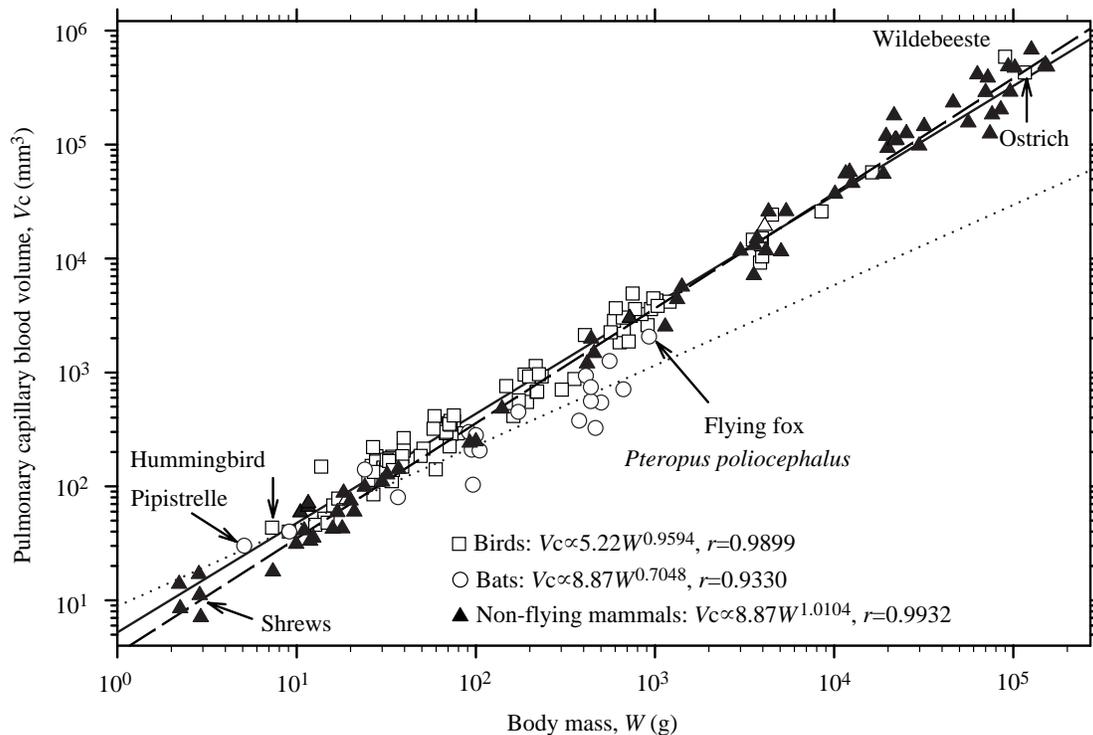


Fig. 6. Relationship between pulmonary capillary blood volume ( $V_c$ ) and body mass ( $W$ ) for bats, birds and non-flying mammals.  $V_c$  in bats is generally lower than in birds except for the smallest of the bat species, *Pipistrellus pipistrellus*. Birds below a body mass of 1 kg have a higher  $V_c$  than non-flying mammals, but above a body mass of more than 10 kg, the non-flying mammals have a significantly greater  $V_c$ . The regression lines are significantly different ( $P < 0.05$ ). See Fig. 2 for sources of data and statistical analysis.

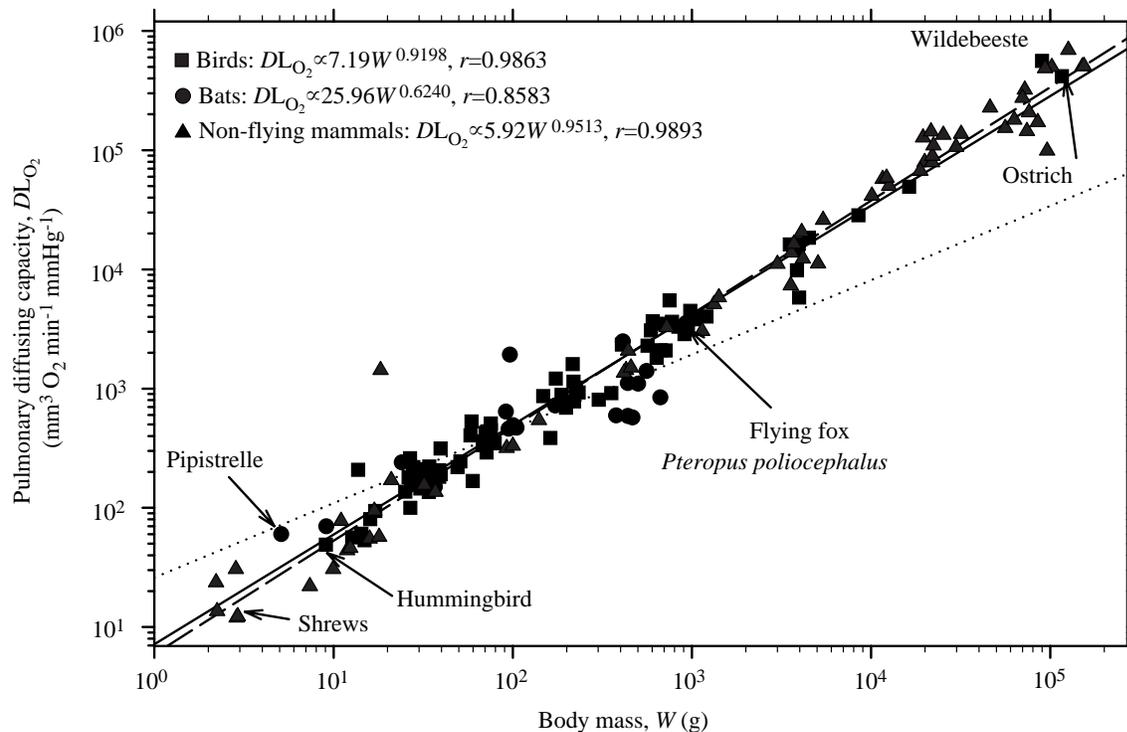


Fig. 7. Relationship between total morphometric pulmonary diffusing capacity ( $DL_{O_2}$ ) and body mass ( $W$ ) in bats, birds and non-flying mammals. Small birds have a greater  $DL_{O_2}$  than non-flying mammals. Bats have a relatively higher  $DL_{O_2}$  than birds and non-flying mammals. The regression lines are significantly different ( $P < 0.05$ ). See Fig. 2 for sources of data and statistical analysis.

passerine species, which operate at a relatively higher body temperature ( $41^\circ\text{C}$ ) than the nonpasserine species ( $39^\circ\text{C}$ ) (King and Farner, 1969), have more specialized lungs (Maina, 1984, 1993). The small highly energetic violet-eared hummingbird *Colibri coruscans* has remarkably efficient lungs (Dubach, 1981), while the gliding and soaring birds such as the gulls, birds that expend less energy in flight (e.g. Baudinette and Schmidt-Nielsen, 1974; Norberg, 1985), have relatively inefficient lungs (Maina and King, 1982a; Maina, 1987). The highest mass-specific respiratory surface area of  $90 \text{cm}^2 \text{g}^{-1}$  was reported in *Colibri coruscans* (Dubach, 1981) and the African rock martin *Hirundo fuligula* (Maina, 1984, 1989; Maina et al., 1989). The very high value of  $800 \text{cm}^2 \text{g}^{-1}$  reported in a hummingbird by Stanislaus (1937) should be treated with caution. The mass-specific respiratory surface area in the hummingbird is substantially greater than that of the shrew ( $43 \text{cm}^2 \text{g}^{-1}$ ), the smallest and the most metabolically highly active extant mammal (Fons and Sicart, 1976; Gehr et al., 1980; Sparti, 1992).

Bird lungs generally have relatively thin blood-gas (tissue) barriers (Maina and King, 1982b; Maina et al., 1989) (Fig. 5). A harmonic mean thickness of  $0.090 \mu\text{m}$  occurs in *Hirundo fuligula* (Maina, 1984) and *Colibri coruscans* (Dubach, 1981); the thickness of the tissue barrier in the shrew is  $0.334 \mu\text{m}$  (Gehr et al., 1980). The domestic fowl *Gallus domesticus* (Abdalla et al., 1982), a bird that has been domesticated for well over 5000 years (e.g. West and Zhou, 1988), and the domestic guinea fowl *Numida meleagris*

(Abdalla and Maina, 1981), a bird that leads an indolent captive lifestyle, have relatively thicker blood-gas barriers, lower respiratory surface areas and pulmonary capillary blood volumes, features that lead to low morphometric pulmonary diffusing capacities (Abdalla and Maina, 1981; Abdalla et al., 1982). The small volant birds have a higher pulmonary capillary blood volume per unit body mass than do equivalent-sized mammals. Over the larger body size range (where most birds are flightless), however, the relationship is reversed (Fig. 6). The same situation occurs for morphometric pulmonary diffusing capacities (Fig. 7). In non-flying mammals, Bartels (1980) observed that mammals in the body mass range between 2.5 and 260 g have a considerably higher mass-specific  $\dot{V}_{O_{2\text{std}}}$  (the  $\dot{V}_{O_2}$  under resting conditions) than that expected from the extrapolation of the regression line covering the entire range of mammals. This shows that small animals are not, at least physiologically, simple extrapolations of the larger ones. A lower blood oxygen-affinity, for example, has been reported in small animals (Schmidt-Nielsen and Larimer, 1958; Bartels, 1964; Lahiri, 1975).

The intersections of the regression lines that are shown here (Figs 2–7) may illustrate intrataxon physiological and structural differences that could be separated by more precise statistical tests. As discussed critically by Maina et al. (1989), such tests may mask the evidently robust intertaxon differences between birds, bats and non-flying mammals. Among birds for which data are available, the emu *Dromaius novaehollandiae*,

a huge bird that in its natural habitat is exposed to few predators, has the poorest morphometrically proficient lungs (Maina and King, 1989). The Humboldt penguin *Spheniscus humboldti*, an excellent diver (Butler and Woakes, 1984), has a relatively thicker blood–gas barrier (Maina and King, 1987); this may prevent the lung from collapsing under high hydrostatic pressures under water (Welsch and Aschauer, 1986).

#### The functional reserves of the avian lung

From observations made over the years, it is evident that bird lungs possess remarkable functional reserves. Cold exposure, for example, does not result in perceptible respiratory distress in the pigeon *Columba livia* (e.g. Bech et al., 1985; Koteja, 1986). Surgical isolation of the thoracic and abdominal air sacs, an operation that renders approximately 70% of the total air capacity non-functional, does not interfere significantly with the gas-exchange efficiency of the respiratory system of the domestic fowl (Brackenbury et al., 1989; Brackenbury, 1990; Brackenbury and Amaku, 1990): after surgery, the birds could run at three times the pre-exercise metabolic rate. Brackenbury (1991) remarked that ‘there is considerable redundancy within the lung/air sac system in terms of its ability to adapt to removal of functional capacity, both at rest and during exercise’. Other investigations corroborate this. In both normoxic and hypoxic conditions, lung oxygen extraction ( $EL_{O_2} = \dot{V}_{O_2} / F_{I_{O_2}} \times \dot{V}_{\min}$ , where  $F_{I_{O_2}}$  is the fraction of oxygen in the inspired gas and  $\dot{V}_{\min}$  is minute ventilation) does not change in exercising Pekin ducks (Kiley et al., 1985). At ambient temperatures between 12 and 22 °C, during flight,  $EL_{O_2}$  does not change in the crows (Bernstein and Schmidt-Nielsen, 1976) and the starlings (Torre-Bueno, 1978). In the bar-headed goose (*Anser indicus*), neither ventilation nor pulmonary gas transfer is limiting in a bird experimentally exercising in a hypoxic environment (7% oxygen) (Fedde et al., 1989). In a simulated environment, the resting bar-headed goose is able to withstand hypoxia to an altitude of 11 km (Black and Tenney, 1980); under such conditions, the  $P_{O_2}$  in the arterial blood is only 0.13 kPa lower than that of the inhaled air. Up to an altitude of 6.1 km, the goose maintains normal gas exchange without hyperventilating, and at approximately 11 km (when the oxygen concentration is only 1.4 mmol l<sup>-1</sup>), it extracts amounts of oxygen adequate to necessitate only a minimal increase in the ventilatory rate (Black and Tenney, 1980).

#### The chiropteran respiratory system

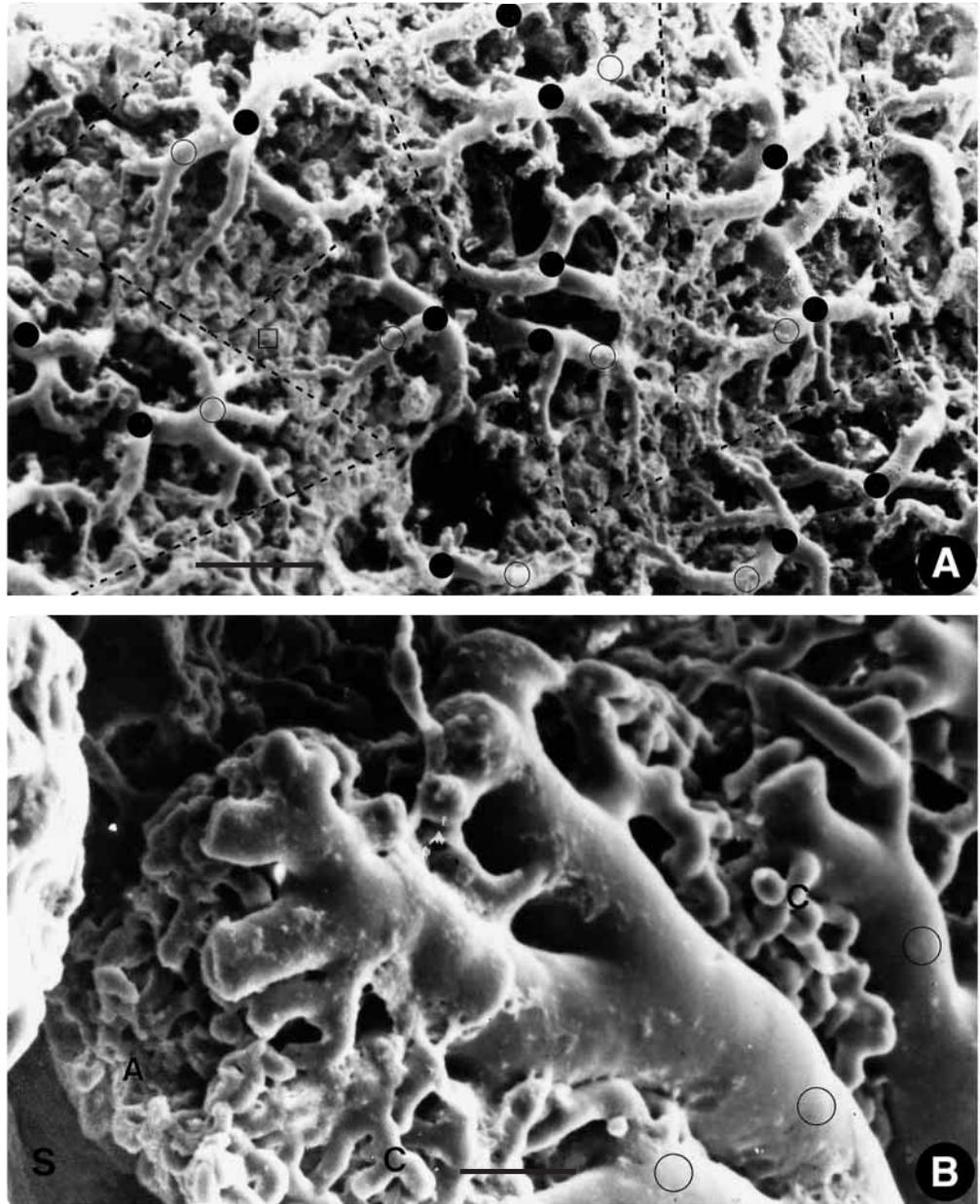
Bats span a body mass range from approximately 1.6 g for the Thai bat *Craeonycteris thonglongyai* to approximately 1.5 kg for the flying fox *Pteropus edulis*. The anatomy of the respiratory system of bats is fundamentally mammalian (Yalden and Morris, 1975). The lungs of bats have, however, been remarkably morphometrically refined (e.g. Maina and Nicholson, 1982; Maina et al., 1982b, 1991; Lechner, 1984; Maina and King, 1984; Maina, 1986) (Fig. 1D–F). By combining anatomical with physiological specializations,

the oxygen uptake capacity of a bat in flight is essentially equal to that of a bird (e.g. Thomas, 1987). The most important factors in this complex arsenal are: (i) a large heart with a huge cardiac output (e.g. Hartman, 1963; Snyder, 1976; Jürgens et al., 1981), (ii) a high haematocrit, haemoglobin concentration, erythrocyte count and blood oxygen-carrying capacity (e.g. Riedesel, 1977; Wolk and Bodgdanowicz, 1987), (iii) superior pulmonary structural parameters (Jürgens et al., 1981; Maina et al., 1982b, 1991; Lechner, 1984; Maina, 1986; Maina and King, 1984) and (iv) an efficient capillary blood supply to the flight muscles (e.g. Mathieu-Costello et al., 1992).

During flight, *Phyllostomus hastatus* can achieve and sustain an  $EL_{O_2}$  of 20%, a value comparable with that of a bird during the metabolic stress of flight (Thomas, 1981; Thomas et al., 1984) or when at rest during exposure to a severe hypoxic stress (Farabaugh et al., 1985). The mean resting  $EL_{O_2}$  at thermoneutral temperature in *Noctilio albiventris* of 18.3% lies between that of birds (20.8%) and that of non-flying mammals (16.6%) of the same body mass: at low ambient temperature,  $EL_{O_2}$  increases from 35 to 40% (Chappell and Roverud, 1990). These values exceed those of most birds under similar conditions (Bucher, 1985). The bat *Tadarida mexicanobrasiliensis*, weighing 13 g, has one of the highest venous haematocrits (75%) reported among vertebrates (Black and Wiederhielm, 1976). In the five species of bat examined by Jürgens et al. (1981), venous haematocrits ranged from 51 to 63% and haemoglobin concentration and erythrocytes numbers were respectively 24.4 g dl<sup>-1</sup> and 26.2 × 10<sup>6</sup> l<sup>-1</sup>. While high haematocrit should enhance the blood oxygen-carrying capacity, the advantages so conferred are soon outweighed by the greater viscosity (e.g. Hedrick et al., 1986; Hedrick and Duffield, 1991), a condition that requires higher energy expenditure for moving the blood. The oxygen-carrying capacity of the blood increases linearly with the haematocrit, while viscosity increases exponentially. An inordinate increase in haematocrit causes a reduction in cardiac output,  $\dot{V}_{O_{2\max}}$  and aerobic scope (Hillman et al., 1985; Tipton, 1986). A suitable haematocrit must be established to optimize the uptake and transport of oxygen (e.g. Crowell and Smith, 1967; Shepherd and Riedel, 1982; Kiel and Shepherd, 1989). In the bats *Antrozous pallidus* (Basset and Wiederhielm, 1984) and *Myotis daubentoni* (Krátký, 1981; Lundberg et al., 1983), the transition of the oxygen-carrying capacity of blood to the adult status coincides with the attainment of volancy. A biological state in which a functional process is synchronized with a developmental factor has been termed ‘programmed physiological heterochrony’ (Spicer and El-Gamal, 1999).

Bats have remarkably big lungs that occupy a large proportion of the coelomic cavity (Maina et al., 1982b, 1991; Maina and King, 1984) (Fig. 2). Compared with the non-flying mammals, certain species of bat (e.g. *Pipistrellus pipistrellus* and *Epomophorus wahlbergi*) have a relatively large respiratory surface area (Fig. 3), a lower surface density of the blood–gas barrier (Fig. 4), a thinner blood–gas barrier

Fig. 8. Double latex cast preparation (latex rubber injected into the airways and into the arterial vasculature) of the lung of the domestic fowl *Gallus domesticus* to show the cross-current design. (A) The venous blood in the intrapulmonary arterioles (○) flows in a perpendicular direction in relation to that of the parabronchial air (dashed lines show the parabronchi and their anastomoses). Gas exchange occurs between stratified blood capillaries (which arise from intraprabronchial arterioles) that interact with the parabronchi along their entire length, the multicapillary serial arterialization system. ●, interparabronchial arteries; □, atria arising from parabronchi. Scale bar 70 μm. (B) A close-up view of an edge of an intraprabronchial artery (○) terminally giving rise to blood capillaries (C) that interdigitate in a counter-current direction with the air capillaries (A) that arise from the atria and infundibulae of the underlying parabronchi. S, interatrial septum. Scale bar 100 μm.



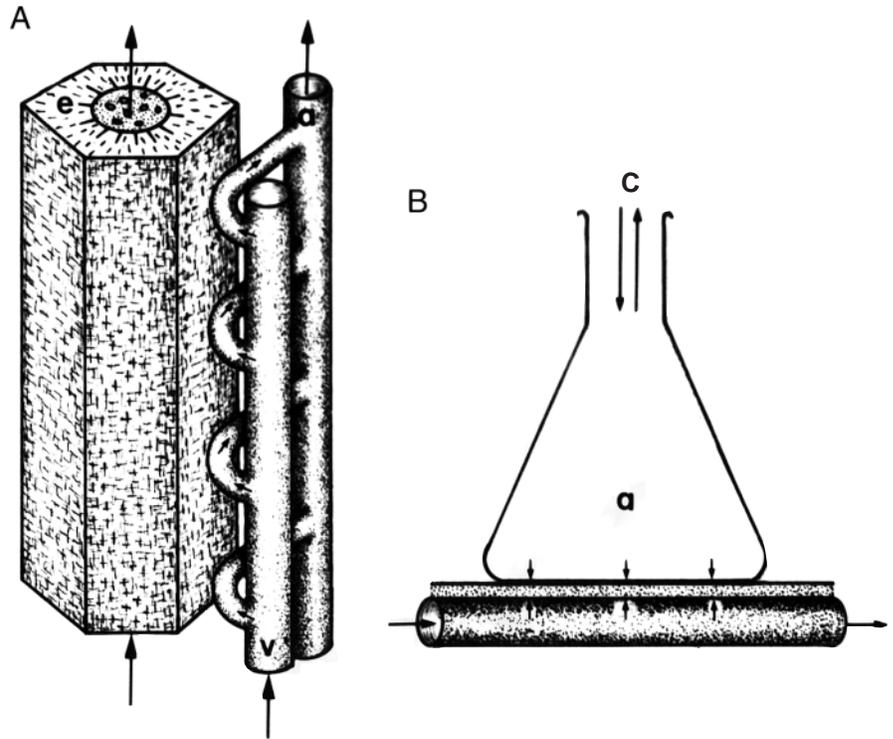
(Fig. 5) and a greater pulmonary capillary blood volume (Fig. 6), variables that lead to a high morphometric pulmonary diffusing capacity in these small species (Fig. 7). The mass-specific respiratory surface area of  $138 \text{ cm}^2 \text{ g}^{-1}$  reported by Maina et al. (1982a) in the epauletted fruit bat *Epomophorus wahlbergi* is the highest value so far reported in a vertebrate lung. The thinnest blood–gas barrier in a mammal is that of  $0.1204 \mu\text{m}$  in the lung of *Phyllostomus hastatus* (Maina et al., 1991), a bat in which  $EL_{O_2}$  is equal to that of an energetic bird of comparable size (Thomas, 1987). Furthermore, *Phyllostomus hastatus* has a high venous haematocrit of 60% (Jürgens et al., 1981). The high demands for oxygen imposed by flight in an animal with a relatively inefficient tidally ventilated lung (Maina, 1998a) may explain why the heaviest bats, the flying foxes (pteropodids), weigh an order of

magnitude less than the heaviest flying birds (e.g. Pennycuick, 1972). In bats, appropriate behaviour and proper selection of ecological niches help to minimize the metabolic selective pressures. Unlike birds, which have dispersed widely and even occupied the remote, arid, cold regions of the world (e.g. Antarctica), bats are largely tropical and neotropical in distribution. While avoiding extremes of temperature, this ensures food (fruit and insect) availability (Wimsatt, 1970; Yalden and Morris, 1975).

#### Respiratory adaptive strategies in birds and bats

Endowed with different genetic resources acquired through their different phylogenetic histories, birds and bats have utilized remarkably different respiratory strategies (e.g. Maina,

Fig. 9. (A) Schematic diagram of the cross-current system in the avian lung. The air flow in the parabronchial lumen (long arrows surrounded by the parabronchial gas-exchange tissue (e) and the blood flow in the intrap parabronchial arterioles (small arrows) is cross-current (i.e. air and blood flow in a direction perpendicular to each other). v, venous blood in the interparabronchial vein; a, arterial blood in the interparabronchial artery. The respiratory gases are exchanged in the periparabronchial tissue, where venous blood is delivered by many intrap parabronchial arterioles and collected by as many intrap parabronchial venules, the multicapillary serial-arterialization system. The flow of air in the parabronchi is continuous and unidirectional. To illustrate the cross- and counter-current dispositions between the air and blood in the avian parabronchus, the diagram has been greatly simplified. The arterioles, blood capillaries and the venules are found in the gas-exchange tissue (e), while the interparabronchial arteries and veins are located in the interparabronchial septa (for details, see Maina, 1988). (B) Diffusion of oxygen and carbon dioxide across the blood-gas barrier (small arrows) of the mammalian system. a, alveolus; c, tidal ventilation of alveoli. The horizontal arrows show the direction of the alveolar capillary blood flow. In the mammalian lung, the geometrical relationship between the alveolar air and the pulmonary capillary blood is described as 'uniform-pool'.



1994, 1998b) independently to develop similar capacities to procure the large amounts of oxygen necessary for powered flight. Synergy of multifarious structural and functional variables has created highly efficient respiratory systems in the two taxa. In the non-flying mammals, Weibel et al. (1992) separated functional and design variables to assess the uptake of oxygen in the lung, its transport to the tissues and its utilization at the mitochondrial level. They observed that, while the design of the internal steps of the respiratory system (mitochondria, capillaries, blood and heart) correlates with functional demands, the lung maintains a variable excess of morphometric diffusing capacity.

In the vast respiratory arsenal of birds, a 'cross-current' arrangement occurs between the parabronchial air flow and the venous blood (e.g. Scheid and Piiper, 1970, 1972) (Figs 8A, 9A), a counter-current design exists between the air and the blood capillaries (Fig. 8B), a multicapillary serial-arterialization system is configured around the parabronchi (Scheid and Piiper, 1972; Scheid, 1979; Abdalla and King, 1975; Maina, 1988) (Fig. 9A), the parabronchi are continuously and unidirectionally ventilated by synchronized action of the air sacs and efficient pulmonary morphometric variables occur. With a respiratory rate as low as  $3 \text{ min}^{-1}$ , the mute swan *Cygnus olor* has an  $EL_{O_2}$  of 33% (Bech and Johansen, 1980) and a ventilation:perfusion ratio of the lung of near unity (i.e. 1.06) (Hastings and Powell, 1986).  $EL_{O_2}$  values as high as 60–70% occur in certain species of bird (e.g. Brent et al., 1984; Stahel and Nicol, 1988), values that exceed

those of 40–45% reported in bats by Chappell and Roverud (1990). The lung of bats has a functionally inferior tidally ventilated (dead-end) alveolar 'uniform pool' design (e.g. Scheid and Piiper, 1970) (Fig. 9B). Because the anatomy of the chiropteran lung is characteristically mammalian (e.g. Yalden and Morris, 1975; Maina et al., 1982b; Maina, 1985, 1986), the respiratory refinements necessary for flight were made within the design constraints inherent in the mammalian lung. The lung was exquisitely structurally refined to exchange respiratory gases during flight at rates equal to the seemingly better-adapted lung of birds. In this regard, the lung/air sac system of birds is not a prerequisite pulmonary design for flight. The bat achieves a  $\dot{V}_{O_2}$  as high as that of the bird by quantitative adaptation of the mammalian lung structure: an example of the functional convergence of two different designs.

Generally small in body size and hence having a relatively high mass-specific resting metabolic rate (e.g. Yalden and Morris, 1975; Carpenter, 1985; Pough et al., 1989), leading an energetic life style (flight) and operating with an 'inferior' (mammalian) lung (Maina, 1998a), bats appear to have been compelled drastically to refine and greatly to exploit many of the morphological and physiological factors involved in oxygen uptake and transport and in energy production. These include pulmonary (e.g. Maina and King, 1984; Maina et al., 1991), flight muscle (e.g. Mathieu-Costello, 1990; Mathieu-Costello et al., 1992) and cardiovascular variables, e.g. haematocrit, haemoglobin concentration and erythrocyte count

(e.g. Black and Wiederhielm, 1976; Jürgens et al., 1981). It is astounding that birds have not exhausted or even utilized certain 'usable' respiratory variables.

Birds have relatively very small lungs (Maina et al., 1989, 1991), and the volume density of the parenchyma (the parabronchial gas-exchange tissue) on average constitutes only approximately 45 % of the lung volume (Maina et al., 1982a) compared with values of 90 % in the mammalian lung (e.g. Gehr et al., 1981; Maina and King, 1984; Maina et al., 1991). Like fish, amphibians and reptiles, among vertebrates, birds have retained the arguably 'primitive' metabolically active nucleated erythrocytes. The venous haematocrit in birds is, on average, 35 %, haemoglobin concentration ranges from 12 to 15 g dl<sup>-1</sup> and oxygen half-saturation pressure ( $P_{50}$ ) is, on average, 4.53 kPa (34 mmHg). These values are lower than or equal to those of the non-flying mammals and are generally lower than those of bats (e.g. Altman and Dittmer, 1970; Lutz et al., 1973, 1974; Palomeque et al., 1980). It is pertinent to point out that robust physiological and morphometrical comparisons of the respiratory variables between bats, birds and non-flying mammals are presently hampered by the high variability of the data in the literature on aspects such as ventilation and the transfer and transport of oxygen. Coupled with this are problems of appropriate standardization of the physiological reference conditions under which the different measurements and determinations of certain variables, some of which are highly susceptible to factors such as temperature, were made.

Locomotory activity is said to offer mechanical assistance to respiratory muscles (Bramble and Carrier, 1983). A 1:1:1 synchronization between wingbeat frequency, respiratory rate and heart rate occurs in bats (e.g. Suthers et al., 1972; Thomas, 1981, 1987; Carpenter, 1985, 1986). The low surface density of the blood-gas barrier in bats compared with that of the non-flying mammals (Fig. 4) suggests that the alveoli in the bat lung are wider. The more extensive respiratory surface area in certain species of bat (Fig. 3) has been generated by a remarkably large lung (Fig. 2) and not by intense internal subdivision, as has evidently been the case in the parabronchial lung of the bird, in which the air capillaries are relatively much smaller in diameter (Maina, 1982, 1988). In bats, in which the respiratory rate is synchronized with the wing beat, wider alveoli may provide an energy-saving scheme by reducing the surface tension forces that have to be overcome in dilating the lung during inspiration. In birds, although the flight muscles attach on the sternum, interestingly, there appears to be very little effect of wing movements on the actual pulmonary air flow and volume (e.g. Zimmer, 1935; Berger et al., 1970; Berger and Hart, 1974; Butler and Woakes, 1980). Matching of respiratory rate with wingbeat frequency occurs in only relatively few species of bird (e.g. Tomlinson, 1963; Berger et al., 1970; Butler and Woakes, 1980; Torre-Bueno, 1985; Funck et al., 1993). The mismatch may be caused by the complex nature of the air flow in the parabronchial lung (Bernstein, 1987). In the European

starling *Sturnus vulgaris*, the ventilatory volume change associated with the wing beat ranges from only 3 to 11 % (Banzett et al., 1992). The synchronization of the wing beat with the breathing cycle should enable bats to ventilate and perfuse their lungs at a relatively lower energy cost and probably more efficiently.

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