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On the allometry of wings

Acerca de la alometría de las alas

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ABSTRACT

The wing spans (mm) of 70 Chilean birds were expressed as functions of body mass (g) by means of Huxley's power equation $Y = a M^b$, where Y is the wing span, a an empirical parameter, M body mass, and b a characteristic exponent. In a geometric similarity (isometry), the exponent for wing span is $b = 1/3$, whereas in "allometric" conditions $b \neq 1/3$. Our results yielded an exponent b of 0.394 (allometry), a result which could be confirmed by means of principal component analysis. Furthermore, we compared our results with those obtained on birds from the northern hemisphere, in which three different aerodynamic models of birds (passerines, shorebirds and ducks) were analyzed separately. An exponent $b \geqq 0.39$ was obtained for all three bird models, confirming the allometry of wing spans.

Key words: Body weight, allometric equation, geometric similarity, wing morphometry, three models of birds.

RESUMEN

La envergadura de las alas (mm) de 70 aves chilenas se expresó en función de la masa corporal (g) por medio de la ecuación de potencia de Huxley $Y = a M^b$, donde Y corresponde a la envergadura alar, a es un parámetro empírico, M la masa corporal y b un exponente característico. En una similitud geométrica (isometría), el exponente para la envergadura alar es $b = 1/3$, en tanto que en condiciones "alométricas" $b \neq 1/3$. Nosotros obtuvimos para la envergadura de las alas un exponente $b = 0{,}394$ (alometría), un resultado que pudo corroborarse mediante el análisis de componentes principales. Además, comparamos nuestros resultados con aquellos provenientes de aves del hemisferio norte, en los cuales se analizaron por separado tres diferentes modelos aerodinámicos de aves (paseriformes, aves de ribera y patos). Un exponente de $b \geqq 0{,}39$ se obtuvo para los tres modelos de aves, con lo cual se confirma la alometría de la envergadura alar.

Palabras claves: Peso corporal, ecuación alométrica, similitud geométrica, morfometría de las alas, tres modelos de aves.

INTRODUCTION

Many attempts have been made to apply dimensional analysis and theories of similarity to the biological sciences (Lambert & Teissier 1927, Thompson 1952, Günther & Guerra 1955, Günther 1975a, 1975b, Stahl 1962, 1963, Schepartz 1980, Mc Mahon 1973, 1975). More recently Heusner (1982, 1983a, 1983b) has discussed biological functions, not only within the framework of dimensional analysis and similarity theories, but also from a thermodynamic point of view by applying a new theoretical approach known as "homomorphism" (Cara 1958, quoted by Heusner (1982).

The first and obvious question to be answered is whether the size and form differences between small and large animals can be quantitatively described by means of a simple "geometric" similarity (isometry), which deals mainly with the dimensions of length (L), areas ($A \alpha L^2$), and volumes ($V \alpha L^3$). In this similarity the constancy of body density ($\rho = ML^{-3}$) must be assured, an assumption wich is validated by the fact that all ani-

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mals placed in water are on the verge of flotation (Economos 1982) due to their almost identical chemical makeup. It is interesting to note that sea mammals (Economos 1982) and fishes (Günther & Morgado 1983) of different sizes follow such a geometric similarity criterion, given that the external morphometry of these aquatic vertebrates varies isometrically. Conversely, the structures and functions of most terrestrial animals agree with a "mechanical" similarity (Günther 1975a, 1975b); the known exceptions being the limb bones of *Bovidae,* which follow the rules of an "elastic" similarity (McMahon 1973, 1975), and the bones of running animals (other than *Bovidae)* which tend to agree with a "geometric" similarity (Alexander 1982).

Our first study on the morphometry and physiometry of bird and insect wings (Günther & Guerra 1957) was based on numerical data from Thompson (1952), which unfortunately included only 2 insects and 4 birds. Furthermore, these specimens were heterogeneous from a taxonomic point of view and their only advantage was their wide body weight range (from a 0.01 g fly to a 3500 g stork).

The experimental data on wing dimensions can be conveniently represented by means of the power equation of Huxley (1932):

$$Y = a\,M^{b} \qquad (1)$$

where Y = any function that can be represented by means of the MLT system of physics; a = empirical parameter; M = body mass (g); and b = exponent.

In a "geometric" similarity the theoretical exponents (b) for any length function is 1/3, for any area 2/3, and for a volume b = 1.0 (Günther 1975a, 1975b). Nevertheless, in our first study we found that the exponent (b)[1] for wing length was b = 0.393, for the flight surface b = 0.664, and for the wing-beat frequency b = −0.382. The only value which agreed with a geometric similarity criterion was the flight surface (b = 2/3), whereas the other two parameters were different from the expected values: b = 1/3 for wing length, and b = −1/3 for the wing-beat frequency. Despite the fact that in all these instances the correlation coefficient (r) was close to unity, only a study performed on numerous specimens of taxonomic homogeneity could resolve whether these numerical values are significantly different from the postulated geometric similarity. Such a study is attempted here on 70 Chilean birds, whose wing spans (L) are expressed as a function of body mass (M). The results are compared with the morphometric data obtained from birds of the northern hemisphere (Müllenhoff 1885, Meunier 1959), and with those of bats, which are the only flying mammals (Norberg 1976, 1981).

MATERIAL AND METHODS

1. Morphometry of wings. Prof. H. Oyarzo (pers. comm. 1984) from the Department of Zoology of the University of Concepción, measured the body mass (expressed in g) and the wing spans (in mm) of 70 Chilean birds. The mass was determined with the precision of 0.1 g and the wing spans, which represent the distances between the tips of the extended wings, with a precision of 0.5 mm. These data are given in Table 1.

2. Statistical analysis. From the logarithms of the wing-span data we calculated the mean values for parameter *a* and exponent *b* of Huxley's equation, together with the 95% confidence limits. The determination coefficient (r^2) of the linear regression line (least squares method) was also calculated. In all statistical tests we accepted $P \leqslant 0.05$ as significant. The principal components analysis (Jolicoeur 1963, 1984) was also submitted to Anderson's (1963) test, in order to validate or to reject the isometry hypothesis (geometric similarity).

RESULTS

From the statistical analysis of the logarithms of wing spans versus the logarithms of body mass we obtained the following allometric equation: $Y = 70.3M^{0.394}$ which yielded a value of 1.847 ± 0.043 (Mean ± SE) for the log of parameter *a,* with 95%

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[1] In this paper we have followed McMahon's (1975) suggestion in the sense that the theoretical predictions of exponent *b* should be expressed as whole fractions of *M, e.g.,* 1/3, 2/3. Experimental results will be expressed as decimal fractional powers, *e.g.,* 0.33, 0.66.

TABLE 1

Taxonomic and morphometric data concerning 70 Chilean birds

Datos taxonómicos y morfométricos concernientes a 70 aves chilenas

Order	Name	Body Mass (g)	Wing Span (mm)
PASSERIFORMES	Turdus falcklandii	90	400
	Sylviorthorrynchus desmursii	10	150
	Pyrope pyrope	37	310
	Scytalopus magellanicus	30	170
	Cinclodes patagonicus	40	290
	Pygochelidon cianoleuca	14	250.5
	Tachycineta leucopyga	15	280.5
	Pteroptochos castaneus	200	290
	Muscisaxicola flavinucha	27	360
	Muscisaxicola alpina	25	310.3
	Muscisaxicola macloviana	20	230
	Phytotoma rara	25	230
	Elaenia albiceps	14	200
	Troglodytes aedon	10	160
	ibidem	10	150
	Mimus thenca	81.7	340
	Agelaius thilius	38	290
	ibidem	46	290.5
	Curaeus curaeus	99	390
	ibidem	66	400
	Sturnella loyca	78	300
	ibidem	110	370
	ibidem	110	390
	Zonotrichia capensis	25	220
	Aphrastura spinicauda	10	160
	ibidem	12	180
	Diuca diuca	26	190
	ibidem	24	190
	ibidem	24	270
	ibidem	24	280
	Anairetes parulus	16	140
STRIGIFORMES	Glaucidium nanum	74	360
	ibidem	75	380
	Bubo virginianus	800	1,100
	Tyto alba	407	680
	ibidem	590	980
	Strix rufipes	620	900
	Athene cunicularia	370	500
PSITTACIFORMES	Enicognathus ferrugineus	500	560
	ibidem	185	480
	ibidem	194	540
	ibidem	200	530
COLUMBIFORMES	Columba livia	284	660
	Zenaida auriculata	120	470
PICIFORMES	Campephilus magellanicus	320	600
	Colaptes pitius	145	470
	ibidem	195	500
	Picoides lignarius	80	260
	ibidem	50	300
CHARADRIFORMES	Charadrius collaris	30	260
	Haematopus palliatus	310	870
	Vanellus chilensis	270	820
	Charadrius falcklandicus	35	510
	Recurvirostra andina	190	790
	Chionis alba	310	710
	Sterna paradisae	106.5	730
	ibidem	110	760
	ibidem	110	770

Table 1 (Cont.)

Order	Name	Body Mass (g)	Wing Span (mm)
ANSERIFORMES	Chloephaga picta	3,250	1,290
	Tachyeres patachonicus	2,500	1,050
FALCONIFORMES	Buteo polyosoma	950	1,235
	Geranoaetus melanoleucus	3,600	1,620
	Parabuteo unicinctus	450	1,100
	Elanus leucurus	270	940
	Circus cinereus	282.2	800
	Milvago chimango	265	760
	ibidem	283	780
	Falco peregrinus	800	1,070
	Falco sparverius	120	580
CAPRIMULGIFORMES	Caprimulgus longirostris	82	460

confidence limits of 1.759 and 1.934; and 0.394 ± 0.020 for exponent *b*, with confidence limits of 0.353 and 0.436. The determination coefficient of exponent *b* was $r^2 = 0.839$. Thus, we may conclude that the wing spans of Chilean birds (Fig. 1) are significantly different ($P \leq 0.05$) from the expected geometric similarity ($b = 1/3$). Furthermore, these results can be compared with the exhaustive quantitative study of the morphological characteristics of birds from the northern hemisphere, which was published a century ago by Müllenhoff (1885), and which —as far as we know— have never been submitted to a statistical analysis. The results of our study are shown in Table 2. It is noteworthy that the 95% confidence intervals of each of the three variables analyzed include the theoretical values which are to be expected from a geometric similarity, *i.e.*, exponent $b = 1/3$ for wing span, $b = 2/3$ for a wing area, and $b = 1/3$ for the wing loading (body weight/wing area) which is expressed in accordance with the original data (g/cm^2). Nevertheless, from a strictly physical point of view the latter dimension should be converted into "force/area" or "Newton's per square meter". But, this dimensional conversion would affect the numerical values of parameter *a* and not that of the allometric exponent (b), which is independent of the physical units employed. Since the main interest of the present study is to decide whether "isometry" or "allometry" are prevalent in wing morphometry, we will concentrate our attention on the latter parameter, *i.e.* on exponent *b*.

In order to elucidate the validity of the conclusions derived from Table 2, namely the eventual existence of a geometric similarity, we applied principal components analysis (Jolicoeur 1963, 1984) to the body mass, wing span, and wing area data obtained from Müllenhoff (1885), which we had previously transformed into decimal logarithms (Table 3). Through the analysis of principal components, the hypothesis of equal relative sizes (isometry) at the $P \leqq 0.05$ level can be decided by means of Anderson's (1963) test. This hypothesis implies, that the first normalized characteristic vectors are equal to $1/\sqrt{3}$, $1/\sqrt{3}$, $1/\sqrt{3}$. In accordance with Table 3 the first characteristic vectors are 0.769, 0.287, 0.570, which correspond to the first characteristic root 0.595. Furthermore, and in accordance with the test proposed by Anderson (1963), the value for $\chi^2 = 1425.92$ (2 DF) indicates that the isometry hypothesis (geometric similarity) must be rejected and, in consequence, body mass and wing morphometry (wing spans and areas) agree instead with an allometric criterion.

Since Müllenhoff's (1885) data include different orders of birds, it is more convenient to classify these animals following the wing loading (aerodynamic criterion) suggested by Greenewalt (1975), *e.g.*, body weight (W) supported per unit wing area (A), which reflects the birds ability to maneuver in its medium. Greenewalt (1975) classified birds into three aerodynamic models, namely, passeriformes, shorebirds, and ducks, which at a given weight show an increase in "wing loading" as one passes from passeriformes through to ducks. When Greenewalt's (1975) criterion was applied to the combined data obtained from the birds studied by Müllenhoff (1885), Oyarzo (pers. comm. 1984), as well as to those of Meunier (1959), we obtained an almost identical allometric exponent (b) for the wing spans of the three models (Table 4, items 1, 2, 3, and Fig. 2). These results also agree with Rayner's (1978) findings for semi-wing-spans (one half wing span), where he obtained *b* exponents of 0.42, 0.40 and 0.41 for passeriform, shorebird, and duck models, respectively. It should be emphasized that our three values (Table 4) are significantly different from the expected value for isometry (b = 1/3); the only slight exception is in the duck model, where the lower limit of the 95% confidence range is almost equal to the theoretically expected figure for isometry.

From a comparative point of view it is interesting to mention Norberg's (1981) studies on the wing spans of bats (Table 4, item 4). She found a *b* exponent for wing spans of 0.30, whose upper 95% confidence limit is within the expected value for a geometric similarity. Finally, the wing spans of hummingbirds (Greenewalt 1975), with their characteristic hovering flight style, yielded —as recalculated by us— an allometric exponent of b = 0.53 (Table 4, item 5), which is also significantly different from the exponent for isometry (b = 1/3).

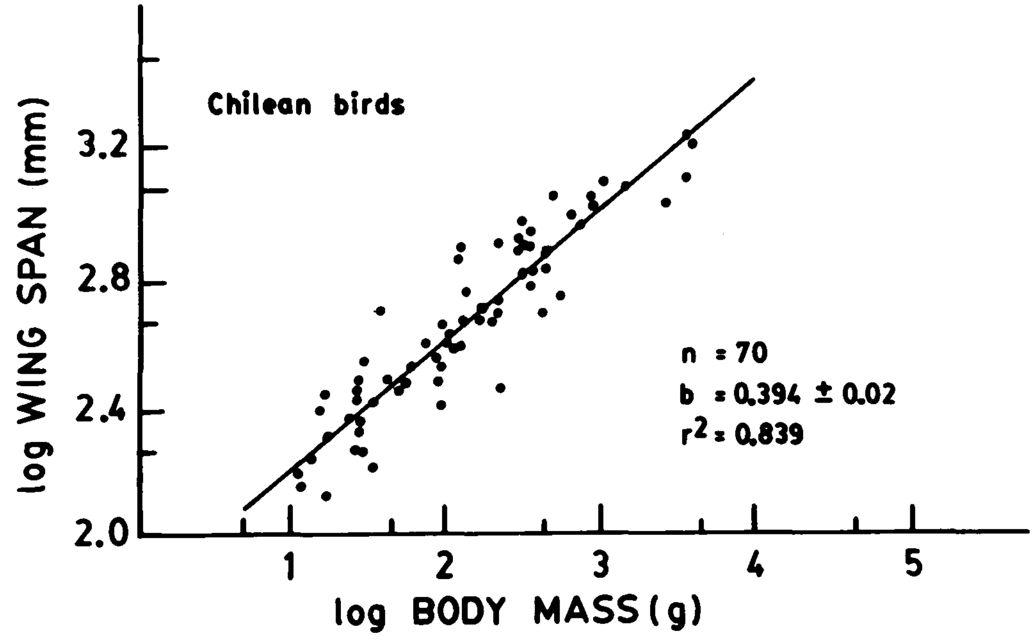

Fig.1: Double logarithmic plot of wing span (mm) as a function of body mass (g) in 70 Chilean birds. Mean values for the exponent *b* are given ± SE (standard error), and also the determination coefficient (r^2).

Representación doblemente logarítmica de la envergadura alar (mm) en función de la masa del cuerpo (g) de 70 aves chilenas. Se especifican, además de los valores promedios del exponente *b*, el error estándar (± SE), así como el coeficiente de determinación (r^2).

TABLE 2

Parameters of the allometric equations for wing dimensions and wing loading of 127 birds (Müllenhoff's 1885 data) as functions of body mass (g).

Parámetros de las ecuaciones alométricas para las dimensiones de las alas y de la intensidad de carga alar de 127 aves (datos de Müllenhoff 1885)- en función de la masa corporal (g).

Item	Function	log (a) (and 95% confidence limits)	Exponent (b) (and 95% confidence limits)	Determination coefficient (r^2)
1	Wing span (cm)	0.96 (0.87, 1.05)	0.35 (0.32, 0.39)	0.79
2	Wing area (cm^2)	1.23 (1.08, 1.37)	0.69 (0.63, 074)	0.84
3	Wing loading (g/cm^2)	−1.23 (−1.37, −1.08)	0.31 (0.25, 0.36)	0.51

TABLE 3

Principal components analysis of wing morphometry for 127 birds (Müllenhoff's 1885 data)

Análisis de los componentes principales de la morfometría de las alas en 127 aves (datos de Müllenhoff 1885)

	Body Mass	Wing Span	Wing Area
Mean vector	2,643	1,890	3,056
Covariance matrix	0,362	0,126	0,250
		0,056	0,103
			0,206
Characteristic roots	**Characteristic vectors**		
0,595	0,769	0,287	0,570
0,025	−0,638	0,387	0,665
0,003	0,029	0,875	−0,481

TABLE 4

Parameters of the allometric equations for wing span (cm) in three models of birds, in *Microchiroptera* and in hummingbirds, as functions of body weight (g).

Parámetros de las ecuaciones alométricas para la envergadura alar (cm) en tres modelos de aves, en microquirópteros y colibríes, en función del peso corporal (g).

Item	Function: Wing span	Sample size	log (a) (and 95% confidence limits)	Exponent (b) (and 95% confidence limits)	Determination coefficient (r^2)	Reference
1	Passeriform model	128	0.81 (0.76, 0.85)	0.42 (0.40, 0.44)	0.93	Müllenhoff (1885)
2	Shorebird model	50	0.81 (0.68, 0.95)	0.42 (0.37, 0.48)	0.84	Meunier (1959) & Oyarzo (pers. comm. 1984).
3	Duck model	24	0.76 (0.60, 0.93)	0.39 (0.33, 0.44)	0.93	
4	Microchiroptera	76	0.04 (−0.008, 0.093)	0.30 (0.27, 0.33)	0.88	Norberg (1981)
5	Hummingbirds	134	0.38 (0.36, 0.40)	0.53 (0.50, 0.56)	0.89	Calc. from Greenewalt (1975).

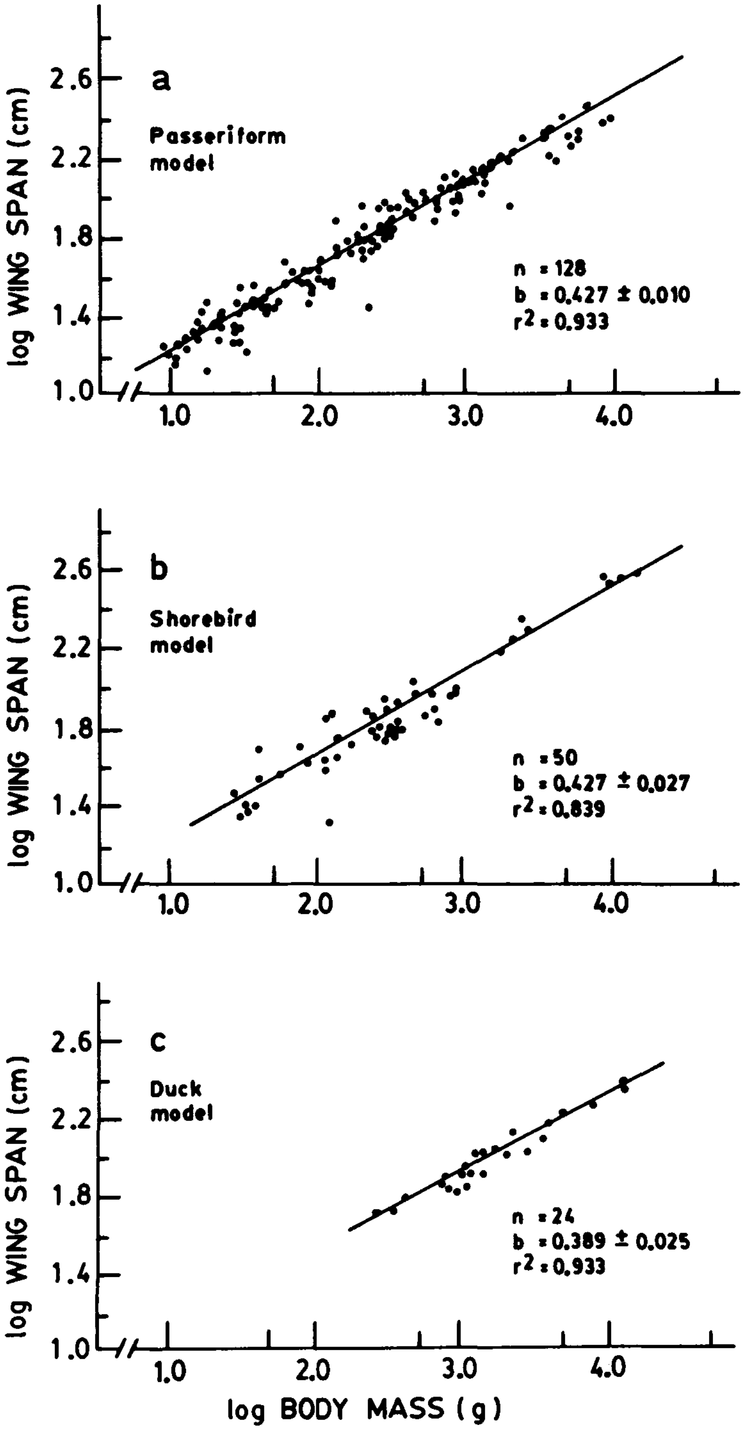

Fig. 2: Logarithm of wing span (cm) versus the logarithm of body mass (g) in three aerodynamic models of birds: a) passerines; b) shorebirds; and c) ducks; based on the numerical data from Müllenhoff (1885), Meunier (1959), and Oyarzo (pers. comm. 1984).

El logaritmo de la envergadura de las alas (cm) versus el logaritmo de la masa corporal (g) en tres modelos aerodinámicos de aves: a) paseriformes; b) aves de ribera; y c) patos; de acuerdo a los datos numéricos de Müllenhoff (1885), Meunier (1959) y Oyarzo (com. pers. 1984).

DISCUSSION

When the numerical data on the wing characteristics of flying animals are analyzed statistically, it is relatively easy to decide whether or not they obey the rules of a "geometric" similarity (isometry). If they do, wing spans should vary in accordance with the cubic root of body mass ($M^{1/3}$); the corresponding wing areas should be proportional to $M^{2/3}$; and wing loading ($M/M^{2/3}$) must vary in accordance to $M^{1/3}$. For this purpose Huxley's (1932) power equation is commonly utilized, since the equation can be obtained directly (least squares method) from the log-log plots of the variables studied. Body mass (M) is generally used as the most convenient reference system, since it represents the sum of the masses of all cells plus that of the extracellular space and of the supporting tissues, which together conform the whole organism. Furthermore, body mass (M) can easily be determined with the required precision as body weight ($W = M \cdot g$) due to the fact that the acceleration of gravity g is practically constant on earth. Nevertheless, many unknown factors may alter the apparently precise determination of body mass. Very often the nutritional and the health status of the captured bird is ignored. In addition, frequently it is not known whether the bird was captured before or after a long flight, a circumstance which is particularly important when the body mass is small, *e.g.*, hummingbirds (Pearson 1955). In summary, many unknown factors may affect body mass measurements.

In our previous paper on wing spans (Günther & Guerra 1957) we obtained an allometric exponent $b = 0.393$, which apparently differed from the expected value for a geometric similarity ($b = 1/3$). Nevertheless, it should be recalled that this result was based on only six measurements, which included both insects and birds. In the present study on 70 Chilean birds measured by Oyarzo (pers. comm. 1984), the calculated exponent was $b = 0.394$, which is in agreement with an allometric criterion (Fig. 1) and whose 95% confidence limits for exponent b were 0.353 and 0.436. When we subjected Müllenhoff's (1985) classical study to a statistical analysis, we obtained $b = 0.35$ for wing spans, and $b = 0.69$ for wing areas, two figures which are in agreement with the hypothesis of isometry. Nevertheless, when Müllenhoff's data (1885) were submitted to a multivariate statistical analysis (Jolicoeur 1963, 1984) and to Anderson's (1963) test, in which three variables were taken into account (body mass, wing span, and wing area), the morphometry of bird wings did not correspond to a geometric similarity. In order to elucidate these conflicting conclusions, we subdivided all available bird wing span data (Müllenhoff 1885, Meunier 1959, Oyarzo pers. comm. 1984) into the three models (passerines, shorebirds, and ducks) proposed by Greenewalt (1975). As shown in Fig. 2, in all three instances the exponent (b) of body mass (M) was allometric ($b \neq 1/3$), with the exception of the duck model, which yielded borderline values for the lower 95% confidence limit. A similar conclusion was reached by Rayner (1979), who obtained exponents (b) of 0.42 for passerines, 0.40 for shorebirds, and 0.41 for duck wings. For the sake of comparison Norberg's (1981) data on *Microchiroptera* are provided in Table 3 (item 4); her data agree with a geometric similarity in the upper 95% confidence limit. Finally, from Greenewalt's (1975) data we calculated an allometric exponent of $b = 0.53$ for the wing length of hummingbirds.

In conclusion, a spectrum of exponents have been obtained for wing lengths[2] or for wing spans as functions of body mass, *i.e.*, from 0.30 for bats to 0.53 for hummingbirds. The exponent b for the three bird models (passerines, shorebirds, ducks) was allometric ($b \sim 0.40$).

The primary assumption of the present study was that the wings of birds should follow the rules of a geometric similarity. This assumption was certainly a great simplification, because body mass determinations and wing morphometry are generally performed *post-mortem* and it is likely that the *in vivo* aerodynamic wing characteristics may eventually be quite different, due to the fact that wing spans and wing areas can change markedly during each wing stroke. Furthermore, several flight styles have been described, *e.g.*: a) flapping forward flight; b) gliding

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[2] Wing length corresponds to the distance from the tip of the longest primary to the first articulated joint (Greenewalt 1975).

flight at fixed angle and zero stroke frequency; c) bounding flight (Rayner 1979); d) soaring flight of the albatross; and e) hovering flight of insects and hummingbirds. To these different flight modes one should add the so-called "clap and fling" movement of chalcid wasps (Weis-Fogh 1973, 1975), and more recently (Somps & Luttges 1985) a whole new class of fluid dynamics has been studied in dragonflies, which disclosed novel and unexpected mechanisms for the production of aerodynamic lift.

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