PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Allometry of Bat Wings and Legs and Comparison with Bird Wings

Ulla M. Norberg

Phil. Trans. R. Soc. Lond. B 1981 **292**, 359-398
doi: 10.1098/rstb.1981.0034

ALLOMETRY OF BAT WINGS AND LEGS AND COMPARISON WITH BIRD WINGS

By ULLA M. NORBERG
Department of Zoology, University of Göteborg, Box 250 59, *S*-400 31 *Göteborg, Sweden*

(*Communicated by Sir James Lighthill, F.R.S. – Received* 31 *July* 1980)

CONTENTS

Allometric equations on wing dimensions versus body mass are given for eight species of megabats and 76 species of microbats, on forearm length versus mass for 14 species of megabats and 90 species of microbats, and on lower leg length versus mass for 11 species of megabats and 45 species of microbats.

Megabats have, on average, shorter wing span, small wing area, higher wing loading and lower aspect ratio than have frugivorous microbats and the insectivorous vespertilionids of similar mass. Vespertilionids have the longest span, largest wing area and lowest wing loading in relation to body mass of the bat groups for which regression lines were calculated (megabats, frugivorous microbats, vespertilionids, molossids), characteristics that are important for slow flight and manoeuvrability for insect capture. Molossids have the highest wing loading of the groups. There is a weak tendency towards higher aspect ratio for larger bats than for smaller ones (positive slope).

The slopes for most characters fit geometric similarity or have confidence intervals including the value for geometric similarity. Only in three cases does the slope lie nearer that for elastic similarity: for the forearm in nycterids and emballonurids and the lower leg length in molossids. Also in these cases the confidence intervals are wide and include the value for elastic similarity and that for geometric similarity as well. In megabats the slope for the lower leg length is much steeper than for geometric similarity. The slope for the forearm length is rather similar to that for wing span in the various groups.

Megabats and frugivorous microbats have rather similar slopes for all the characters measured, but differ from the other groups only in wing area, wing loading and aspect ratio. The two frugivorous bat groups also have about the same elevation of the regression lines for aspect ratio and forearm length. Megabats and frugivorous microbats thus show a close convergence in wing area, wing loading, aspect ratio and forearm length.

The regression equations provide 'norms' for the respective bat groups. Those species that deviate 10% or more from the mean trends for wing measurements are divided into different groups, based on the wing's aspect ratio and loading.

Bats with *low aspect ratio* wings usually have large pinnae, which improve the ability to discover small objects such as insects on leaves. Families or species of bats with wings of low aspect ratio are, for instance, Megadermatidae, Nycteridae, *Rhinolophus ferrumequinum* (Rhinolophidae), *Chrotopterus auritus* (Phyllostomidae) and *Plecotus* (Vespertilionidae).

The group with *average aspect ratio* wings contains bats with different kinds of flight style and foraging behaviour, for instance many pteropodids, phyllostomids and vespertilionids.

Bats with *high aspect ratio* wings are, for instance, Molossidae, *Rhynchonycteris naso* (Emballonuridae) and *Nyctalus leisleri* (Vespertilionidae).

The regression lines for wing span, area and loading in megabats lie almost in the region of the lines for Greenewalt's (1975) passeriform group, whereas the span and area for vespertilionid bats are larger and the wing loading much smaller than for most birds of similar mass. Molossid bats have a larger relative wing span and aspect ratio than have most birds, and a wing area and loading similar to those of small birds of the passeriform group. Vespertilionid bats have about the same aspect ratio as birds of the passeriform group, whereas megabats have somewhat lower ratios.

Molossid bats show strong convergence with swifts and swallows in foraging behaviour and in wing form. Similar convergences can be found between various vespertilionid bats, flycatchers and swallows.

1. Introduction

Comparisons of the morphology of the locomotor apparatuses of animals of different size have shown that geometric similarity does not always prevail, i.e. differently sized animals do not always have the same body proportions.

The purpose of this investigation is to find how the flight membrane, forearm and lower leg of bats change with mass of the animal, i.e. whether the various structures scale with total mass according to the rule of geometric similarity or that of elastic similarity (a model introduced by McMahon (1973), or otherwise. The found regression equations will be used also for finding out if these relations are different between bats of different sub-orders (Mega- and Microchiroptera) and among bats with different food habits (which requires different types of flight). I base my analysis on own data of living as well as dead bats and on data available in the literature.

Greenewalt (1962, 1975) compiled data from different sources on various morphological characters of flying animals, including 16 species of bats. Lawlor (1973) gave allometric equations of wing dimensions for 25 species of neotropical bats. My investigation differs from Greenewalt's and Lawlor's works by treating different categories of bats separately.

Findley *et al.* (1972) estimated various wing characters from study skins of 136 species of bats. They plotted masses of many specimens of living bats against head and body lengths and established a curve from which they estimated masses of the skinned specimens, based on their lengths.

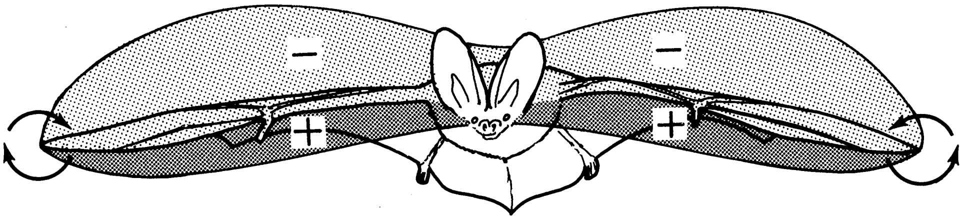


FIGURE 1. Schematic diagram of a flying bat with wings in the middle of the downstroke, showing pressure distribution around the wings and therefrom resulting trailing vortices behind the wing tips (arrows). The pressure distribution in different phases of the stroke depends on local areas and velocities. (The indicated departure from the elliptical lift distribution, characteristic of a fixed-wing state, is due to spanwise differences in relative air velocity because of wing flapping.) The body prevents circulation and, hence, pressure equalization at the wing bases and so helps in maintaining a pressure difference along the entire span. Therefore I include the part of the body between the wings in measurements of (functional) wing areas (cf. figure 2).

The dimensions of the femur relative to body mass were analysed in 45 species of bats by Howell & Pylka (1977). They found that insectivorous and frugivorous bats fit geometric similarity, whereas vampires (with agile quadrupedal locomotion) are an exception and fit elastic similarity.

2. MATERIALS, METHODS AND DEFINITIONS

I collected data on mass, wing area, wing span, and lengths of forearm and lower leg from the literature, and made my own measurements of living as well as dead bats, as indicated in tables 1 and 2. The analyses comprise 130 species altogether (84 for wing measurements, 104 for forearm length and 56 for lower leg length).

Wing area, *S*. During flight the negative pressure above the wings is maintained also over the body (figure 1; see, for example, Pennycuick 1972). The wing area thus should be defined as if the wings were continuous through the body (figure 2*a*). With bats there is, nevertheless, some uncertainty as to what to include of the tail membrane (uropatagium) between the legs. Various conventions of measuring wing area appear in figure 2*b–e*. In contrast to birds, the bats move their legs up and down during the wing-beat cycle, thus moving the entire tail membrane with them (Norberg 1976*b*). The tail membrane thereby gives some useful aerodynamic forces during the wing strokes. Therefore, I suggest that the wing area in bats be defined as the area of the two wings, the entire tail membrane and the body part in between (head excluded; figure 2*b*). This area is used in this investigation, and was also used by Lawlor (1973).

Vaughan (1959, 1966) also included the body part and tail membrane in between the two wings, but excluded the tip of the tail membrane (figure 2*c*). Mouillard (in Müllenhoff 1885), Müllenhoff (1885), Gaisler (1959), and Farney & Fleharty (1969) took the projection of the entire bat, including the outline of the head (figure 2*d*). Furthermore, others gave the area of the wings only (figure 2*e*; see, for example, Harting (in Müllenhoff 1885) and Betz 1958), whereas Puranik *et al.* (1976) took the combined area of the wings and the uropatagium (but nothing of the body). I recalculated the data on wing area from these various sources to be comparable with Lawlor's and my data, as follows.

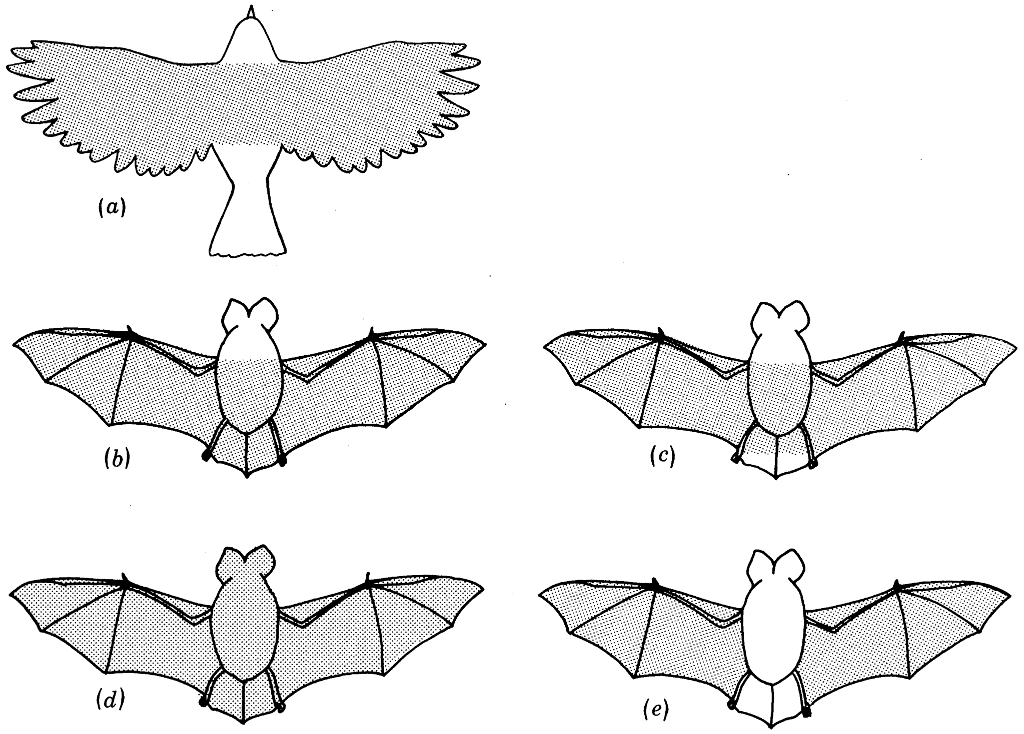


FIGURE 2. Convention used in defining wing area (shaded) in birds (see, for example: Pennycuick 1968; Norberg 1979) and different ways of defining wing area in bats. (*a*) Wing area in birds. (*b*) Wing area in bats used in this investigation and by Lawlor (1973). (*c*) Wing area in bats corresponding to that in birds. This area was used by Vaughan (1959, 1966). (*d*) Wing area in bats used by Mouillard (Müllenhoff 1885), Müllenhoff (1885), Gaisler (1959) and Farney & Fleharty (1969). (*e*) Wing area in bats used by Harting (Müllenhoff 1885) and Betz (1958).

The outer part of the tail membrane (uropatagium) was not included in Vaughan's measurements and he presented no drawings of it. Therefore I estimated its area (as a percentage of the rest of the wing area) from drawings of outlines of wings and tail membranes of the same species in Farney & Fleharty (1969; figure 1) and added it to Vaughan's data. All molossids included in Vaughan's data were not represented in Farney & Fleharty, but I assume that they all have the same proportions. The addition varied between 1.5% (for molossids, the same value used for all) and 6% (for *Myotis yumanensis*).

On drawings of bats in Farney & Fleharty (1969) and on own drawings of different bat species I estimated the head to make up on average 3% of the total silhouette, and this amount was subtracted from the values of Farney & Fleharty (1969), Gaisler (1959), Mouillard (in Müllenhoff 1885) and Müllenhoff (1885). On a drawing of a pteropodid bat (*Cynopterus marginatus*) in Puranik *et al.* (1976) I estimated its body area to be 11.5% of the area of its wings and uropatagium, and this was added to their value of wing area.

The possible errors in the estimated changes of wing area cannot change the recalculated wing area to any greater extent; so this procedure should be satisfactory. Some authors gave the area of the total membrane (body excluded) or of the wings only, but I did not use these data, because of the larger errors a recalculation of these areas would give. An exception is the data from Puranik *et al.* (1976; see above), who gave a drawing with the body area/wing area proportions.

Body mass, M, is the total mass of the bat.

Wing span, b, is the distance between the wing tips of a bat with extended wings.

Wing loading, W/S, is the weight divided by the wing area.

Aspect ratio is the wing span squared, divided by the wing area, b^2/S.

The *forearm* and *lower leg lengths*, l_{fa} and l_{ll} respectively, are conventionally measured as the distance between the two ends when the extremities are flexed. In some cases (indicated in table 2) the length of the tibia, instead of the lower leg, is given and used here. This is somewhat shorter than the lower leg (which includes soft parts and also small parts of femur and tarsus at the joints), but does not affect the result to any larger extent.

The relations between various dimensions and body mass are expressed by the power function

$$y = \alpha M^{\beta},$$

where y is the variable in question, M is body mass, and α and β are constants fitted to the data with the least square method on a HP 67 calculator. When plotted in a double-logarithmic diagram the curve is a straight line with slope β (figures 1–6).

Before calculating the exponents of the allometric equations, I separated the bats into different groups based on systematics and food habits. These groups are defined in tables 1–6.

Differences in y-intercepts (α) and regression coefficients (β) among the various bat groups were tested with the t-test. Student's t-tests were also used to see whether the calculated regression coefficients differ from those for geometric or elastic similarity. In each comparison the variances are assumed to be equal. A weighted variance was then used for all groups and tests.

The sample sizes, n, in the tables give the numbers of species measured. When there are data from more than one author for one species I used the mean value.

3. Results and discussion

3.1. *Differences in regression equations among various bat groups*

Data on wing characteristics of eight species of megachiropteran bats and 76 species of microchiropteran bats are given in table 1. Data on forearm length of 14 megabats and 90 microbats and on lower leg length of 11 megabats and 45 microbats are given in table 2. The relations between various dimensions and body mass are expressed as power functions, which

TABLE 1. WING DIMENSIONS AND CHARACTERISTICS OF 87 SPECIES OF BATS

(The food habits are indicated in dominance order in the second column, where fr. means frugivore, n. nectarivore, i. insectivore, p. piscivore, c. carnivore and s. sanguivore. When separating bats according to food habits for fitting of allometric equations, I include the species in the food category mentioned first. The data on mass and dimensions originate from different sources, identified in the rightmost column as follows:

1 Puranik *et al.* (1976);
2 own data;
3 Kingden (1974);
4 Harting (from Müllenhoff 1885);
5 Mouillard (from Müllenhoff 1885);
6 Betz (1958);
7 Lawlor (1973);
8 Gaisler (1959);
9 Vaughan (^{a}1959, ^{b}1966);
10 Farney & Fleharty (1969);
11 Peterson & Smith (1973);
12 Stebbins (^{a}1968*a*, ^{b}*b*);
13 Müllenhoff (1885).

When two reference numbers are indicated, the first refers to body mass. The different quantities are calculated as described in the methods section. The number of specimens measured are given in parentheses.)

species	food habit	mass, M kg	wing span, b m	wing area, S m²	wing loading, W/S N m^{-2}	aspect ratio, b^2/S	ref. no.
Pteropodidae							
Cynopterus marginatus	fr.	(10) 0.0489	(12) 0.468	(12) 0.0343	14.00	6.38	1
Eidolon helvum	fr.	(32) 0.274	(32) 0.777	(32) 0.0879	30.73	6.87	2
Epomophorus anurus	fr.	0.0730	(2) 0.428	(2) 0.0307	23.65	5.97	3, 2
Macroglossus minimus	fr., n.	0.0214	0.245	0.0102	20.58	5.88	4
Pteropus edulis	fr.	1.38	1.20	0.178	76.18	8.10	4
P. geoffroyi	fr.	0.053	0.484	0.0297	17.51	7.89	5
P. giganteus	fr.	(1) 0.347	(1) 0.939	(1) 0.168	20.25	5.25	6
Rousettus aegyptiacus	fr.	(4) 0.145	(8) 0.577	(8) 0.0555	25.63	6.00	2
Emballonuridae	i.						
Rhynchonycteris naso		(3) 0.0039	(3) 0.239	(3) 0.0088	4.35	6.54	7
Saccopteryx bilineata		(6) 0.0075	(6) 0.275	(6) 0.0125	5.89	6.05	7
Taphozous saccolaimus		0.0187	0.295	—	—	—	4
Noctilionidae							
Noctilio labialis	i.	(7) 0.0296	(7) 0.403	(7) 0.0209	13.89	7.77	7
N. leporinus	p., i.	(1) 0.0590	(1) 0.584	(1) 0.0380	15.23	8.82	7
Nycteridae	i.						
Nycteris hispida		(1) 0.0080	(3) 0.266	(3) 0.0146	5.38	4.89	2
Megadermatidae	i.						
Lavia frons		0.0320	(1) 0.320	(1) 0.0208	15.09	4.92	3, 2
Rhinolophidae	i.						
Rhinolophus euryale		(4) 0.0109	(4) 0.285	(4) 0.0132	8.10	6.15	8
R. ferrumequinum		(4) 0.0226	(4) 0.332	(4) 0.0182	12.18	6.06	8
Rhinolophus sp. (Uganda)		(4) 0.0122	(4) 0.308	(4) 0.0135	9.04	7.02	2
R. hipposideros		(10) 0.0068	(10) 0.231	(10) 0.0094	7.10	5.68	8
Phyllostomidae							
Artibeus jamaicensis	fr., i.	(6) 0.0470	(6) 0.420	(6) 0.0277	16.65	6.36	7
A. lituratus	fr., i.	(3) 0.0596	(3) 0.448	(3) 0.0330	17.72	6.09	7
A. phaotis	fr.	(10) 0.0104	(11) 0.258	(11) 0.0106	9.62	6.28	7
Carollia perspicillata	fr., i.	(9) 0.0191	(9) 0.316	(9) 0.0165	11.36	6.05	7
Chiroderma villosum	fr.	(4) 0.0229	(4) 0.320	(4) 0.0161	13.95	6.36	7
Choeroniscus godmani	fr. n.	(1) 0.0084	(1) 0.238	(1) 0.0088	9.36	6.38	7
Chrotopterus auritus	fr., c.	(1) 0.0809	(1) 0.539	(1) 0.0532	14.92	5.46	7
Glossophaga soricina	fr., n., i.	0.0146	0.240	—	—	—	4
		(6) 0.0106	(6) 0.252	(6) 0.0099	10.15	6.40	7
Lichonycteris obscura	fr., n.	(2) 0.0065	(2) 0.224	(2) 0.0076	8.39	6.60	7
Macrotus californicus	i., fr.	(12) 0.0141	(6) 0.295	—	—	—	9^{a}
Mormops sp.	i.	0.0208	0.287	—	—	—	4
Phyllostomus discolor	fr., i.	(4) 0.0422	(4) 0.416	(4) 0.0262	15.80	7.13	7
P. hastatus	fr., i., c.	(2) 0.110	(2) 0.586	(2) 0.0441	24.47	7.79	7
Sturnira lilium	fr.	(6) 0.0150	(6) 0.281	(6) 0.0121	12.16	6.52	7
Uroderma bilobatum	fr., i.	(3) 0.0154	(3) 0.307	(3) 0.0150	10.07	6.31	7
Vampyrodes carracioloi	fr.	(2) 0.0388	(2) 0.411	(2) 0.0260	14.64	6.50	7
Vampyrops helleri	fr.	(4) 0.0133	(4) 0.270	(4) 0.0114	11.45	6.40	7
Desmodontidae	s.						
Desmodus rotundus		(9) 0.0285	(9) 0.366	(9) 0.0200	13.98	6.70	7
Thyropteridae	i.						
Thyroptera tricolor		(4) 0.0035	(4) 0.224	(4) 0.0083	4.14	6.04	7

species	food habit	mass, M / kg	wing span, b / m	wing area, S / m^2	wing loading, W/S / $N\ m^{-2}$	aspect ratio, b^2/S	ref. no.
Vespertilionidae	i.						
Barbastella barbastellus		(10) 0.0103	(10) 0.258	(10) 0.0111	9.10	6.00	8
Eptesicus fuscus		(3) 0.0166†	(56) 0.325	(56) 0.0166	9.81	6.36	10
E. nilssoni		(1) 0.0092	(1) 0.272	(1) 0.0112	8.06	6.61	8
E. serotinus		(6) 0.0223	(6) 0.341	(6) 0.0180	12.15	6.46	8
Glauconycteris argentata		(44) 0.0092	(57) 0.313	—	—	—	11
G. gleni		(15) 0.0107	(13) 0.301	—	—	—	11
G. variegata		(14) 0.0112	(8) 0.314	—	—	—	11
Lasionycteris noctivagans		(35) 0.0106†	(35) 0.289	(35) 0.0127	8.19	6.58	10
Lasiurus borealis		(1) 0.0131†	(2) 0.312	(2) 0.0147	8.74	6.62	10
L. cinereus		(32) 0.0270†	(51) 0.400	(51) 0.0208	12.73	7.69	10
Minipterus schreibersi		(10) 0.0142	(10) 0.309	(10) 0.0137	10.17	6.97	8
Myotis bechsteini		(2) 0.0104	(2) 0.255	(2) 0.0112	9.11	5.81	8
		(1) 0.0094	(2) 0.274	—	—	—	12^{a}
M. daubentoni		(10) 0.0070	(10) 0.248	(10) 0.0098	7.01	6.28	8
M. emarginatus		(2) 0.0067	(2) 0.235	(2) 0.0093	7.07	5.94	8
M. evotis		(5) 0.0062	(5) 0.228	(5) 0.0083	7.33	6.26	9^{b}
		(22) 0.0075†	(38) 0.270	(38) 0.0123	5.98	5.93	10
M. grisescens		(113) 0.0102†	(113) 0.281	(113) 0.0124	8.07	6.37	10
M. keenii		(34) 0.0070†	(40) 0.241	(40) 0.0101	6.80	5.75	10
M. leibii		(1) 0.0065†	(1) 0.242	(1) 0.0096	6.64	6.10	10
M. lucifugus		(5) 0.0081	(5) 0.233	(5) 0.0088	9.03	6.17	9^{b}
M. l. lucifugus		(4) 0.0067†	(13) 0.239	(13) 0.0095	6.92	6.01	10
M. l. occultus		(8) 0.0087†	(8) 0.264	(8) 0.0117	7.29	5.96	10
M. myotis		(10) 0.0265	(10) 0.383	(10) 0.0233	11.16	6.30	8
M. mystacinus		(7) 0.0054	(7) 0.213	(7) 0.0075	7.06	6.05	8
M. nattereri		(10) 0.0070	(10) 0.268	(10) 0.0113	6.08	6.36	8
M. nigricans		(1) 0.0042	(1) 0.210	(1) 0.0068	6.06	6.53	7
M. oxygnathus		(6) 0.0210	(6) 0.369	(6) 0.0204	10.10	6.67	8
M. thysanodes		(5) 0.0085†	(68) 0.285	(68) 0.0134	6.22	6.06	10
M. velifer		(20) 0.0086	(6) 0.249	—	—	—	9^{a}
		(7) 0.0091†	(52) 0.296	(52) 0.0142	6.29	6.17	10
M. volans		(16) 0.0104†	(61) 0.267	(61) 0.0123	8.29	5.80	10
M. yumanensis		(5) 0.0052	(5) 0.203	(5) 0.0065	7.85	6.34	9^{b}
Nyctalus leisleri		(1) 0.0169	(1) 0.260	(1) 0.0086	19.28	7.86	8
N. noctula		(8) 0.0265	(8) 0.344	(8) 0.0161	16.15	7.35	8
Pipistrellus hesperus		(1) 0.0044†	(1) 0.190	(1) 0.0063	6.85	5.73	10
P. nathusii		(1) 0.0068	(1) 0.206	(1) 0.0066	10.11	6.43	8
P. pipistrellus		(39) 0.0052	(7) 0.212	(7) 0.0064	7.97	7.02	12^{b}, 2
		0.0056	0.235	—	—	—	4
		(10) 0.0051	(10) 0.202	(10) 0.0062	8.07	6.58	8
		(39) 0.0052	(40) 0.223	—	—	—	12^{b}
		0.0037	0.198	0.0055	6.60	7.09	13
P. subflavus		(40) 0.0059†	(40) 0.237	(40) 0.0090	6.43	6.24	10
Plecotus auritus		(1) 0.0090	(1) 0.270	(1) 0.0123	7.18	5.93	2
		0.0104	0.260	—	—	—	4
		(10) 0.0098	(10) 0.254	(10) 0.0119	8.08	5.42	8
P. townsendi		(5) 0.0091	(5) 0.245	(5) 0.0105	8.50	5.72	9^{b}
		(30) 0.0105†	(37) 0.293	(37) 0.0145	7.10	5.92	10
Rhogeessa tumida		(1) 0.0039	(1) 0.187	(1) 0.0056	6.83	6.26	7
Vespertilio murinus		(10) 0.0115	(10) 0.278	(10) 0.0111	10.16	6.96	8
Molossidae	i.						
Eumops perotis		(5) 0.0535	(5) 0.446	(5) 0.0209	25.11	9.52	9^{b}
Molossus longicaudatus		0.0335	0.352	—	—	—	4
M. molossus		(3) 0.0161	(3) 0.274	(3) 0.0095	16.63	7.88	7
M. sinaloae		(5) 0.0238	(6) 0.328	(6) 0.0133	17.56	8.06	7
Otomops martiensseni		(3) 0.0355	(9) 0.467	(7) 0.0234	14.88	9.32	2
Tadarida brasiliensis		(5) 0.0122	(5) 0.251	(5) 0.0074	16.17	8.51	9^{b}
		(39) 0.0125†	(39) 0.301	(39) 0.0110	11.15	8·24	10
T. molossa		(3) 0.0162	(3) 0.313	(3) 0.0103	15.43	9.51	9^{b}
T. pumila		(3) 0.0080	(4) 0.248	(1) 0.0073	10.75	8.43	2

† Mass calculated from wing loading and area in Farney & Fleharty (1969).

Table 2. Body mass, forearm length (of 104 species) and lower leg length (of 57 species)

(The food habits are indicated in dominance order in the second column as in table 1. When separating bats according to food habits for fitting of allometric equations, I include the species in the food category mentioned first. The data on mass and dimensions originate from different sources, identified in the rightmost column as follows:

1–13 As in table 1;
14 Andersen (1912);
15 Kock (1969);
16 Verschuren (1957);
17 Bergmans (^{a}1979, ^{b}1978);
18 Fleming *et al.* (1972);
19 Findley & Wilson (1974);
20 Findley & Traut (1970);
21 Fenton & Peterson (1972).

When two reference numbers are indicated, the first refers to body mass. The number of specimens measured is shown in parentheses.)

species	food habit	mass, M / kg	forearm length, l_{fa} / mm	lower leg length, l_{ll} / mm	ref. no.
Pteropodidae					
Eidolon helvum	fr.	(32) 0.274	125†	49.5†	2, 14
		(32) 0.274	113	—	2, 15
		0.281†	123†	—	3
Epomophorus anurus	fr.	0.073†	—	(2) 31.2	3, 2
		0.0765†	72.5†	—	3
		(5) 0.0788	(21) 76.4	—	16
E. labiatus	fr.	0.0540†	62.5†	—	3
E. wahlbergi	fr.	0.0870†	85.0†	—	3
		0.0755†	—	(2) 34.3^{t}	3, 17^{a}
E. pousarguesi	fr.	(1) 0.145	(1) 94.8	—	17^{b}
Epomops franqueti	fr.	0.118†	93.0†	—	3
		0.104†	—	(2) 35.4^{t}	3, 17^{a}
Macroglossus minimus	fr., n.	0.0214	42.3†	16.5†	4, 14
Megaloglossus woermanni	fr.	0.0160†	43.3†	—	3
Micropteropus pusillus	fr.	0.0300†	52.5†	—	3
		0.0300†	(31) 51.1	(12) 22.1^{t}	3, 17^{a}
Myonycteris torquata	fr.	0.0300	62.5†	21.3†^{t}	3
Pteropus edulis	fr.	1.38	185†	87.5†	4, 14
P. giganteus	fr.	(1) 0.347	170†	83.5†	6, 14
Rousettus aegyptiacus	fr.	(4) 0.145	(8) 93.9	(8) 43.7	2
Stenonycteris lanosus	fr.	0.145	90.0	40.0^{t}	3
Rhinopomatidae	i.				
Rhinopoma hardwickei		0.0110†	55.5†	—	3
Emballonuridae	i.				
Rhynconycteris naso		(3) 0.0039	(21) 38	—	7, 18
Saccopteryx bilineata		(6) 0.0075	(11) 44	—	7, 18
Taphozous hildegardeae		0.0235†	67.5†	—	3
T. mauritianus		0.0225†	61.5†	—	3
		0.0225†	(11) 63.2	(9) 25.4^{t}	3, 16
T. perforatus		0.0235†	63.5†	—	3
T. nudiventris		0.0600	73.0	—	3
		0.0600	(1) 74.0	(1) 32.0^{t}	3, 16
T. peli		0.0985†	90.5†	—	3
Noctilionidae					
Noctilio labialis	i.	(7) 0.0296	(2) 57	—	7, 18
N. leporinus	p., i.	(1) 0.0590	(13) 82	—	7, 18
Hipposideridae	i.				
Hipposideros camerunensis		0.0370†	74.5†	—	3
H. commersoni		0.130	97.5†	—	3
H. cyclops		0.0345†	65.0†	—	3
		0.0345†	(35) 67.7	(33) 32.0^{t}	3, 16
Triaenops persicus		0.0115†	52.5†	—	3
Nycteridae	i.				
Nycteris aethiopica		0.0125†	48.5†	—	3
		0.0125†	50.2	25.9^{t}	3, 16

species	food habit	mass, M / kg	forearm length, l_{fa} / mm	lower leg length, l_{ll} / mm	ref. no.
N. arge		0.0090†	41.5†	—	3
		0.0090†	(8) 43.4	(9) 22.8^{t}	3, 16
N. grandis		0.0305†	61.5†	—	3
		0.0305†	(1) 60.0	(1) 34.0^{t}	3, 16
N. hispida		0.0080†	40.5†	—	3
		0.0080†	(75) 40.2	(67) 19.6^{t}	3, 16
		(1) 0.0067	(1) 39.6	(1) 19.0^{t}	16
N. macrotis		0.0115†	47.5†	—	3
N. nana		0.0065†	34.0†	—	3
		0.0065†	(28) 34.8	(26) 16.7^{t}	3, 16
N. thebaica		0.0205†	47.0†	—	3
		0.0205†	(1) 43.0	(1) 23.0^{t}	3, 16
Megadermatidae	i.				
Cardioderma cor		0.0280†	56.5†	—	3
Lavia frons		0.0320†	59.7†	—	3
		0.0320†	57.2	31.0	3, 15
		0.0320†	(25) 59.5	(27) 32.9^{t}	3, 16
Rhinolophidae	i.				
Rhinolophus euryale		(4) 0.0109	(4) 48.5	(4) 20.5	8
R. ferrumequinum		(4) 0.0226	(4) 57.0	(4) 25.0	8
Rhinolophus sp. (Uganda)		(4) 0.0124	(4) 42.4	(4) 17.3	2
R. hipposideros		(6) 0.0075	(6) 37.0	—	6
		(10) 0.0068	(10) 39.5	(10) 18.0	8
Phyllostomidae					
Artibeus jamaicensis	fr., i.	(6) 0.0470	(1167) 63	—	7, 18
A. lituratus	fr., i.	(3) 0.0596	(109) 70	—	7, 18
A. phaotis	fr.	(10) 0.0104	(77) 39	—	7, 18
Carollia perspicillata	fr., i.	(9) 0.0191	(726) 43	—	7, 18
Chiroderma villosum	fr.	(4) 0.0229	(12) 46	—	7, 18
		(4) 0.0229	45.8	—	7, 19
Choeroniscus godmani	fr., n.	(1) 0.0084	33.5	—	7, 19
Chrotopterus auritus	fr., c.	(1) 0.0809	(2) 81	—	7, 18
Lichonycteris obscura	fr., n.	(2) 0.0065	32.4	—	7, 19
Phyllostomus hastatus	fr., i., c.	(4) 0.110	(17) 90	—	7, 18
Sturnira lilium	fr.	(6) 0.0150	(116) 40	—	7, 18
Uroderma bilobatum	fr., i.	(3) 0.0154	(366) 43	—	7, 18
Vampyrodes caraccioi	fr.	(2) 0.0388	(9) 55	—	7, 18
Vampyrops helleri	fr.	(4) 0.0133	(8) 39	—	7, 18
Desmodontidae	s.				
Desmodus rotundus		(6) 0.0296	(147) 59	—	7, 18
Thyropteridae	i.				
Thyroptera tricolor		0.0040	36.2	—	19
		(4) 0.0035	(1) 35	—	7, 18
Vespertilionidae	i.				
Barbastella barbastellus		(7) 0.0092	(7) 39.0	—	6
		(10) 0.0103	(10) 38.5	(10) 19.0	8
Eptesicus nilssoni		(1) 0.0092	(1) 43.0	(1) 20.0	8
E. serotinus		(6) 0.0223	(6) 51.5	(6) 22.5	8
E. tenuipinnis		0.0053†	30.5†	—	3
Glauconycteris argentata		(44) 0.0092	(67) 41.7	(61) 18.3	11
G. gleni		0.0118†	42.0†	—	3
		(15) 0.0107	(15) 40.5	(15) 16.2^{t}	11
G. variegata		0.0120†	43.3†	—	3
		(14) 0.0112	(30) 42.2	(28) 19.4^{t}	11
Lasiurus borealis		0.0131	39.6	—	10, 19
Mimetillus moloneyi		0.0088†	28.3†	—	3
Miniopterus inflatus		0.0125†	47.5†	—	3

[*continued overleaf*

TABLE 2—*cont.*

species	food habit	mass, M / kg	forearm length, l_{fa} / mm	lower leg length, l_{ll} / mm	ref. no.
M. screibersi		0.0080†	44.5†	—	3
		(10) 0.0142	(10) 45.5	(10) 20.5	8
Myotis bechsteini		(2) 0.0104	(2) 42.5	(2) 21.5	8
		(1) 0.0094	(2) 41.1	—	12^{a}
M. bocagei		0.0070†	38.0†	—	3
M. daubentoni		(10) 0.0070	(10) 38.0	(10) 17.5	8
M. emarginatus		(2) 0.0067	(2) 37.0	(2) 19.0	8
M. myotis		(31) 0.0213	(31) 48.0	—	6
		(10) 0.0265	(10) 61.5	(10) 26.5	8
M. mystacinus		(7) 0.0054	(7) 34.0	(7) 15.0	8
M. nattereri		(10) 0.0070	(10) 41.5	(10) 17.5	8
M. nigricans		(1) 0.0042	(5) 34	—	9
M. oxygnathus		(6) 0.0210	(6) 59.0	(6) 26.5	8
M. tricolor		0.0095†	49.5†	—	3
M. welwitschii		0.0100	54.0†	—	3
Nyctalus leisleri		(1) 0.0169	(1) 43.5	(1) 17.0	8
N. noctula		(8) 0.0265	(8) 53.5	(8) 20.5	8
Nycticeius schlieffeni		0.0075†	32.0†	—	3
		0.0075†	(2) 31.5	(2) 12.5^{t}	3, 16
Pipistrellus hesperus		0.0044	(221) 32.0	(194) 11.9^{t}	10, 20
P. kuhli		0.0060†	31.0†	—	3
P. nanulus		0.0053†	23.0†	—	3
P. nanus		0.0030†	28.8†	—	3
		0.0030	(57) 30.9	(56) 12.5^{t}	3, 16
P. nathusii		(1) 0.0068	(1) 33.0	(1) 13.5	8
P. pipistrellus		(39) 0.0052	(7) 31.3	(7) 11.6	12^{b}, 2
		(10) 0.0051	(10) 31.0	(10) 11.5	8
		(39) 0.0052	(40) 31.5	—	12^{b}
Plecotus auritus		(1) 0.0090	(5) 39.2	(6) 18.5	2
		(7) 0.0077	40.0	—	6
		(10) 0.0098	(10) 39.5	(10) 18.5	8
Rhogeessa tumida		(1) 0.0039	(3) 30	—	7, 18
		(1) 0.0039	30.4	—	7, 19
Scotophilus nigrita		0.0300†	57.5†	—	3
		0.0300†	(2) 51.2	(2) 22.3^{t}	3, 16
Vespertilio murinus		(10) 0.0115	(10) 44.5	(10) 17.5	8
Molossidae	i.				
Otomops martiensseni		(3) 0.0355	(8) 70.4	(8) 22.1	2
		0.0348†	67.0	—	3
Tadarida aloysiiabaudiae		(11) 0.0261	(14) 51.2	(12) 17.8^{t}	21
T. bivittata		0.0200†	49.0†	—	3
T. brachyptera		0.0110†	30.3†	—	3
T. condylura		0.0350†	47.5†	—	3
		0.0350†	(41) 48.4	(14) 18.5^{t}	3, 16
T. congica		0.0530†	57.0	—	3
T. leonis		0.0255†	39.5†	—	3
T. midas		0.0508†	62.0†	—	3
		0.0508†	(21) 62.6	(21) 22.2^{t}	3, 13
		(1) 0.0460	(1) 63.0	(1) 22.5^{t}	16
T. nanula		0.0110†	30.3†	—	3
T. pumila		(3) 0.0080	39.7	13.2	2
		0.0118†	39.2†	—	3
		0.0118†	(1) 39.5	(1) 15.8^{t}	3, 16
T. thersites		0.0255†	39.5	—	3
T. trevori		0.0460	53.0	—	3
		0.0460	(1) 53.5	(1) 20.0^{t}	3, 16
T. russata		(6) 0.0171	(7) 43.9	(7) 13.9^{t}	21

† Average value as calculated from maximum and minimum values in the original source when this does not contain means.

^{t} Length of tibia.

are listed in tables 3 and 4, together with results from other authors. Each power function is plotted in log–log diagrams in figures 3–8.

3.1.1. *Wing span versus body mass*

For geometrically similar bats, wing span should vary with the one-third power of the mass, $b \propto M^{0.33}$. In megabats (Pteropodidae) the slope is 0.36, and in microbats 0.30 (table 3; figure 3). This means that the span increases slightly more with body mass in megabats and slightly less in microbats than would be predicted from the rule of geometric similarity. However, this comparison is somewhat misleading, since the microbats consist of several families and also contain bats of different food categories, while the fruit-eating megabats are rather homogeneous both taxonomically and ecologically. Clutton-Brock & Harvey (1979) state that it appears to be a common biological phenomenon that size-dependent variables show progressively shallower slopes, when regressed on body size, the lower the taxonomic level that is considered. As a result, smaller species within any family would tend to show positive deviations from a regression line based on a higher taxonomic group, and larger species negative deviations. This holds for several mammals. Also in bats the slopes of regression lines for different families are different from those for higher taxonomic groups. But, for the bats, the slopes for

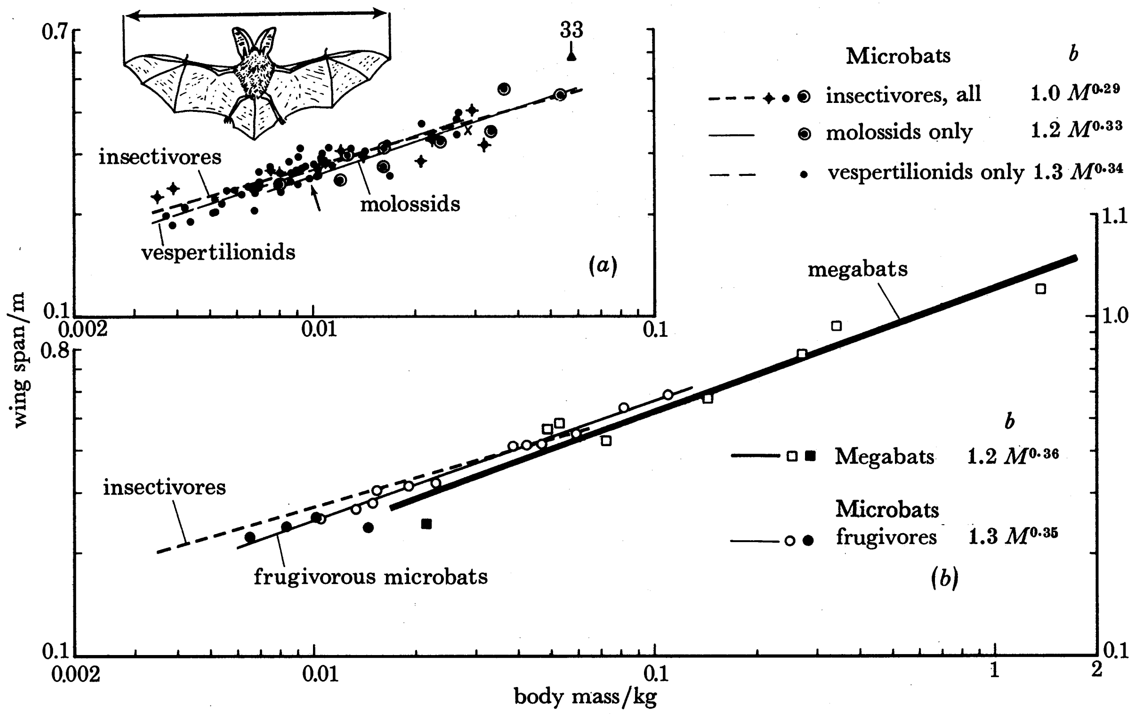


FIGURE 3. Wing span *b* plotted on logarithmic coordinates against body mass for micro- and megachiropteran bats.

(*a*) Insectivorous microbats. The number refers to species listed in table 5. ✦, Insectivores except vespertilionids and molossids; ●, vespertilionids only; ◉, molossids only; ▲, piscivore; ×, sanguivore. The inset bat is *Plecotus auritus* (at the arrow).

(*b*) Megabats and frugivorous microbats. The line for insectivores is marked for comparison. □, Frugivorous megabat; ■, nectarivorous megabat; ○, frugivorous microbat; ●, nectarivorous microbat.

TABLE 3. POWER FUNCTIONS OF BAT WING DIMENSIONS AND OTHER AERODYNAMIC CHARACTERISTICS VERSUS TOTAL MASS M

(The exponents for geometric and elastic similarity and the power functions from other investigators are given for comparison. n, Number of species or †number of observations. ‡ Recalculated from Greenewalt (1975).)

			(a) wing span, $b = \alpha M^{\beta}$				(b) wing area, $S = \alpha M^{\beta}$			
	mass range kg	equation no.	n	α (and 95 % confidence limits)	β (and 95 % confidence limits)	r	n	α (and 95 % confidence limits)	β (and 95 % confidence limits)	r
geometric similarity					0.33				0.67	
elastic similarity					0.25					
Megachiroptera	0.016–1.4	1 (*a*)–(*d*)	8	1.21 (1.07–1.37)	0.362 ± 0.050	0.96	8	0.210 (0.166–0.266)	0.691 ± 0.099	0.95
Microchiroptera										
all		2 (*a*)–(*d*)	76	1.10 (0.98–1.24)	0.304 ± 0.027	0.94	69	0.148 (0.117–0.188)	0.559 ± 0.054	0.92
insectivores, all	0.0035–0.13	3 (*a*)–(*d*)	59	1.03 (0.87–1.22)	0.288 ± 0.037	0.91	52	0.106 (0.075–0.151)	0.486 ± 0.077	0.85
Vespertilionidae only	0.0030–0.027		38	1.28 (0.98–1.34)	0.335 ± 0.057	0.91	35	0.179 (0.106–0.305)	0.597 ± 0.112	0.88
Molossidae only	0.0080–0.054		8	1.18 (0.78–1.79)	0.327 ± 0.107	0.92	7	0.146 (0.060–0.352)	0.624 ± 0.222	0.94
frugivores only	0.0084–0.11	4 (*a*)–(*d*)	15	1.26 (1.02–1.55)	0.351 ± 0.054	0.99	15	0.234 (0.155–0.354)	0.686 ± 0.107	0.99
Microchiroptera (Lawlor 1973)	0.0035–0.11		30†	1.11	0.314	0.96	30†	0.146	0.586	0.96
Mega- + Microchiroptera (Greenewalt 1975)	0.0037–1.4						15	0.150‡	0.656‡	
passeriform model (Greenewalt 1975)	*ca.* 0.006–2.9		139†	1.13–1.65‡	0.417‡		555†	0.163–0.334‡	0.784‡	
shorebird model (Greenewalt 1975)	*ca.* 0.022–1.2		41†	1.16‡	0.403‡		263†	0.129‡	0.714‡	
duck model (Greenewalt 1975)	*ca.* 0.12–5.8		15†	0.90–0.93‡	0.409‡		58†	0.078–0.083‡	0.714‡	
hummingbirds (Greenewalt 1975)	0.0020–0.020		134†	2.31‡	0.455‡		65†	0.417‡	1.00‡	

	mass range / kg	equation no.	(c) wing loading, $W/S = \alpha M^{\beta}$				(d) aspect ratio, $b^2/S = \alpha M^{\beta}$			
			n	α (and 95% confidence limits)	β (and 95% confidence limits)	r	n	α (and 95% confidence limits)	β (and 95% confidence limits)	r
geometric similarity					0.33				0.00	
Megachiroptera	0.016–1.4	1 (*a*)–(*d*)	8	46.8 (37.5–58.3)	0.309 ± 0.092	0.81	8	6.94 (6.04–7.97)	0.033 ± 0.058	0.30
Microchiroptera										
all		2 (*a*)–(*d*)	69	66.5 (53.3–83.0)	0.441 ± 0.050	0.88	69	8.71 (7.58–10.0)	0.065 ± 0.032	0.37
insectivores, all	0.0035–0.13	3 (*a*)–(*d*)	52	92.9 (67.1–129)	0.515 ± 0.071	0.86	52	10.9 (8.88–13.4)	0.112 ± 0.045	0.49
Vespertilionidae only	0.0030–0.027		35	55.1 (33.8–89.9)	0.404 ± 0.104	0.79	35	8.99 (6.61–12.2)	0.075 ± 0.066	0.50
Molossidae only	0.0080–0.054		7	66.9 (29.5–152)	0.373 ± 0.206	0.86	7	11.4 (6.81–19.1)	0.069 ± 0.130	0.54
frugivores only	0.0084–0.11	4 (*a*)–(*d*)	15	42.2 (28.8–61.9)	0.317 ± 0.100	0.95	15	6.69 (5.26–8.52)	0.011 ± 0.063	0.12
Mega- + Microchiroptera (Greenewalt 1975)	0.0037–1.4		15	65.4‡	0.344‡					
passeriform model (Greenewalt 1975)	*ca.* 0.006–2.9		398†	60.2–29.4‡	0.216‡			7.83–8.15‡	0.049‡	
shorebird model (Greenewalt 1975)	*ca.* 0.022–1.2			76.0‡	0.286‡			10.4‡	0.104‡	
duck model (Greenewalt 1975)	*ca.* 0.12–5.8			12.6–18.0‡	0.286‡			10.4‡	0.092‡	
hummingbirds (Greenewalt 1975)	0.0020–0.020			23.5‡	0.000‡			4.92‡	0.090‡	

TABLE 4. POWER FUNCTIONS OF LENGTHS OF BAT FOREARM (l_{fa}) AND LOWER LEG (l_{ll}) VERSUS TOTAL MASS M

(The exponents for geometric and elastic similarity and the power function of the length of femur (l_{fem}) versus total mass from Howell & Pylka (1977) are given for comparison. † Including insectivores, piscivores and frugivores. ‡ Calculated from data on ulna in Prange *et al.* (1979).)

	mass range kg	equation no.	n	forearm length $l_{fa} = \alpha M^{\beta}$ α (and 95% confidence limits)	β (and 95% confidence limits)	r
geometric similarity					0.33	
elastic similarity					0.25	
Megachiroptera	0.016–1.4	5 (*a*)	14	192 (168–219)	0.361 ± 0.051	0.97
Microchiroptera						
all		6 (*a*)	90	166 (147–187)	0.306 ± 0.028	0.88
insectivores, all	0.0030–0.13	7 (*a*)	75	163 (142–188)	0.299 ± 0.032	0.85
Emballonuridae only	0.0039–0.099		7	167 (121–231)	0.264 ± 0.081	0.98
Nycteridae only	0.0065–0.031		7	156 (75.5–322)	0.282 ± 0.164	0.87
Vespertilionidae only	0.0030–0.030		35	180 (131–248)	0.323 ± 0.068	0.82
Molossidae only	0.0080–0.053		13	169 (112–254)	0.349 ± 0.108	0.81
frugivores	0.0084–0.11		13	195 (160–237)	0.367 ± 0.071	0.99
birds (Prange *et al.* 1979)	0.0036–80.9		16	103‡	0.304‡	0.82‡

	mass range kg	equation no.	n	lower leg length $l_{ll} = \alpha M^{\beta}$ α (and 95% confidence limits)	β (and 95% confidence limits)	r	femur length $l_{fem} \propto M^{\beta}$ β
geometric similarity					0.33		0.33
elastic similarity					0.25		0.25
Megachiroptera	0.016–1.4	5 (*b*)	11	92.6 (78.0–110)	0.415 ± 0.069	0.97	
Microchiroptera							
all							
insectivores, all	0.0030–0.13	7 (*b*)	45	61.2 (47.9–78.2)	0.266 ± 0.056	0.72	
Emballonuridae only	0.0039–0.099						
Nycteridae only	0.0065–0.031		6	107 (44.7–256)	0.349 ± 0.197	0.87	
Vespertilionidae only	0.0030–0.030		24	75.3 (49.0–116)	0.315 ± 0.093	0.81	
Molossidae only	0.0080–0.053		7	48.7 (24.9–95.1)	0.274 ± 0.181	0.88	
frugivores	0.0084–0.11						
Microchiroptera (Howell & Pylka 1977):	0.0026–0.10						
'AOB bats'†							0.36
insectivores							0.33
vampires	0.020–0.050						0.18
birds (Prange *et al.* 1979)	0.0036–80.9						0.36

different families for various direct measurements (span, area, forearm length, lower leg length) are instead steeper than for microbats or insectivores taken together (i.e. than for bats of higher taxonomic status). As for regression lines, it is therefore important to compare the megabats with different microbat *families* as far as possible.

The slopes of regression lines differ statistically significantly between megabats and all microbats, treated as a group, as regards wing span ($P < 0.05$), wing area ($P < 0.05$) and wing loading ($P < 0.02$), between megabats and insectivorous microbats as a group as regards wing span ($P < 0.02$), wing area ($P < 0.002$), wing loading ($P < 0.001$), aspect ratio ($P < 0.05$) and lower leg length ($P < 0.002$), and between frugivorous microbats and insectivorous microbats as a group as regards wing area ($P < 0.01$), wing loading ($P < 0.002$) and aspect ratio ($P < 0.05$). But, when different insectivorous *families* are compared with megabats or frugivorous microbats (each of *family* status), the differences usually are not significant.

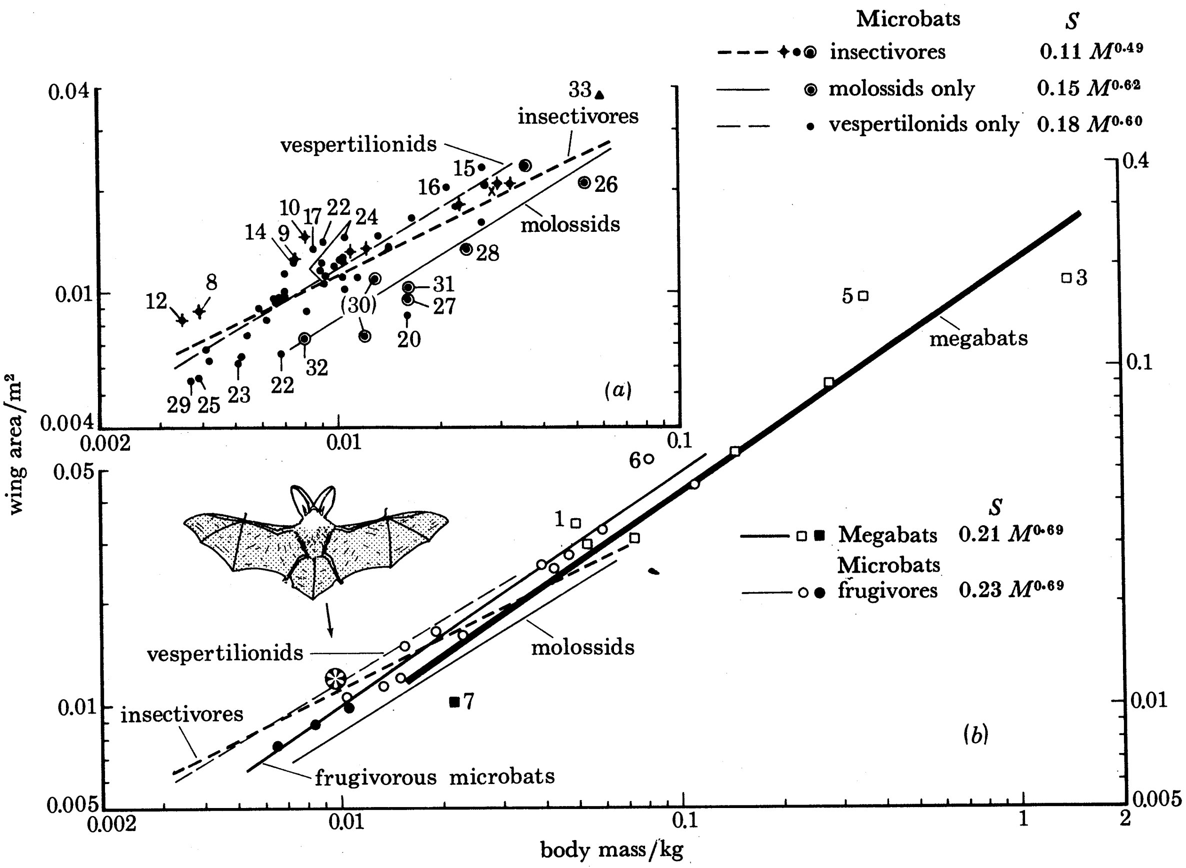


FIGURE 4. Wing area S plotted on logarithmic coordinates against body mass for micro- and megachiropteran bats.

(*a*) Insectivorous microbats.

(*b*) Megabats and frugivorous microbats. Lines for insectivores are marked for comparison. The frugivorous microbats show convergence toward the megabats which also are frugivorous (and/or nectarivorous).

The numbers refer to species listed in table 5. The same symbols are used as in figure 3. The inset bat and star is *Plecotus auritus.*

There are significant differences in y-intercepts between different groups in many characters, especially between megabats and all microbats treated as a group and between megabats and insectivorous microbats as a group, but in some cases the y-intercepts almost coincide (as for megabats and frugivorous microbats; see the 95% confidence limits in tables 3 and 4). There also seem to be different trends among various families, especially among families with very different food habits and/or foraging behaviours. In many cases the lack of significance may be due to the small sample of separate families.

The slope for wing span body mass for frugivorous microbats (Phyllostomidae) is 0.35 and for the group of nine families of insectivorous microbats 0.29. However, when this insectivore group is split into groups of lower taxonomic level, the slope becomes 0.34 for vespertilionids and 0.33 for molossids, i.e. almost the same as the slope for frugivorous microbats and not significantly different from it. Vespertilionids have the highest local elevation of the four groups for which regression lines were calculated, i.e. the longest span in relation to body mass. Megabats have the lowest elevation, while molossids and frugivorous microbats have almost the same, intermediate, local elevation (figure 3). The y-intercepts of the regression lines do not necessarily reflect the elevation of the lines within the intervals of interest.

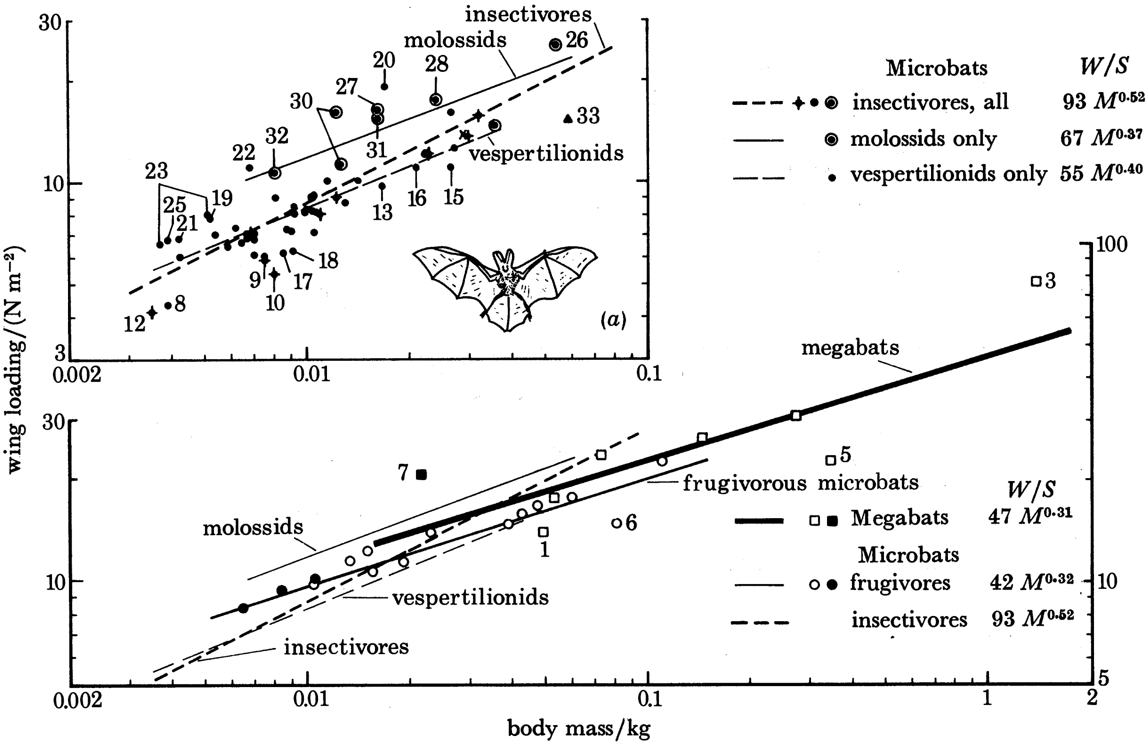


FIGURE 5. Wing loading W/S plotted on logarithmic coordinates against body mass for micro- and megachiropteran bats.

(*a*) Insectivorous microbats. The inset bat is *Nycteris hispida* (no. 10).

(*b*) Megabats and frugivorous microbats. Lines for insectivores are marked for comparison. Convergence as described in legend to figure 4*b*.

The numbers refer to species listed in table 5. The same symbols are used as in figure 3.

3.1.2. *Wing area versus body mass*

If geometric similarity would prevail, the wing area should vary with the two-thirds power of the body mass, $S \propto M^{2/3} = M^{0.67}$. The regression analysis gives slope 0.69 for megabats, 0.69 for frugivorous microbats, 0.60 for vespertilionids and 0.62 for molossids (figure 4). The slope for all microbats together is 0.56, and for all insectivores only 0.49. Thus, the wing area increases faster with increasing body mass for frugivores and slower for insectivores than for geometrically similar bats. Vespertilionids have the highest local elevation of the regression line of the four groups, i.e. the largest wing area among bats of similar mass. Molossids have the lowest elevation, and megabats the second lowest.

3.1.3. *Wing loading versus body mass*

The relation between wing loading and body mass for geometrically similar bats is $W/S \propto M^{0.33}$. The empirically found slope is 0.31 for megabats, 0.32 for frugivorous microbats, 0.40 for vespertilionids, and 0.37 for molossids (figure 5). The slope is 0.44 for all microbats together, and 0.52 for all insectivores taken together.

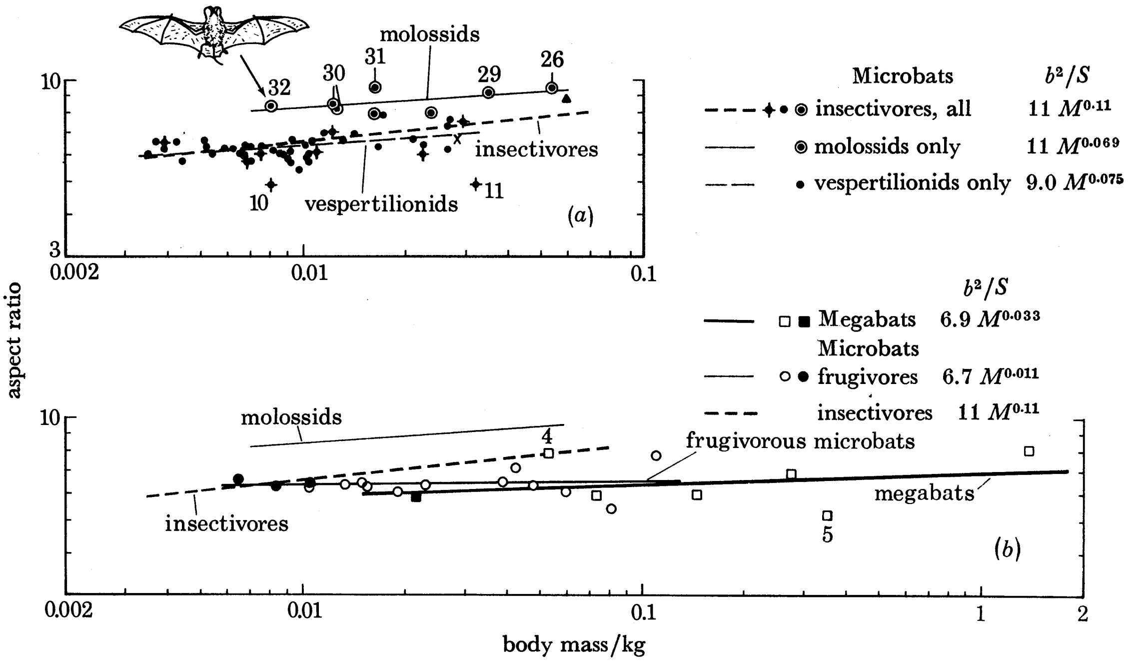


FIGURE 6. Aspect ratio plotted on logarithmic coordinates against body mass for micro- and megachiropteran bats.

(*a*) Insectivorous microbats. The inset bat is *Tadarida pumila* (no. 32).

(*b*) Megabats and frugivorous microbats. Lines for insectivores are marked for comparison. Convergence as described in legend to figure 4*b*.

The numbers refer to species listed in table 5. The same symbols are used as in figure 3.

As a result of their small wing area, molossids have higher wing loading than have frugivorous microbats and other insectivores of similar mass. Megabats also have high wing loading for their size, whereas vespertilionids have the lowest wing loading of the four groups for which regression lines were calculated.

The exponents for wing area and loading in frugivorous microbats are much more similar to those for megabats than to those for insectivorous microbats.

3.1.4. *Aspect ratio versus body mass*

The aspect ratio should be constant for geometrically similar bats and not vary with body mass. However, the analysis gives a slope of 0.033 for megabats, 0.011 for frugivorous microbats, 0.075 for vespertilionids and 0.069 for molossids (figure 6; table 3); a slight increase of aspect ratio with body mass in all groups. This is also found in birds (Greenewalt 1975; table 3). The slopes are 0.065 for all microbats and 0.11 for all insectivores together, which are significantly different from zero ($P < 0.001$). Of the separate families the slope is significantly different from zero only in vespertilionids ($P < 0.05$). Molossids have the highest aspect ratio of the four families.

Again, the slope for frugivorous microbats is more similar to that for megabats than to that for insectivores. But the correlation coefficients for all aspect ratio gradients are low (0.12–0.54).

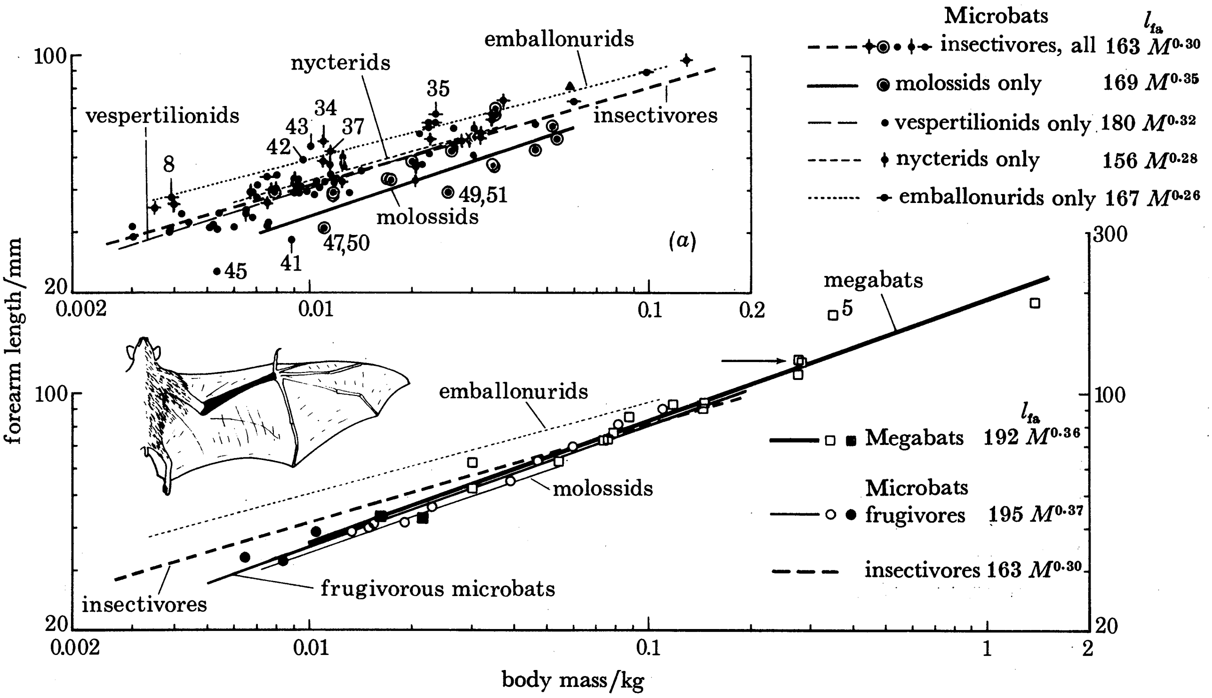


FIGURE 7. Forearm length l_{fa} plotted on logarithmic coordinates against body mass for micro- and megachiropteran bats.

(*a*) Insectivorous microbats. ɸ, Nycterids only; -●-, emballonurids only; -✦-, insectivores except nycterids, emballonurids, molossids and vespertilionids.

(*b*) Megabats and frugivorous microbats. Lines for insectivores are marked for comparison. Very close convergence of the same sort as described in legend to figure 4*b*.

The numbers refer to species listed in table 6. Other symbols as in figure 3. The inset bat is *Eidolon helvum* (at the arrow).

3.1.5. *Forearm length versus body mass*

The length of the forearm in the different categories of bats increases with about the same exponent as for wing span (table 4; figure 7). Thus, the forearm/wing span ratio is almost the same for bats of various sizes within the respective group. The slope is 0.36 for megabats, 0.37 for frugivorous microbats and 0.30 for insectivores. When the insectivores are separated into families, the slope is 0.26 for emballonurids, which is significantly different from that for megabats ($P < 0.05$), and 0.28 for nycterids, both being near elastic similarity (0.25), whereas it is 0.32 for vespertilionids and 0.35 for molossids, which fit geometric similarity (0.33). Molossids, frugivorous microbats and small megabats have the shortest forearm in relation to body mass, and emballonurids have the longest of the groups within their mass range. Large megabats have, however, proportionately longer forearms than have any other group (see figure 7).

3.1.6. *Lower leg length versus body mass*

The slope for the length of the lower leg (or tibia) is as much as 0.42 in megabats and only 0.27 in insectivores (table 4; figure 8). However, there is rather a large variation about the regression line for the insectivores ($r = 0.72$). For instance, the molossids differ in having much shorter tibia, and the nycterids much longer tibia, in relation to body mass than have the other insectivores. The slope is 0.27 for molossids, 0.35 for nycterids and 0.32 for vespertilionids. Data on lower leg length for frugivorous microbats are lacking.

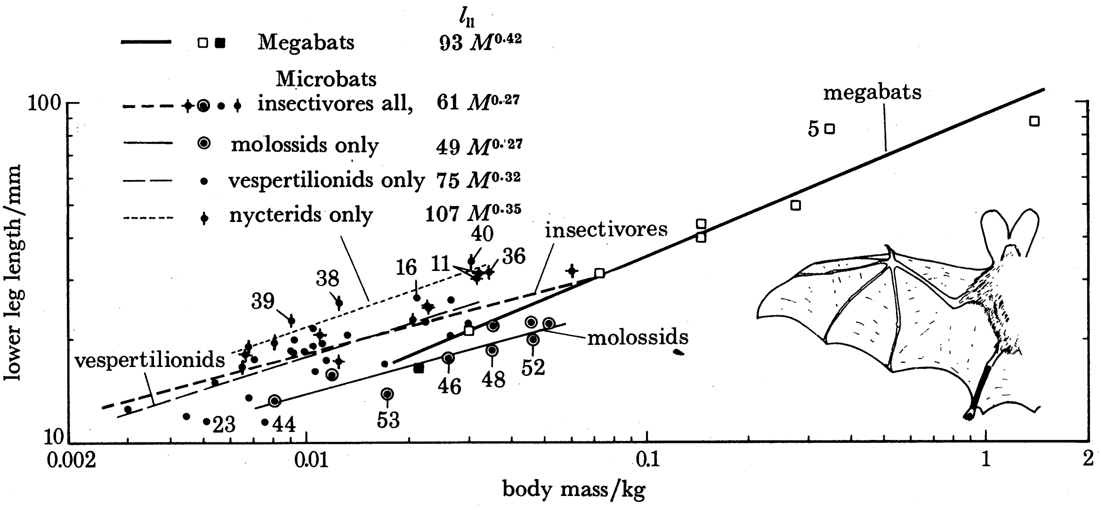


FIGURE 8. Lower leg length l_{II} plotted on logarithmic coordinates against body mass for mega- and microchiropteran bats. I have no data on frugivorous microbats. The numbers refer to species listed in table 6. The same symbols are used as in figures 3 and 7*a* except for ✦, which here is for insectivores except nycterids, molossids and vespertilionids. The inset bat is *Lavia frons* (no. 11).

In summary, megabats have, on average, shorter wing span, smaller wing area, higher wing loading and lower aspect ratio than have frugivorous microbats and the insectivorous vespertilionids of similar mass. Megabats and frugivorous microbats have very similar slopes for all these characters and also for the forearm length. They also differ from the insectivores by having a somewhat steeper slope for wing area and shallower slopes for wing loading and aspect ratio than have the insectivores. The megabats and frugivorous microbats show obvious convergence in the slopes for wing area, wing loading, aspect ratio and forearm length. As for wing span the regression lines for some insectivore families do not differ much from that for the frugivorous microbats. Nevertheless, the frugivorous mega- and microbats show similar trends also in this character. Within their mass range vespertilionids have the longest span, largest wing area and lowest wing loading in relation to body mass of the bat groups for which regression lines were calculated. The correlation between aspect ratio and body mass is very low, but there is a weak tendency towards higher aspect ratios for larger bats. Further, molossids have a higher ratio than have any of the other groups. The slope for the forearm length versus body mass is rather similar to that for wing span in the various bat groups. It lies near that for elastic similarity in emballonurids and near that for geometric similarity in the other groups (except for nycterids). The slope for the lower leg length is much larger than that for geometric similarity in megabats.

3.2. *Geometric or elastic similarity?*

In geometrically similar organisms a characteristic length is proportional to $M^{0.33}$, a characteristic area to $M^{0.67}$, and the diameter of, for example, a bone or muscle to its length. However, McMahon (1973, 1975*a*) formulated a theory of elastic similarity. It states that elastically similar animals are those whose structures are similarly threatened by elastic failure under their own weight. Consequently, the length of a body segment would be proportional to $M^{0.25}$ and its diameter to $M^{0.375}$. Data from trees (McMahon & Kronauer 1976), birds (Maloiy *et al.* 1979) and antelopes (Bovidae) (McMahon 1975*b*; Alexander 1977; Alexander *et al.* 1979) fit the theory, as do data on limb bone diameters from other mammals (Insectivora, Primates, Rodentia, Fissipedia) (Alexander *et al.* 1979). But the limb bone lengths of these latter mammals tend to be proportional to $M^{0.35}$ (Alexander *et al.* 1979), which is consistent with geometric similarity. More than half of the bat dimensions treated here follow geometric similarity, a few elastic similarity, whereas the rest fit neither, or have wide 95% confidence limits, as summarized in tables 3 and 4.

Megabats and the frugivores belonging to Microchiroptera (within family Phyllostomidae) fit geometric similarity in wing span (0.36 and 0.35 respectively), wing area (both 0.69) and wing loading (0.31 and 0.32 respectively; table 3). The 95% confidence limits are, however, wide, probably because of the small samples, especially of megabats ($n = 8$ and 15 respectively).

In vespertilionids the wing span exponent (0·34) fits geometric similarity, whereas the exponents for wing area (0.60) and wing loading (0.40) are lower and higher, respectively. But for area and loading the exponents for geometric similarity (0.67 and 0.33 respectively) are not outside the respective 95% confidence limits for the family. In molossids the mean values for both span and loading are near to those for geometric similarity, but they have extremely wide 95% confidence limits (the molossid sample being small).

As regards aspect ratio, frugivorous microbats are nearer geometric similarity than are the other bat groups, the others having larger exponents (but not significantly different from zero in megabats and molossids).

The exponents for the lengths of skeletal elements of wings and legs would be expected to fit elastic similarity. Among the bats in this investigation this is nearly so only for the forearm in nycterids ($\beta = 0.28$) and emballonurids ($\beta = 0.26$), and for the lower leg (tibia) in the molossids ($\beta = 0.27$; table 4). But in none of these families is the slope significantly different from that for geometric similarity.

The exponent for the forearm length is near to that for geometric similarity in megabats (0.36), vespertilionids (0.32), molossids (0.35) and frugivorous microbats (phyllostomids; 0.37), but in molossids 0.25 is not outside the 95% confidence limits. The exponent for the lower leg length is well above that for geometric similarity in megabats (0.42), whereas it is near that for geometric similarity in nycterids (0.35) and vespertilionids (0.32). Nonetheless, the exponent for elastic similarity, 0.25, is not outside the 95% confidence limits in nycterids and vespertilionids. Data on lower leg length for frugirovous microbats are lacking.

Overall, therefore, there is a tendency for more than half of the data (in 17 out of 26 cases) for wings and legs of various families to fit geometric similarity, whereas the slopes lie near that for elastic similarity only in three cases (the forearm in nycterids and emballonurids, and the lower leg in molossids). The 95% confidence limits are, however, very wide for these three families, probably due to the small samples (7).

Howell & Pylka (1977) found that the femur fits geometric similarity in insectivorous and frugivorous microbats, whereas 'quadrupedal' vampires (often running on all fours) are an exception, their femur being closer to elastic similarity (table 4).

3.3. *Aerodynamic and flight characteristics*

3.3.1. *Introduction*

Before considering specific differences in morphology of the wings and legs of the bats, and associated differences in food niche and locomotor pattern, I will give some general aspects on wing characters and flight style.

A bat with low mass is often more manoeuvrable and agile than larger bats. Low mass and low wing loading is to advantage especially for slow flight and hovering since the lift force L, which must balance the weight, is proportional to the product of the square of the speed with wing area,

$$L \propto W \propto V^2 S,$$

so that $V \propto (W/S)^{\frac{1}{2}}$, where V is some characteristic speed. Low wing loading thus enables a bat to produce enough lift in slow flight and in hovering, without having to use excessively high wing beat frequencies that would result in large moments of inertia and hence an unnecessary waste of energy for production of inertial power (the power needed to accelerate the wings).

A good wing should have a shape that allows it to obtain sufficient lift without much drag. Higher lift to drag ratios (L/D) can be obtained with long narrow wings (high aspect ratio wings) than with short broad ones (low aspect ratio wings).

Narrow wings obviously tend to have small areas and thus high wing loadings (unless they are compensatorily long). A bat with high wing loading must fly fast to obtain sufficient lift, and by flying fast it reduces the induced power (power needed to support the weight), but increases wing profile power and parasite power (power needed to overcome body drag). The longer the wings the less the induced power (for a constant speed), which is especially large in hovering and slow flight. On the other hand, the longer the wings the larger the profile power and the inertial power (power needed to accelerate the wings) and, consequently, the inertial loads on the wing skeletons. Long wings are also some hindrance for bats when flying in dense vegetation, and to manoeuvrability.

In summary, bats flying in dense vegetation should have short but broad wings (to get large wing area), those flying slowly in open areas should have medium wing span but relatively broad wings, and those flying fast in the open should have narrow wings. Bats that often carry heavy food (fruits, prey) should have large wing area to be able to fly with extra load.

Wing span is nearly geometrically similar for bats of various mass, with slight differences among groups. For example, the insectivorous vespertilionids, which have great demands for manoeuvrability for insect capture, have a longer span than have frugivores (mega- as well as microbats) of similar mass. This long span contributes to making the wing area large (figure 4), and thereby the wing loading low (figure 5), and to decrease the induced power, all of which are important for slow flight (although long wings tend to detract from manoeuvrability).

3.3.2. *Species deviating from mean trends*

The regression equations provide 'norms' for the respective bat groups. By comparing a particular species with these norms any morphological specialization can easily be identified with reference to the norm. Tables 5 and 6 show the species that in one measurement or other differ from the mean trend for the various measurements. I will consider species that in some measurement deviate 10% or more from the regression line for the respective group (megabats, frugivorous microbats, insectivorous microbats, or all microbats), and discuss their flight characteristics. When data originate from more than one author for one species, the average value was used to characterize the species. In the figures and tables, however, I have indicated the average value from each author.

All but two (75%) of the species investigated among the family Pteropodidae and 35% of the family Phyllostomidae differ 10% or more from the mean trends for wing dimensions of respective bat group. Among the vespertilionids 62% differ 10% or more from the mean trends for the insectivores, as do all of the molossids.

Among the insectivores the families Emballonuridae (two species), Nycteridae (one species), Thyropteridae (one species) and Vespertilionidae (*Lasiurus*, *Myotis*) have species with large wing area and low wing loading as compared with the mean values given by the regression lines. The family Vespertilionidae also contains genera with relatively small wing span and area and high wing loading, such as *Nyctalus* and *Pipistrellus*. The molossid bats have narrow wings (high aspect ratios), small wing area and thereby high wing loading, except for *Otomops*, which have large wing area and low wing loading because of its long wings.

The only fish-eater included has small aspect ratio, indicating narrow wings.

Those species that have long forearms and/or long lower legs also have large wing area. Likewise, those with short lower legs have a small wing area. This is rather obvious since long legs are coupled with a large tail membrane which is included in the wing area. An exception is the frugivorous bats, mega- as well as microchiropteran, which have a reduced tail membrane but not necessarily short legs.

Those species that deviate 10% or more from the mean trends for wing measurements are divided into different groups, based on the wing aspect ratio and on the wing loading. These species are listed in table 5. Species deviating 10% or more in forearm and lower leg length are listed in table 6.

I denote aspect ratio, wing loading etc. as low, intermediate and high when their values are, respectively, $\geqslant$ 10% lower than the average value, within 10% of the average value and $\geqslant$10% higher than the average value, predicted from the model.

Aspect ratio. (*a*) *Bats with low aspect ratio wings* (figure 9*a*). It is characteristic for bats with low aspect ratio to have slow and highly manoeuvrable flight and to fly among vegetation. Their wing loading is low or intermediate.

(i) Bats with low wing loading. Species with large wing area and thereby low wing loading are *Nycteris hispida* (Nycteridae) (figure 9*a*), *Myotis myotis*, *Plecotus townsendi* (both Vespertilionidae) and *Chrotopterus auritus* (Phyllostomidae). These species have intermediate wing spans. Both *N. hispida* and *C. auritus* have large tail membranes. *N. hispida* is a small bat and has a very manoeuvrable flight, as has *P. townsendi*. So has probably *C. auritus*, which is a large

TABLE 5. SPECIES IN WHICH AT LEAST ONE OF THE FOUR WING MEASUREMENTS LISTED BELOW DEVIATES AT LEAST 10% FROM THE MEAN TREND FOR THE RESPECTIVE GROUP

(Deviations are measured relative to the values predicted from the model (fitted regression equation) for the respective groups 'frugivores' (equations (1) and (4)), 'nectarivores' (equation (1)), 'insectivores' (equation (3)) and 'piscivore' (equation (2)). Deviations (negative or positive) from the regression line are indicated as follows: 0 for $<10\,\%$; − and + for 10–20 %; − − and + + for 20–30 %; − − − and + + + for $\geqslant 30\,\%$. A dot means that data are lacking. The numbers on the left refer to the numbers of graph points in figures 3–6.)

species	wing span	wing area	wing loading	aspect ratio
frugivores (eqs (1) and (4))				
1 *Cynopterus marginatus* (Pteropodidae, eq. (1))	+	+ + +	− −	0
2 *Epomophorus anurus* (Pteropodidae, eq. (1))	−	−	+	0
3 *Pteropus edulis* (Pteropodidae, eq. (1))	−	− − −	+ + +	+
4 *P. geoffroyi* (Pteropodidae, eq. (1))	+	0	0	+ +
5 *P. giganteus* (Pteropodidae, eq. (1))	+	+ + +	− − −	− −
Chiroderma villosum (Phyllostomidae, eq. (4))	0	0	+	0
6 *Chrotopterus auritus* (Phyllostomidae, eq. (4))	0	+ +	− −	−
Phyllostomus discolor (Phyllostomidae, eq. (4))	0	0	0	+
P. hastatus (Phyllostomidae, eq. (4))	0	−	+	+
Uroderma bilobatum (Phyllostomidae, eq. (4))	0	+	−	0
nectararivore (eq. (1))				
7 *Macroglossus minimus* (Pteropodidae)	−	− − −	+ + +	0
insectivores (eq. (3))				
8 *Rhynconycteris naso* (Emballonuridae)	+	+ +	−	+
9 *Saccopteryx bilineata* (Emballonuridae)	0	+ +	− −	0
10 *Nycteris hispida* (Nycteridae)	0	+ + +	− − −	− −
11 *Lavia frons* (Megadermatidae)	−	0	0	− − −
Rhinolophus euryale (Rhinolophidae)	0	+	−	0
R. ferrumequinum (Rhinolophidae)	0	0	0	−
Mormops sp. (Phyllostomidae)	−	.	.	.
12 *Thyroptera tricolor* (Thyropteridae)	+	+ +	−	0
13 *Eptesicus fuscus* (Vespertilionidae)	0	+	− −	0
E. serotinus (Vespertilionidae)	0	0	−	0
Glauconycteris argentata (Vespertilionidae)	+	.	.	.
G. variegata (Vespertilionidae)	+	.	.	.
Lasiurus borealis (Vespertilionidae)	0	+	−	0
L. cinereus (Vespertilionidae)	+	+	−	0
Myotis bechsteini (Vespertilionidae)	0	0	0	−
14 *M. evotis* (Vespertilionidae)	0	+ +	−	0
15 *M. myotis* (Vespertilionidae)	0	+ +	− −	−
M. mystacinus (Vespertilionidae)	0	−	+	0
M. nattereri (Vespertilionidae)	0	+	−	0
16 *M. oxygnathus* (Vespertilionidae)	0	+ +	− −	0
17 *M. thysanodes* (Vespertilionidae)	0	+ +	− −	0
18 *M. velifer* (Vespertilionidae)	+	+ + +	− −	0
M. volans (Vespertilionidae)	0	0	0	−
19 *M. yumanensis* (Vespertilionidae)	−	−	+ +	0
20 *Nyctalus leisleri* (Vespertilionidae)	−	− − −	+ + +	+
N. noctula (Vespertilionidae)	0	−	+	0
21 *Pipistrellus hesperus* (Vespertilionidae)	−	−	+ +	0
22 *P. nathusii* (Vespertilionidae)	−	− −	+ + +	0
23 *P. pipistrellus* (Vespertilionidae)	0	− −	+ + +	0
Plecotus auritus (Vespertilionidae)	0	0	0	−
24 *P. townsendi* (Vespertilionidae)	0	+ +	−	−
25 *Rhogeessa tumida* (Vespertilionidae)	−	− −	+ +	0
26 *Eumops perotis* (Molossidae)	0	−	+ +	+ +
27 *Molossus molossus* (Molossidae)	−	− − −	+ + +	+
28 *M. sinaloae* (Molossidae)	0	− −	+ +	+
29 *Otomops martiensseni* (Molossidae)	+	+	−	+ +
30 *Tadarida brasiliensis* (Molossidae)	0	−	+ +	+ +
31 *T. molossa* (Molossidae)	0	− −	+ + +	+ + +
32 *T. pumila* (Molossidae)	0	− −	+ + +	+ + +
piscivore (eq. (2))				
33 *Noctilio leporinus* (Noctilionidae)	+ +	+ +	− −	+

bat. Lawlor (1973) suggests that this species may feed on other bats, and this would increase the demand for a large wing area.

Pteropus giganteus (Pteropodidae) belongs to this category though having very long wings. Findley *et al.* (1972) wrote that pteropodid bats have short wings. However, the frugivorous megabats in this investigation are rather diverse in wing structure and the family has members in all three aspect ratio groups.

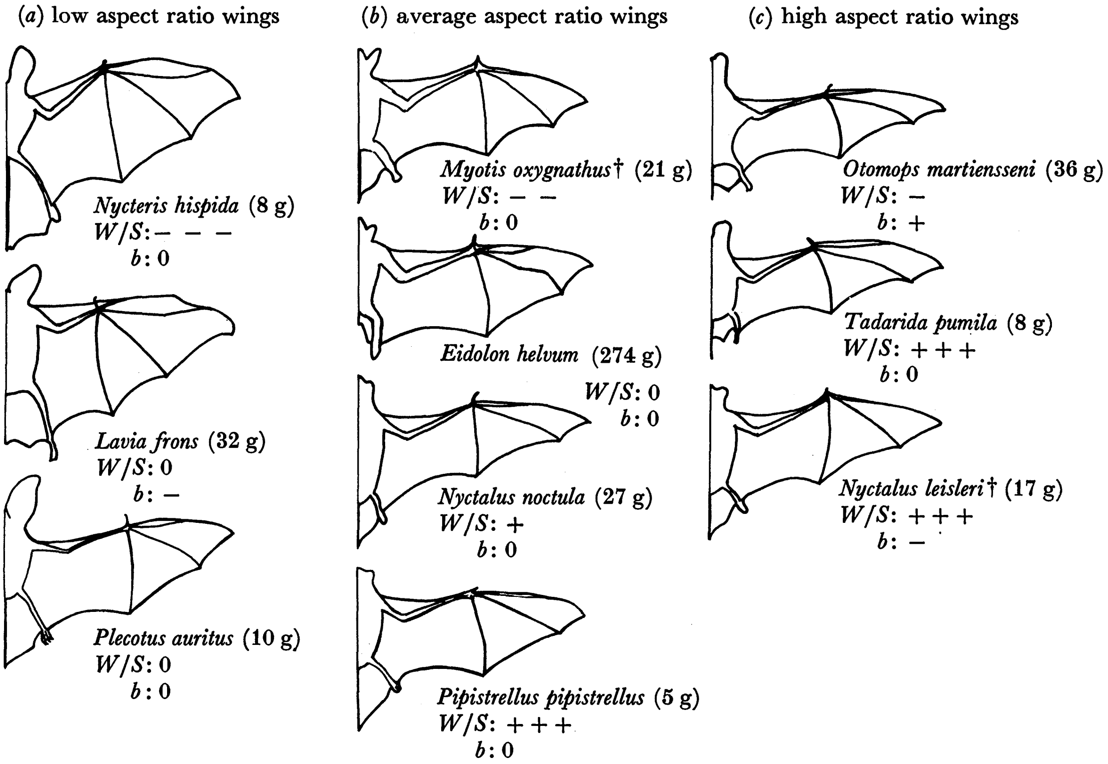


FIGURE 9. Wing planform of some bats with different shapes of the wings and tail membrane. The bats are put in different aspect ratio categories. Deviations of the wing loading (W/S) and wing span (b) from the regression line for the respective groups are indicated as follows: 0 for $< 10\,\%$ deviation, − and + for 10–20 % deviation, − − and + + for 20–30 % deviation, and − − − and + + + for $\geqslant 30\,\%$ deviation (cf. table 5). The bats within each aspect ratio category are arranged from low (top diagrams) to high (bottom diagrams) wing loading. They are drawn to different scales so that the half-span becomes equal in all figures.

(*a*) Bats with low aspect ratio wings. This group includes species that have $\geqslant 10\,\%$ lower aspect ratio than the model for the respective bat group predicts.

(*b*) Bats with average aspect ratio wings. This group includes species with aspect ratios deviating less than 10 % from the value predicted by the model.

(*c*) Bats with high aspect ratio wings. This group includes species that have $\geqslant 10\,\%$ higher aspect ratio than the model predicts.

† Modified from Gaisler (1959).

(ii) Bats with average wing loading. Species with average wing area and thereby average wing loading are the following: *Lavia frons* (Megadermatidae) (figure 9*a*), with proportionally short wings, *Rhinolophus ferrumequinum* (Rhinolophidae), *M. bechsteini*, *M. volans*, and *Plecotus auritus* (figure 9*a*) (all Vespertilionidae), all four with average wing span. *L. frons* has a very large tail membrane, like *N. hispida*, contributing to a large wing area in spite of short wings.

Findley *et al.* (1972) estimated the wing span of *N. hispida* and *L. frons* to be large, which is contradictory to my results. *L. frons* has a slow, fluttering and highly erratic flight. It roosts in bushes and trees, and hunts insects like a flycatcher, often by day; it typically searches for insects from a hanging position in a tree, makes a short flight, catches the insect and flies back again to eat it (own observations in Tanzania in 1972). *R. ferrumequinum* and *P. auritus* also hunt somewhat like a flycatcher. Further, *P. auritus* often hovers and usually catches insects among the foliage of trees.

(iii) Bats with high wing loading. There is none in this category in this investigation.

Aspect ratio. (*b*) *Bats with average aspect ratio wings* (figure 9*b*). About 73 % of the species investigated have intermediate aspect ratios. About 56 % of these also have intermediate wing span, wing area and wing loading (for example *Eidolon helvum*, Pteropodidae, figure 9*b*); the rest differ from the mean trends for these characters as follows.

(i) Bats with low wing loading. Those species with a proportionately low wing loading, following from a large wing area, have a long or intermediate wing span, and are morphologically very similar to the bats of §3.3.2. (*a*) (i). This group includes species with slow and medium flying speeds, and also some hoverers. The following species belong to this category: *Cynopterus marginatus* (Pteropodidae), *Saccopteryx bilineata* (Emballonuridae), *R. euryale*, *Thyroptera tricolor* (Thyropteridae), *Eptesicus fuscus*, *Lasiurus borealis*, *L. cinereus*, *M. evotis*, *M. nattereri*, *M. oxygnathus* (figure 9*b*), *M. thysanodes*, *M. velifer* (all belonging to Vespertilionidae), and *Uroderma bilobatum* (Phyllostomidae). *E. serotinus* belongs to this group but differs from the others by having an intermediate wing area. According to Lawlor's (1973) calculation, *S. bilineata* and *T. tricolor* have low aspect ratios.

(ii) Bats with average wing loading. About 41 % of the bats in this investigation (those not listed in table 5) have average values of all wing characters, and thus belong to this category. This group includes for example the pteropodids *Eidolon* and *Rousettus*, two-thirds of the frugivorous phyllostomids (among them the three nectarivores), one-third of the vespertilionids (for example *Barbastella*, *Lasionycteris*, *Miniopterus* and *Vespertilio*), and *Desmodus* (Desmodontidae).

(iii) Bats with high wing loading. The species within this group have short or intermediate wing span. This group includes species with medium and fast flying speeds (vespertilionids), but also hovering nectar-feeding bats and frugivores. Some examples follow.

Vespertilionids. *M. yumanensis*, *Pipistrellus hesperus*, *P. nathusii*, and *Rhogeessa tumida* have short narrow wings. *P. pipistrellus* and *Nyctalus noctula* (figure 9*b*) also have narrow wings but intermediate wing span. *Pipistrellus* flies rather rapidly. *N. leisleri* also has short, narrow wings, extremely high wing loading but a high aspect ratio, and is therefore put in the next section. *N. noctula* and *N. leisleri* both have a rapid and relatively straight flight.

Frugivores and nectar-feeders. The fruit-eating pteropodid *Epomophorus anurus* and phyllostomid *Chiroderma villosum* and the nectar-feeding pteropodid *Macroglossus minimus* belong to this group. *Chiroderma villosum* has a medium wing span, whereas the other two have short span in relation to body mass. The nectar-feeding bats often hover and should benefit from long wings, but long wings may be disadvantageous in dense vegetation, and this might limit the wing length in these bats. These bats have to manoeuvre among vegetation when flying from flower to flower. The glossophagine bats are characterized by long hand wings (Findley *et al.* 1972), which may promote hovering as suggested by these authors. The shorter the arm wing (and thus the longer the hand wing) is, in relation to the total length of the wing, the more proximally the main mass of the wing will be located, and the less the inertial power and inertial loads on the wing skeleton become (both tending to be large in slow and hovering flight because of high stroke frequency and/or large stroke amplitude; Norberg 1979). The three nectar-feeding phyllostomids in this investigation have average values throughout (cf. above).

Aspect ratio. (*c*) *Bats with high aspect ratio wings* (figure 9*c*). This group includes species with medium or fast flying speeds.

(i) Bats with low wing loading. Those species with proportionately long span also have large wing area and thereby low wing loading. A large wing area is to the advantage for bats carrying heavy prey. The fish-eating noctilionid *Noctilio leporinus* has large wing area, long wings and low wing loading, while the insect-eating *N. labialis* is intermediate in all these wing characters. *N. leporinus* hunts fish by lagging its feet in the water surface. It has not a particularly rapid flight (Walker 1964). It benefits from long wings since it hunts in open areas.

Otomops martiensseni (figure 9*c*) is the only molossid bat investigated that has long span and thereby large wing area and low wing loading. It has a rapid and straight flight and often flies long distances at high altitudes. It is a proficient flyer that can make rapid manoeuvres, such as series of sideslips with somewhat flexed wings, to cause rapid loss of height for instance when descending towards roosting caves (Norberg 1976*a*).

Rhynchonycteris naso (Emballonuridae) is another bat with long wings, large wing area and low wing loading. *Glauconycteris variegata* (Vespertillionidae) also has very long wings and, according to Findley *et al.* (1972), a very high aspect ratio, which suggests rapid flight in open areas. Data on wing area are lacking for this species.

(ii) Bats with average wing loading. *Pteropus geoffroyi* (Pteropodidae) and *Phyllostomus discolor* (Phyllostomidae) belong to this group. The former has a large span whereas the latter has an intermediate one.

(iii) Bats with high wing loading. The molossid bats have narrow wings, and all molossids in this investigation but *O. martiensseni* have extremely small wing area and thereby high wing loading. *Molossus molossus* has proportionately short wings, whereas *Eumops perotis*, *M. sinaloae*, *Tadarida brasiliensis*, *T. molossa* and *T. pumila* (figure 9*c*) have medium wing span. Several authors, for instance Vaughan (1966), write that molossids, in general, have long wings, which thus is false (probably a misinterpretation of the wings' narrowness). All molossids have rapid flight and usually fly in open areas. Many of them also perform long flights.

Nyctalus leisleri (figure 9*c*) and *Pteropus edulis* belong to this group. Both have short, narrow wings and extremely small wing area and thereby high wing loading.

Findley *et al.* (1972) stated that *Lasionycteris noctivagans* (Vespertilionidae) has a high aspect ratio, which is contradictory to the present data, which show aspect ratio to be intermediate, as are all the other wing characters.

Forearm length. Species deviating $\geqslant 10\,\%$ from the mean trend for forearm length in the respective group are listed in table 6. The wing span is correlated with the length of the forearm in some species but not in others. Long forearm as well as long wing span occur in, for instance, *Pteropus giganteus*, *Rhynconycteris naso*, *Thyroptera tricolor* and *Otomops martiensseni*.

Rhinopoma hardwickei (Rhinopomatidae) and *Myotis welwitschii* both have extremely long forearms. Other bats with long forearm are all the hipposiderids investigated, *Nycteris aethiopica*, *N. macrotis* and all emballonurids but one. Species of the genera *Myotis* have long or medium length of forearm. None of the *Myotis* species investigated has a proportionately short forearm.

Species with short forearm and short wing span are *Macroglossus minimus* and *Nyctalus leisleri*.

Molossids and pipistrellines have short or medium length of forearm (except *Otomops*, which has a long forearm). Other species with short forearm are *Nycteris thebaica*, *Eptesicus tenuipinnis*, *Lasiurus borealis*, *Mimetillus moloneyi* and *Nycticeius schlieffeni* (all but *Nycteris* belonging to Vespertilionidae).

Lower leg length (table 6). The species with large tail membrane usually have a long tibia as, for instance, *Nycteris hispida*, *Lavia frons*, *Rhinolophus ferrumequinum*, *Eptesicus nilssoni*, *Myotis bechsteini*, *M. emarginatus*, *M. myotis* and *M. oxygnathus*. Among these the tail membrane contributes to a large total wing area and low wing loading in *N. hispida* (figure 9*a*), *M. myotis* and *M. oxygnathus* (figure 9*b*).

The frugivore *Pteropus giganteus* also has a long tibia though a small tail membrane as in all frugivores, mega- as well as microchiropteran. Other species with long tibia are *Taphozous mauritianus* (Emballonuridae), *T. nudiventris*, *Hipposideros cyclops* (Hipposideridae), *N. aethiopica*, *N. grandis*, and *N. arge*, on which data on wing area and loading are lacking.

Species with relatively short tibia are *Macroglossus minimus*, *Pteropus edulis*, *Glauconycteris gleni*, *Nyctalus leisleri*, *N. noctula*, *Nycticeius schlieffeni* and all pipistrellines and molossids investigated. Most of them have high wing loading and high aspect ratio wings.

3.3.3. *Big pinnae in bats with low aspect ratio wings*

Some bat species have remarkably large and erect pinnae. Disproportionately many of these are low speed, low aspect ratio bats, a fact that strongly indicates functional interrelationships among these characters. Some species with extremely large ears occur in the genera *Lavia*, *Nycteris* and *Plecotus*, whereas *Chrotopterus auritus* and *Myotis myotis* are examples of species with rather large ears. Many species with large ears are carnivores or partly carnivores, such as the megadermatids *Megaderma* and *Macroderma*, and the phyllostomids *Mimon* and *Chrotopterus auritus*. Data on wing characters of the three former genera are lacking. Other genera with large ears and slow manoeuvrable flight are *Antrozous* and *Euderma* (both Vespertilionidae).

A common reason why long-eared bats are slow fliers is that detection and localization of insects on leaves etc. require proficient auditory capabilities as well as capability to fly slowly and to hover among vegetation and close to surfaces where insects sit. Large pinnae can catch the echoes from the emitted echo-location signals very effectively, and improve the ability to discover small objects. For instance, some insectivorous bats with very large pinnae (Nycteridae and *Plecotus* of the Vespertilionidae) can take insects from solid surfaces (Sales & Pye 1974).

Hipposiderids and rhinolophids are slow-flying bats with rather large and highly mobile pinnae which are moved alternatingly and in synchrony with the emission of ultrasonic pulses (Pye 1968).

Great mobility of the pinnae is also shown by the Pteropodidae and by many phyllostomids (convergence; see §3.4.). But in these bats ear movements appear to play a part in auditory localization of external sources rather than in echo-location (Pye 1968).

Pinnae may also have aerodynamic effects. One might expect that only a bat that specializes in low speed flight can afford to have big, upright, drag-producing, ears (the drag increasing with the square of the speed). At low speeds the bat's main expense is induced power and the addition of more frontal area, and hence parasite power (power needed to overcome the profile drag of the body), does not make much difference to the total power. The large ears in *Plecotus auritus* have a projected frontal area about 65% of that of the body exclusive of the ears (Norberg 1976*b*); they increase the body drag by about 65%. Large forwardly directed ears may also give some lift in forward flight.

Table 6. Species in which the forearm length and/or lower leg length deviate at least 10% from the mean trend for the respective group

(Deviations are measured relative to the values predicted from the model (fitted regression equation, see table 4) for the respective groups 'frugivores' (equation (7)), 'nectarivores' (equation (7)), 'insectivores' (equation (9)) and 'piscivore' (equation (8)). Deviations (negative and positive) from the regression line are indicated as follows: 0 for $<10\%$; – and + for 10–20%; – – and + + for 20–30%; – – – and + + + for $\geqslant 30\%$. A dot means that data are lacking. The numbers on the left refer to the numbers of graph points in figures 7 and 8.)

	species	forearm length	lower leg length
	frugivores (eq. (5))		
	Myonycteris torquata (Pteropodidae)	+	0
	Pteropus edulis (Pteropodidae)	–	–
5	*P. giganteus* (Pteropodidae)	+ +	+ + +
	nectarivore (eq. (5))		
	Macroglossus minimus (Pteropodidae)	–	–
	insectivores (eq. (7))		
34	*Rhinopoma hardwickei* (Rhinopomatidae)	+ + +	·
8	*Rhynconycteris naso* (Emballonuridae)	+ +	·
	Saccopteryx bilineata (Emballonuridae)	+	·
35	*Taphozous hildegardeae* (Emballonuridae)	+ +	·
	T. mauritianus (Emballonuridae)	+	+
	T. nudiventris (Emballonuridae)	0	+
	T. perforatus (Emballonuridae)	+	·
	T. peli (Emballonuridae)	+	·
	Hipposideros camerunensis (Hipposideridae)	+	·
	H. commersoni (Hipposideridae)	+	·
36	*H. cyclops* (Hipposideridae)	+	+ +
37	*Triaenops persicus* (Hipposideridae)	+ +	·
38	*Nycteris aethiopica* (Nycteridae)	+	+ + +
39	*N. arge* (Nycteridae)	0	+ + +
40	*N. grandis* (Nycteridae)	0	+ + +
	N. hispida (Nycteridae)	0	+
	N. macrotis (Nycteridae)	+	·
	N. thebaica (Nycteridae)	–	0
11	*Lavia frons* (Megadermatidae)	0	+ + +
	Rhinolophus euryale (Rhinolophidae)	+	+
	R. ferrumequinum (Rhinolophidae)	0	+
	Thyroptera tricolor (Thyropteridae)	+	·
	Eptesicus nilssoni (Vespertilionidae)	0	+
	E. tenuipinnis (Vespertilionidae)	–	·
	Glauconycteris gleni (Vespertilionidae)	0	–
	Lasiurus borealis (Vespertilionidae)	–	·
41	*Mimetillus moloneyi* (Vespertilionidae)	– –	·
	Myotis bechsteini (Vespertilionidae)	0	+
	M. emarginatus (Vespertilionidae)	0	+
	M. myotis (Vespertilionidae)	0	+
	M. nattereri (Vespertilionidae)	+	0
16	*M. oxygnathus* (Vespertilionidae)	+	+ +
42	*M. tricolor* (Vespertilionidae)	+ +	·
43	*M. welwitschii* (Vespertilionidae)	+ + +	·
	Nyctalus leisleri (Vespertilionidae)	0	–
	N. noctula (Vespertilionidae)	0	–
44	*Nycticeius schlieffeni* (Vespertilionidae)	–	– –
	Pipistrellus hesperus (Vespertilionidae)	0	–
	P. kuhli (Vespertilionidae)	–	·
45	*P. nanulus* (Vespertilionidae)	– – –	·
	P. nathusii (Vespertilionidae)	0	–
23	*P. pipistrellus* (Vespertilionidae)	0	– –
	Otomops martiensseni (Molossidae)	+	–
46	*Tadarida aloysiiabaudiae* (Molossidae)	0	– –

species	forearm length	lower leg length
47 *T. brachyptera* (Molossidae)	– –	
48 *T. condylura* (Molossidae)	–	– –
49 *T. leonis* (Molossidae)	– – –	·
T. midas (Molossidae)	0	–
50 *T. nanula* (Molossidae)	– –	·
T. pumila (Molossidae)	0	–
51 *T. thersites* (Molossidae)	– –	·
52 *T. trevori* (Molossidae)	–	– –
53 *T. russata* (Molossidae)	·	– – –
piscivore (eq. (6))		
Noctilio leporinus (Noctilionidae)	+	

3.4 *Convergence between* Megachiroptera *and frugivorous* Microchiroptera

The very first bats may have been insectivores, which later entered diversified dietary niches (Jepsen 1970). Most microbats are insectivores, but one fruit-eating family has evolved, Phyllostomidae (which also contains nectar-feeders, insectivores and carnivores). All megabats are vegetarians (fruit- and nectar-feeders). These bats often make long flights between roosting place and feeding areas, and climb among vegetation or hover in front of flowers when searching for and collecting food. They may not have the same demands for ability of making rapid manoeuvres as have the insectivores when catching insects.

Nectarivores and frugivores have reduced tail membrane, which allows the feet to be moved freely, and this probably is an adaptation for better ability of climbing around in bushes and trees, where these bats eat and roost. This reduced tail membrane probably is the main cause of the small wing area in some species. Drastic reduction of the tail membrane has occurred independently in the Old World's megachiropteran bats and the New World's microchiropteran phyllostomids that are nectar- or fruit-eaters. Thus, there has obviously been convergent evolution in the morphology of the tail membrane because of similar behaviour.

The present study has revealed evident convergence between these two groups (the pteropodids and the phyllostomids) as regards the exponents of the allometric equations for wing area, wing loading, aspect ratio and forearm length. The frugivorous mega- and microbats show similar trends also for wing span, but in this character the frugivorous microbats do not differ from all insectivorous groups.

The allometric equations for the frugivorous mega- and microbats and for all the insectivores taken together are quite different and one gets the impression of an extraordinary convergence between the two frugivorous groups (tables 3, 4). However, as described above (§3.1.1.) the slopes of regression lines for the direct measurements tend to be steeper for families than for taxonomic groups of higher rank among bats. Since the claimed convergence of frugivorous microbats upon the megabats mostly involves increase of the slope it should be evaluated to what extent this is a result of treating the frugivorous microbat family separately. Therefore, the heterogeneous insectivore group among microbats is split into families to clarify whether or not the frugivore family deviates also from separate insectivore families, in the direction of microbats, as regards slope of regression lines. Actually, the slopes for the individual families of insectivores come nearer to those for the frugivores, but differences still do remain and they are in the sense suggesting convergence between the two frugivore families. The exponents for the various dimensions for the frugivorous mega- and microbats and some insectivorous groups are reviewed here to show the degree of convergence.

The *wing span* exponent is 0.36 for megabats and 0.35 for frugivorous microbats, whereas it is only 0.29 for the insectivores taken together. Treated separately, however, the vespertilionids have the slope 0.34 and the molossids 0.33. There is thus almost no difference between frugivorous microbats and the two insectivorous groups in this respect. The *wing area* exponent is 0.69 for megabats and frugivorous microbats, whereas it is 0.60 for vespertilionids and 0.62 for molossids. Thus, the exponents for the two frugivorous groups are similar and differ from those of the insectivores. The wing area increases somewhat faster with body mass in frugivores than in insectivores. On the other hand, most insectivores have relatively longer span and larger wing area than have frugivores of similar mass (figures 3, 4).

The *wing loading* exponent is 0.31 for megabats and 0.32 for frugivorous microbats, and as much as 0.40 for vespertilionids and 0.37 for molossids. Thus, the wing loading increases faster with body mass in insectivores than in frugivores (figure 5). Again, frugivorous microbats are more similar to megabats than to other microbats.

The correlation coefficients for all *aspect ratio* gradients are low, and, therefore, the exponents are rather uncertain. But there is a trend for the frugivorous microbats to resemble the megabats more than they resemble the separate families of insectivores in this respect. The exponent is 0.033 for megabats and 0.011 for frugivorous microbats, and about 0.07 for vespertilionids and molossids. Furthermore, the regression lines for megabats and frugivorous microbats have almost the same elevation (figure 6).

The exponent for the *forearm length* for megabats and frugivorous microbats (0.36 and 0.37, respectively) do not differ much from those for vespertilionids (0.32) and molossids (0.35), but are much higher than those for nycterids (0.28) and emballonurids (0.26). The exponents almost agree with the exponents for the wing span for the various bat groups. Also as regards the forearm length, the regression lines for megabats and frugivorous microbats have almost the same elevation (figure 7).

Eisenberg & Wilson (1978) concluded that the family Phyllostomidae shows a strong convergence of brain/body mass ratios toward the pattern shown by the Pteropodidae.

In summary, the frugivorous (and/or nectarivorous) New World microbats (Phyllostomidae) and the Old World megabats (Pteropodidae) show close convergence in several characters:

(i) the exponents of the allometric equations for wing area, wing loading, and aspect ratio (and also for wing span and forearm length, although some insectivorous groups do not differ from the frugivores in these characters);

(ii) the elevation of the regression lines for aspect ratio and forearm length;

(iii) reduced tail membrane;

(iv) brain size (Eisenberg & Wilson 1978); and

(v) outer ear function (auditory detection and localization by external sounds rather than by echoes from emitted echo-location sounds (Pye 1968; see §3.3.3.)).

In view of the close relationship between insectivorous and frugivorous microbats, the divergence between them, and the close convergence of the frugivorous microbats towards the megabats (which are all frugivorous and/or nectarivorous), strongly suggest that the morphological characters concerned are related to their similar food habits.

3.5. *Comparisons between bats and birds*

I have recalculated regression equations for various wing parameters of birds from Greenewalt (1975) to be comparable with those for the bats. The recalculated equations are given in table 3 for four categories of birds: the passeriform group, the shorebird group, ducks and hummingbirds. Except for passeriforms, the passeriform model also includes species of other families and orders, for example Ardeidae, Apodidae, Laridae, Picidae, Falconiformes and Strigiformes. Except for various waders, swans and geese, the shorebird group includes for example Columbidae and Psittacidae.

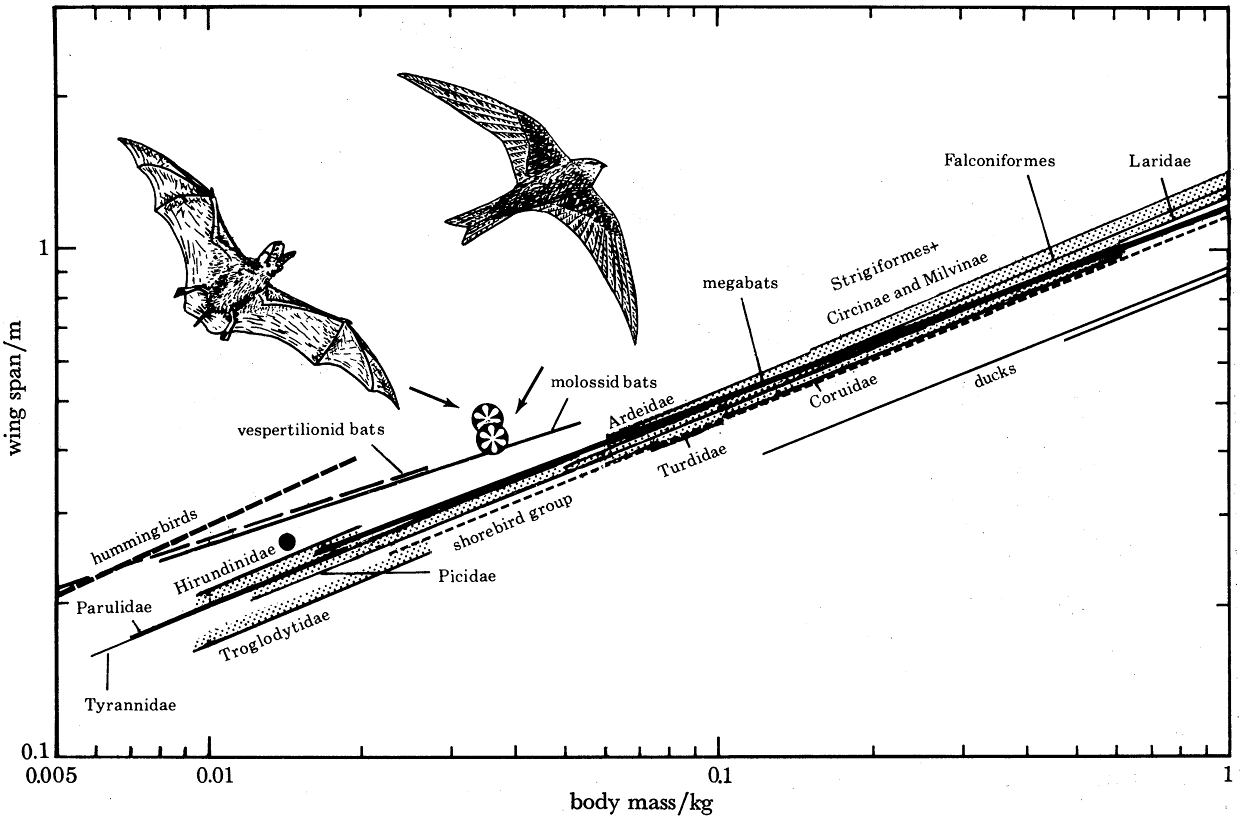


FIGURE 10. Wing span plotted on logarithmic coordinates against body mass for some groups of birds and bats. The regression equations for birds are recalculated from Greenewalt (1975; see table 3). The stippled area shows the range for Greenewalt's passeriform group, which includes birds other than passeriforms (see §3.5). The line for megabats lies within the range of passeriforms, whereas the lines for vespertilionids and molossids lie higher than that. The inset bird is a swift (*Apus apus*, family Apodidae). It has about the same span (lower ⊛) as a molossid of similar mass (here represented by *Otomops martiensseni*, upper ⊛). The flycatcher *Muscicapa striata* (●) has a long relative wing span.

The regression lines for various wing dimensions of birds are shown in figures 10–13, which also contain regression lines for some bat groups (megabats, vespertilionids and molossids) for comparison. Although being of quite different origin, birds and bats coincide in many cases.

3.5.1. *Wing span*

The values for megabats lie in about the same region as the passeriform group (figure 10). Vespertilionids and molossids have proportionately longer wings than have passeriforms of

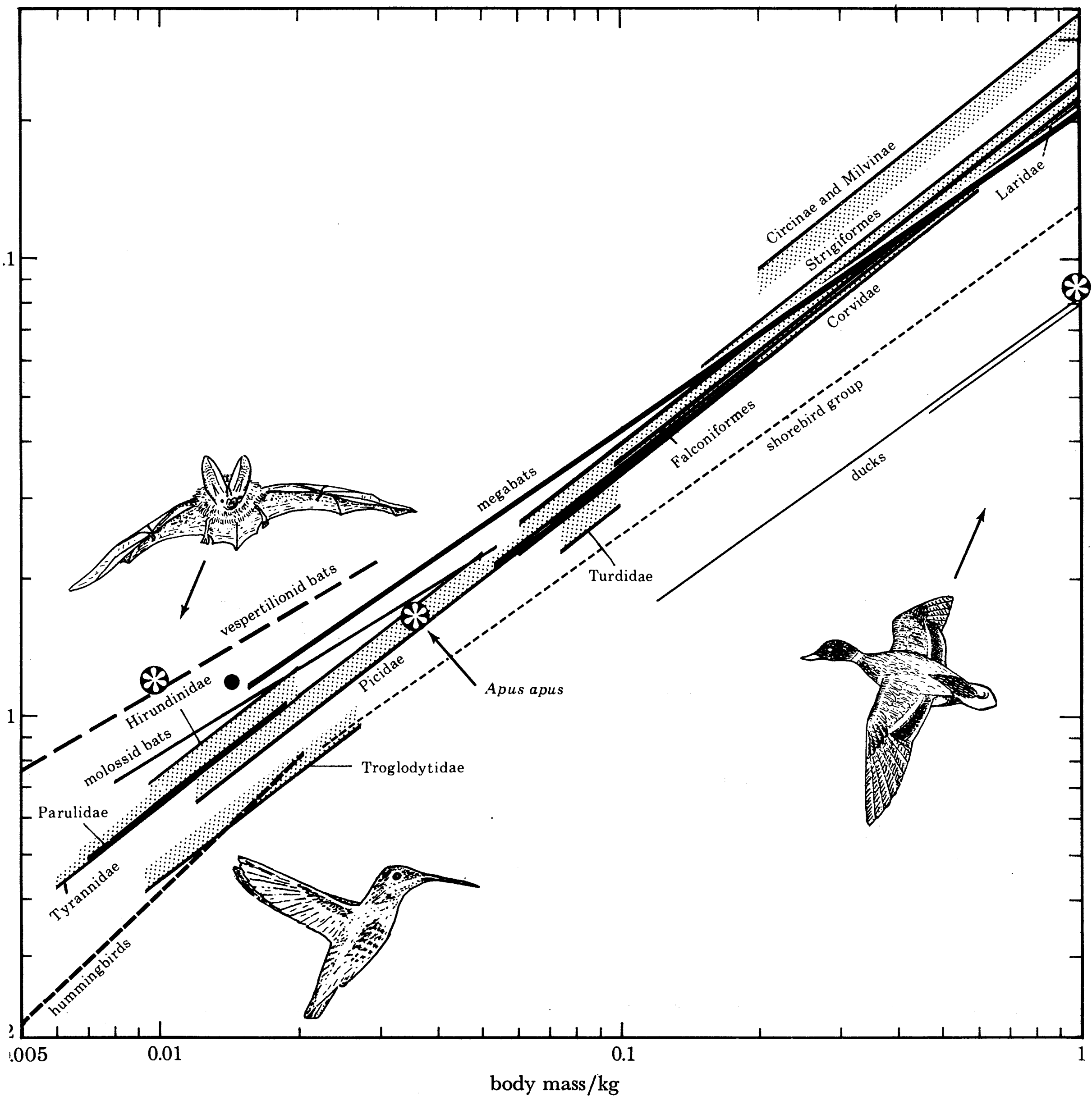


FIGURE 11. Wing area plotted on logarithmic coordinates against body mass for some birds and bats. The stippled area is the range for Greenewalt's (1975) passeriform group (description as for figure 10). The line for megabats lies partly within the range of the passeriform group. Vespertilionid bats have larger wing area than do birds of similar mass. They lie rather near flycatchers (here represented by *Muscicapa striata*, ●), which have a large wing area in comparison with other passeriforms of similar mass. The line for molossids lies near that for swallows (Hirundinidae) and near the value for swifts (*Apus apus*, ❂). The inset bat is *Plecotus auritus* and the birds a mallard (*Anas platyrhynchos*; at symbols ❂) and a hummingbird.

similar mass, and, in the lower mass range, nearly the same span as hummingbirds, which have proportionately much longer wings than have other birds. However, the slope of the regression line for hummingbirds is much steeper (0.46) than that for the insectivorous bats (0.33). This means that small hummingbirds have shorter span than, for example, vespertilionids, and large hummingbirds have longer span than equally large insectivorous bats. The lines for these bats lie nearest to swifts (Apodidae) flycatchers (Muscicapidae), swallows (Hirundinidae) and the larger tyrannids of the passerifom group.

3.5.2. *Wing area*

Greenewalt (1975, appendix) wrote that there is some uncertainty as to whether or not wing area, as measured by several investigators (and used by Greenewalt), includes the projection of the body area in between the two wings. According to Greenewalt, this area is relatively small and probably within the error of estimate. I have measured this area in *Parus* to be about 20% of the area of the two wings. In, for example, harriers and kites this percentage is much smaller, but in wrens and thrushes is maybe as large or larger. Therefore, the true regression lines for the different birds may lie somewhat higher for the wing area and lower for the wing loading and aspect ratio than they do in figures 11–13. Members of the passeriform group (except for Troglodytidae) have, on average, a larger wing area in relation to body mass than have hummingbirds, shorebirds and ducks (figure 11). Ducks have the smallest relative wing area. Hummingbirds differ in having a much higher slope of the regression line (1.0, table 3)

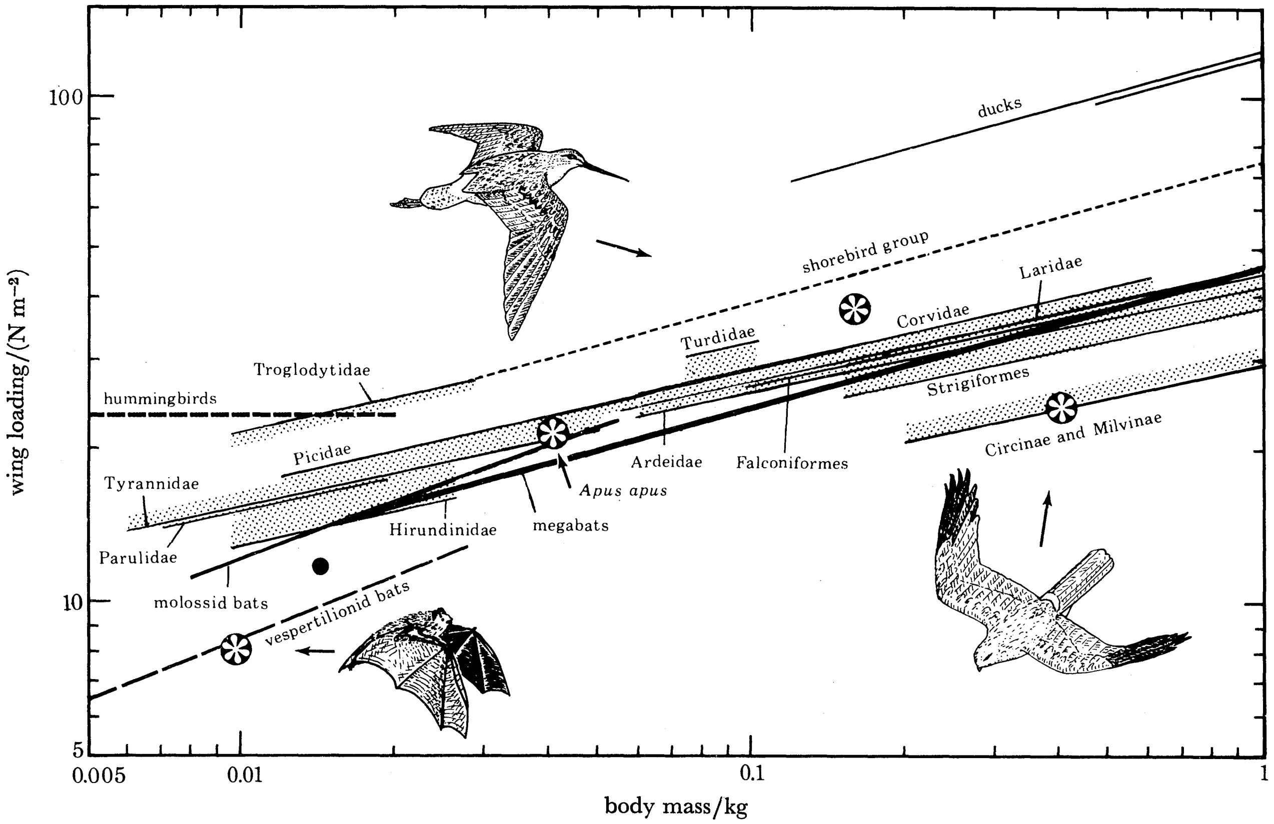


FIGURE 12. Wing loading plotted on logarithmic coordinates against body mass for some birds and bats. The stippled area is the range for Greenewalt's (1975) passeriform group (description as for figure 10). The lines for megabats and molossid bats lie partly within the range of the passeriform group. The swift (*Apus apus*) has about the same loading as a molossid bat of similar mass. As compared with other small passeriforms, flycatchers (represented by *Muscicapa striata*, ●) have low wing loading, similar to that of a vespertilionid bat of similar mass. The inset bat is *Eptesicus nilssoni* and the birds are a greenshank (*Tringa nebularia*, shorebird group) and a hen harrier (*Circus cyaneus*, family Circinae), whose coordinates are marked with symbols ⊛.

for wing area than have the other birds (0.71–0.78) and the bats (0.49–0.69). Within their mass range vespertilionid bats have a much larger wing area in relation to body mass than have any of the birds. Molossid bats have about similar wing area to swallows, flycatchers, swifts and larger tyrannids. Small megabats have a somewhat larger area than have members of the passeriform group of similar mass, whereas larger megabats have an area within the range of the passeriform group.

3.5.3. *Wing loading*

Because of their small wing area, ducks have a higher wing loading than have bats and other birds (figure 12). Megabats lie in about the same range as the passeriform group. Vespertilionid bats have a much lower wing loading than have any of the birds of similar mass, and molossids lie in about the same region as swifts, swallows and larger tyrannids. Hummingbirds differ strikingly from the others by having a constant wing loading (2.75 N m^{-2}) irrespective of mass.

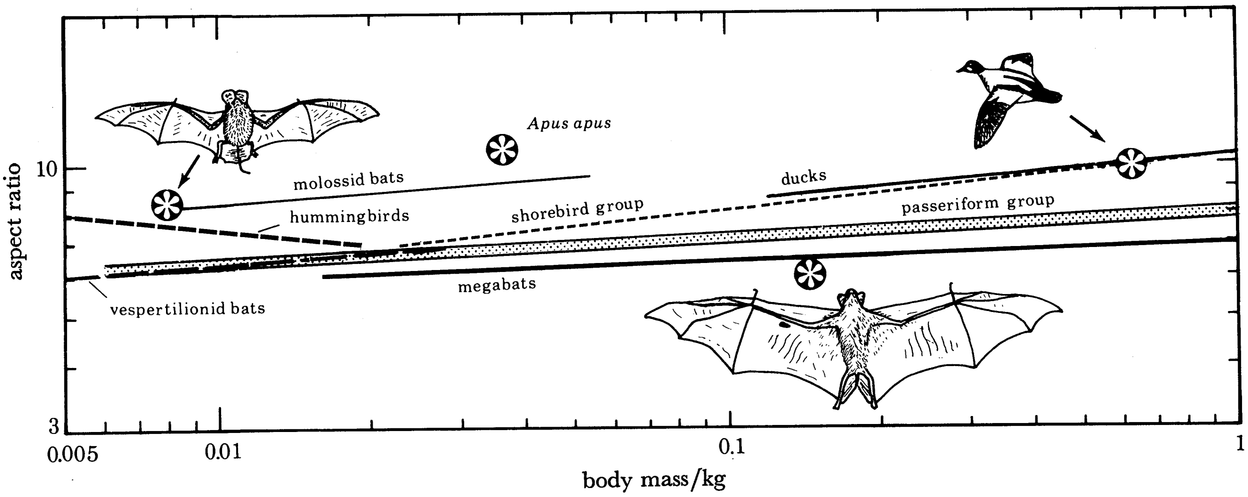


FIGURE 13. Aspect ratio plotted on logarithmic coordinates against body mass for some birds and bats. The stippled area is the range for Greenewalt's (1975) passeriform group (description as for figure 10). The lines for vespertilionid bats and small birds of the passeriform group coincide. The inset bats are *Tadarida pumila* (left) and *Rousettus aegyptiacus* (right), and the duck is *Bucephala clangula* (coordinates marked with symbols ⊛). The aspect ratio of the swift (*Apus apus*) is most similar to that of a molossid among the bats.

3.5.4 *Aspect ratio*

The aspect ratio is about the same for vespertilionid bats and small passeriforms (figure 13). Molossids have larger ratio than have any other bat and most birds of similar mass (one exception is the swift, *Apus apus*). Megabats have somewhat lower ratios than have members of the passeriform group. In contrast to that for bats and other birds, the line for hummingbirds has a negative slope.

3.5.5. *Forearm length*

Prange *et al.* (1979) gave data on lengths of humerus, ulna, femur and tibiotarsus from 16–22 species of birds from different families. They also gave regression equations for the lengths of humerus (slope 0.48) and femur (slope 0.36) versus body mass. Using their data, I calculated the slope for ulna (forearm) to be 0.30, which is the same as the slope for the forearm length in insectivorous bats (table 4). The y-intercept for the birds is, however, much lower than for any bat group, which means that bats have longer forearm in relation to body mass than have birds.

Molossid bats, swifts and, to a certain extent, swallows show strong convergence in foraging behaviour: rapid flight in open areas and mostly above tree tops (swallows usually at somewhat lower levels than the others). The wing form and size of these birds and bats reflect this convergence (figures 10–13).

Many vespertilionid bats fly among vegetation with slow manoeuvrable flight, sometimes hovering. Many of them forage like flycatchers. On the other hand, some species fly in a molossid-like manner. Among the birds, the relative wing span of vespertilionid bats is most similar to that for hummingbirds, swifts, flycatchers and swallows, and the aspect ratio is most similar to that for small passeriforms (including swallows and flycatchers; figures 10, 13). But the wing area and loading of vespertilionid bats are larger and lower, respectively, than of any bird of similar mass; they are nearest to those for flycatchers (represented by *Muscicapa striata* (● in figures 11 and 12)).

4. Conclusion

Comparisons of the morphology of wings and legs of bats show that there are different allometric equations for wing and leg dimensions for different groups of bats, and that geometric similarity prevails for about half of the characters of different groups of bats and elastic similarity only in a few characters of some families. For some families the samples are small, which results in wide 95% confidence limits and thereby lack of significant differences. But for these families the correlation coefficients usually are high, indicating rather reliable equations. In any case, various bat groups show different trends for many characters. Different foraging behaviour and thereby locomotor pattern are correlated with these morphological trends.

Table 7 shows associations between various characters among bats. The insectivorous microbats are highly diverse in wing structure and make up different groups with different flight habits. Nycterids and megadermatids (and probably also hipposiderids) are bats with low wing loading and low aspect ratio wings, and some genera within the Vespertilionidae (for instance *Plecotus*) have similar morphology. All are slow fliers with high manoeuvrability. Many small insectivorous bats usually fly slowly, hunting insects among vegetation. During foraging they need higher manoeuvrability than do frugivores. Slow manoeuvrable flight is coupled with large wing area and thereby low wing loading. The small insectivores usually have a large tail membrane.

There are few very large insectivores, and middle-sized insectivores have proportions in between those of megabats and frugivorous microbats. Some large microbats are carnivorous and need a large wing area (low wing loading) to be able to carry heavy prey. These bats usually have larger than average wing areas.

The molossids differ from most other insectivores in flight habits and wing morphology. They use open areas as foraging places and fly very fast, but are rather manoeuvrable. Their wings are very narrow, which should reduce profile and induced powers. To be good manoeuvrers, their wings must not be too long. However, narrow wings with average span have high wing loading, which tends to reduce manoeuvrability. On the other hand, their high flight speed may make up for the small wing area since the aerodynamic forces needed for manoeuvres increase with the speed squared.

Table 8 shows the gross taxonomy of bats and evolutionary divergences and convergence among subgroups. Two unrelated bat groups that are rather similar to each other and show similar trends in allometry, are the Old World megachiropteran bats (family Pteropodidae) and the New World phyllostomids (Microchiroptera), which both are vegetarians (fruit- and/or nectar-feeders). Members of both groups have reduced tail membrane, which allows the feet to be moved freely. This is probably an adaptation for climbing about in bushes and trees, where they roost and feed. This reduced tail membrane contributes to making the wing area smaller and thereby wing loading higher in small frugivorous microbats than in most insectivores, except molossids, of similar mass. The wing span, and thereby wing area, however, increase somewhat faster with body mass in the frugivores (mega- as well as microbats) than in insectivores, resulting in similar wing loadings in larger frugivorous microbats, as in, among others, vespertilionids of similar mass (figures 3–5).

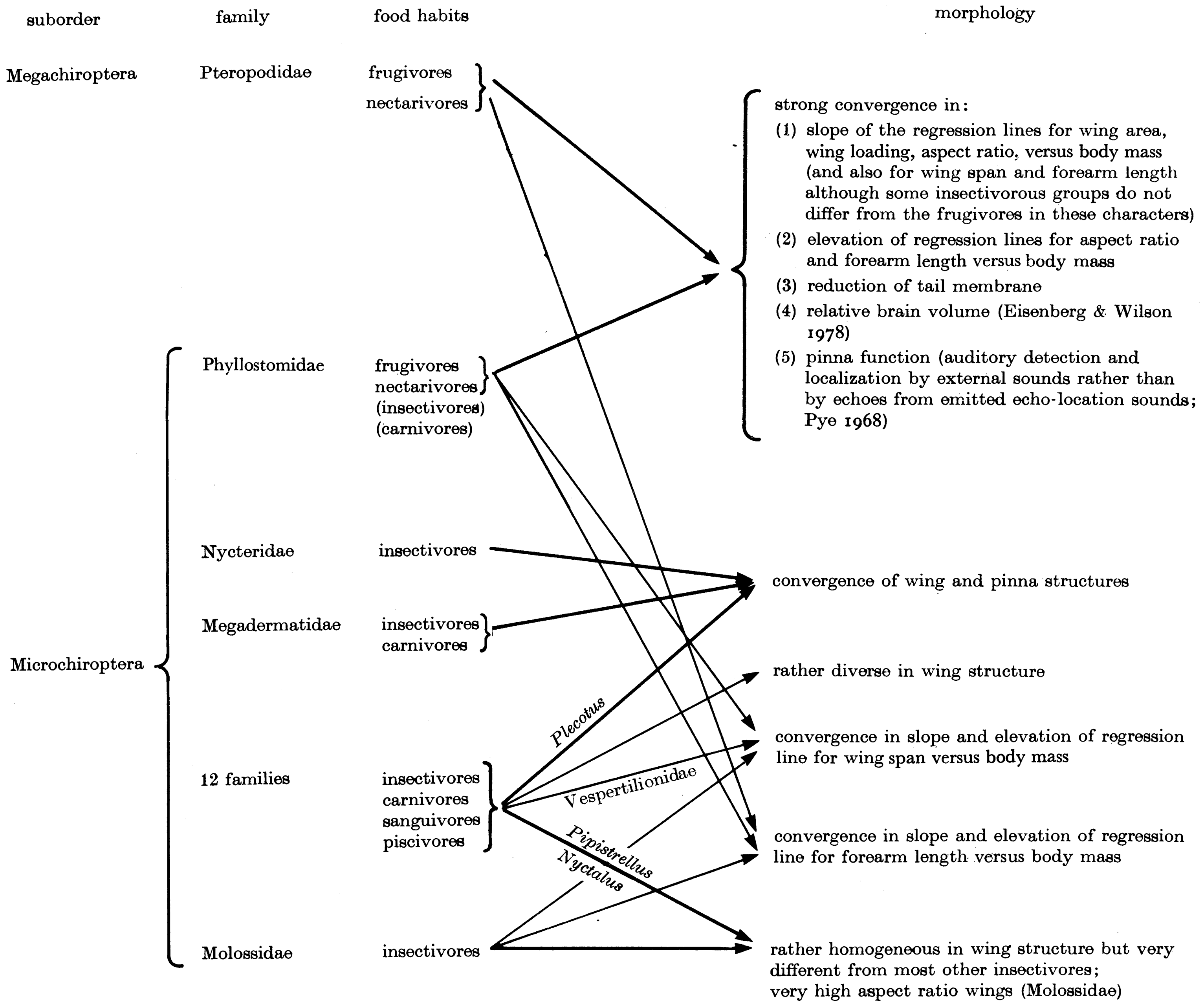
TABLE 7. ASSOCIATIONS AMONG VARIOUS CHARACTERS IN BATS

Vertical grouping according to aspect ratio; other characters listed in the leftmost column.

	low aspect ratio (–, – –, – – –)	average aspect ratio (0)	high aspect ratio (+, + +, + + +)
wing span	short or average	mostly average	mostly average but large variation
wing area	average or large	mostly average	mostly small
wing loading	low or average	mostly average	mostly high
foraging in habitat type	among vegetation, not above tree top level in forest	among vegetation and in open areas; often along vegetation edges, usually at or below tree top level in forest	in open areas, often at high altitudes
foraging behaviour	often sallying in flycatcher style; hovering and picking insects off vegetation, etc.	straight flight (megabats); hovering (mainly nectarivores); patrolling to and fro at various levels (insectivores)	straight flights over large distances
flight style	slow and manoeuvrable	slow and rather manoeuvrable; average; fast	medium and fast
hovering ability	often good	good in some species (nectarivores); not very good in others	none
pinna size	often extremely big and upright	small or average	often adpressed and forwardly pointing
percentage species (of those investigated)	12	71	17
examples of families and species	Megadermatidae, Nycteridae, *Rhinolophus ferrum-equinum* (Rhinolophidae), *Chrotopterus auritus* (Phyllostomidae), *Plecotus* (Vespertilionidae)	Pteropodidae, Phyllostomidae, Vespertilionidae	Molossidae, *Rhynchonycteris naso* (Emballonuridae), *Noctilio leporinus* (Noctilionidae), *Phyllostomus* (Phyllostomidae), *Nyctalus leisleri* (Vespertilionidae)

The large frugivores belong to suborder Megachiroptera and the small ones to family Phyllostomidae (Microchiroptera), there being only little overlap in size between the two

TABLE 8. GROSS TAXONOMY AND EVOLUTIONARY DIVERGENCE AND CONVERGENCE AMONG SUBGROUPS OF BATS



groups. Frugivorous megabats often make long and straight flights between roosting and feeding places, and are not as manoeuvrable as the smaller phyllostomids and nectarivorous megabats. The smallest frugivores are mostly nectarivorous, which often use hovering flight. In hovering and slow flight the induced power is a large power drain. The induced power becomes smaller the larger the wing disc area and thus the longer the wings. However, long wings may hinder bats flying among vegetation. This may be the reason why small frugivores (most of which are also nectarivorous and often hover among vegetation) have somewhat shorter span than have insectivores of similar mass (figure 3). Hoverers may instead increase the wing disc area by increasing the stroke amplitude, an efficient way of reducing induced power in hovering (Rayner 1979).

Phyllostomids show similar trends as megabats in various dimensions. The slope of the regression lines for wing span, wing area, wing loading, aspect ratio and forearm length versus body mass are almost the same for megabats and frugivorous microbats. Moreover, the elevation of the lines for aspect ratio and forearm length are similar for these bat groups. For wing span the slope and elevation in molossids and vespertilionids are rather similar to those of the frugivorous microbats (the similarity in this respect between the two frugivorous groups therefore distinguishing them only from some insectivorous groups and characters). Molossids also have about the same slope and elevation of the regression line for forearm length as have the frugivores (mega- as well as microbats). Still, one can state that megabats and frugivorous microbats converge as regards the regression lines for wing area, loading, aspect ratio and forearm length (figures 4–7). Data on lower leg length in frugivorous microbats are lacking. The regression line for the lower leg length is much steeper for megabats than for any of the insectivorous groups (figure 8).

The insectivorous microbats make up rather a heterogeneous group of bats with different food habits and thereby different locomotor pattern and wing morphology. Therefore, there is very large scatter of values, except for wing span, among insectivorous microbats (figures 4–8). Maximum and minimum values differ by a factor of about 2 for bats of similar mass as regards wing area, wing loading and aspect ratio, and by a factor of about 1½ as regards forearm and lower leg lengths.

Molossid bats show strong convergence with swifts and, to a certain degree, swallows in foraging behaviour and also in wing form and size. Various vespertilionid bats show similarities with flycatchers and swallows in flight during foraging and in various wing characters. Megabats and various members of the passeriform group are very similar in wing form.

I am most grateful to Colin Pennycuick and Festo Mutere for their help in the field in east Africa and for supplying me with several bat species. I am especially grateful to Linda and Colin Pennycuick and Pat and Derek Pomeroy for their kind hospitality during my stay in east Africa. I further thank Gustaf Rudebeck for giving me specimens of *Pipistrellus pipistrellus*. I am indebted to Neill Alexander and Åke Norberg for reading the manuscript, and to Bo Ericson for advice on the statistics. This work was supported by grants (B 4455–100) from the Swedish Natural Science Research Council. Two visits to east Africa were made possible by grants from the Paul and Marie Berghaus Donation-fund, the Helge Ax:son Johnson Foundation, the Wilhelm and Martina Lundgren Science Foundation and the Längman Cultural Foundation.

REFERENCES

Alexander, R. McN. 1977 Allometry of the limbs of antelopes (Bovidae). *J. Zool.* **183**, 125–146.

Alexander, R. McN., Jayes, A. S., Maloiy, G. M. & Wathuta, E. M. 1979 Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J. Zool.* **189**, 305–314.

Andersen, K. 1912 Megachiroptera. *Catalogue of the* Chiroptera *in the collection of the British Museum*, vol. 1 (2nd edn). London: British Museum.

Bergmans, W. 1978 Rediscovery of *Epomophorus pousarguesi* Trouessart, 1904 in the Central African Empire (Mammalia, Megachiroptera). *J. nat. Hist.* **12**, 681–687.

Bergmans, W. 1979 Taxonomy and zoogeography of the fruit bats of the People's Republic of Congo, with notes on their reproductive biology (Mammalia, Megachiroptera). *Bijdr. Dierk.* **48**, 161–186.

Betz, E. 1958 Untersuchungen über die Korrelation der Flugmechanismen bei den Chiropteren. *Zool. Jb.* **77**, 491–526.

Clutton-Brock, T. H. & Harvey, P. H. 1979 Comparison and adaptation. *Proc. R. Soc. Lond.* B **205**, 547–565.

Eisenberg, J. F. & Wilson, D. E. 1978 Relative brain size and feeding strategies in the chiroptera. *Evolution, Lancaster Pa* **32**, 740–751.

Farney, J. & Fleharty, E. D. 1969 Aspect ratio, loading, wing span, and membrane areas of bats. *J. Mammal.* **50**, 362–367.

Fenton, M. B. & Peterson, R. L. 1972 Further notes on *Tadarida aloysiiabaudiae* and *Tadarida russata* (Chiroptera: Molossidae-Africa). *Can. J. Zool.* **50**, 19–24.

Findley, J. S., Studier, E. H. & Wilson, D. E. 1972 Morphologic properties of bat wings. *J. Mammal.* **53**, 429–444.

Findley, J. S. & Traut, G. L. 1970 Geographic variation in *Pipistrellus hesperus*. *J. Mammal.* **51**, 741–765.

Findley, J. S. & Wilson, D. E. 1974 Observations on the neotropical disk-winged bat, *Thyroptera tricolor spix*. *J. Mammal.* **55**, 562–571.

Fleming, T. H., Hooper, E. T. & Wilson, D. E. 1972 Three central american bat communities: structure, reproductive cycles, and movement patterns. *Ecology* **53**, 555–569.

Gaisler, J. 1959 Beitrag zum vergleichenden Studium des Flugapparates der Fledermäuse (Microchiroptera). *Folia zool.* **8**, 37–62.

Greenewalt, C. H. 1962 Dimensional relationships for flying animals. *Smithson. misc. Collns* **144**, 1–46.

Greenewalt, C. H. 1975 The flight of birds. *Trans. Am. phil. Soc.* **65** (4), 1–67.

Howell, D. J. & Pylka, J. 1977 Why bats hang upside down: a biomechanical hypothesis. *J. theor. Biol.* **69**, 625–631.

Jepsen, G. L. 1970 Bat origins and evolution. In *Biology of bats*, vol. 1 (ed. W. A. Wimsatt), pp. 1–64. New York: Academic Press.

Kingden, J. 1974 East African mammals. *An atlas of evolution in Africa*, vol. 2, pt A. London and New York: Academic Press.

Kock, D. 1969 Die Fledermaus-Fauna des Sudan. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*. Frankfurt am Main: Verlag Waldemar Kramer.

Lawlor, T. E. 1973 Aerodynamic characteristics of some neotropical bats. *J. Mammal.* **54**, 71–78.

McMahon, T. A. 1973 Size and shape in biology. *Science, N.Y.* **179**, 1201–1204.

McMahon, T. A. 1975*a* Using body size to understand the structural design of animals: quadripedal locomotion. *J. appl. Phys.* **39**, 619–627.

McMahon, T. A. 1975*b* Allometry and biomechanics: limb bones of adult ungulates. *Am. Nat.* **109**, 547–563.

McMahon, T. A. & Kronauer, R. E. 1976 Tree structures: deducing the principle of mechanical design. *J. theor. Biol.* **59**, 443–466.

Maloiy, G. M. O., Alexander, R. McN., Njau, R. & Jayes, A. S. 1979 Allometry of the legs of running birds. *J. Zool.* **187**, 161–167.

Müllenhoff, K. 1885 Die Grösse der Flugflächen. *Pflügers Arch. ges. Physiol.* **35**, 407–453.

Norberg, U. M. 1976*a* Some advanced flight manoeuvres of bats. *J. exp. Biol.* **64**, 489–495.

Norberg, U. M. 1976*b* Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. *J. exp. Biol.* **65**, 179–212.

Norberg, U. M. 1979 Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. *Phil. Trans. R. Soc.* **287**, 131–165.

Pennycuick, C. J. 1968 A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 509–526.

Pennycuick, C. J. 1972 Animal flight. *Studies in biology*, vol. 2. London: Edward Arnold.

Peterson, R. L. & Smith, D. A. 1973 A new species of *Glauconycteris* (Vespertilionidae, Chiroptera). *Occ. Pap. R. Ont. Mus. Zool.* **22**, 1–12.

Prange, H. D., Anderson, J. F. & Rahn, H. 1979 Scaling of skeletal mass to body mass in birds and mammals. *Am. Nat.* **113**, 103–122.

Puranik, P. G., Gopalakrishna, G. & Chari, N. 1976 Flight parameters of the short-nosed fruit bat *Cynopterus marginatus*. *Proc. Indian Acad. Sci.* B **83**, 160–165.

Pye, J. D. 1968 Hearing in bats. In *Hearing mechanisms in vertebrates. A Ciba foundation symposium* (ed. A. V. S. De Reuck & J. Knight), pp. 66–84. London: J. & A. Churchill.

Rayner, J. M. V. 1979 A new approach to animal flight mechanics. *J. exp. Biol.* **80**, 17–54.

Sales, G. D. & Pye, J. D. 1974 *Ultrasonic communication by animals.* London: Chapman and Hall.

Stebbins, R. E. 1968*a* Bechstein's bat (*Myotis bechsteini*) in Dorset 1966–67. *J. Zool.* **155**, 228–231.

Stebbins, R. E. 1968*b* Measurements, composition and behaviour of a large colony of the bat *Pipistrellus pipistrellus. J. Zool.* **156**, 15–33.

Walker, E. P. 1964 *Mammals of the world*, vol. 1. Baltimore: Johns Hopkins.

Vaughan, T. A. 1959 Functional morphology of three bats: *Eumops, Myotis, Macrotus. Univ. Kans. Publs Mus. nat. Hist.* **12**, 1–153.

Vaughan, T. A. 1966 Morphology and flight characteristics of molossid bats. *J. Mammal.* **47**, 249–260.

Verschuren, J. 1957 *Ecologie, biologie et systematique des chiroptères. Éxploration Parcs Nationals Congo Belge.* Brussels: Institute Parcs Nationals Congo Belge.