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Biomechanic consequences of differences in wing morphology between *Tadarida brasiliensis* and *Myotis chiloensis*

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The wing morphology of bats is very diverse, and may correlate with energetic, behavioural, and ecological demands. If these demands conflict, wing shape may reflect compromise solutions. In this study, we compared the wing morphology of two bats, *Tadarida brasiliensis* (Geoffroy, 1824) and *Myotis chiloensis* (Waterhouse, 1828), that differ in body size, habitat, and foraging behaviour. We analyzed features of biomechanical and energetic relevance, and sought evidence of compromise solutions to energetic, ecological, and behavioural demands. We found that wing span of both species conformed to expectations based on allometric relationships, but that although the wing area of *M. chiloensis* did not differ from predictions, the wing area of *T. brasiliensis* was lower. *M. chiloensis* possessed an unusually low second moment of area of the humerus. Wing form of *M. chiloensis* is consistent with highly maneuverable flight needed to live between shrubs and wooded habitats, and its low aspect ratio and low wing loading indicate a high energetic cost and a low flight speed, respectively. The low humeral second moment of area may be related to a reduction of wing mass and may result in decreased inertial power. In contrast, *T. brasiliensis* showed high aspect ratio and wing loading, characteristic of high speed, energetically economic flight.

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Introduction

The wing shape of flying vertebrates influences both the energetic costs of flight and ecological and behavioural aspects, such as flight pattern, foraging behaviour, habitat selection, and size of food items (Norberg 1987). As flight is an expensive mode of locomotion (Norberg 1994), there should be strong selection for reduction of flight costs, favoring specific wing shapes. The wing morphology of bats is very diverse, and may be correlated to energetic, behavioural and ecological constraints (Norberg 1987, 1994). This may mean that energetics *per se* is not the only critical design parameter for wing, and that lifestyle, behaviour, and habitat demands may

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be relevant. If these demands conflict, wing shape may reflect functional compromises. For example, bats that live in dense vegetation need to be highly maneuverable and to fly at low speed. These requirements are facilitated by a low wing loading. If the energetic costs of flight are relevant to the survival and reproduction of the bats, we expect to find narrow wings that minimize the work needed to fly by minimizing the power to generate lift and thrust (Rayner 1979, Norberg 1987). However, these ecological and energetical demands are not compatible. A bat with narrow wings will have small wing areas and thus high wing loading unless their wings are also long. Energetic demands predict bats will possess narrow wings, and habitat constraints predicts low wing loading and hence bats with large wing span, but large wings are very impractical in cluttered areas.

The wide spectrum of wing forms of bats, from short and wide to long and narrow, have been related to flight patterns and foraging behaviour (Findley *et al.* 1972, Kopka 1973, Lawlor 1973, Norberg 1981, Baagøe 1987, Norberg 1987, 1994, 1996, Norberg and Rayner 1987, De la Cueva *et al.* 1995, Spear and Ainley 1997, Webb *et al.* 1998, Norberg *et al.* 2000). In this study, we compared the wing morphology of two Chilean bats that differ in body size, habitat, and foraging behaviour. We analyzed differences between these species from an energetic perspective based on aerodynamic theory, and looked for evidence of compromise solutions to divergent energetic, ecological, and behavioural demands.

Material and methods

We compared the molossid *Tadarida brasiliensis* (Geoffroy, 1824) (body mass $m_b = 11.95 \pm 0.32$ (SE) g, $n = 27$) and the vespertilionid *Myotis chiloensis* (Waterhouse, 1828) ($m_b = 6.76 \pm 0.09$ g, $n = 59$) caught in Santiago, Chile, and donated to us by Servicio Metropolitano de Salud del Medio Ambiente (SESMA). In this region, *T. brasiliensis* commonly colonizes urban buildings (Gantz and Martínez 2000) and its diet consists mostly of small moths and beetles caught in open areas while flying (Nowak 1999, Gantz and Martínez 2000). *M. chiloensis,* an endemic species, has the most southerly distribution of all bat species, and usually lives in thickets, near watercourses, and occasionally colonizes human dwellings (Nowak 1999). It feeds primarily on nematoceran dipterans (Gantz and Martínez 2000).

Wing span (B = the distance between the wing tips) was measured directly with calipers (± 0.1 mm) from individuals with outstretched wings. Great care was taken to keep the leading edges of the arm wings and parts of the hand wing along a straight line. Wing area (S = area of body between the wings and tail membrane) was estimated following Norberg (1994) by fully extending the right wing and the trailing edge of uropatagium aligned with the midline of the body, tracing the wing outline onto white paper and weighing it in an analytical balance (± 0.1 mg). Marks were made on paper to identify three wing zones: (1) propatagium (membrane that run from the shoulder to the wrist and is the leading edge of the wing), (2) dactylo- plus plagiopatagium (membrane spanning digits 2–5 plus membrane including area from 5th digit to body, respectively), and (3) uropatagium (membrane between hind limbs).

External diameter (D_h) and medullar cavity diameter (d_h) were measured from radiographs of the wing (Fig. 1). Diameters were measured at midshaft. A distance focus-film of 1 m was used to avoid size distortion of actual bone dimensions. From these measurements, several parameters were computed: aspect ratio $AR = B^2/S$, wing loading $P_w = m_b\, g/S$ (g = gravitational acceleration), and second moment of area of the humerus at midshaft $I_h = \pi\ (D_h^4 - d_h^4)/64$, a measure of the amount and geometrical distribution of material in a beam cross-section and thus a measure of resistance to

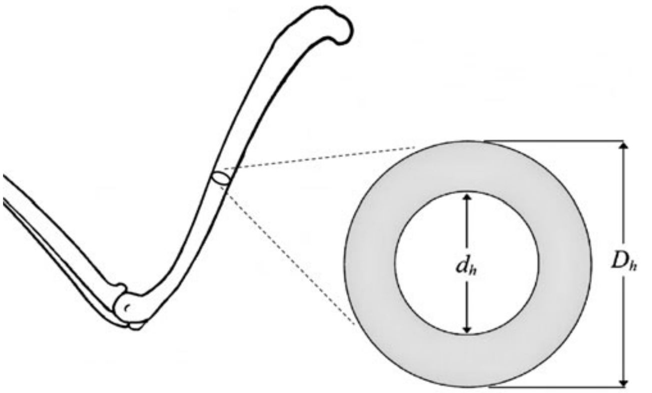

Fig. 1. Scheme of bat arm indicating the measurements used to acquire cross-sectional data of midshaft humerus. D_h – external diameter of humerus, d_h – internal diameter of humerus.

bending (Wainwright *et al*. 1982, Biknevicius 1993). Means for the two species were compared with a Student's t-test for unpaired samples. Wing span, wing area, and humeral second moment of area were compared with values predicted from body mass by allometric equations (Kirkpatrick 1994). One-sample Student's t-tests were performed to test deviations from the allometric predictions by computing the ratio R = observed/expected and testing H_0: R = 1 vs H_1: R ≠ 1.

Results

The body mass of *Tadarida brasiliensis* (*Tb*) was nearly double that of *Myotis chiloensis* (*Mc*) (Table 1). Both species showed wingspans within allometric predictions (*Tb*: $t = -0.7$, df = 26, $p > 0.05$; *Mc*: $t = -1.7$, df = 38, $p > 0.05$) (Fig. 2a). Wing area of *M. chiloensis* was within the predicted range (t = 0.4, df = 46, $p > 0.05$), in contrast to the significantly lower wing area of *T. brasiliensis*

Table 1. Mean values and 95% confidence interval (CI) of body mass, wing shape and strength parameters measured in *Tadarida brasiliensis* and *Myotis chiloensis* captured in central Chile. See text for description of parameters.

Parameter	*Tadarida brasiliensis*		*Myotis chiloensis*	
	n	Mean ± 95% CI	*n*	Mean ± 95% CI
Body mass (g)	27	11.95 ± 0.62	49	6.76 ± 0.18
Wing area (cm^2)	24	100.14 ± 4.61	47	98.29 ± 3.47
Wing span (cm)	27	28.65 ± 0.63	39	2.70 ± 0.39
Second moment of area (× 10^{-6}) (cm^4)	18	11.15 ± 2.61	43	3.89 ± 0.49
Wing loading (N/m^2)	24	11.56 ± 0.66	47	6.80 ± 0.23
Aspect ratio	24	8.12 ± 0.16	37	5.76 ± 0.16

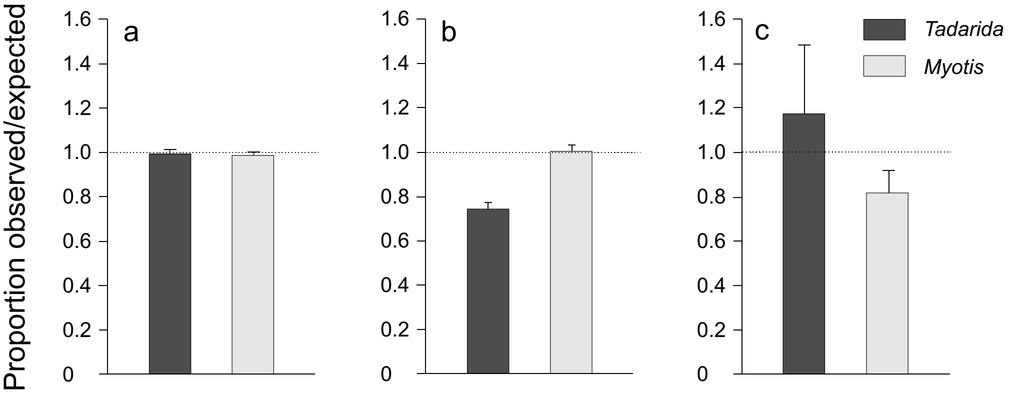

Fig. 2. Relationships between observed values measured in this study and expected values obtained from literature of (a) wing span (B), (b) wing area (S), and (c) second moment of area of humerus (I_h). Bars correspond to 95% confidence interval. Expected values were calculated from Kirkpatrick's (1994) equations: (a) $B = 1.248\ m_b^{0.33}$ ($r = 0.969$), (b) $S = 0.190\ m_b^{0.59}$ ($r = 0.979$), (c) $I_h = 2.68 \times 10^{-11}\ B^{4.42}$ ($r = 0.964$).

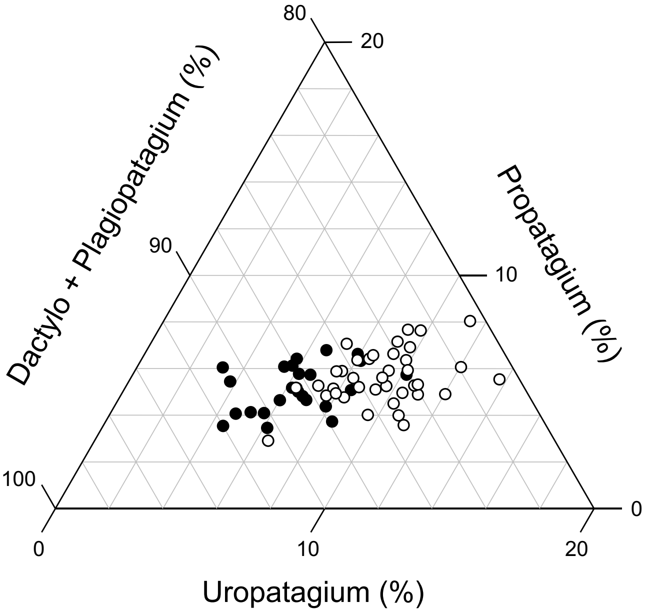

Fig. 3. Ternary plot showing the percentage of propatagium, dactylo+plagiopatagium and uropatagium respect total patagium area of *Tadarida brasiliensis* (closed circles) and *Myotis chiloensis* (open circles).

(t = –15.6, df = 23, p <0.0001) (Fig. 2b). When we compare wing area in absolute terms we observe no differences between these species (t = 0.617, df = 69, p > 0.5), in spite of their differences in size. Analysis of proportion of different zones of patagium respect to total patagium shows that whereas proportion of propatagium area is similar in both species (t = –1.6, df = 61, p > 0.1), proportion of dactylo + plagiopatagium in *T. brasiliensis* is 4.0% higher that of *M. chiloensis* (t = 6.7, df = 61, p < 0.001). Conversely, the uropatagium is proportionately 46.5% higher in *M. chiloensis* than in *T. brasiliensis* (t = –7.2, df = 61, p < 0.001) (Fig. 3). The second moment of area of the humeral midshaft of *T. brasiliensis* did not differ from the allometric prediction (t = 1.1, df = 17, p > 0.05), but that of *M. chiloensis* was significantly lower than predicted (t = –3.6, df = 31, p < 0.01) (Fig. 2c).

Discussion

The body mass of the two study species differs by a factor of two. As a consequence, flight mechanics and energetics also differ, because metabolism and wing loading, for example, vary allometrically with body mass. The proportion of patagium area varies among species; *T. brasiliensis* has a relatively larger dactylo+plagiopatagium area and a strongly reduced proportion of uropatagium compared with *M. chiloensis*. The large uropatagial area of *M. chiloensis* might facilitate rapid changes of direction and effective use of the uropatagium to catch insects in flight (Norberg 1994). On the other hand, this large membrane would increase tail drag and therefore energetic costs of flight (Norberg 1995). Despite the large difference in mass, the absolute wing area differs by less than 2%. This is because the wing area of *M. chiloensis* is close to that predicted allometrically and the wing area of *T. brasiliensis* is far lower than expected based on body mass alone. As a consequence, the average wing loading is higher in *T. brasiliensis* (11.56 N/m^2) than in *M. chiloensis* (6.80 N/m^2). Aerodynamic theory indicates that minimum speed needed to fly scales as $(\text{wing loading})^{0.5}$, and therefore, only bats with low wing loading can fly slowly, while bats with high wing loading must fly at higher minimum speeds (Norberg 1994). Average speeds between 6 m/s (Hayward and Davis 1964) and 11.3 m/s (Svoboda and Choate 1987) have been attributed to *T. brasiliensis,* near the highest recorded speeds for bats (Norberg 1987). Aspect ratio can be interpreted as a measure of the aerodynamic efficiency of flight (Norberg 1994). Low total flight power is obtained with a high aspect ratio wing, by decreasing profile power (power needed to overcome the form and friction drag of wings) in fast flight and by decreasing induced power (power needed to generate lift and thrust) in slow flight (Norberg 1987, Rayner 1982). The relatively reduced wing area of *T. brasiliensis* is linked to a high aspect ratio (8.12). This wing design allows fast and economical flight, and is consistent with the requirements of species that fly long distances such as *T. brasiliensis*, which have been reported to feed up to 60 km from their nest sites and to migrate over 1000 km (Norberg 1994). In contrast, *M. chiloensis* has a low wing loading, compared to that of other bats and a lower aspect ratio than *T. brasiliensis.* The wing configuration of *M. chiloensis* indicates relatively more energetically expensive flight and lower minimum flight speeds than in *T. brasiliensis.*

In active flight, the skeleton of the upper extremities of bats must support the dynamic loads of flapping. The wing skeleton of bats is not aligned with the wing's center of pressure, therefore the main forces exerted on the humerus are torsional (Swartz *et al.* 1992, Biewener and Dial 1995). The ability of a bone to resist torsional forces is proportional to the polar second moment of area (J) of the bone's cross-section, which is twice the second moment of area (I) for a bone with a circular cross-section (Swartz 1997). *T. brasiliensis* possesses humeri with second moments of area typical of bats of its body mass, but, in contrast, second moments of area in the humerus of *M. chiloensis* are low, suggesting poorer resistance to bending and torsional forces. The ratio between the stress at which a structure will fail to the maximum stresses imposed by vigorous activity is defined as the safety factor of the structure. The safety factor of large bones in terrestrial and flying vertebrates is typically 2 or higher (Biewener 1990, Kirkpatrick 1994), but bat wing bones have the lowest safety factors among extant vertebrates studied to date, estimated at about 1.4 during hovering (Kirkpatrick 1994). They are therefore susceptible to damage to the wing skeleton during flight, particularly during hovering in which the wing beat frequency and mechanical demands are highest (Rayner 1984). Although *M. chiloensis* belongs to a genus in which hovering is common, as one might expect based on its low wing loading and small size (Norberg 1994), the low second moment of area of humerus might constrain this possibility. On the other hand, the low aspect ratio and low wing loading indicate energetically expensive and slow flight, respectively. As a consequence, induced and inertial power (power needed to oscillate the wings) figure importantly in their flight energy budgets (Rayner 1982). It has been observed that inertial power in nectar-feeding bat, *Glossophaga soricina*, comprises around 55% of the total mechanical power required during hovering (Norberg *et al.* 1993). Thus, a reduction of wing mass by means of a reduction of humeral mass might reduce inertial power (Tholleson and Norberg 1991, Van den Berg and Rayner 1995). The second moment of area of humerus is 18% lower than allometric expectations for *M. chiloensis*. If the proportion between external diameter (D_h) and medullary diameter (d_h) remain unchanged, a reduction of second moment of area of this magnitude would produce a reduction of 5% in humerus diameter, and therefore a reduction of cortical cross-section area about 10%. If humeral length remains constant and if cortical area decrement occurs homogeneously throughout bone, the diminution of cortical area would result in a 10% reduction in humeral mass. This reduction in wing mass and hence in wing moment of inertia, might be a way to reduced energetic costs by reducing inertial power of *M. chiloensis*, which possess a fragile energetic equilibrium characterized by alternating occurrence of euthermic and torpor periods to allow a positive energy budget (Bozinovic *et al.* 1985). On the other hand, a reduction in wing mass that decreases wing moment of inertia may improve flight maneuverability (defined as minimum turning radius the animal can attain) and agility (maximum roll acceleration during initiation of a turn, a measure of ability to alter flight path) (Tholleson and Norberg 1991). Maneuverability can be also increased by low body mass and low wing loading and high agility can be obtained by low wing moment of inertia and large aerodynamic torque (Tholleson and Norberg 1991). Bats at low flight speed increase aerodynamic torque by low aspect ratio (broad wings) and large wing span, although torque also can be increased by increasing flight speed. Moreover, agility can be improved in high speed bats through short wing span and high aspect ratio (narrow wings). Thus, *M. chiloensis* shows a wing morphology (broad wings, low wing loading and large uropatagial area) and biomechanical wing bone properties (low second moment of area and hence low wing moment of inertia) consistent with the highly maneuverable flight needed to live amongst shrubs in densely wooded habitats. In contrast, *T. brasiliensis* is characterized by high aspect ratio and wing loading, typical of fast and energetically inexpensive flight, needed for long distance flights.

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