Biomechanical, Respiratory and Cardiovascular Adaptations of Bats and the Case of the Small Community of Bats in Chile

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Biomechanical, Respiratory and Cardiovascular Adaptations of Bats and the Case of the Small Community of Bats in Chile

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1. Introduction

Bats are unique among mammals for their ability to fly. The acquisition of powered flight required a series of morphological and physiological changes in the basic mammal body plan. The structure of the limbs is the most obvious specialization, however, adaptations for powered flight encompass most organ systems, in particular the cardiovascular and respiratory apparatus. Flight performance is strongly determined by wing morphology, which in turn is associated with the biomechanics and energetics of flight, as well as ecological aspects such as foraging behavior and habitat selection.

In this chapter we focus on respiratory, cardiac and wing morphology characteristics of some bat species present in Chile, correlating the results with ecological and behavioral information. The small community of Chilean bat species shows a pattern similar to that found in other bat communities. With respect to wing morphology we found that *Tadarida brasiliensis*, *Desmodus rotundus* and *Mormopterus kalinowskii* have small wing areas, while molossids have high aspect ratios and that of *D. rotundus* is only moderate. *D. rotundus* has a smaller mass specific wing span, and the highest wing loading. *Myotis chiloensis* has a second moment of area of humerus (Ih), lower than expected from allometric predictions, suggesting poorer resistance. Based on these results four functional groups may be recognized: i) species with high wing loading and low wing span such as *D. rotundus*, capable of rapid flight with moderate power consumption, ii) species with high wing loading and high aspect ratio, such as the molossids *T. brasiliensis and M. kalinowski*, which are capable of fast flight and low power consumption, characteristic of foragers in open areas; iii) species with low wing loading and low wing span such as most vespertilionids, capable of slow and maneuverable flights in a bat that inhabits wooded areas; and iv) *L. cinereus*, forming an isolated group characterized by high speed and agility.

Also the respiratory and cardiovascular systems of bats are modifications or refinements that allow them to survive this extreme way of life. Bats have lung volumes about 72% greater than non-flying mammals of the same size. Pulmonary ventilation can rapidly increase 10 to 17 times as flight begins. These respiratory adaptations, along with structural changes of lungs, lead to higher oxygen consumption than other mammals of similar size, reaching up to 22 mlO_2/gh at low temperatures and during hovering. We found that the bronchial morphology of *T. brasiliensis* shows an optimization of the proximal airway with minimum entropy production during mechanical ventilation. In addition, bats have a very thin alveolar-capillary barrier, yielding an oxygen diffusion capacity similar to birds. Also, the heart of bats is larger than in all other mammals, representing about 1% of body weight, reaching in some cases 2%. Birds and bats reach very similar aerobic capacities. However, while birds have a large set of structural changes in their respiratory system, bats have a cardiorespiratory system optimized to their extreme life style.

The order Chiroptera ("winged hands") is practically defined by saying that it is constituted by flying mammals. These animals require deep structural changes associated with their lifestyle, but based on a mammalian model. Flight influences its main characteristic: wings formed by a membrane called a patagyum. The arms are the dominant limbs while legs are reduced, contributing to the reduction in body mass which is necessary for flight. These structural changes are also associated with the colonization of the crepuscular and nocturnal air space which required the specialization of the visual system in megachiropterans and the development of echolocation in michrochiropterans, where excepting macro chiropterans the vision contributes little, but where the emission and reception of ultrasound, or echolocation, allows the recognition of the surrounding environment; the ear is the main organ sense of the group.

2. Body size

Body size is associated with flight behavior, diet selection, reproductive behavior, physiology and practically all aspects of the biology of bats. (Swartz et al., 2003). Bat body sizes vary from 2 g and 16 cm wingspan in the mammal with the lowest body mass known *Craseonycteris thonglongyai*, to 1.5 Kg and 2 m wingspan in the Asian flying foxes (Megachiroptera; Pteropodidae) (Fenton, 1992).

The superior limit of body size is not imposed by flight, because among birds there are species which weigh up to 14 Kg, such as Koris`s bustard, and the extinct pterosaurs reached giant sizes. It is possible that in bats the superior limit to body mass is imposed by a combination of behavioral, ecological and physiological factors. Insectivorous bats would have aerodynamic and sensorial restrictions. Barclay & Brigham (1991) proposed that associated with an increase in the body mass there is a decrease in the maneuverability that prey detection at long distances requires. However, this would condition the use of low frequencies during echolocation, with a decrease in spatial resolution. Thus, the abundance of large prey could be a limiting factor of body size in these bats, which is corroborated in part by the positive correlation between prey size and body size of bats (Aldridge & Rautenbach 1987; O'Neil & Taylor, 1989). However, this does not apply to large fruit bats that do not use echolocation. In the latter restrictions derived from muscle physiology may operate; kinematics of flight or wing loading and mechanical stress imposed on the bones by flight (Marden, 1994). While the force per unit mass generated by a muscle is approximately constant, the mass-specific power to fly scales positively with mass, resulting in less lift generation per unit of muscle power (Marden, 1994). Similarly, the mechanical power required for flight grows faster (α Mb $^{1.185}$) than the oxygen consumption of bats (Maina et al., 1991; Maina 2000) helping to establish an upper limit of about 1.5 Kg for bats (Carpenter 1986, Maina 2000).

3. Limbs

Limbs of bats are completely conditioned by flight. While the forelimbs are large and strong, the legs are small, contributing to a reduced mass allowing flying. However, these latter have adaptations such as the joint mechanism of the claws, which pivot on the distal phalanges. While an elastic ligament extends the dorsal claw, the long plantar tendon inserts on the ventral side of the base of the claw, flexing it. Thus, when bats hang inverted during rest, the body weight flexes the claw and allows it to catch on a branch or a cliff (Neuweiler, 2000). In most mammals the diameter of the femur scales with body mass raised to the 1/3 power (geometric similarity), but in bats femur diameter is smaller than that of other mammals of similar size. An exception to this generalization is the vampire bat *Desmodus rotundus* in which the diameter of the femur follows the curve of non-flying mammals (Swartz, 1997). This species has a semi-quadrupedal locomotion while feeding, being able to travel on all four limbs and even start flight with a jump (Schutt et al., 1997).

The body and forelimbs are significantly modified for flight. The thin patagium is richly vascularized with muscles that allow tension and bending, thus contributing dynamically to flight. Occipitopollicalis muscles, Dorsoplagiopatagialis, Humeropatagialis, Coracocutaneus, Uropatagialis and Plagiopatagial Tensor contribute to this dynamic tension, while the adductor of the fifth digit causes the arched profile necessary for flight. While bird wing movement is controlled mainly by two muscles and the point of rotation of the wing is slightly medial or dorsal to the level of shoulder joint, in the bats this point is shifted ventrally to the sterno –clavicular articulation, allowing the scapula to participate in wing movements. In the movement of bat wings at least 17 muscles are involved (Neuweiler, 2000). The main lift muscles are the Trapezium, rhomboids, Acromiodeltoideus and Spinodeltoideus, while the lowering of the wings is controlled mainly by Pectoralis, Serratus, Clavodeltoid and Subscapularis. Extension and flexion of the wing are governed by a special muscle arrangement that automates these movements. Both the triceps (extensor, dorsal) and the biceps (flexor, ventral) are inserted from the scapula to the forearm, bypassing the humeral insertion. Also the extensor carpi radialis and flexor carpi ulnaris bypass the radius. Thus the contraction of the triceps causes the extension of the radio-carpal extensor and the whole wing in an almost automatic form (Neuweiler, 2000).

Wing morphology is highly variable, associated with the biomechanics and energetics of flight (Rayner 1979, 1982), and with ecological and behavioral factors such as flight pattern, foraging behavior and habitat selection (Norberg & Rayner 1987, Norberg 1994; Canals et al. 2001, Iriarte-Díaz et al. 2002, Canals et al., 2005).

There are four important parameters related to the aerodynamics of flight: 1) wing loading:

$$W_L = mg / S \tag{1}$$

which represents the weight per unit area (N/m^2) to be supported by the wings; 2) wingspan (B), corresponding to the length of the wings from tip to tip, 3) the aspect ratio:

$$AR = B^2 / S \,, \tag{2}$$

which is a dimensionless measure of the relative length to width of the wings, so high AR values correspond to long, thin wings and vice versa, and finally 4) wing acuity ratio (i.e., tip length ratio: TL = length of third finger / arm length) (Neuweiler, 2000) .

4. Flight

In its most simple terms, a bat must move the air with its wings in such a way as to produce aerodynamic force. The component of the aerodynamic force that propels the bat forward is thrust and the component that keeps the bat from falling is lift. These forces are opposed by drag (an aerodynamic force) and gravity, respectively. In contrast to planes that continuously produce thrust and lift (by their engines and the constant flow over the wings), bats generate aerodynamic force in a cyclic manner due to the flapping of the wings. Thus, flight in bats is dependent of an appropriate modulation of wing kinematics in order to generate enough aerodynamic force.

Unlike terrestrial locomotion, where limbs push against a solid substrate, aerial fliers use their wings to push against fluids, which distort and swirl to form a complex wake (Dickinson et al., 2000). Although it is the wing motion that is directly responsible for the generation of lift and thrust, we can estimate the aerodynamic forces by looking at the fluid motion left behind a flying animal. Newton's third law requires that the forces exerted by the air upon the wings must be equal and opposite to the forces exerted by the wings upon the air. The wake left behind the wing thus contains a complete 'footprint' of its force generation. An everyday example of this are the vapor trails left by airplane wings, the tip vortices, that arise directly from the aerodynamic forces produced as the plane moves through the atmosphere. Bats also leave an aerodynamic wake and this wake can be measured by looking at the movement of the air left behind.

An aerodynamic wake can be efficiently analyzed in terms of its *vortex structure*. Vorticity is the local angular or rotational velocity of the fluid, and a vortex is somewhat subjectively defined as a concentration of vorticity. Tornados and swirling motions of water draining are familiar examples of vortices. Visualization and quantification of these vortices can be used to estimate aerodynamic forces. Early studies of bat's wake structures, using helium-filled bubbles, suggested that the upstroke function and wingbeat gaits may vary to flight speed, with lift being produced during upstroke at high speeds but not during slow flights (Rayner et al., 1986). These differences in lift generation would be expressed as discrete vortex rings during slow flight in contrast to the ondulating but constant vortex lines observed at fast flight speeds (figure 1). Recent studies using digital particle image velocimetry (DPIV) have allow us to study the wake left behind flying bats with much higher temporal and spatial resolution than those original studies. The emerging picture of the aerodynamic footprint left by bats is that the wake structures are more complex than expected, potentially because of the more complex wing kinematics than that of birds and insects as well as the compliant characteristics of the wing membrane, and currently it is an area of very active research (e.g., Hedenström et al., 2007; Johansson et al., 2008; Muijres et al., 2008; Hedenström et al., 2009; Hubel et al., 2009; Hubel et al., 2010; Wolf et al., 2010).

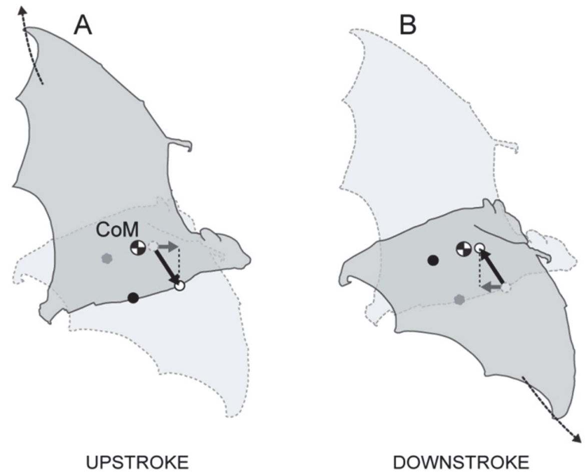

Fig. 1. Effect of the oscillation of the wings on the position of the center of mass (COM) and accelerations of the body. When external forces, such as aerodynamic and gravitational forces, are absent, the position of the COM will remain constant but the body moves in opposition to the flapping wings to conserve momentum. Closed and open symbols correspond to the pelvis and chest markers, respectively. During upstroke (A), the upward and backward acceleration of the wings will produce an inertial force (black arrow) that will move the body forward and downward with respect to the downstroke. This force will produce a forward-oriented component, or inertial thrust, during upstroke (grey arrow). During downstroke (B), the downward and forward acceleration of the wings will produce an inertial force (black arrow) that will move the body backward and upward while keeping the position of the COM constant. The horizontal component of this inertial force will produce negative inertial thrust during downstroke (grey arrow).

Aerodynamic theory predicts that the wing loading, the wing span and aspect ratio are significant parameters in determining performance in flight. For example, during flight the organism should generate sustained lift (L) to support body weight and thrust (T) to overcome drag (D). Thus, the power required to fly is:

$$P = D \cdot v = T \cdot v \,, \tag{3}$$

where v is the relative velocity of air over the wings. The cost of transport (C), which corresponds to the work done to move a unit of weight for a unit of distance is inversely proportional to the speed:

$$C = P \,/\, mgv = T \,/\, L \,, \tag{4}$$

with P = power, m the body mass and g gravity acceleration). Furthermore, the speed is proportional to $W_L{}^{1/2}$, so that both high wing loading and high flight speeds are associated with low transportation costs (Norberg 1987).

The energy per unit time (power) required to fly can be decomposed into that needed to move the wings (inertial power: P_{in}) and the power required to produce the aerodynamic force (R). The latter can be decomposed into the power required to overcome the resistance of the body (parasite power: P_{PAR}), the profile of the wings (Power Profile: P_{PRO}) and the power to generate lift and thrust (induced power: P_I). Thus the total aerodynamic power is the sum these:

$$P = (P_{PAR} + P_{PRO} + P_I) + P_{in} . \tag{5}$$

Plotting the power according to flight speed a typical "U" curve is obtained, whose minimum determines the speed at which it produces the minimum energy expenditure (V_{MP}). It is also possible to calculate the speed which determines the minimum cost of transport (V_{MR}), which is determined by the intersection between the curve and the tangent to it passing through the point (v = 0) (Norberg, 1987).

All these components of energy expenditure of flight are correlated with B and WL, for example $P_{par} \alpha\ v^3\ \alpha\ (W_L)^{3/2}$, $P_{pro}\ \alpha\ S(B/\tau)^3$ during hovering, where τ is the wing beat period, $P_I\ \alpha\ (Mg)^{3/2}/B$ during hovering and $P_I \alpha\ (Mg)^2/(B^2 v)$ during forward flight, and $P_{in}\ \alpha\ B^2$ (Norberg, 1987). In addition, the minimum resistance (D_{min}) and the minimum power required to fly (P_{min}) are inversely correlated with the aspect ratio:

$$D_{\min} = 2mg(C_r / \pi AR)^{1/2} , \tag{6}$$

and

$$P_{\min} = [0.95(mg)^{3/2} C_r^{\,1/4}] / B(AR)^{1/4} , \tag{7}$$

where C_r is the combined parasite and profile friction coefficient. Thus high values of AR are critical in reducing both parameters; AR is considered to be a measure of aerodynamic efficiency (Norberg, 1994). Another important aspect is the high wing acuity (i.e., TL) that allows adequate air movement dynamics around the wings without turbulence. By contrast, rounded wings can generate turbulent flow by increasing the resistance to movement and therefore P_{PRO}.

Norberg and Rayner (1987) attempted to establish a relationship between lifestyle and major aerodynamic parameters of wing morphology, being able to classify four groups of bats: i) bats of open space and faster flight have long and narrow wings, with high wing loadings up 20N/m^2 and aspect ratios as high as 14.3 in some Molossidae (Fenton 1992, Norberg & Rayner 1987), ii) slow-flying bats of forested areas with short and broad wings, with low wing loading, about 5 to 6 N/m^2, and low aspect ratios, about 5 (Canals et al. 2001, Iriarte-Díaz et al. 2002), iii) fast flying bats with stationary or short flights, which have high wing loading but low aspect ratios, and finally iv) slow-flying bats in open spaces, which have high aspect ratios but low wing loading (Figure 2).

Species that forage in and around foliage tend to have short, rounded wings with low values of AR and TL, which produces low wing loading. They have a relatively slow flight, between 2.5 and 6 m / s, and are very maneuverable (Neuweiler, 2000). Many of them can use hovering to locate and capture prey over the foliage or to feed on pollen or nectar. Species that forage on leaves are slender, with long, thin wings (high AR) and high wing loading. Their flight speed is high, between 9 and 15 m / s. These bats have less maneuverability. However, their agility, defined as the ability to accelerate and stop quickly, is increased, as is an ability related to wing loading (Norberg & Rayner, 1987). An example of such bats is the Molossidae, for example *Tadarida brasiliensis* in which the highest flight speed has been registered: 27 m / s (Neuweiler, 2000). Some species of bats feed by fishing or hunting on bodies of water, such as *Noctilio leporinus*, requiring a great generation of thrust (T) in flight, plus an important handling. Thus they have higher TL, AR moderate and relatively low wing loading.

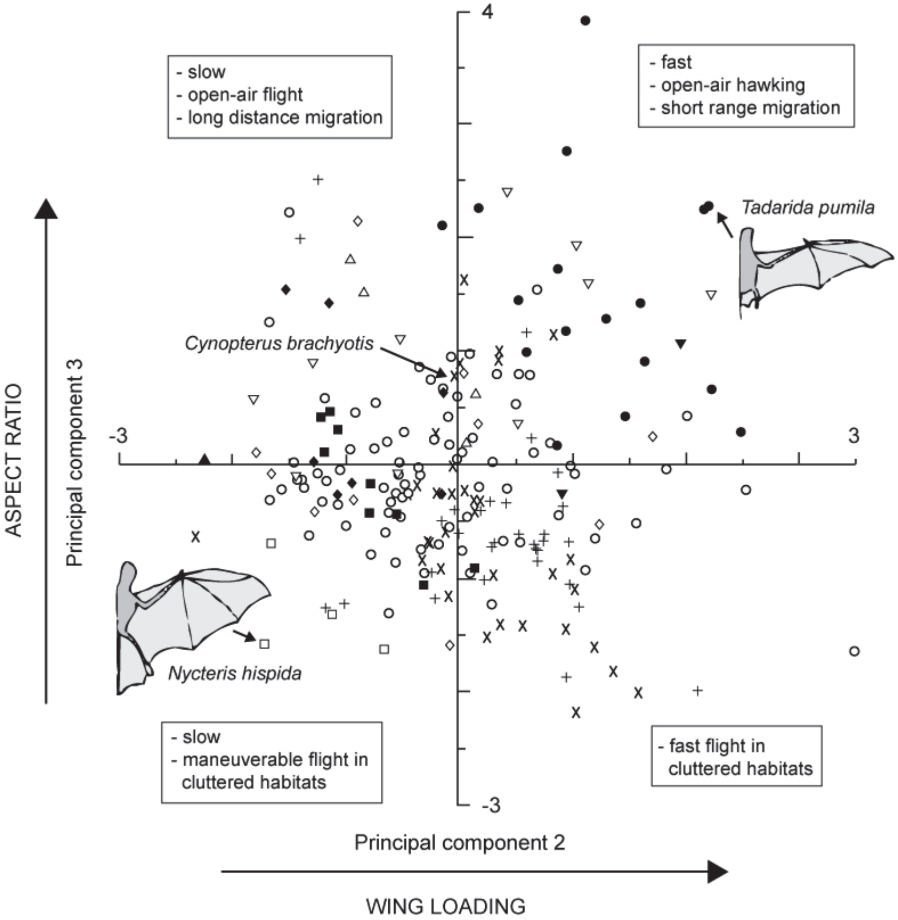

Fig. 2. Principal components for morphological characteristics in several bat species. The first component was explained for body mass, but second and third components are related with wing loading (WL) and the aspect ratio (AR) respectively. This analysis allow recognize different eco-morphological groups of bats. Modified from Wainwright & Reilly 1994.

Frugivorous bats usually fly long distances for foraging, occasionally flying over 27 km. This requires sustained flight and highly developed flight muscles that result in high wing loading, however, their wings are broad and rounded (Neuweiler 2000). The same is true in the vampire bat *Desmodus rotundus* (Canals et al., 2005). Bats which plane using convection currents such as some Pteropodidae usually have larger wingspan and wing loadings lower than those using flapping flight (Norberg et al., 2000).

4.1 Studies in Chile

In a series of studies, Canals et al (2001), Iriarte et al (2002) and Canals et al (2005) examined some aspects of the wing morphology of 8 species of bats present in Chile, correlating the results with available ecological information. They estimated aspect ratio, wingspan, wing surface, and wing loading of the molossids *Mormopterus kalinowskii* and *Tadarida brasiliensis*, the Phyllostomidae *Desmodus rotundus* and the vespertilionids *Myotis chiloensis, Histiotus montanus, Histiotus macrotus, Lasiurus borealis* and *Lasiurus cinereus* (Table 1).

Species	**M_b (g)**	**B (cm)**	**S (cm^2)**	**W_L (N/m^2)**	**AR**	**I_h (cm^{4}x10^{-6})**
Myotis chiloensis (49)	6.76 ± 0.18	23.69 ± 0.39	98.29 ± 3.47	6.8 ± 0.23	5.76 ± 0.16	3.89 ± 0.49
Histiotus montanus (1)	12.5	29.2	-	-	-	23.1
Histiotus macrotus (3)	9.37 ± 0.29	29.67 ± 0.58	129.67 ± 4.20	7.08 ± 0.19	6.78 ± 0.06	21.17 ± 3.52
Lasiurus borealis (3)	7.87 ± 1.12	25.37 ± 2.49	93.73 ± 8.87	8.20 ± 0.46	6.87 ± 0.70	12.68 ± 9.30
Lasiurus cinereus (2)	19.55 ± 6.58	30.20 ± 1.41	165.45 ± 52.07	15.42 ± 5.75	5.72 ± 1.29	26.78 ± 5.06
Tadarida brasiliensis (27)	11.95 ± 0.62	28.65 ± 0.63	100.14 ± 4.61	11.56 ± 0.66	8.12 ± 0.16	11.15 ± 2.61
Mormopterus kalinowskii (2)	3.10 ± 1.13	17.25 ± 0.35	32.4 ± 2.26	9.28 ± 2.77	9.20 ± 0.27	5.85 ± 5.98
Desmodus rotundus (1)	33.48	33.5	167.23	19.61	6.71	68.3
Histiotus montanus (1)	4.3	19.7	58.8	7.17	6.6	9.3
Lasiurus cinereus (4)	12.23 ± 2.71	27.33 ± 0.68	93.50 ± 8.18	12.74 ± 2.07	8.01 ± 0.44	21.24 ± 14.01

* From Iriarte-Díaz & Canals 2002 and Canals et al., 2005.

Mb = body mass, B = wing span, S = wing surface, W_L = wing loading, AR = aspect ratio and I_h = second moment of humeral area in median section. Asterisks indicate juvenile individuals. In one adult *H. montanus* it was not possible to estimate the wing surface. Numbers in parentheses indicate sample sizes.

Table 1. Summary of the aerodynamic characteristics of the wings of eight bats.

The free-tailed bat *T. brasiliensis* and *D. rotundus* have no tail membrane and a low wing area, but while the molossids have high aspect ratios, that of *D. rotundus* is only moderate. *D. rotundus* has a smaller wingspan for its body mass, and the highest wing loading. Furthermore, these authors estimated radiographically the second moment of area of humerus (I_h), which corresponds to a measure of bone strength to bending. *Myotis chiloensis* had a value lower than expected from allometric predictions, suggesting poor resistance. All other vespertilionids showed a high second moment of area, which may be explained by their costly form of locomotion, especially in species with high parasite load as a result of their long ears. The high I_h shown by *D. rotundus* may be explained by the low aspect ratio and high body mass, which increase the torque produced by the weight during quadrupedal locomotion.

The small community of Chilean bats showed a similar pattern to that found by Norberg and Rayner for many species, but at a small scale. Principal components analysis showed two axes, the first correlated positively with wing loading and negatively with wingspan and the second positively correlated with the aspect ratio. In these species 4 functional groups can be recognized, one for each quadrant in the graph:

i. *D. rotundus*, with high wing loading but low wingspan (relative to its body size), located in the high agility and rapid flight zone with moderate power consumption, which is likely related to long flights to their resting places and their particular form of locomotion;
ii. The molossids *T. brasiliensis* and *M. Kalinowski* in the area of high flight speed and low power consumption as is characteristic of high speed open area foragers;
iii. Most of vespertilionids in the zone of high maneuverability and low speed which correspond to bats which inhabit wooded areas;
iv. *L. cinereus* forming an isolated group in a zone of high speed and agility.

4.2 The mechanics of flight: Kinematics

The differences in flight performance observed in bats can be associated with higher energy expenditure efficiency as well as very high levels of maneuverability. For example, among animals of comparable body size, hovering flight of nectar-feeding bats is 40 and 60% less costly metabolically that that of hawkmoths and hummingbirds, respectively (Winter, 1998; Winter and von Helversen, 1998; Voigt and Winter, 1999), suggesting that bats have more efficient mechanisms of lift generation than member of other groups. Although the kinematics of hovering of bats differ from those of insects and hummingbirds, we lack experimental measurements that can explain such differences in efficiency. In a recent study using PIV methods, it was shown that bats can increase lift generation during slow flights by 40% by using attached leading-edge vortices around the wings (Muijres et al., 2008), similar to those used by insects (Fry et al., 2005) and hummingbirds (Warrick et al., 2005) during hovering flight. Why hovering flight in bats is energetically cheaper than that of insects and hummingbirds of similar size is still unclear.

4.3 Maneuvering during flight

The ability to quickly alter flight direction and speed is essential for bats to successfully navigate complex three-dimensional environments, to capture prey, and to avoid predators. Despite the importance of this task, maneuvering abilities and its mechanisms have been barely investigated. A flying organism has six degrees-of-freedom of movement: translation in three dimensions in space and rotation around three orthogonal axes centered on the center of mass, termed yaw, pitch, and roll.

In its most basic form, a turning maneuver requires the reorientation of the body in such a way that the net aerodynamic force is tilted laterally effectively producing a centripetal force that will drive the bat through the turn. The most common method in the literature is the bank turn. In this kind of turn, the body rolls into a bank, which orients the lift vector towards the direction of the turn, producing a centripetal force. When the turn is complete, the body rolls back into the unbanked position such that centripetal force is no longer produced. Airplanes use this mechanism, it has been observed in insects and birds, and it has been assumed that bats use it as well. If a flying organism performs a banked turn, then for any given lift coefficient and bank angle, the turning radius depends directly of the wing loading or body weight per unit wing

area; there is some evidence consistent with this relationship from bats in both field and obstacle course settings (Aldridge, 1986; Aldridge and Rautenbach, 1987; Stockwell, 2001).
However, growing evidence suggest that differences in turning techniques (e.g., gliding versus flapping turns, Aldridge, 1987b) and changes in wing posture throughout the turn (Lentink et al., 2007) can substantially alter the turning performance. The only study to investigate the mechanisms of turning in bats suggest a more complex mechanism. Detailed analysis of the wing motion and body orientation during 90-degree turns in the pteropodid *Cynopterus brachyotis* showed that during the upstroke the body rotates into the direction of the turn, a mix of roll and yaw rotations, without changes in flight direction. This body rotation allows the bat to use part of the thrust generated during the downstroke to enhance the centripetal force from the bank turn, thus allowing the bat to perform tighter turns than predicted by wing morphology alone (Iriarte-Díaz and Swartz, 2008). These results highlights the importance of studying the mechanics flight performance and that using morphological proxies to estimate performance (e.g., wing loading and aspect ratio) might severely underestimate flight abilities of bats.

4.4 The effect of wing inertia during flight

One aspect of flight performance that remains virtually unstudied is the importance of inertial forces generated by the flapping motion of relatively massive wings. The wings of bats comprise a significant portion of total body mass, ranging from 11 to 20% in a few measured species (Thollesson and Norberg, 1991; Watts et al., 2001) and consequently, inertial forces produced by accelerating these masses are expected to be high and the potential effect of these forces on flight performance is still not well understood. In a recent study, the effect of wing's inertial forces was studied on *C. brachyotis* during forward, steady flight (Iriarte-Díaz et al., 2011 in press). At any speed, the tip of the wings move upwards and backwards relatively to the body, but if the speed of the body is low enough, the tip can sometimes move backwards relatively to the still air during the upstroke. This backward movement of the wingtip has been called "tip-reversal upstroke" (Aldridge, 1987a) and for decades has been thought that it provides additional thrust to slow-flying bats, partially because the observation that the bat's trunk accelerate forward during upstroke. However, for *C. brachyotis*, the forward acceleration of the body is the result of forwardly directed inertial forces produced by the motion of the wings. When the wings swing backwards, approximately 20% of the bat's mass moves backward relative to the center of mass. In order to maintain the momentum, other portions of the body must move forward relative to the center of mass, which is reflected in the forward acceleration of the trunk. Using a model of the mass distribution of the trunk and wings, inertial accelerations were estimated and removed in order to estimate the acceleration of the center of mass. When inertial forces were removed, forward acceleration of the center of mass only occurred during the downstroke (Iriarte-Díaz et al., 2011). Thus, inertial forces may be potentially important during flight, although when and how they can be used is not known. Preliminary evidence suggest that inertial forces might be important during turning (Iriarte-Díaz and Swartz, 2008) and when performing landing maneuvers (Riskin et al., 2009).

5. Physiology and energy of bats

The first law of thermodynamics states that energy is neither created nor destroyed, only transformed. Living organisms as physical systems obey this principle, acquiring, converting, assigning, storing and dissipating energy. The transformation of energy plays a crucial role in the evolution, ecology and physiology of organisms. Thus the internal and external boundaries of the use and transformation of energy affect their fitness and may affect species richness, reproductive effort, activity patterns, habitat use and life history (McNab 2002, Cruz-Neto et al 2003; 2006).

Field metabolic rate (FMR) integrates all the energy costs of free-living organisms, including the costs of thermoregulation, locomotion etc. This has been quantified in the Australian bat *Syconycteris australis* with doubly labeled water, reaching 7 times the basal metabolic rate (Geiser & Coburn 1999), one of the highest values described in endotherms. This is attributable to the prolonged nocturnal flight (Geiser 2006). The mass specific metabolism of bats is 1.6 times that of non-flying mammals (Thomas, 1987). Also, during flight metabolism increases to 20 or 30 times the standard rate (Thomas, 1975). During flight, about 25% of metabolism is converted into work, so that 75% is dissipated as heat. This is done primarily in two ways: via airway and skin. The airway dissipates only about 15% because little or no frequency change is possible during flight, since there is a synchrony between wing beat and respiration. Thus the skin must remove the remaining heat (85%). Its large area and conductance allow this removal of heat by convection and radiation, which is favored by vasodilatation and opening of arteriovenous shunts in the wings and by the greater thermal difference between the body and the environment during nocturnal flying.

The thermal conductance of a microchiropteran of 10 g is about 6 times that of a mega-chiropteran of 500 g (Geiser 2006). Thus the maintenance of homeothermy is especially relevant in small bats with large membranous wings and large lungs. Bats have a respiratory area 6 times greater and a conductance between 1.5 and 4 times greater than non-flying mammals (Neuweiler, 2000), although the minimum conductance at rest appears to be similar (see Speakman & Thomas 2003). Despite this, bats can remain active and euthermic within wide temperature ranges.

To maintain their temperature bats may use different behavioral and physiological strategies. Behaviorally they can avoid overheating by wing movements that favor convection or licking the surface of their skin to increase evaporation, since they do not have sweat glands. Small bats find microenvironments with high thermal stability in caves or shelters, and can travel to other shelters to avoid overheating at times of high temperatures. Thus, the solitary bat *Syconycteris australis* resting under leaves selected thermal environments in the middle of wooded patches in spring and autumn, protected from the extreme temperatures, while in winter it moved to the extremes (Law 1993) . To avoid cold behaviorally, many species have a social grouping behavior (huddling) (Roveroud & Chappel 1991), or nest in caves forming large colonies of hundreds to millions of individuals, raising the temperature up to 8° C above that of the rest of the cave (Dwyer & Harris 1972).

The first physiological response to cold is to increase muscle tone generating heat, followed by shivering, which actually consists of rhythmic but asynchronous fibrillary muscle contractions. However, heat generation consumes so much energy that with limited resources it is not convenient for long periods.

When ambient temperatures fall below the lower limit of thermoneutrality, bats have the "option" to maintain their body temperature at a high energy cost, or to enter into torpor, maintaining a temperature similar to that of the environment with a significant decrease in energy expenditure. Entering into torpor seems to depend upon the interaction among resource availability, reproductive status and body size. McNab (1983) proposed a boundary line of endothermy, allometrically related to body size with an exponent -0.67, which intersects the Kleiber line for mass-specific metabolism at 37 g. Thus, individuals under this line and weighing less than 37 g may use torpor as a physiological response to save energy. During torpor, animals enter into a rhythmic pattern of breathing and apnea; the periods are longer as the temperature drops. . These periods allow the accumulation of CO_2 that triggers breathing and prevents evaporation in the lungs. The mechanism that triggers the awakening is still unknown. Many bats have facultative stupor, maintaining significant fluctuations of oxygen consumption and body temperature (heterothermy), saving a great amount of energy. Some examples of this behavior are found in *Eptesicus fuscus, Rhinolophus ferrunequinum, bechteinii Myotis, Myotis evotis, Lasiurus cinereus* (Willis 2006) and *Myotis chiloensis* (Bozinovic et al. 1985). These bats have different patterns, such as the presence of lethargy in the daily rhythm with no difference between sexes, preference in pregnant and breast-feeding and preference for males. These depend on the fine balance between the costs of endothermy, reproduction and locomotion costs imposed by the high wing loading in the pregnant females. For example, if the costs are very high, some bats prefer to rest in cold and go into torpor, avoiding the cost of endothermy and negative energy balance (Willis 2006).

Another long-term mechanism for energy saving is hibernation, in which metabolism falls to extremely low levels; heart rate can also decrease from more than 400 beats to a few beats per minute and the peripheral circulation and urine output may fall to almost nil. The respiratory quotient drops to 0.6-0.7, indicating that metabolism of lipids and blood glucose values may reach about 25 mg / dl. In contrast to torpor in which the values of Q10 (ratio of metabolic change with 10° C of temperature change) are around 2, during hibernation they are temperature-dependent, increasing from 2 to 4 with an increase of temperature, which suggests an active metabolic depression. For example at 20° C the metabolism of a bat in torpor is twice that of a hibernating bat.

This metabolic depression could be due to metabolic acidosis, low thyroid hormone or mediated by fatty acids (Neuweiler, 2000). The mechanisms that trigger hibernation have not been established, although it has been postulated that hibernation is regulated autonomously. Temperature, energy depletion and loss of water have been postulated as triggers that regulate arousal.

5.1 Energy balance: *Myotis chiloensis*, a case study

The perpetuation of animals over time requires an average positive energy balance, which is particularly difficult for small mammals such as the insectivorous bat *Myotis chiloensis*. Bozinovic et al (1985) studied the oxygen consumption of 25 individuals (5.78 ± 0.9g) at different temperatures. There were two responses: a) euthermic metabolic levels (36.6 ± 2.2° C) with an average oxygen consumption of 1.76 mlO_2/gh b) torpor metabolic levels, where the temperature was only 0.5° C above room temperature with metabolic reductions of 81 to 98% (Figure 3). In continuous records *M. chiloensis* showed a daily rhythm with only three hours in which animals were euthermic.

The torpor in *M. chiloensis* was as expected for a small mammal, under the endothermy limit proposed by McNab (1983); however it does not explain why this species does not maintain high metabolism all the time.

The answer seems to come from the energy balance

$$Intake - Egestion = M_{activity} + M_{euthermia} + M_{torpor} + E\ , \tag{8}$$

where M is metabolism and E the energy balance.

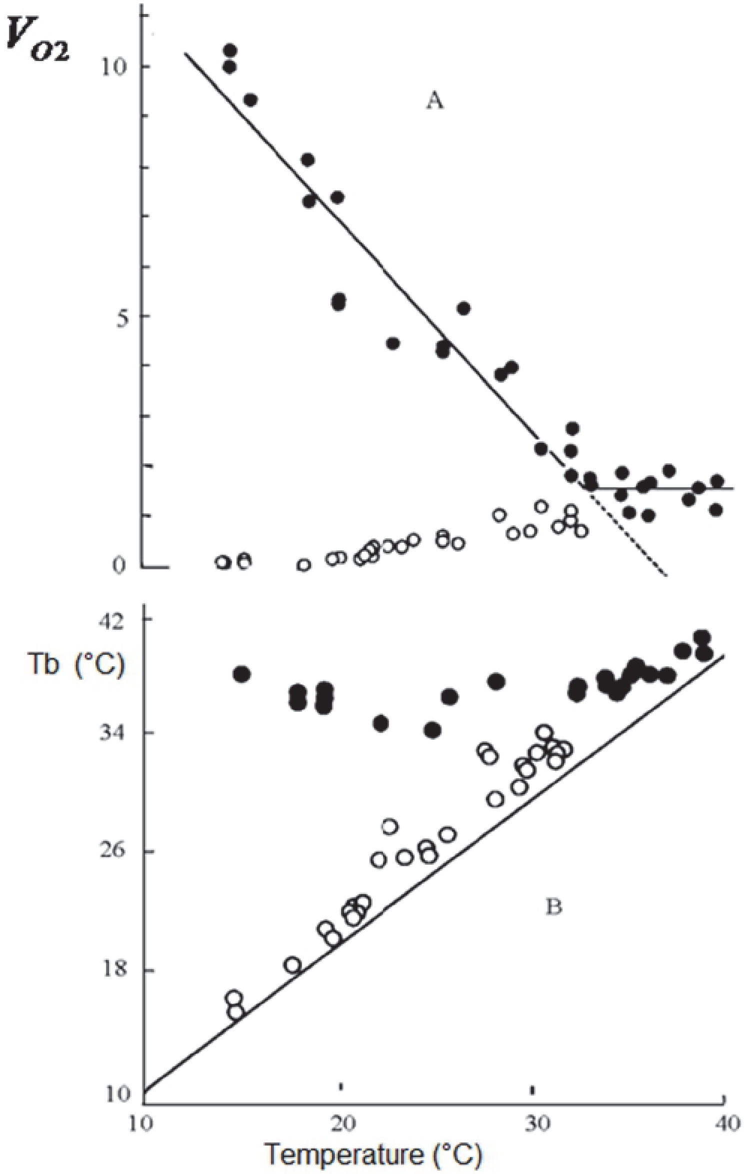

Fig. 3. A) Relation between ambient temperature and metabolism (MR, mlO_2/gh) and B) Relation between ambient temperature and body (Tb, °C) in *Myotis chiloensis* in euthermic state (black circles) and in torpor (white circles) (Modified from Bozinovic et al., 1985).

Data on the chemical composition of various flying insects indicates that their assimilated energy is approximately 5.3 Kcal / g; thus an individual of 5.8 g which ingested 11% of its weight in insects every day assimilates 5.8 x0, 11x5, 32 = 3.39 kcal / day. Therefore this individual may have two situations:

a. Euthermy: The temperature the shelters of *Myotis chiloensis* averages 19.5° C and metabolism at this temperature is 36 cal / gh, so that in the 21 hours of resting the minimal euthermic energy expenditure is 5.8 x36x21 = 4.38 kcal. The rest of the time (3 hours) *M. chiloensis* is flying and feeding. Assuming that the metabolic activity is at least three times BMR, the energetic cost would be 5.8 x36x3x3 = 1.88 kcal. Thus we have the following relationship: 3.39 = 4.38 + 1.88 + E, where the euthermic energy budget would be E = -2.87 kcal / day, i.e., the individual would have an energy imbalance equivalent to a mass loss of 5 to 10% per day.
b. Torpor: If instead it spends 20 hours in torpor with a metabolism of 1.2 cal / gh, 1 hour of euthermic rest (30 min before and after feeding) and the same three hours of activity, it would expend 5.8 x1, 2x20 = 0.14 Kcal in torpor, the same 1.88 Kcal during activity and 1x36x5, 8 = 0.21 Kcal at euthermic rest, giving a balance 3.39 = 0.21 + 1.88 + 0.14 + E. Now the energy budget is positive: E = +1.16 kcal / day.

6. The respiratory system

Endothermic animals depend on aerobic metabolism for most of their vital functions. The energy from food is allocated to different functions such as maintenance of homeostasis (i.e. temperature), reproduction, exchange mechanisms, maintenance of tone and locomotion. As most bats are small and therefore have a large surface area per unit volume, they have trouble maintaining their body temperature high and constant as consequence of the significant energy loss through the skin. Moreover, flight requires high energy expenditure, especially since many bats are exposed to cold nights and fly at high altitudes with low oxygen partial pressures (Harrison & Roberts 2000). In this sense bats may be considered as mammals adapted to extreme environments where oxygen management is crucial. Both the respiratory and cardiovascular systems undergo changes or refinements that allow them to optimize the acquisition and delivery of oxygen to tissues, and thus survive this extreme way of life.

Breathing in mammals consists basically of two connected events: ventilator convection and alveolar diffusion. The first is the displacement of a volume of air through the airway and the second in the effective exchange of oxygen and CO_2 at the alveolar level.

7. Ventilator convection

Alveolar ventilation ($\dot{V}$) may be expressed as the product of effective tidal volume (tidal volume (Vc) minus dead space (E)) and the respiratory rate (f_r):

$$\dot{V} = (Vc - E) \cdot f_r \,. \tag{9}$$

Thus increments in ventilation are possible only through effective tidal volume or respiratory rate increments. However, increasing alveolar ventilation may be costly in energetic terms as the movement of larger volumes of air results in greater breathing work. Moreover, the work of breathing (T_r) not only depends on the volume but also on the pressure necessary to mobilize this volume:

$$T_r = \int P dV \,. \tag{10}$$

This in turn is a direct function of the resistance to air movement which is influenced by a) a geometric factor:

$$R_g = \frac{8\eta l}{\pi r^4}\,, \tag{11}$$

(Poiseuille Law), where l is the length of the airway, η the air viscosity and r the radius of the bronchi, which basically indicates that the resistance to flow is inversely proportional to the fourth power of the radius, and b) a dynamic factor:

$$R_v = k_1 \cdot v + k_2 \cdot v^2 \,, \tag{12}$$

where v is the velocity of air flow, which indicates higher resistance at higher flow rates (or breathing rates). Thus the total resistance to airflow through the airway as a function of breath rate follows a U-shaped curve, determining for each species, according to the geometric characteristics of the airway, an optimal respiratory rate with minimal resistance. Murray (1926) and later Weibel and Gomez (1962) and Wilson (1967) established that respiratory geometry could be adapted to a minimum overall work of breathing and minimum entropy dissipation during mechanical ventilation, following approximately the Murray law "For minimum breathing work, ventilation (Q: minute volume) should be proportional to the third power of the radius (r):

$$Q = k \cdot r^3 \,. \tag{13}$$

However, mammals have considerable deviations from this pattern, especially due to the presence of asymmetries in diameter in the bronchial bifurcations and non-uniform length of segmental and subsegmental bronchi (Horstfield, 1990, Canals et al., 2002).

Bats have a much greater lung volume than non-flying mammals and they remove about 60% of the total lung capacity with each breath during flight (Neuweiler, 2000). Lung volume is about 72% greater than in non-flying mammals of similar weight (Canals et al, 2005a) (Table 2). At rest, pulmonary ventilation is similar to that of non-flying mammals. However, this can rapidly increase 10 to 17 times when flight begins (Thomas, 1987). This is due to increases of 3 to 5 times in breath rates and 2 to 4 times in tidal volume. The respiratory rate is synchronized to the wing beat frequency, reaching a value of 400 min^{-1}. These respiratory adaptations function together with structural changes of lung yield in oxygen consumption reaching to 2.5 to 3 times higher than mammals of equal size (Thomas, 1987) and high maximum oxygen consumption, which can reach 22 to mlO_2/gh at low temperatures (Canals et al., 2005b) and during hovering (Winter et al., 1998, Voigt & Winter, 1999; Voigt, 2004).

The morphology of the airways also appears to play a role in saving energy during flight. Canals et al. (2005) studied the airway of *Tadarida brasiliensis*, finding that this species showed fine adjustments in the geometry of the bronchial bifurcations leading to a better optimization of the proximal airway. As the airway is responsible for 80% of lung resistance and 80% of this is generated in the proximal airway, the optimization of the proximal airway can mean less energy loss during flight (Figure 4).

Species	Mb (g)	LV (cc)	RLV=LV/Mb (cc/g)
Tadarida brasiliensis	11.95 ± 1.36	0.654 ± 0.091	0.055 ± 0.011
Mormopterus kalinowski	3.1 ± 1.13	0.162 ± 0.024	0.054 ± 0.021
Myotis chiloensis	6.95 ± 0.54	0.406 ± 0.071	0.058 ± 0.009
Histiotus macrotus	9.80 ± 0.666	0.602 ± 0.094	0.061 ± 0.005
Histiotus montanus	12.5	0.696	0.056
Lasiurus borealis	6.8 ± 2.05	0.455	0.064 ± 0.004
Lasiurus cinereus	16.06 ± 7.62	1.025 ± 0.389	0.066 ± 0.010
Phyllostomus hastatus *	97.8 ± 2.56	4.95 ± 0.255	0.051 ± 0.007
Pteropus lyley *	456.0 ± 20.87	15.37 ± 1.93	0.034 ± 0.011
*Pteropus alecto**	667.0	22.20	0.033
Pteropus poliocephalus *	928.0	39.24	0.042

Table 2. Lung volume (LV) and relative lung volume (RLV) in several species of bats (from Canals et al 2005a and Maina et al., 1991*)

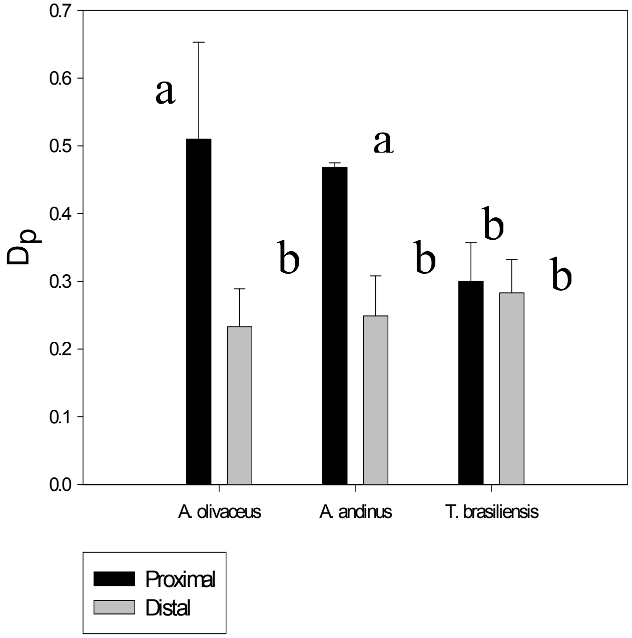

Fig. 4. Optimization of the proximal airway of *Tadarida brasiliensis. T. brasiliensis* is compared with the rodents *Abrothrix olivaceus* and *A. andinus.* The ordinate is the distance from the optimum value determined by the geometry of the bronchial bifurcations. While rodents have values farther from the optimum, *T. brasiliensis* shows a better optimization in the proximal zone, which is the key to a reduction in respiratory work, dissipating less energy. Different letters represent statistically significant differences

8. Alveolar diffusion

The diffusion of oxygen through the alveolar-capillary barrier depends directly on the gradient of partial pressure of oxygen between the alveoli and the capillary (ΔPO_2) and the respiratory surface (A), and inversely on the thickness of the alveolar-capillary membrane (τ_h) This can be expressed as:

$$\dot{V}_{O2} = \kappa \frac{dSa \cdot Vp}{\tau_h} \cdot \Delta PO_2 , \tag{14}$$

where the alveolar surface is expressed as the product of lung volume (V_p) and the surface density per unit of lung volume (dSa), κ is Krogh's constant and VO_2 is the oxygen consumption (Weibel et al., 1981). Thus, high oxygen consumption may be achieved through increases in alveolar surface density or lung volume, or by reducing the thickness of the alveolar-capillary barrier. The factor:

$$DO_2 = \kappa \frac{dSa \cdot Vp}{\tau_h} , \tag{15}$$

is known as conductance or oxygen diffusing capacity (DO_2). As mentioned above, bats have a lung volume 1.72 to 1.75 times that of non-flying mammals, however, alveolar surface density is similar to that of non-flying mammals (Maina, 2000). As a result, the total respiratory area of bats is larger than in non-flying mammals. In addition, these animals have a very thin alveolar-capillary barrier (Maina et al., 1991; Maina, 2000a) that may reach a value of 0.1204 microns in *Phyllostomus hastatus*, the lowest measured in mammals. So bats have very high oxygen diffusion capacity, similar to those of birds (Table 3).

9. The cardiovascular system

Respiratory adaptations are insufficient to ensure adequate oxygen delivery to tissues, so these must be accompanied by changes in the cardiovascular system. Here the blood flow generated by the heartbeat, the resistance to flow, and transport of oxygen in the blood are all relevant.

9.1 The heart

Blood flow (Q) can be expressed as the product of volume ejected in each beat (V_E) and heart rate (f_c) or as the ratio between the gradient of pressure to generate the flow (ΔP) and peripheral resistance (R):

$$Q = V_E \cdot f_c = \Delta P / R . \tag{16}$$

Peripheral resistance follows a Poiseuille relationship and cardiac work, similar to respiratory work, depends on expulsive volume and pressure:

$$T_c = \int P dV . \tag{17}$$

Thus high flow is obtained by increasing the expulsive volume or heart rate and by decreasing peripheral resistance.

Rodents	**Mb (g)**	**τh (μm)**	**Dsa (cm-1)**	**VLp (cm3)**	**DtO_2/Mb ($mlO_2\ s^{-1}\ Pa^{-1}\ g^{-1}$)**
Abrothrix olivaceus	26.3 ± 2.00	0.303 ± 0.037	589.37 ± 45.26	0.846 ± 0.28	$2.565x10^{-6}$
Abrothrix andinus	25.48 ± 1.93	0.345 ± 0.057	791.8 ± 229.68	0.972 ± 0.12	$3.589x10^{-6}$
Phyllotis darwini	75.0 ± 4.96	0.223 ± 0.033	1140.5 ± 92.0	1.91 ± 0.17	$4.92\ x10^{-6}$
Bats					
Tadarida brasiliensis	11.25 ± 0.50	0.230 ± 0.086	690.28 ± 156.96	0.585 ± 0.09	$6.398x10^{-6}$
Myotis chiloensis	6 ± 0.10	0.219 ± 0.015	2020.3 ± 71.0	0.360 ± 0.01	$20.4x10^{-6}$
Birds					
Zenaida auriculata	142 ± 1.55	0.171 ± 0.026	3102.9 ± 175	3.77 ± 0.06	$9.28x10^{-6}$
Columbina picui	39.9± 1.4	0.302 ±0.118	2328.9 ±426.4	1.04± 0.04	$4.19x10^{-6}$
Metropelia melanoptera	78.4± 2.4	0.186± 0.008	2580.4± 190.3	2.11 ±0.07	$7.04\ x10^{-6}$
Notoprocta predicaría	398 ± 11.7	0.469 ± 0.019	1811.3 ± 27	11.32 ± 0.43	2.07x10-6

Table 3. Pulmonary parameters of some Chilean species rodents, bats and birds. Mb = body mass; τh6 = harmonic mean of alveolo-capillary barrier thickness; Dsa = density of respiratory surface; VLp = volume of lung parenchyma and DtO2/Mb = mass-specific oxygen diffusion capacity of the alveolo-capillary barrier (data from Canals et al., 2005b; Figueroa et al., 2006; Alfaro et al., 2010).

Bats have the largest hearts of mammals relative to body mass, usually representing about 1% of body weight (Neuweiler, 2000), but reaching 2% (Jurgens et al., 1981, Canals et al., 2005a) (Table 4). They have great development of the right ventricle associated with better lung perfusion and high density of capillaries per unit volume. They also have the highest level of energy reserves in the form of ATP that has been measured in the heart of any animal (Neuweiler, 2000). Despite increased cardiac output, the volume expelled is similar to other mammals, somewhat greater than 1.5 ml / kg, indicating that the increase in heart size is mainly at the expense of muscle hypertrophy. The heart rate is extremely variable and may range from a few beats per minute during hibernation to over 1000 beats per minute during flight (Wolf & Bogdanowics, 1987, Neuweiler, 2000).

Species	**Mb (g)**	**Mh (g)**	**RHM=Mh/Mb (%)**	**Mh obs Mh exp**
Tadarida brasiliensis	11.25 ± 1.13	0.145 ±0.033	1.29 ± 0.23	0.943 ± 0.176
Mormopterus kalinowski	3.1 ± 1.13	0.057 ± 0.018	1.88 ± 0.10	1.041 ± 0.022
Myotis chiloensis	6.88 ± 0.47	0.096 ± 0.0145	1.40 ± 0.20	0.921 ± 0.137
Histiotus macrotus	9.65 ± 0.61	0.166 ± 0.0350	1.71 ± 0.03	1.213 ± 0.237
Histiotus montanus	12.5	0.272	2.18	1.627 ± 0
Lasiurus borealis	7.87 ± 1.10	0.120 ± 0.02	1.55 ± 0.27	1.046 ± 0.169
Lasiurus cinereus	12.76 ± 2.74	0.173 ± 0.042	1.40 ± 0.04	1.042 ± 0.279
Pipistrellus pipistrellus *	4.85 ± 0.18	–	1.26 ± 0.24	–
Myotis myotis *	20.6 ± 0.9	–	0.98 ± 0.08	–
Molossus ater *	38.2 ± 1.4	–	0.97 ± 0.01	–
Phyllostomus discolor *	45.2 ± 1.34	–	0.94 ± 0.09	–
Rousettus aegyptiacus *	146.0 ± 7.5	–	0.84 ±0.08	–

Table 4. Heart size of several bat species. Mb = body mass; Mh = heart mass; RHM = relative heart mass; Mhobs/Mhexp = ratio of observed to that expected by allometry. (Data from Canals et al., 2005a; Jurgens et al., 1981*)

9.2 Vessels, the resistance to flow and oxygen transport in blood

The vessels of bats follow a mammalian pattern, with some arterial and venous modifications. Unlike other mammals, the venous return of the forelimbs occurs through two vena cava; inferior vena cava have a muscular zone that allow regulation of venous return, lower during rest and high during flight. The arteries of the wing branch into arterioles with a muscle base which can regulate the flow to the wings and maintain the arteriovenous differential pressure. There are also arteriovenous shunts and venous vessels with pulsating zones (venous hearts) that can regulate the return of blood from the wings. The volume of blood is similar to other mammals as well as the affinity of hemoglobin. However, bats have the highest levels of hematocrit measured in mammals and may reach values above 70% in *Tadarida brasiliensis* and *Miniopterus minor*. Red blood cells are smaller (Figueroa et al., 2007) and hemoglobin has been found in higher concentrations (18-24 g/100ml blood), similar to that found in hummingbirds (Johansen et al., 1987). Consequently, bats have a transport capacity of oxygen in the blood of 25 to 30%. In comparison, non-flying mammals have an oxygen-carrying capacity of about 18% (Thomas, 1987; Neuweiler, 2000).

10. The narrow-based, high keyed strategy

By comparing the structural and functional adaptations in birds and bats it can be established that they reach very similar aerobic capacities. However, strategies to achieve these high performances during flight are different. Birds have a large set of structural changes in their respiratory system, such as air bags, parabronchi systems, respiratory capillaries, cross-current flows, etc. In contrast, bats have a cardio-respiratory system fully modified to accomplish an extreme way of life. This mammalian structural base is highly refined, operating near maximum values (Maina, 1998) (Table 5). Thus, Maina (1998) comparing a set of 7 parameters including birds, bats and non-flying mammals, found that bats have higher "degrees" of optimization in 5 of them: resting respiratory rate, hematocrit, hemoglobin concentration, resting heart rate and blood count.

Optimization Strategy	
Respiratory Adaptations	**Cardiovascular Adaptations**
Increase of lung volumen	Increase of heart size
Thin alveolo-capillary membrane	Development of right half of the heart
Small alveoles	Regulation of venous return
High oxygen diffusing capacity	High hematocrit
High respiratory frequency	Small GR
Proximal airway adjusted to lower energy loss	Greater concentration of hemoglobin
	Greater oxygen transport capacity

Table 5. Strategy of respiratory and cardiovascular optimization in bats.

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