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ECOLOGICAL MORPHOLOGY AND FLIGHT IN BATS (MAMMALIA; CHIROPTERA): WING ADAPTATIONS, FLIGHT PERFORMANCE, FORAGING STRATEGY AND ECHOLOCATION

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[Plates 1 and 2]

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Bat wing morphology is considered in relation to flight performance and flight behaviour to clarify the functional basis for eco-morphological correlations in flying animals. Bivariate correlations are presented between wing dimensions and body mass for a range of bat families and feeding classes, and principal-components analysis is used to measure overall size, wing size and wing shape. The principal components representing wing size and wing shape (as opposed to overall size) are interpreted as being equivalent to wing loading and to aspect ratio. Relative length and area of the hand-wing or wingtip are determined independently of wing size, and are used to derive a wingtip shape index, which measures the degree of roundedness or pointedness of the wingtip.

The optimal wing form for bats adapted for different modes of flight is predicted by means of mechanical and aerodynamic models. We identify and model aspects of performance likely to influence flight adaptation significantly; these include selective pressures for economic forward flight (low energy per unit time or per unit distance (equal to cost of transport)), for flight at high or low speeds, for hovering, and for turning. Turning performance is measured by two quantities: manoeuvrability, referring to the minimum space required for a turn at a given speed; and agility, relating to the rate at which a turn can be initiated. High flight speed correlates with high wing loading, good manoeuvrability is favoured by low wing loading, and turning agility should be associated with fast flight and with high wing loading. Other factors influencing wing adaptations, such as migration, flying with a foetus or young or carrying loads in flight (all of which favour large wing area), flight in cluttered environments (short wings) and modes of landing, are identified. The mechanical predictions are cast into a size-independent principal-components form, and are related to the morphology and the observed flight behaviour of different species and families of bats. In this way we provide a broadly based functional interpretation of the selective forces that influence wing morphology in bats.

Measured flight speeds in bats permit testing of these predictions. Comparison of open-field free-flight speeds with morphology confirms that speed correlates with mass, wing loading and wingtip proportions as expected; there is no direct relation between speed and aspect ratio.

Some adaptive trends in bat wing morphology are clear from this analysis. Insectivores hunt in a range of different ways, which are reflected in their morphology. Bats hawking high-flying insects have small, pointed wings which give good agility, high flight speeds and low cost of transport. Bats hunting for insects among vegetation, and perhaps gleaning, have very short and rounded wingtips, and often relatively short, broad wings, giving good manoeuvrability at low flight speeds. Many insectivorous species forage by 'flycatching' (perching while seeking prey) and have somewhat similar morphology to gleaners. Insectivorous species foraging in more open habitats usually have slightly longer wings, and hence lower cost of transport. Piscivores forage over open stretches of water, and have very long wings giving low flight power and cost of transport, and unusually long, rounded tips for control and stability in flight. Carnivores must carry heavy loads, and thus have relatively large wing areas; their foraging strategies consist of perching, hunting and gleaning, and wing structure is similar to that of insectivorous species with similar behaviour. Perching and hovering nectarivores both have a relatively small wing area: this surprising result may result from environmental pressure for a short wingspan or from the advantage of high speed during commuting flights; the large wingtips of these bats are valuable for lift generation in slow flight.

The relation between flight morphology (as an indicator of flight behaviour) and echolocation is considered. It is demonstrated that adaptive trends in wing adaptations are predictably and closely paralleled by echolocation call structure, owing to the joint constraints of flying and locating food in different ways.

Pressures on flight morphology depend also on size, with most aspects of performance favouring smaller animals. Power rises rapidly as mass increases; in smaller bats the available energy margin is greater than in larger species, and they may have a more generalized repertoire of flight behaviour. Trophic pressures related to feeding strategy and behaviour are also important, and may restrict the size ranges of different feeding classes: insectivores and primary nectarivores must be relatively small, carnivores and frugivores somewhat larger.

The relation of these results to bat community ecology is considered, as our predictions may be tested through comparisons between comparable, sympatric species. Our mechanical predictions apply to all bats and to all kinds of bat communities, but other factors (for example echolocation) may also contribute to specialization in feeding or behaviour, and species separation may not be determined solely by wing morphology or flight behaviour. None the less, we believe that our approach, of identifying functional correlates of bat flight behaviour and identifying these with morphological adaptations, clarifies the eco-morphological relationships of bats.

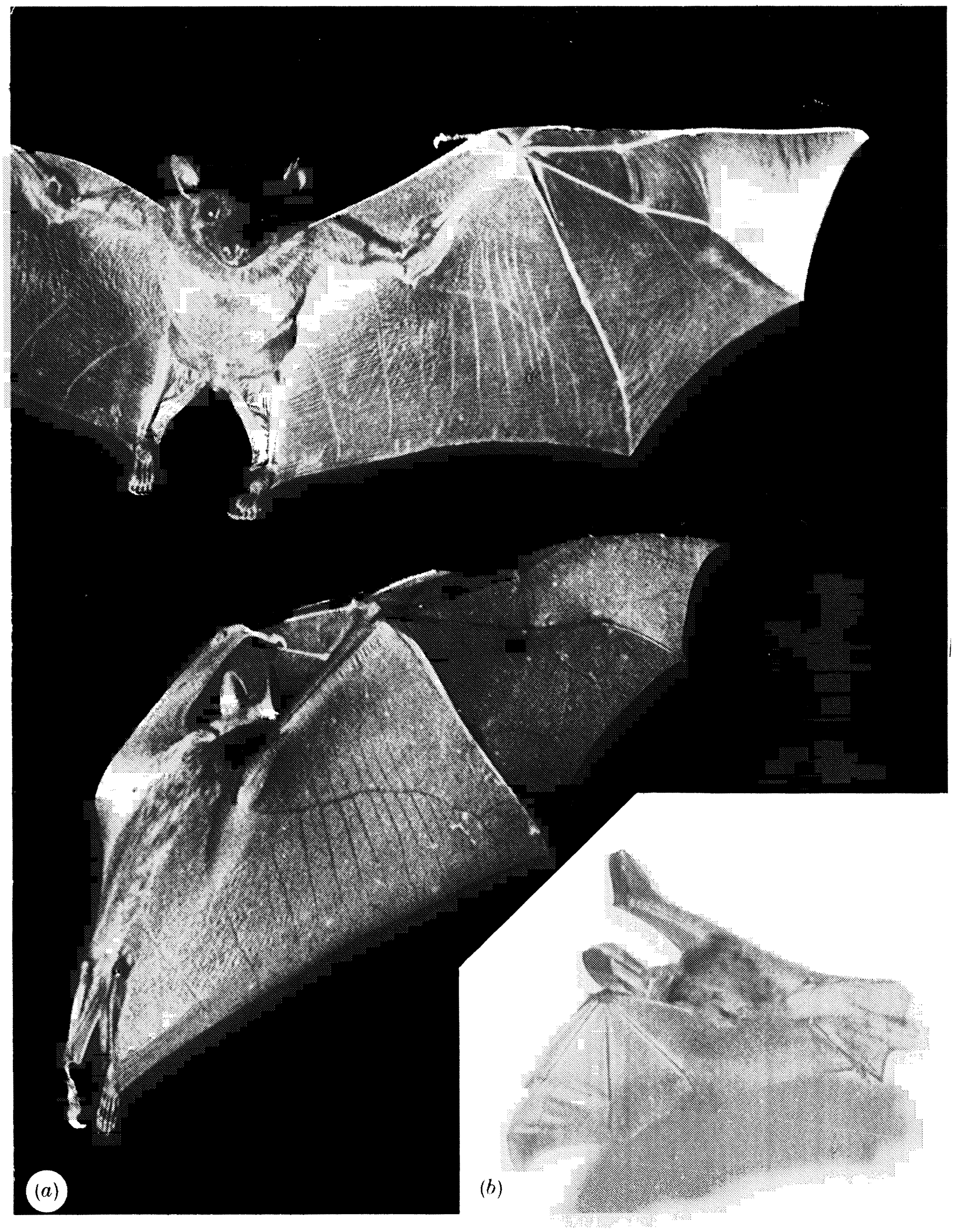
1. INTRODUCTION

Flight modes and behaviour vary among flying animals and depend on habitat structure, choice of food, foraging behaviour and many other factors. By selective adaptation of the flight apparatus, evolution permits a species to improve its capacity to use certain food sources in certain ways. Natural selection may favour a wing shape that makes possible particular flight achievements or that minimizes the work needed to fly in the manner, and at the speed, optimal for the animal. In this paper we explore flight performance in bats, and demonstrate how mechanical constraints imposed by flight give rise to pronounced correlations between flight morphology, flight behaviour and ecological role.

Steady, sustained flight performance is crucial in determining the wing adaptations of flying animals, but it is by no means the sole significant factor; the ability to control flight and to turn also has considerable influence on morphology, particularly in bats exploiting cluttered habitats and needing to locate and catch active and flying prey. Many aspects of flight performance favour smaller bats; a bat with low mass has a higher power : mass ratio and tends to be more manoeuvrable and agile than a larger animal; low mass and large wing area (low wing loading) are especially advantageous for slow flight and for hovering. Insectivory and nectarivory demand higher manoeuvrability than do frugivory or other feeding strategies: flight manoeuvres during insect capture often involve rapid turns, rolls, dives and climbs, and nectar-feeders must fly slowly and hover close among vegetation. Some bats are migratory, and some commute over substantial distances; these species must be capable of sustained steady flight. Flight in clutter requires slow speeds and high manoeuvrability, and also constrains a bat to a short wing, because long wings can be a physical hindrance. The optimal wing size and shape for any bat is a compromise between a mosaic of different, and sometimes conflicting, selection forces. Figure 1 (plates 1 and 2) illustrates some examples of bats with different wing forms.

Because the emphasis of this study is the classification of bat flight morphology in terms of aerodynamic theory and of observed flight behaviour, we have selected simple morphological parameters with clear functional interpretations; our choices have been governed by conventional aerodynamic usage. Our aims are: (i) to present a multivariate statistical analysis of bat flight morphology; (ii) to interpret this in terms of the various selection forces acting on flight adaptations; (iii) to explore how these selection forces interact; and (iv) to develop a means of predicting from morphology the expected flight performance and the ecological and trophic relationships of flight of other species of bats.

Body mass, wingspan and wing area are the primary measures of design in flying machines and organisms. They are widely used in studies of animal flight morphology; from them are derived wing loading and aspect ratio, describing respectively the size and shape of the wings. Conventional aerodynamic theory applied to flapping flight does not address the problem of the optimal wing proportions or wing shape, and although these familiar aerodynamic quantities are powerful for interpreting the adaptive function of overall wing morphology, they are less effective in describing the shape and size of the component portions of the wing, and in particular of the wingtip.



Description of plates 1 and 2

Figure 1. Photographs showing typical flying bats with different wing morphology. (*a*) *Rousettus aegyptiacus* (Pteropodidae) with low aspect ratio and average wing loading. (*b*) *Nycteris hispida* (Nycteridae) with very low aspect ratio and wing loading. (*c*) *Plecotus auritus* (Vespertilionidae) with low aspect ratio and low wing loading. (*d*) *Otomops martiensseni* (Molossidae) with very high aspect ratio and average wing loading. (*e*) *Eptesicus nilssonii* (Vespertilionidae). Photographs by U.M.N.

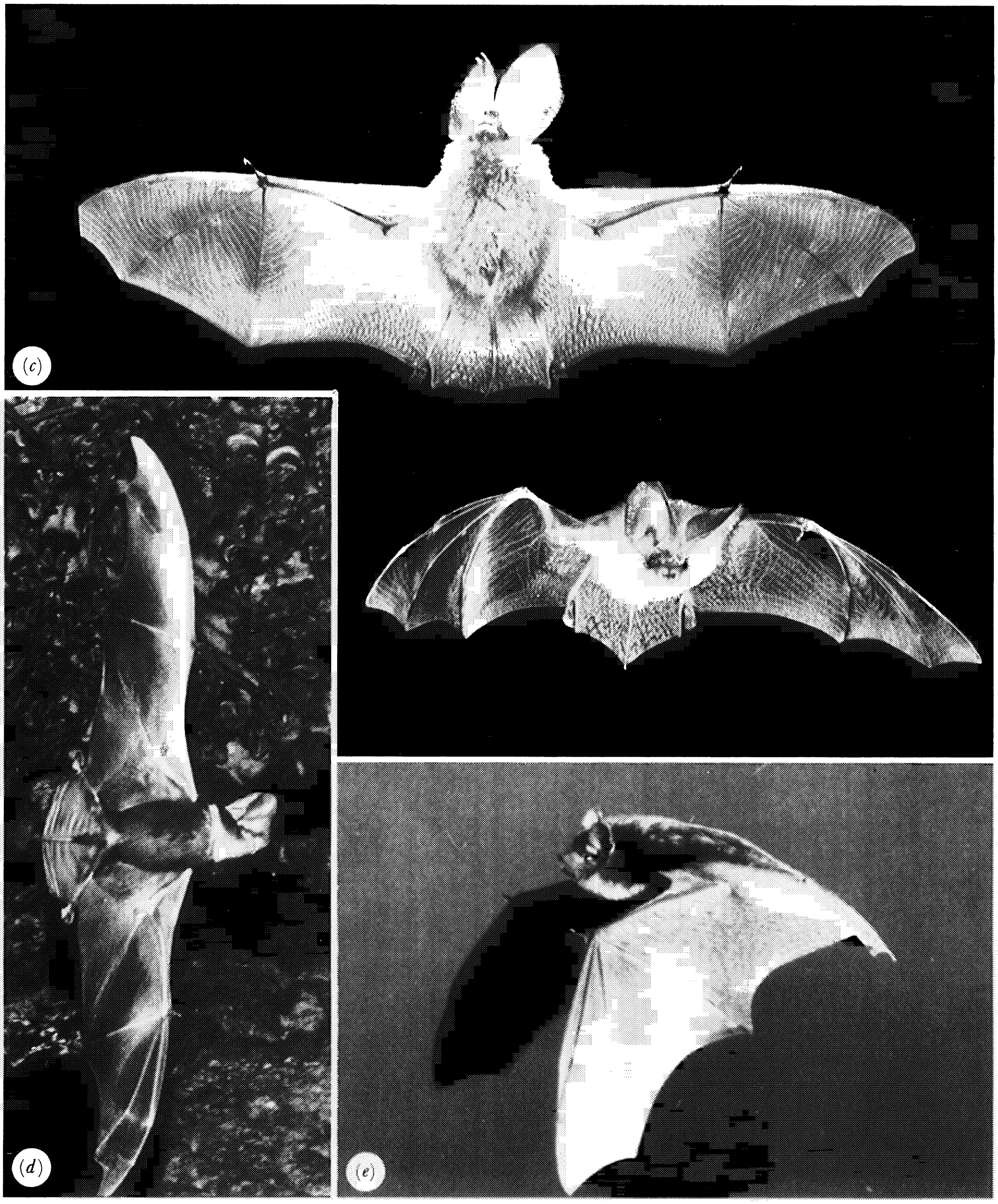


Figure 1*c*, *e*. For description see overleaf.

The configuration of the wing skeleton in bats makes it natural to consider the wingtip or hand-wing as that portion of the wing distal to the fifth digit, that is the area of membrane spanned by the second to fifth digits; the arm-wing is the portion of wing between the body and the fifth digit. Various quantities have been proposed as measures of the size of the wingtip and of the shape of the wing membrane at the wingtip, including the tip index of Findley *et al.* (1972) and the alpha angle of Smith & Starrett (1979). Both measures can be obtained from museum specimens, but because they both correlate with aspect ratio and indicate the overall shape of the wing, neither addresses the shape of the wingtip region alone.

To resolve this difficulty, we introduce three wingtip indices to describe the proportions and shape of the wingtip or hand-wing. We have selected wingtip length and area ratios that are less dependent on the wing's aspect ratio, and derived an index of wingtip shape that is a powerful indicator of wingtip geometry independent of the overall size and shape of the wing or of the hand-wing. We use these indices together with statistical measures of wing loading and aspect ratio independent of overall size to identify major trends in wing adaptations among different taxonomic and ecological groups of bats.

Many authors have previously considered bat flight morphology, and attempts to relate wing proportions to flight patterns have been made by, for example, Revilliod (1916), de Fenis (1921), Betz (1958), Gaisler (1959), Struhsaker (1961), Hartman (1963), Dwyer (1965), Vaughan (1959, 1966), Farney & Fleharty (1969), Fenton (1972, 1975), Findley *et al.* (1972), Kopka (1973), Lawlor (1973), Pirlot (1977), Strickler (1978*a*, *b*), Smith & Starrett (1979) and Norberg (1981*a*, *b*). Greenewalt (1962), Kopka (1973), Lawlor (1973) and Pirlot (1977) have determined allometric equations for the size or body-mass variation of bat wing dimensions; Norberg (1981*a*) computed regression analyses of wing and leg dimensions for different families of bats. Most of Norberg's data are also used in this investigation. Norberg found that deviations from average morphology could be related to different foraging behaviour and locomotor patterns. Mortensen (1977) and Freeman (1981*a*) have performed multivariate analyses of wing and head morphology, and use a large complex of characters to predict feeding and foraging strategies in phyllostomine and molossid bats. Findley *et al.* (1972) estimated indices for wing length, wing area, wing loading and aspect ratio from study skins of 136 species of bat, but estimated body mass from the lengths of the skinned specimens; they used factor analysis to find trends in the data, correlating wing parameters with flight characteristics. Most recently, Aldridge (1985, 1986) has considered turning behaviour in microchiropteran bats in relation to wing morphology, and Baagøe (1987) has related features of wing osteology in Scandinavian microchiroptera to flight behaviour (in particular to flight speed, turning radius and foraging height).

2. MATERIALS AND METHODS

2.1. *Morphological measurements*

We used measurements of the overall size of the animal (body mass), the size and shape of its wings (wingspan, wing area and aspect ratio), and the relative size of the wings (wing loading). We also determined the size and shape of the wingtips by using the length and area of the hand- and arm-wings; from these we derived wingtip indices.

We measured mass, wingspan and wing area or obtained these data from the literature (table 1). The analysis includes 257 species from 16 of the 18 living families of bats. Fourteen of the specimens could be identified only to the genus, and may coincide with con-geners

[text continues on p. 346]

Table 1. Body mass and wing dimensions of bats

(The quantities tabulated are measured or calculated as described in the methods section: in some cases they consist of aggregate measurements from different individual bats and from various sources. Values of body mass M in brackets were estimated from wingspan or forearm length by using correlation equations for the appropriate family or genus, provided that the animals were known to be of similar size; bracketed wing loadings are estimated from these masses with measured wing areas. Taxonomic names given in brackets were used in the original sources of the data. The sources of these data are identified in the following list (where several reference numbers are given, body mass has generally been drawn from the first): 1, Norberg $^{\mathrm{a}}$(1981*a*) $^{\mathrm{b}}$unpublished data; 2, Puranik *et al.* (1977); 3, Pennycuick (1973); 4, R. E. Goodwin (1979); 5, B. Gaskell, personal communication; 6, Habersetzer (1982*a*, 1986); 7, Rosevear (1965); 8, Kopka (1973); 9, de Fenis (1921); 10, Betz (1958); 11, Tucker (1973); 12, T. J. Roberts (1977); 13, Perez (1973); 14, Carpenter $^{\mathrm{a}}$(1975) $^{\mathrm{b}}$(1968); 15, Stephan & Nelson (1981); 16, Dwyer (1965); 17, Harting (1869); 18, Leen & Novick (1969); 19, C. Jones $^{\mathrm{a}}$(1972) $^{\mathrm{b}}$(1967); 20, Lang & Chapin (1917); 21, Kingdon (1974); 22, Kock (1969); 23, Pirlot (1977); 24, Strickler (1978*a*); 25, Nicoll & Suttie (1982); 26, Lawlor (1973); 27, Museum of Zoology, Ann Arbor, personal communication; 28, Bradbury & Vehrencamp (1976); 29, Strahan (1983); 30, Banks (1930); 31, Sterndale (1884); 32, H. D. J. N. Aldridge & I. L. Rautenbach, personal communication; 33, Habersetzer (1982*b*), *cit.* Neuweiler (1983); 34, Wood (1982); 35, Fenton *et al.* (1987); 36, E. Kulzer, personal communication; 37, T. A. Vaughan $^{\mathrm{a}}$personal communication $^{\mathrm{b}}$(1959) $^{\mathrm{c}}$(1966); 38, A. Roberts (1951); 39, Gaisler (1959); 40, Kuzyakin (1950); 41, R. E. Stebbings $^{\mathrm{a}}$personal communication $^{\mathrm{b}}$(1968*a*) $^{\mathrm{c}}$(1977) $^{\mathrm{d}}$(1968*b*) $^{\mathrm{e}}$(1970); 42, Eisentraut (1951); 43, Hartman (1963); 44, Barbour & W. H. Davis (1969); 45, S. P. Thomas, personal communication; 46, Walker (1964); 47, D. E. Wilson, personal communication; 48, Howell (1979); 49, B. Richardson, personal communication; 50, J. Scott Altenbach & J. S. Findley, personal communication; 51, W. R. Phillips, personal communication; 52, Farney & Fleharty (1969); 53, Poole (1936); 54, M. B. Fenton, personal communication; 55, Peterson & D. A. Smith (1973); 56, Peterson $^{\mathrm{a}}$(1982) $^{\mathrm{b}}$(1974) $^{\mathrm{c}}$(1972); 57, B. Hickey, personal communication; 58, Barrett-Hamilton (1910); 59, C. Jones & Suttkus (1971); 60, Czaplewski (1983); 61, Daniel (1979); 62, E. D. Pierson, personal communication; 63, Willig (1985). Food habits are indicated in dominance order in the right hand column, where f indicates frugivore; n, nectarivore; i, insectivore; p, piscivore; c, carnivore; and s, sanguivore.

species	code	total mass, M/kg	wing-span, B/m	wing area, S/m^2	aspect ratio, A	wing loading, $\dfrac{Mg/S}{\mathrm{N\,m^{-2}}}$	tip length ratio, T_l	tip area ratio, T_S	tip shape index, I	source	food
PTEROPODIDAE											
Pteropodinae											
Eidolon helvum	*Eih*	0.274	0.777	0.0879	6.9	30.6	1.32	0.72	1.20	1$^{\mathrm{a}}$	fn
Rousettus sp.	*Ro*	0.0836	0.520	—	—	—	—	—	—	2	fn
R. aegyptiacus	*Roa*	0.140	0.572	0.0558	5.9	24.6	1.08	0.64	1.45	1$^{\mathrm{a}}$,3	fn
(*Pteropus geoffroyi*)											
R. amplexicaudatus	*Rom*	0.0750	0.529	—	—	—	—	—	—	4	fn
R. celebensis	*Roc*	0.0680	0.486	0.0391	6.0	17.1	1.30	0.66	1.03	5	fn
R. leschenaulti	*Rol*	0.0824	0.458	0.0350	6.0	23.1	—	—	—	6	fn
Myonycteris torquata	—	—	0.292	—	—	—	—	—	—	7	fn
Pteropus sp.	*Pt*	0.210	0.587	0.0583	5.9	35.3	2.13	0.64	0.43	8	fn
		0.311	—	0.124	—	24.5	2.90	0.70	0.32	9	fn
		0.470	—	0.163	—	28.3	—	—	—	9	fn
		0.500	—	0.183	—	26.9	—	—	—	9	fn
		0.875	0.953	—	—	—	—	—	—	8	fn
		0.347	0.990	0.177	5.5	19.2	—	0.34	—	10	fn
P. alecto	*Pta*	0.780	1.19	—	—	—	—	—	—	11	fn
(*P. gouldi*)											
P. giganteus	*Ptg*	1.180	1.25	—	—	—	—	—	—	12	fn
(*P. medius*)											
P. griseus	*Ptr*	0.270	0.844	—	—	—	—	—	—	4	fn
P. mariannus	*Ptm*	0.457	0.980	—	—	—	—	—	—	13	fn
P. poliocephalus	*Ptp*	0.770	1.14	—	—	—	—	—	—	14$^{\mathrm{a}}$	fn
P. scapulatus	*Pts*	0.375	0.904	0.112	7.3	32.8	—	—	—	15,16	fn
P. tokudae	*Ptt*	0.152	0.650	—	—	—	—	—	—	17	fn
P. tonganus	*Pto*	0.558	1.00	0.141	7.1	39.0	1.42	0.69	0.95	8	fn
P. vampyrus	*Ptv*	1.179	1.30	0.200	8.4	57.8	1.30	0.72	1.24	17,18,4,1$^{\mathrm{b}}$	fn
(*P. edulis*)											
Acerodon mackloti	*Acm*	0.518	1.02	—	—	—	—	—	—	4	fn
Styloctenium wallacei	*Slw*	0.150	0.652	0.0635	6.7	23.2	1.44	0.69	0.92	5	f
Dobsonia moluccense	*Dom*	0.378	0.852	0.106	6.8	34.9	1.18	0.57	0.93	5	fn
D. peronii	*Dop*	0.224	0.778	—	—	—	—	—	—	4	fn
D. viridis	*Dov*	0.238	0.770	0.0884	6.7	26.4	1.25	0.58	0.87	5	fn
Hypsignathus monstrosus	*Hym*	0.427	0.882	0.115	6.7	36.3	1.27	0.81	1.76	8	fn
Epomops franqueti	*Eof*	0.109	0.600	0.0552	6.5	19.4	—	—	—	19$^{\mathrm{a}}$,20	fn
Epomophorus anurus	*Epa*	0.0730	0.428	0.0307	6.0	23.3	1.49	0.83	1.26	21,1$^{\mathrm{a}}$,1$^{\mathrm{b}}$	fn
E. gambianus	*Epg*	0.158	0.584	0.0575	5.9	27.0	—	—		9,7	fn
E. labiatus	—	—	0.485	—	—	—	—	—		22	fn

TABLE 1. (*cont.*)

species	code	total mass, M/kg	wing-span, B/m	wing area, S/m^2	aspect ratio, A	wing loading, Mg/S $\mathrm{N\,m^{-2}}$	tip length ratio T_l	tip area ratio T_S	tip shape index I	source	food
Epomophorus minor	*Epm*	0.0670	—	0.0240	—	27.4	—	—	—	9	fn
E. wahlbergi	—	—	0.520	—	—	—	—	—	—	20	fn
Micropteropus pusillus	*Mzp*	0.0211	0.378	0.0164	8.7	12.6	—	—	—	19[a],22	fn
Nanonycteris veldkampii	—	—	0.178	—	—	—	—	—	—	7	nf
Scotonycteris ophiodon	—	—	0.330	—	—	—	—	—	—	7	fn
S. zenkeri	—	—	0.229	—	—	—	—	—	—	7	fn
Cynopterus brachyotis	*Cyb*	0.0265	0.390	0.0198	7.7	13.1	1.38	0.78	1.33	5,23,1[b]	fn
C. horsfieldi	*Cyh*	0.0529	0.489	0.0302	7.9	17.2	—	—	—	23	fn
C. sphinx	*Cys*	0.0415	0.415	0.0258	6.7	15.6	1.50	0.86	1.34	6,24	fn
Thoopterus nigrescens	*Ton*	0.0660	0.494	0.0367	6.7	17.6	1.30	0.65	1.00	5	f
Balionycteris maculata	*Bnm*	0.0139	0.311	0.0120	8.1	11.4	—	—	—	23	f
Harpyionycterinae											
Harpyionycteris celebensis	*Hac*	0.104	0.566	0.0529	6.1	19.3	1.46	0.79	1.18	5	f
Nyctimeninae											
Nyctimene sp.	*Nt*	0.0900	0.449	0.0371	5.4	23.8	1.93	0.78	0.68	8	f
N. aello	*Nta*	0.0890	0.542	0.0473	6.2	18.5	1.42	0.72	1.03	5	f
N. albiventer	*Ntl*	0.0310	0.382	0.0232	6.3	13.1	1.27	0.71	1.27	5	f
N. cephalotes	*Ntc*	0.0470	0.440	0.0314	6.2	14.7	1.25	0.61	0.95	5	f
N. robinsoni	*Ntr*	0.0464	0.400	0.0284	5.6	16.0	1.68	0.83	0.98	8	f
Paranyctimene raptor	*Par*	0.0220	0.331	0.0190	5.8	11.4	1.27	0.63	0.98	5	f
Macroglossinae											
Eonycteris spelaea	*Ens*	0.0428	0.434	0.0218	8.6	19.3	—	—	—	23	n
Megaloglossus woermanni	—	—	0.241	—	—	—	—	—	—	7	n
Macroglossus sp.	*Ma*	0.0453	0.392	0.0242	6.3	18.4	2.27	0.90	0.66	8	n
		0.0131	0.233	0.0096	5.7	13.4	1.63	0.78	0.92	8	n
M. minimus	*Mam*	0.0135	0.264	0.0108	6.5	12.3	1.42	0.85	1.49	5	n
M. sobrinus	*Mas*	—	—	—	—	—	1.40	0.84	1.50	24	n
Syconycteris australis	*Sya*	0.0170	0.279	0.0125	6.2	13.3	1.54	0.89	1.37	5	fn
Notopteris macdonaldii	*Npm*	0.0450	0.407	0.0270	6.1	16.3	1.42	0.71	1.00	8	n
RHINOPOMATIDAE											
Rhinopoma hardwickii (*R. cystops*)	*Rph*	0.0163	0.280	0.0114	6.9	14.0	0.89	0.64	2.56	6,24	i
R. microphyllum	*Rpm*	0.0320	0.350	0.0153	8.0	20.5	1.10	0.61	1.24	1[b]	i
EMBALLONURIDAE											
Emballonurinae											
Emballonura monticola	*Emm*	0.0053	0.264	0.0090	7.7	5.8	—	—	—	23	i
E. semicaudata	*Ems*	0.0056	0.262	0.0097	7.1	5.7	1.15	0.71	1.61	8	i
Coleura afra	—	—	0.311	—	—	—	—	—	—	22	i
C. seychellensis	*Cos*	0.0104	0.286	0.0126	6.5	8.1	—	—	—	25	i
Rhynchonycteris naso	*Ryn*	0.0039	0.239	0.0088	6.5	4.3	—	—	—	26	i
Saccopteryx bilineata	*Sab*	0.0075	0.275	0.0125	6.1	5.9	1.29	0.78	1.53	26	i
Balantiopteryx plicata	*Bpp*	0.0065	—	—	—	—	1.14	0.81	2.45	27,28,23	i
Taphozous flaviventris	*Tpf*	0.0450	0.489	0.0304	7.9	14.5	—	—	—	29,16	i
T. longimanus	*Tpl*	0.0282	0.390	0.0155	9.8	17.8	—	—	—	9,30,31	i
T. melanopogon	*Tpa*	0.0391	0.385	0.0148	10.0	25.9	—	—	—	6	i
T. perforatus	*Tpp*	0.0188	0.326	0.0142	7.5	13.0	1.22	0.63	1.07	8,24	i
T. saccolaimus	*Tps*	0.0187	0.295	—	—	—	—	—	—	17	i
T. peli (*Saccolaimus peli*)	—	—	0.685	—	—	—	—	—	—	20	i
T. nudiventris (*T. kachhensis*)	Tpn	0.0499	0.456	0.0219	9.5	22.4	1.41	0.75	1.14	6,33	i
CRASEONYCTERIDAE											
Craseonycteris thonglongyai	*Crt*	0.0019	0.160	0.0036	7.1	5.2	1.07	0.57	1.14	34,1[b]	i
NYCTERIDAE											
Nycteris arge	—	—	0.267	—	—	—	—	—	—	20	i
N. grandis	*Ncg*	0.0320	0.380	0.0277	5.2	11.4	—	—	—	35	ic
N. hispida	*Nch*	0.0080	0.266	0.0146	4.8	5.4	1.60	1.07	2.02	1[a],1[b]	i
N. macrotis	*Ncm*	0.0115	0.288	0.0159	5.2	7.1	1.62	1.05	1.84	21,7	i
N. major	—	—	0.311	—	—	—	—	—	—	20	i
N. nana	—	—	0.152	—	—	—	—	—	—	7	i
N. thebaica	*Nct*	0.0110	0.307	0.0171	5.5	6.3	1.57	1.23	3.62	32,24	i
MEGADERMATIDAE											
Megaderma lyra	*Mel*	0.0375	0.440	0.0312	6.2	11.8	1.70	0.96	1.30	6,33	ci
M. spasma	*Mes*	—	0.344	—	—	—	1.24	0.80	1.82	1[b],24	ic
Macroderma gigas	*Mdg*	0.123	0.660	0.0717	6.1	16.8	1.50	0.68	0.83	36	ci
Cardioderma cor	—	—	0.328	—	—	—	1.49	—	—	1[b]	ic
Lavia frons	*Lvf*	0.0260	0.340	0.0213	5.4	12.0	1.45	0.91	1.69	37[a],1[a],1[b]	i

TABLE 1. (*cont.*)

species	code	total mass, M/kg	wing-span, B/m	wing area, S/m^2	aspect ratio, A	wing loading, $\frac{Mg/S}{\mathrm{N\ m^{-2}}}$	tip length ratio T_l	tip area ratio T_S	tip shape index I	source	food
RHINOLOPHIDAE											
Rhinolophus blasii (*R. empusa*)	—	—	0.288	—	—	—	—	—	—	38	i
R. capensis	—	—	0.325	—	—	—	—	—	—	38	i
R. clivosus (*R. geoffroyi*)	—	—	0.348	—	—	—	—	—	—	38	i
R. darlingi	*Rhd*	0.0110	0.295	0.0138	6.3	7.8	—	—	—	32	i
R. eloquens	—	—	0.380	—	—	—	—	—	—	38	i
R. euryale	*Rhe*	0.0109	0.285	0.0132	6.2	8.1	—	—	—	39,24	i
R. ferrumequinum	*Rhf*	0.0226	0.332	0.0182	6.1	12.2	1.22	0.84	2.13	39,8,24,40	i
R. fumigatus	*Rhu*	0.0129	0.333	0.0165	6.7	7.7	1.21	0.88	2.67	32,1[a],1[b]	i
R. hildebrandtii	*Rhh*	0.0243	0.407	0.0243	6.8	9.8	—	—	—	32	i
R. hipposideros	*Rhi*	0.0068	0.231	0.0094	5.7	7.1	1.04	0.75	2.59	39,8,40,41[a]	i
R. landeri	*Rhl*	0.0090	0.290	0.0132	6.1	6.7	—	—	—	32	i
R. megaphyllus	*Rhm*	0.0098	0.281	0.0130	6.1	7.4	1.04	0.71	2.15	15,16	i
R. mehelyi	*Rhy*	0.0165	—	0.0139	—	11.6	—	—	—	9	i
R. simulator	—	—	0.265	—	—	—	—	—	—	38	i
R. swinnyi	*Rhs*	0.0070	0.268	0.0109	6.6	6.3	—	—	—	32	i
R. trifoliatus	*Rht*	0.0283	—	0.0198	—	14.0	—	—	—	30	i
HIPPOSIDERIDAE											
Hipposideros abae	—	—	0.320	—	—	—	—	—	—	20	i
H. beatus (*H. nanus*)	—	—	0.206	—	—	—	—	—	—	20,7	i
H. bicolor	*Hib*	0.0062	0.249	0.0100	6.2	6.1	1.00	0.76	3.17	6,33	i
H. caffer	*Hic*	0.0093	0.294	0.0138	6.3	6.6	1.18	0.81	2.11	32,1[b]	i
H. cineraceus	*Hii*	0.0038	0.245	0.0079	7.6	4.7	—	—	—	1[b]	i
H. commersoni	*Hio*	0.089	0.654	0.0556	7.7	15.7	—	—	—	32	i
H. cyclops (*H. langi*)	—	—	0.413	—	—	—	—	—	—	20,7	i
H. diadema (*Phyllorhina diadema*)	*Hid*	0.0498	0.489	0.0384	6.2	12.7	—	—	—	9,4,30	i
H. speoris	*His*	0.0110	0.280	0.0121	6.5	8.9	0.97	0.87	8.7	6,33	i
Triaenops persicus (*T. afer*)	Trp	0.0109	0.293	0.0116	7.4	9.2	0.98	0.66	2.06	8	i
NOCTILIONIDAE											
Noctilio albiventris (*N. labialis*)	*Noa*	0.0296	0.403	0.0209	7.8	13.9	1.48	1.02	2.22	26,24	ipf
N. leporinus	*Nol*	0.0590	0.584	0.0380	9.0	15.2	1.55	1.07	2.23	26,8,24,42	pif
MORMOOPIDAE											
Pteronotus sp. (*Chilonycteris* sp.)	*Pn*	0.0081	0.260	0.0090	7.5	8.8	1.02	0.69	2.09	8	i
P. davyi	*Pnd*	0.0109	0.334	0.0134	8.3	8.0	1.18	0.68	1.36	23,24	i
P. gymnonotus (*P. suapurensis*)	*Png*	0.0082	0.297	0.0110	8.0	7.3	1.06	0.65	1.59	8	i
P. parnellii (*Chilonycteris rubiginosa*)	*Pnp*	0.0229	—	—	—	—	1.17	0.71	1.54	27,24	if
Mormoops megalophylla (*Aello* sp.)	*Mrm*	0.0170	0.325	0.0149	7.1	11.2	1.32	0.69	1.10	8,17	i
PHYLLOSTOMIDAE											
Phyllostominae											
Micronycteris megalotis	*Mnm*	0.0071	0.231	0.0095	5.6	7.3	—	—	—	23,43	if
Macrotus californicus	*Mcc*	0.0141	0.295	0.0136	6.4	10.2	—	—	—	37[b]	if
M. waterhousii	*Mcw*	0.0095	0.340	0.0128	9.0	7.3	—	—	—	9,44	if
Mimon crenulatum	*Mmc*	0.0148	0.386	0.0179	8.3	8.1	—	—	—	23	if
Phyllostomus discolor	*Phd*	0.0422	0.416	0.0262	6.6	15.8	1.33	0.85	1.77	26,1[b],24	fin
P. hastatus	*Phh*	0.107	0.562	0.0417	7.6	25.2	1.63	0.76	0.87	26,45	fic
Trachops cirrhosus	*Tcc*	0.0438	0.422	0.0281	6.3	15.3	—	—	—	43	ic
Chrotopterus auritus	*Cha*	0.0809	0.539	0.0532	5.5	14.9	1.73	1.42	4.58	26,46	cif
Vampyrum spectrum	*Vas*	0.158	0.676	0.0844	5.4	18.4	1.62	0.83	1.05	47	cifn
Glossophaginae											
Glossophaga longirostris	—	—	0.212	—	—	—	1.34	—	—	1[b]	nfi
G. soricina	*Gls*	0.0106	0.252	0.0099	6.4	10.5	1.79	1.17	1.89	26,8,24	nfi
Leptonycteris nivalis	*Len*	0.0338	0.410	—	—	—	1.41	1.12	3.86	24,44	nfi
L. yerbabuenae (*L. sanborni*)	*Ley*	0.0195	0.325	0.0180	5.9	10.6	1.42	1.00	2.38	48,49,1[b]	nfi
Anoura geoffroyi	*Ang*	0.0141	0.282	0.0111	7.2	12.5	1.68	1.26	3.00	8	nfi
Lichonycteris obscura	*Lio*	0.0065	0.224	0.0076	6.6	8.4	—	—	—	26	ni
Choeroniscus godmani	*Cng*	0.0084	0.238	0.0088	6.4	9.4	—	—	—	26	ni
C. minor	*Cnm*	0.0088	0.227	0.0083	6.2	10.4	1.69	1.04	1.60	8	nfi
Choeronycteris mexicana	*Ccm*	0.0182	0.300	0.0130	6.9	13.7	1.58	1.20	3.16	50,24	nf
Carolliinae											
Carollia brevicauda	*Cab*	0.0157	0.262	0.0124	5.5	12.4	1.85	0.99	1.15	8	f
C. perspicillata	*Cap*	0.0191	0.316	0.0165	6.1	11.4	1.61	1.11	2.22	26,1[b],24	fin

TABLE 1. (*cont.*)

species	code	total mass, M/kg	wing-span, B/m	wing area, S/m^2	aspect ratio, A	wing loading, $\frac{Mg/S}{\mathrm{N\ m^{-2}}}$	tip length ratio T_l	tip area ratio T_S	tip shape index I	source	food
Sturnirinae											
Sturnira lilium	*Stil*	0.0150	0.281	0.0121	6.5	12.2	1.59	0.93	1.41	26,1^{b}	fni
S. ludovici	*Stu*	0.0173	0.295	0.0132	6.6	12.9	1.63	1.25	3.29	8	f
Stenodermatinae											
Uroderma bilobatum	*Urb*	0.0154	0.307	0.0150	6.3	10.1	—	—	—	26	fi
Vampyrops helleri	*Vph*	0.0133	0.270	0.0114	6.4	11.4	—	—	—	26	fi
Vampyrodes caraccioli	*Vdc*	0.0383	0.411	0.0260	6.5	14.5	—	—	—	26	f
Chiroderma villosum	*Civ*	0.0229	0.320	0.0161	6.4	14.0	—	—	—	26	f
Artibeus jamaicensis	*Arj*	0.0470	0.420	0.0277	6.4	16.6	—	—	—	26	fin
A. lituratus	*Arl*	0.0596	0.448	0.0330	6.1	17.7	1.77	0.99	1.27	26,8	fin
A. phaeotis	*Arp*	0.0104	0.258	0.0106	6.3	9.6	—	—	—	26	fni
Stenoderma rufum	*Snr*	0.0223	0.266	0.0120	5.9	18.2	2.19	1.10	1.01	8	f
Centurio senex	*Ces*	0.0220	—	—	—	—	1.47	0.71	0.93	27,24	f
Brachyphyllinae											
Erophylla sezekorni	*Ers*	0.0163	0.273	0.0122	6.1	13.1	1.45	0.94	1.84	8	fni
Desmodontinae											
Desmodus rotundus	*Der*	0.0285	0.366	0.0200	6.7	14.0	1.12	0.65	1.38	26,1^{b},24	s
Diaemus youngi	*Diy*	0.0361	0.419	0.0206	8.5	17.2	—	—	—	23	s
Diphylla ecaudata	*Dpe*	0.0329	0.356	0.0190	6.7	16.5	1.53	0.95	1.64	8,24	s
NATALIDAE											
Natalus stramineus (*N. mexicanus*)	*Nas*	0.0039	0.240	0.0099	5.8	3.9	1.34	0.99	2.83	8,24	i
THYROPTERIDAE											
Thyroptera discifera	*Thd*	0.0031	0.211	0.0075	5.9	4.1	1.46	0.93	1.75	8	i
T. tricolor	*Tht*	0.0035	0.224	0.0083	6.0	4.1	1.25	0.86	2.21	26,24	i
VESPERTILIONIDAE											
Vespertilioninae											
Myotis adversus	*Myad*	0.0103	0.292	0.0127	6.7	7.9	1.32	0.89	2.08	51	ip
M. albescens	*Mya*	0.0059	0.230	0.0077	6.9	7.5	—	—	—	43,1^{b}	i
M. auriculus	—	—	0.270	—	—	—	—	—	—	44	i
M. austroriparius	—	—	0.254	—	—	—	—	—	—	44	i
M. bechsteini	*Myb*	0.0101	0.256	0.0110	6.0	9.0	1.02	0.83	4.37	39,41^{a},41^{b}	i
M. bocagii	*Mybo*	0.0080	0.323	0.0123	8.5	6.4	—	—	—	32	i
M. californicus	*Myc*	0.0042	0.220	0.0086	5.6	4.8	1.45	1.13	3.53	27,52	i
M. capaccinii	*Mycp*	0.0060	—	0.0056	—	10.5	—	—	—	9	i
M. dasycneme	*Myd*	0.0114	0.271	0.0108	6.8	10.4	1.43	0.78	1.20	8	i
M. daubentonii	*Mydb*	0.0070	0.248	0.0098	6.3	7.0	1.22	0.82	2.05	39,41^{a}	i
M. emarginatus	*Mye*	0.0067	0.235	0.0093	5.9	7.1	1.16	0.78	2.05	39,8	i
M. evotis	*Myev*	0.0073	0.265	0.0118	6.0	6.1	1.01	0.80	3.81	37^{c},52	i
M. grisescens	*Myg*	0.0104	0.281	0.0124	6.4	8.2	1.09	0.70	1.79	52	i
M. keenii	*Myk*	0.0070	0.241	0.0101	5.8	6.8	1.10	0.76	2.24	52	i
M. leibii	*Myl*	0.0065	0.242	0.0096	6.1	6.7	1.11	0.83	2.96	52	i
M. lucifugus	*Mylu*	0.0071	0.237	0.0093	6.0	7.5	1.05	0.80	3.20	37^{c},52,24	i
M. myotis	*Mym*	0.0265	0.383	0.0233	6.3	11.2	1.22	0.80	1.89	39,41^{a},42	i
M. oxygnathus (*M. myotis oxygnathus*)	*Myo*	0.0210	0.369	0.0204	6.7	10.1	1.41	0.76	1.17	39,40	i
M. mystacinus	*Myms*	0.0054	0.213	0.0075	6.0	7.1	1.14	0.79	2.26	39,41^{a}	i
M. nattereri	*Myn*	0.0070	0.268	0.0113	6.4	6.1	1.31	0.76	1.38	39,41^{a}	i
M. nigricans	*Myni*	0.0042	0.210	0.0068	6.5	6.1	—	—	—	26	i
M. occultus (*M. lucifugus occultus*)	*Myoc*	0.0087	0.264	0.0117	6.0	7.3	1.20	0.61	1.03	52	i
M. sodalis	*Mys*	0.0068	0.234	0.0102	5.4	6.5	1.05	0.89	5.56	52,53	i
M. thysanodes	*Myt*	0.0084	0.285	0.0134	6.1	6.2	—	—	—	52	i
M. tricolor	*Mytr*	0.0160	0.344	0.0191	6.2	8.2	—	—	—	32	i
M. velifer	*Myv*	0.0091	0.296	0.0142	6.2	6.3	1.08	0.67	1.63	52	i
M. volans	*Myvo*	0.0104	0.267	0.0123	5.8	8.3	1.15	0.63	1.21	52	i
M. yumanensis	*Myy*	0.0052	0.203	0.0065	6.3	7.8	1.24	0.95	3.28	37^{c},52	i
Pizonyx vivesi	*Pzv*	0.0250	0.448	0.0271	7.4	9.0	1.41	0.97	2.20	14^{b},42,24	ip
Lasionycteris noctivagans	*Lnn*	0.0106	0.289	0.0127	6.6	8.2	1.26	0.79	1.68	52	i
Pipistrellus ceylonicus	*Pic*	0.0082	0.256	0.0083	7.9	9.6	—	—	—	6	i
P. hesperus	*Pih*	0.0044	0.190	0.0063	5.7	6.9	1.12	0.60	1.15	52	i
P. javanicus	*Pij*	0.0055	—	0.0068	—	7.9	—	—	—	9	i
P. kuhli	*Pik*	0.0047	0.185	0.0054	6.3	8.5	—	—	—	8	i
P. mimus	*Pim*	0.0034	0.187	0.0053	6.6	6.2	1.23	0.73	1.46	6,33	i
P. musciculus	—	—	0.162	—	—	—	—	—	—	20	i
P. nanulus	*Pin*	0.0025	0.152	—	—	—	1.36	—	—	7,1^{b}	i
P. nanus	*Pia*	0.0050	0.206	0.0058	7.3	8.4	—	—	—	32	i
P. nathusii	*Piu*	0.0067	0.219	0.0067	7.2	9.8	1.44	0.77	1.15	8,39,41^{c}	i

TABLE 1. (*cont.*)

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Pipistrellus pipistrellus	*Pip*	0.0052	0.218	0.0063	7.5	8.1	1.18	0.75	1.74	$1^{a},39,41^{d},1^{b}$	i
P. rueppelli	*Pir*	0.0070	0.252	0.0101	6.3	6.8	—	—	—	32	i
P. rusticus	*Pii*	0.0050	0.218	0.0070	6.8	7.0	—	—	—	32	i
P. subflavus	*Pis*	0.0051	0.237	0.0090	6.2	5.6	1.16	0.78	2.05	52	i
P. tasmaniensis	*Pit*	0.0223	0.364	0.0147	9.0	14.8	1.29	0.73	1.32	51	i
P. tenuis	—	—	0.199	—	—	—	—	—	—	4	i
Scotozous dormeri (*Pipistrellus dormeri*)	*Szd*	(0.0078)	0.256	0.0084	6.9	(9.1)	1.23	0.76	1.62	33	i
Nyctalus leisleri	*Nyl*	0.0169	0.260	0.0086	7.9	19.3	1.40	0.76	1.19	$39,41^{a}$	i
N. noctula	*Nyn*	0.0265	0.344	0.0161	7.4	16.1	1.43	0.71	0.99	$39,1^{b}$	i
Eptesicus capensis	*Etc*	0.0070	0.249	0.0097	6.4	7.1	—	—	—	32	i
E. fuscus	*Etf*	0.0159	0.325	0.0166	6.4	9.4	1.15	0.60	1.09	$1^{b},52,54$	i
E. guineensis	—	—	0.198	—	—	—	—	—	—	22	i
E. hottentotus	*Eth*	0.0300	0.389	0.0210	7.2	14.0	—	—	—	32	i
E. nilssonii	*Etn*	0.0092	0.272	0.0112	6.6	8.1	—	—	—	39	i
E. platyops	—	—	0.254	—	—	—	—	—	—	7	i
E. pumilus	*Etp*	0.0055	0.232	0.0073	7.4	7.3	—	—	—	15,16	i
E. regulus	*Etr*	0.0056	0.238	0.0083	6.8	6.6	1.36	0.76	1.25	51	i
E. rendalli (*E. faradjeus*)	—	—	0.267	—	—	—	—	—	—	20	i
E. sagittula	*Ets*	0.0069	0.262	0.0106	6.5	6.4	1.20	0.82	2.16	51	i
E. serotinus	*Ete*	0.0223	0.341	0.0180	6.5	12.2	1.18	0.72	1.57	$39,41^{a}$	i
E. tenuipinnis (*E. ater*)	*Ett*	0.0053	0.190	0.0052	5.5	9.9	1.53	1.03	2.06	21,7	i
E. vulturnus	*Etv*	0.0045	0.227	0.0069	7.5	6.4	1.44	0.78	1.17	51	i
E. zuluensis	*Etz*	0.0040	0.210	0.0069	6.4	5.7	—	—	—	32	i
Vespertilio murinus	*Vem*	0.0115	0.278	0.0111	7.0	10.2	1.50	0.73	0.95	39,40	i
Tylonycteris pachypus	*Typ*	0.0015	0.155	—	—	—	—	—	—	18	i
T. robustula	*Tyr*	0.0080	0.221	0.0059	8.3	13.3	—	—	—	23	i
Mimetillus moloneyi	*Mtm*	0.0088	0.180	0.0048	6.7	18.0	1.25	0.52	0.71	21,7	i
Glauconycteris argentata	*Gna*	0.0092	0.313	—	—	—	—	—	—	55	i
G. gleni	*Gng*	0.0107	0.301	—	—	—	—	—	—	55	i
G. poensis	—	—	0.229	—	—	—	—	—	—	7	i
G. variegata	*Gnv*	0.0112	0.314	—	—	—	—	—	—	55	i
G. kenyacole	*Gnk*	0.0070	0.296	—	—	—	—	—	—	56^{a}	i
Chalinolobus dwyeri	*Cld*	0.0085	0.275	0.0126	6.0	6.6	—	—	—	29,16	i
C. gouldii	*Clg*	0.0153	0.331	0.0140	7.8	10.7	1.29	0.72	1.28	51	i
C. morio	*Clm*	0.0099	0.284	0.0109	7.4	8.9	1.38	0.85	1.58	51	i
Nycticeius humeralis	*Neh*	0.0096	0.244	0.0088	6.8	10.7	1.67	0.84	1.01	$19^{b},51,1^{b}$	i
N. rueppellii (*Scoteinus rueppelli*)	*Ner*	0.0300	0.378	0.0226	6.3	13.0	—	—	—	29,16	i
N. schlieffenii	*Nes*	0.0050	0.224	0.0073	6.9	6.7	—	—	—	32	i
Scotorepens orion (*Scoteinus orion*)	*Spo*	0.0117	0.273	0.0103	7.2	11.1	1.14	0.63	1.24	16	i
Rhogeessa tumida	*Rgt*	0.0039	0.187	0.0056	6.2	6.8	—	—	—	26	if
Scotophilus borbonicus	*Scb*	0.0160	0.337	0.0151	7.5	10.4	—	—	—	32	i
S. dinganii (*S. nigrita*)	*Scd*	0.0240	0.372	0.0190	7.3	12.4	1.48	1.31	7.71	32,38	i
S. heathii	*Sch*	0.0345	0.425	0.0225	8.0	15.0	—	—	—	6	i
S. kuhlii	—	—	0.339	—	—	—	—	—	—	4	i
S. nigrita (*S. gigas*)	—	—	0.584	—	—	—	—	—	—	22	i
Lasiurus castaneus	*Lac*	0.0116	0.246	0.0079	7.7	14.4	1.00	0.49	0.96	8	i
L. cinereus	*Lai*	0.0330	0.398	0.0196	8.1	16.5	1.51	0.93	1.60	1^{b}	i
L. borealis	*Lab*	0.0167	0.281	0.0117	6.7	14.0	1.58	0.88	1.26	$57,1^{b}$	i
L. seminolus	—	—	0.300	—	—	—	—	—	—	44	i
Dasypterus ega (*Lasiurus ega*)	—	—	0.345	—	—	—	—	—	—	44	i
D. intermedius (*Lasiurus intermedius*)	—	—	0.370	—	—	—	—	—	—	44	i
Barbastella barbastellus	*Bab*	0.0103	0.258	0.0111	6.0	9.1	1.20	0.84	2.33	39,58	i
Plecotus auritus	*Pla*	0.0090	0.267	0.0124	5.7	7.1	1.19	0.70	1.43	$1^{a},41^{a},41^{e},1^{b}$	i
P. austriacus	*Pls*	0.0100	0.276	0.0124	6.1	7.9	1.27	0.82	1.82	41^{a}	i
P. rafinesquii	*Plr*	0.0083	0.286	0.0138	5.9	5.9	1.39	—	—	$59,1^{b}$	i
P. townsendii	*Plt*	0.0102	0.287	0.0140	5.9	7.2	1.29	0.90	2.31	$37^{c},52$	i
Idionycteris phyllotis	*Idp*	0.0120	0.323	0.0179	5.8	6.6	1.23	0.79	1.80	60,52	i
Miniopterinae											
Miniopterus australis	*Mia*	0.0071	0.276	0.0112	6.8	6.2	—	—	—	15,16	i
M. inflatus	*Mii*	0.0125	0.290	0.0097	8.7	12.6	1.48	1.01	2.15	21,7	i
M. minor (*M. breyi*)	—	—	0.280	—	—	—	—	—	—	20	i
M. schreibersi	*Mis*	0.0142	0.309	0.0137	7.0	10.2	1.46	0.74	1.03	39,40,16	i

TABLE 1. (*cont.*)

species	code	total mass, M/kg	wing-span, B/m	wing area, S/m^2	aspect ratio, A	wing loading, $\frac{Mg/S}{\mathrm{N\,m^{-2}}}$	tip length ratio T_l	tip area ratio T_s	tip shape index I	source	food
Murinae											
Murina leucogaster (*M. hilgendorfi*)	*Mul*	—	—	—	—	—	1.44	0.74	1.06	40	i
Kerivoulinae											
Kerivoula argentata	*Kea*	0.0100	0.301	0.0149	6.1	6.6	—	—	—	32	i
K. cuprosa	—	—	0.250	—	—	—	—	—	—	20	i
K. hardwickii	*Keh*	—	0.251	0.0091	6.9	—	1.31	0.94	2.54	8	i
K. lanosa	—	—	0.254	—	—	—	—	—	—	38	i
K. phalaena	—	—	0.197	—	—	—	—	—	—	7	i
Nyctophilinae											
Antrozous pallidus	*Azp*	0.0173	0.357	0.0210	6.1	8.1	1.16	0.70	1.52	50,52	ifc
Nyctophilus geoffroyi	*Nlg*	0.0080	0.276	0.0109	7.0	7.2	1.23	0.70	1.33	51	i
N. gouldi	*Nlo*	0.0112	0.311	0.0141	6.9	7.8	1.34	0.78	1.40	51	i
N. timoriensis	*Nlt*	0.0095	0.294	0.0140	6.2	6.7	1.07	0.74	2.24	16	i
MYSTACINIDAE											
Mystacina robusta (described in error as *M. velutina* (= *M. tuberculata*); probably extinct)	*Msr*	0.0245	0.330	0.119	9.2	20.2	—	—	—	9,61	ifn
Mystacina tuberculata	*Mst*	0.0135	0.274	0.0108	7.0	12.3	1.19	0.70	1.43	61,62	ifn
MOLOSSIDAE											
Tadarida sp.	*Ta*	0.0330	—	0.0148	—	21.9	—	—	—	9	i
		0.0220	0.361	0.0139	9.4	15.5	—	—	—	32	i
Tadarida aegyptiaca	*Taa*	0.0159	0.354	0.0130	9.7	12.0	—	—	—	6	i
Tadarida ansorgei (*Nyctinomus ansorgei*)	—	—	0.331	—	—	—	—	—	—	20	i
Tadarida australis	*Tas*	0.0360	0.446	0.0180	11.1	19.6	1.46	0.88	1.52	16	i
Tadarida brasiliensis (*Nyctinomus musculus*)	*Tab*	0.0125	0.295	0.0106	8.2	11.5	1.38	0.82	1.48	37^{b},52,27	i
T. condylura	*Tac*	0.0260	0.359	0.0142	9.1	18.0	—	—	—	32	i
T. congica	*Tao*	0.0529	0.439	—	—	—	—	—	—	56^{c}	i
T. demonstrator (*Mops faradjius*)	—	—	0.316	—	—	—	—	—	—	20,22	i
T. femorosacca	—	—	0.345	—	—	—	—	—	—	44	i
T. fulminans	*Taf*	0.0330	0.457	0.0160	14.3	20.2	—	—	—	32	i
T. lobata	—	—	0.419	—	—	—	—	—	—	56^{b}	i
T. major (*Chaerophon abae*)	—	—	0.327	—	—	—	—	—	—	20,7,22	i
T. midas	*Tai*	0.0441	0.457	0.0235	8.9	11.4	—	—	—	32	i
T. nanula (*Mops nanulus*)	—	—	0.222	—	—	—	—	—	—	20	i
T. plicata	*Tap*	0.0236	0.343	0.0106	11.1	21.8	—	—	—	23	i
T. pumila	*Tau*	0.0105	0.274	0.0087	8.6	11.8	1.57	0.98	1.66	32,1^{a},1^{b}	i
T. russata (*Chaerophon russatus*)	—	—	0.292	—	—	—	—	—	—	20	i
T. teniotis	*Tat*	—	—	—	—	—	1.62	0.74	0.84	40	i
T. thersites (*Mops occipitalis*)	—	—	0.272	—	—	—	—	—	—	20	i
T. trevori (*Mops trevori*)	—	—	0.384	—	—	—	—	—	—	20	i
Mormopterus acetabulosus	—	—	0.240	—	—	—	—	—	—	38	i
Otomops martiensseni	*Otm*	0.0355	0.467	0.0234	9.3	14.9	1.42	0.81	1.33	1^{a},1^{b}	i
Sauromys petrophilus (*Platymops petrophilus*)	—	—	0.285	—	—	—	—	—	—	38	i
Myopterus albatus	—	—	0.374	—	—	—	—	—	—	20	i
M. whitleyi (*Eomops whitleyi*)	*Mpw*	0.0120	—	0.0074	—	15.9	—	—	—	9	i
Molossops abrasus	*Mla*	0.0350	—	0.0173	—	19.8	—	—	—	9	i
Neoplatymops mattogrossensis	*Nmm*	0.0058	0.215	0.0063	7.3	9.0	—	—	—	63	i
Eumops glaucinus	—	—	0.470	—	—	—	—	—	—	44	i
E. perotis	*Eup*	0.0535	0.446	0.0209	9.5	25.1	1.38	0.83	1.51	37^{c}	i
E. underwoodi	*Euu*	0.0400	0.520	—	—	—	—	—	—	44	i
Promops nasutus (*Molossus nasutus*)	*Prn*	0.0375	—	0.0149	—	24.7	—	—	—	9	i
Molossus ater	*Moa*	0.0286	0.365	0.0120	11.1	23.4	1.59	0.92	1. 37	23,24	i
M. bondae	*Mob*	0.0176	0.284	0.0092	8.8	18.8	—	—	—	43	i
M. molossus (*Tadarida molossa*)	*Mom*	0.0162	0.294	0.0099	8.7	16.0	—	—	—	26,37^{c}	i
M. sinaloae	*Mos*	0.0238	0.328	0.0133	9.1	17.6	—	—	—	26	i
Cheiromeles sp.	*Cm*	0.0892	0.460	0.0245	8.6	35.7	—	0.91	—	8	i
C. torquatus	*Cmt*	0.1355	—	0.0384	—	34.6	—	—	—	9	i

tabulated separately. These data include the 84 species used by Norberg (1981*a*), with adjustments where we have since obtained additional data. Measurements of mass, wingspan and wing area were obtained from the same specimens for 215 species, and we have information on wingtip ratios for 155 species. Where data for any one species are from more than one source, we have used the weighted arithmetic mean of the available records. For some species (*Pteropus vampyrus*, *Cynopterus brachyotis* and *Nycticeius humeralis*) only two of the three basic measurements were given in each of two or three sources. Although a simple combination of the available data could give an adequate mean, we corrected for possible size variations by finding the gradient of the correlation lines between the missing quantities and body mass for the family or subfamily in question (see below and table 4); we then used the available data to determine the appropriate constants for the correlation equations for the species concerned, and used the weighted mean mass to determine the mean wingspan and/or wing area for the species concerned (values in table 1). We obtained measurements of wingspan alone for an additional 52 species; these are included in table 1 for reference, but play no part in our statistical analyses.

We have used the taxonomic classifications of Corbet & Hill (1986) for species and subfamily names and of Hill & J. D. Smith (1984) for family and superfamily names. In some areas *Hipposideros ruber* cannot be distinguished from *H. caffer* by external features, but they are commonly treated as separate species (Fenton 1986); we have assigned records for these species to *H. caffer*. Bracketed species and genus names in table 1 were used in the source references. In the figures, species are identified by the abbreviations following each specific name in table 1.

Body mass and wing parameters are defined as follows:

(i) Body mass, M (kg). The masses used are mostly from fresh specimens (78% of the species) and are, as far as possible, from the same specimens as those for which wing dimensions have been measured. However, for some species (9%) mass is taken from one source and wing dimensions from another. De Fenis (1921) and Kopka (1973) used preserved specimens, and their measures of mass may be overestimates. Furthermore, body mass in bats fluctuates during the year with pregnancy and, for some species, with hibernation (see, for example, Beasley *et al.* 1984). Stebbings (1970) measured seasonal body mass changes in *Plecotus auritus* and *P. austriacus* (Vespertilionidae), and found that hibernation mass loss amounts to 22–29% of mean annual mass; similar mass variations are typical of other insectivorous species. Because masses given in the literature are rarely specific as to time of year or to age and condition of the individual, variation in body mass is a source of error which cannot adequately be controlled.

(ii) Wingspan, B (m), is the distance between the wingtips of a bat with wings extended so that the leading edge is straight (figure 2). Some authors (Betz 1958; Struhsaker 1961; Hartman 1963; Kopka 1973) give only the length of the wing distal to the body or to the humeral joint. Examination of various species indicated that the wingspan is about 10% longer than the combined length of the two wings excluding the body width, and we have, where appropriate, added 10% to the combined wing length measurements to estimate wingspan.

(iii) Wing area, S (m^2), is the combined area of the two wings, the entire tail membrane and the portion of the body between the wings (Norberg 1981*a*); this is the shaded area in figure 2. Other definitions used in the literature range from the area of the wings alone, to the wings and tail membrane but excluding the body, to the total flight silhouette including the projected area of the head (table 2). We measured the areas of the tail membrane, of the body between

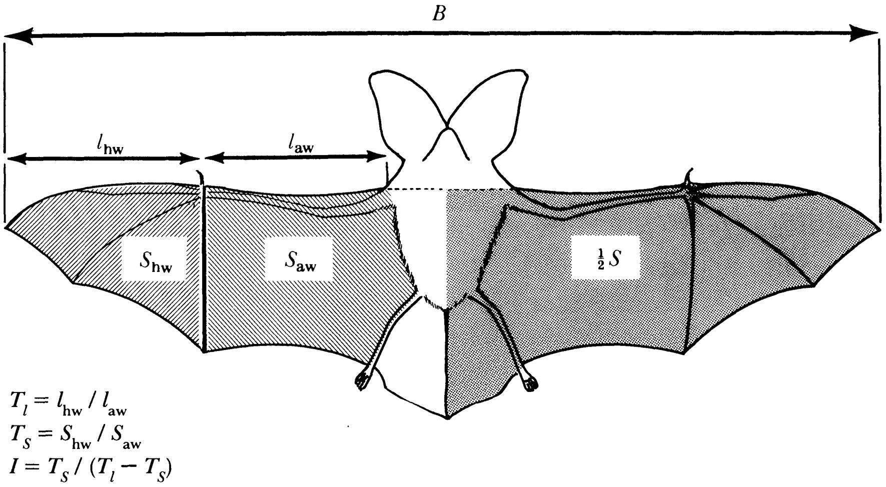


FIGURE 2. Definitions of morphological quantities used in this paper to describe bat wings. The wingspan, B, is measured from tip to tip of the extended wings; S is the wing area, including the tail membrane (when present) and the area of the body between the wings, but excluding the projected area of the head; aspect ratio and wing loading are defined from these quantities with body mass M and gravitational acceleration $g = 9.81$ m s^{-2}. S_{hw} and S_{aw} are the areas of the hand- and arm-wings, that is the areas distal to the fifth digit and between the fifth digit, the body and the legs. l_{hw} and l_{aw} are the corresponding lengths. These quantities are used to define the tip length and tip area ratios, T_l and T_S, and the wingtip shape index, I.

TABLE 2. WING AREAS MEASURED IN BATS

(Definitions of wing area used by the various sources together with corrections applied to convert published areas to accord with our definition (see (1) below and figure 2). The source numbers refer to the sources listed in table 1, and the number of species, n, refers to those for which the different areas were calculated (including the necessary corrections). Among these, 14 species (*Tpl*, *Hid*, *Mrm*, *Myb*, *Myev*, *Mylu*, *Piu*, *Pip*, *Etf*, *Neh*, *Plt*, *Azp*, *Tab*, *Mom*) are represented twice, because measurements of their wing area were given by two different authors using different conventions. The total number of species in the right column ($n = 243$) is therefore greater than the number of species for which wing area is given in table 1 ($n = 229$). Asterisks indicate: *, area calculated from published figure of bat outline; **, source gives area of a rectangle enclosing wings and tail membrane times a correction factor (0.72–0.75).)

definition of 'wing area'	source	correction	n
1. areas of wings, tail membrane and body (head excluded)	1[a], 1[b], 3, 5*, 6, 7*, 16, 23**, 26, 32, 33*, 35, 36, 41, 42*, 43, 45, 47, 49, 50, 62	none	128
2. areas of wings, tail membrane (exclusive of the tail tip) and body (head excluded)	19, 37	addition to area for tail tip: Molossidae 1.5% Vespertilionidae 6%	11
3. areas of wings, tail and ventral furred area	51	ventral furred area, about equal to body+head area substracted, body area calculated from figures and added	10
4. area of the silhouette	39, 52, 63	3% substrated from given area for head	39
5. areas of wings and tail membrane	8, 9, 10	10% added to given area for part of body between wings	47
6. area of wings	16, 17, 25, 30, 59	10% added to given area for body area; for tail add: Emballonuridae, Rhinolophidae, Hipposideridae and Mormoopidae, 10%; Vespertilionidae, 15%; Phyllostomidae, 6%.	8

the wings and of the head in various families of bats to obtain average relations between the different areas, and used these (table 2) to correct published wing area measurements to achieve consistency.

(iv) Aspect ratio, A, is the square of the wingspan divided by the wing area; $A = B^2/S$. A higher aspect ratio usually corresponds with greater aerodynamic efficiency and lower energy losses in flight.

(v) Wing loading, Mg/S ($\mathrm{N\ m^{-2}}$), is the weight (mass times gravitational acceleration g) divided by the wing area, and is related to the mean pressure on the wings. Therefore, flight speed is proportional to the square root of wing loading.

Aspect ratio correlates well with the outline of wing shape, because wings with rounded tips naturally have low aspect ratio. But not all shape variation in bat wings is expressed by aspect ratio alone. We have measured wingtip shape by the tip length ratio T_l, the tip area ratio T_S and the tip shape index I.

(vi) Tip length ratio, T_l, is the ratio of the length of the hand-wing, l_{hw}, to the length of the arm-wing, l_{aw} (figure 2); $T_l = l_{\mathrm{hw}}/l_{\mathrm{aw}}$. Kovtun (1978) used a similar measure and related it directly to manoeuvrability; the ratio is also similar to the tip index of Findley *et al.* (1972) based on the length of the third digit.

(vii) Tip area ratio, T_S, is the ratio of the hand-wing area (chiropatagium), S_{hw}, to the arm-wing area (plagiopatagium plus propatagium), S_{aw} (figure 2); $T_S = S_{\mathrm{hw}}/S_{\mathrm{aw}}$.

(viii) Tip shape index, I, is particularly valuable because it is independent of the overall size and shape of the arm- and hand-wings, but is determined simply by their relative size. The derivation and significance of the tip index is based in part on modelling the plan form of the wing by assuming that the wing chord is constant over the arm-wing, but reduces monotonically as a power function with index I over the hand-wing. Then the chord at a point on the wing, at distance l distal from the humeral joint, may be written

$$c(l) = \begin{cases} S_{\mathrm{aw}}/l_{\mathrm{aw}}, & 0 \leqslant l \leqslant l_{\mathrm{aw}}, \\ (S_{\mathrm{aw}}/l_{\mathrm{aw}})\{1-[(l-l_{\mathrm{aw}})/l_{\mathrm{hw}}]^I\}, & l_{\mathrm{aw}} \leqslant l \leqslant l_{\mathrm{aw}}+l_{\mathrm{hw}}. \end{cases} \tag{1}$$

The tangent of the angle between leading and trailing edges of the wings at the wingtip is calculated as $\mathrm{d}c(l)/\mathrm{d}l$ at $l = l_{\mathrm{aw}}+l_{\mathrm{hw}}$, and is evaluated as $IS_{\mathrm{aw}}/l_{\mathrm{aw}}\,l_{\mathrm{hw}}$. Because the wingtip has widest chord $S_{\mathrm{aw}}/l_{\mathrm{aw}}$ at the fifth digit, and has length l_{hw} from fifth digit to tip, the index I is a measure of wingtip angle and hence of wingtip shape independent of the extent of the hand-wing. Moreover, by integration of (1) the area of the hand-wing can be evaluated in terms of the arm-wing dimensions and the hand-wing length as $S_{\mathrm{hw}} = IS_{\mathrm{aw}}\,l_{\mathrm{hw}}/[(I+1)l_{\mathrm{aw}}$. From this relation the index I can be evaluated simply as

$$I = T_S/(T_l - T_S). \tag{2}$$

We have used equation (2) to determine the tip shape indices in table 1. High index values indicate rounded or nearly square wingtips, with the hypothetical value infinity corresponding to a completely rectangular wing. The value $I = 1$ corresponds (according to our model of wing chord) to triangular wingtips, and with lower values the wingtip becomes more acute and the wing thins considerably as the tip is approached.

The underlying assumption that chord decreases monotonically from the end of the fifth digit to the wingtip means that we ignore the role of the fourth digit in spreading the trailing edge of the hand wing. The value of the assumption in providing a direct measure of wingtip shape overrides this drawback.

2.2. *Statistical analysis*

We have computed bivariate correlations between body mass and wingspan, wing area, aspect ratio and wing loading. We averaged measurements (see above) so that each species is represented by a single point, because we are concerned only with interspecific variation in size and shape. We assume that each record represents a real average for healthy adult specimens of the species; we neglect sexual dimorphism, geographical (subspecies or clinal) variation and ontogenetic change in morphology within species.

In determining the simultaneous variation of two morphological quantities it is not usually possible to define one as an 'independent' variable. Furthermore, all measurements are subject to error (as noted above), including any intraspecific variation removed by averaging. For these reasons linear regression is not a suitable model for the bivariate correlation or structural relation, and we have used the reduced major axis (RMA) (Rayner 1985*a*). In most cases we use the bivariate relations to test significance of functional relations between mechanical quantities against a biomechanical hypothesis. Therefore, the equations considered are of the form $S = aM^b$, where, in this example, M is body mass, S is wing area and a and b are constants; we derive these equations by applying linear methods to logarithmically transformed values of S and M. (Units of metres, kilograms and seconds are used throughout.)

We used principal-components analysis to clarify and display our results, and included just three absolute measures of body mass and wing dimensions (M, B, S) in the analysis. Within the data sample, variation in size (quantified for instance by body mass) represents the greatest proportion of the variation, and bivariate correlations between size-dependent quantities obscure size-independent shape variation. Principal components analysis concentrates the dependence into a single derived quantity (the first principal component Q_s), leaving size-independent or shape variation expressed by the remaining two components (Q_l and Q_a). The components are dependent on the data sample used, and can only reflect the trends of variation between species: they are not in themselves fundamental measures of adaptation. The method permits a convenient display of shape variation in bat wings more clearly than conventional bivariate scatter plots, and provides a numerical measure of the deviation in shape of any one species from the average. In this it parallels Norberg's (1981*a*) use of deviations from regression lines, with the advantage that deviation in wingspan and wing area are considered simultaneously, and without the disadvantages associated with the use of regression models in morphometrics.

Principal components are derived by familiar methods (see, for example, Chatfield & Collins 1980). All morphological quantities are logarithmically transformed and are standardized to have zero mean and unit standard deviation before computation of the components. This is essential if the components are to be used to explore hypotheses expressed in power-law form (as we have done in §§4.3 and 4.5), and is equivalent to using the reduced major axis for a bivariate sample (Rayner 1985*a*): in a multivariate data set with positive correlations between all variables, the first standardized principal component is necessarily strongly correlated with size, and projects onto the RMA lines derived from bivariate calculations with each pair of variates taken independently of the third. Subsequent components must be ratios between the initial morphological parameters, and in this analysis are particularly valuable since they turn out to have a form consistent with wing loading and aspect ratio, and so act as measures of the relative size and shape of the wings. An advantage of the principal components is that by definition these components are independent of the size of the animal and of each other.

Computations were performed on a Research Machines 380Z microcomputer with programs written in Microsoft BASIC by J.M.V.R.

2.3. *Food choice and foraging behaviour*

To relate morphology and foraging strategies, we have classified bats into broad feeding classes; these are shown in table 1, as far as possible in order of preference. These food classes are generalizations; many species feed opportunistically or show seasonal and geographical variations in diet. Such variations are most pronounced in phyllostomids; for instance, glossophagine bats are usually called flower bats, but they often take insects and fruit depending on availability. Moreover, the diet of many bats is poorly known.

We have drawn the data on food choice mainly from Walker (1964), Brosset (1966), Fleming *et al.* (1972), Wilson (1973), Howell & Burch (1974), Heithaus *et al.* (1975), Gardner (1977), Mortensen (1977), Vestjens & Hall (1977), Strickler (1978*a*), Howell (1980), Heithaus (1982), Humphrey *et al.* (1983), Marshall (1983, 1985) and Dobat & Peikert-Holle (1985). Using these data, we have classified bats into six feeding classes: frugivores (including all plant material other than nectar and pollen), nectarivores (including pollen), insectivores (including all arthropods), carnivores (vertebrate meat other than fish), piscivores and sanguivores. These follow the classes considered by Eisentraut (1951), Brosset (1966), Wilson (1973) and Hill & J. D. Smith (1984). To cover bats taking a range of foods, we also distinguish 'primary' food classes, which consist of bats taking that food type as the sole or dominant portion of their diet.

We have not attempted rigorously to classify feeding behaviour (the repertoire of locomotion and other behaviours associated with food location, acquisition and handling), primarily because adequate observations of a sufficient number of species are lacking, and also because many bats show considerable behavioural plasticity in feeding. In our feeding classes the insectivores show the greatest range of feeding behaviour, and within this class we identify the following broad categories: fast, long-range hawking; slow hawking in open spaces; slow, short-range hawking; trawling for aquatic insects; gleaning and hovering; and flycatching and perch-hunting. These are discussed in detail in §§3.8 and 6.2; they are neither complete nor exclusive, and may overlap. Bats in other feeding classes show parallel specializations; carnivores also use gleaning and perch-hunting, some nectarivores and frugivores use hovering, and so on.

2.4. *Flight performance calculations*

We have identified various criteria which are important in determining the contribution of flight adaptations to selection on flight morphology (see §3). Flight speed and mechanical power consumption were predicted by applying a model of flapping-flight aerodynamics (Rayner 1986, 1987) to a representative sample of bats chosen as the mean morphology (mass, wingspan, wing area) of each bat family. The results were related to morphology in power-law form by linear and multiple linear logarithmic regression. This method gives formulae for estimating performance in any bat, and also demonstrates how power and speed vary with wing morphology.

2.5. *Flight speeds*

One of the predictions we derive in §3.2 relates flight speed in bats to body mass and wing morphology. Preliminary assessments of morphological correlations with measurements of speed were made by Findley *et al.* (1972); Norberg (1987) listed speed measurements for several bat species collected from the literature and from her own measurements. Analysis of these data demonstrated that speed increased significantly with wing loading. We used these data, with additional measurements from Habersetzer (1981); 9.1 m s^{-1} in open field in *Rhinopoma hardwickei*), Belwood & Fullard (1984); 11.1 m s^{-1} in open-field foraging in wide circles in *Lasiurus cinereus semotus*) and Baagøe (1987; a range of Scandinavian vespertilionids). We admitted only 'reliable' speed records (Norberg 1987) for bats in straight, free flight in the open field, and these data were compared to mean morphological measurements as appropriate (table 1).

3. Aerodynamic performance and its morphological correlates

3.1. *Compromise adaptation of flight morphology*

Bat wing morphology has evolved so that the animals' intrinsic flight performance is matched to their ecological roles. In this section we identify aspects of flight performance likely to contribute most strongly to selection on flight morphology, and model the likely morphological correlates of performance specialization. In selecting potentially significant or informative aspects of performance we have been guided by Andersson & R. Å. Norberg (1981), who considered the size (body mass) scaling of various aspects of flight performance in aerial predatory birds. We extend their analysis to incorporate the influence of relative wing dimensions and wing shape on forward flight, on manoeuvrability, and on other flight tasks. We do not imply that wing morphology in any bat species or family has evolved as a response to a single adaptive pressure. Wing morphology must represent a compromise within a mosaic of contraints, and must have evolved so that flight morphology itself constrains the ecological role(s) and behaviour(s) a bat may adopt. In addition to the aerodynamic factors considered here (and which later we show to relate directly to flight behaviour) these constraints also comprise limitations imposed by physiology, sensory performance, the strength of bones, muscles and other tissues, and by many other aspects of the animals' biology and behaviour. At this stage and relative importance of these other constraints is not clear; we do not discuss them in any detail, and concentrate here on mechanical factors.

Equally, we cannot determine the relative importance of the various mechanical factors or assess comparatively the contribution of quantities such as turning ability or flight speed to fitness. It would be naive to claim that a useful selective currency in one species (for example flight energy) should be equally valid for all. An 'average' bat might adequately accomplish all of the flight tasks it encounters and might readily meet its ecological needs so that the most critical constraints on morphology might either be independent of flight or might reflect the bat's need to retain a broad repertoire of flight behaviour. By the same token, a more specialized species might retain sufficient flexibility to cope *in extremis* with all likely situations, but its morphology may be determined by the most important or most critical of the ecological conditions it experiences. Perhaps wing morphology should more realistically be seen as influenced more strongly by the breadth of the environmental conditions commonly experienced than any single factor.

This dilemma can be resolved indirectly. By determining the *expected* morphological response under the assumption that a single aerodynamic or mechanical factor predominates, and by then relating these results to the known morphology and flight behaviour of individual species, families and feeding classes of bats, we can explore the relative significance of different mechanical constraints on flight and on the morphology of flying vertebrates. But we are not using these data and observations to test whether adaptation has taken place; rather, we assume that bats are adapted to fulfil a particular role, and we try to establish which factors have had the greatest influence, and to explore how compromise solutions have come about, as bats evolved and radiated to their present morphological and ecological diversity. We use morphological measurements, observations of flight and foraging behaviour and mechanical and aerodynamic theory as tools to guide our judgments.

3.2. *Steady forward flight*

Forward flight performance is usually assessed in terms of power requirements because of the large energy rates demanded by active flapping flight. Aspects of the mechanics and aerodynamics of flapping flight in bats have been considered by Eisentraut (1936), Vaughan (1970*a*, *b*), Norberg (1976*a*, *b*, 1986*a*, 1987) and Rayner (1986, 1987). The anatomy and functional morphology of the flight organs have been widely studied (see, for example, Vaughan (1959, 1970*a*), Norberg (1970*a*, 1972*a*), Strickler (1978*a*, *b*), Altenbach (1979) and Altenbach & Hermanson (1987)). Flight physiology and energetics have been reviewed by S. P. Thomas (1975, 1987) and Carpenter (1985, 1986).

A simple mechanical model based on fixed-wing aircraft and helicopter analysis to predict power consumption in flight was proposed by Pennycuick (1968, 1969); subsequent modifications have resulted in a model more closely related to flight metabolism (Tucker 1973; Pennycuick 1975, 1978). We have used a comparable model (Rayner 1979, 1986, 1987) which is more realistic for flying vertebrates and allows for periodic variation in lift generation by flapping wings. Mechanical power in flight may be written as a function of flight speed, V, in the form

$$P(V) = p_{\mathrm{i}} M^2 g^2 / B^2 V + \tfrac{1}{2}\rho (p_{\mathrm{par}} + p_{\mathrm{pro}}) S V^3, \tag{3}$$

where M is body mass, B is wingspan, S is wing area, ρ is air density (1.205 kg m^{-3}) and g is the gravitational acceleration (9.81 m s^{-2}). Equation (3) displays explicitly the principal sources of variation in power with speed and with morphology (M, B, S); additional factors causing variation of the power components are encompassed in the non-dimensional coefficients p_{i}, p_{par} and p_{pro}. The first term, p_{i}, represents the induced power, which is the rate of working required to generate a vortex wake whose reaction both sustains and propels the animal. The remaining terms, p_{par} and p_{pro}, are the parasite and profile powers, representing the work done against form and friction drag on the body and wings respectively. The components of mechanical power and the summed curve of total power against speed, computed by using this model (Rayner 1986), for a noctule (*Nyctalus noctula*) are shown in figure 3. The model is based on a realistic model of wingbeat kinematics (Rayner 1986, 1987) and of vortex wake structure (Rayner 1985*b*, 1987; Rayner *et al.* 1986), and the calculation allows for changes in wingbeat frequency and amplitude with speed so that thrust and drag are always in equilibrium.

Beyond the explicit variation of power with morphology shown in equation (3), factors influencing power fall broadly into two categories: variation with speed owing to variation of wingbeat kinematics or gait, and variation with both speed and overall size related to Reynolds' number effects. Over the size range of bats Reynolds' number does not change significantly; any associated effects are probably small enough to be neglected, and p_{par} and p_{pro} are taken

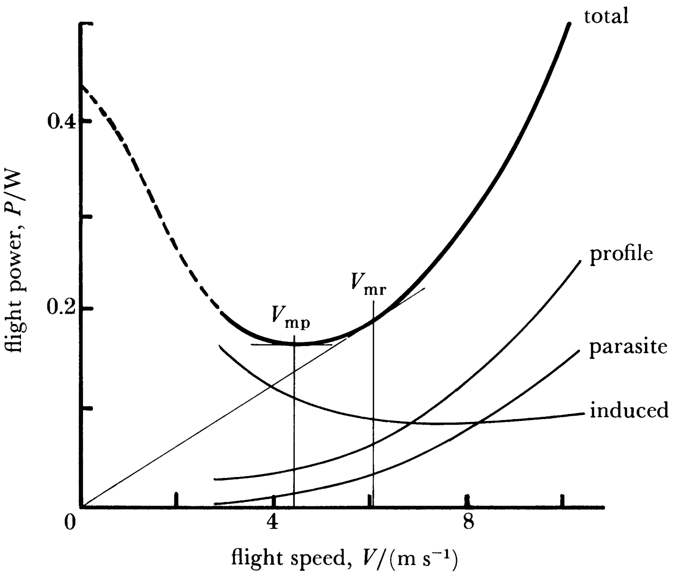


FIGURE 3. Estimated mechanical power plotted against speed for a noctule, *Nyctalus noctula*, derived by using the model of Rayner (1986, 1987). The rise in induced power at high flight speeds correlates with a change in wingbeat kinematics and reflects the greater thrust required to balance drag at these speeds. For minimum energy per unit time the bat should fly at speed V_{mp}, and for maximum range or minimum cost of transport (energy per unit distance) it should select speed V_{mr}. Bats hawking insects in the air should fly slightly faster than V_{mp} (Norberg 1981 *b*), whereas those commuting to return food to a central place should fly as fast as possible, and will probably exceed V_{mr} (R. Å. Norberg 1981 *a*).

as approximately constant. However, the effects of gait changes are important. The aerodynamic life generated by the wings is responsible for thrust to balance drag as well as for weight support; the behaviour of induced power with flight speed is influenced by variation in drag, and it is not reasonable to assume that p_i is constant with speed (Rayner 1986, 1987). With fixed wings, lift acts solely to balance weight, induced power decays as V^{-1} (compare Pennycuick 1968) and p_i is constant. In flapping flight, however, lift must also provide thrust; at relatively low speeds, thrust is needed primarily to balance induced drag (the cost of generating lift), and so induced power falls with increasing speed. At high speeds, friction drag rises and becomes dominant; accordingly the thrust must also rise, and there is a small rise in induced power.

The U-shape of the mechanical power curve (figure 3) is common to all flying birds and bats, and determines the typical speeds adopted in flight. The bottom point of the curve defines the minimum power speed V_{mp}, which should be used by the bat to maximize flight time with a given amount of energy (Pennycuick 1969, 1975); it should be selected, for instance, by nectar- and pollen-feeding bats waiting turns to feed, as reported in glossophagine bats by Howell (1979). At the maximum range speed, V_{mr}, the power:speed ratio (equivalent to the cost of transport, $C = P/MgV$, or the energy required to transport unit weight of the animal through unit distance) is minimum; it is found by drawing a tangent to the curve from the origin. This speed should be selected whenever a long distance is to be covered on a given amount of energy regardless of time (e.g. during migration) (Pennycuick 1969). Recent wind-tunnel measurements of flight metabolism in the large pteropodid *Pteropus poliocephalus* (Carpenter 1985) and with smaller pteropodids *Eidolon helvum*, *Hypsignathus monstrosus* and

Rousettus aegyptiacus (Carpenter 1986) suggested that endurance of these species is greater when flying at V_{mp}. If these results are representative, bats may be unable to use V_{mr} for sustained flight. *P. poliocephalus*, however, is very large ($M = 0.65$–0.8 kg), and this apparently anomalous result may be a consequence of the relatively large size of pteropodids. Large birds may not have sufficient flight-muscle performance available for them to fly as fast as V_{mr} (Pennycuick 1969). Because there are no comparable observations of endurance in other flying vertebrates the question of how representative these results are remains unanswered.

During foraging in flight (for example while catching insects) a bat should fly faster than V_{mp} (R. Å. Norberg, personal communication, cited in Norberg 1981*b*), but while commuting to a feeding area the bat should fly faster than V_{mr} (R. Å. Norberg 1981). In both situations the goal is maximization of net energy gain per unit time (foraging plus commuting), and the precise flight speed adopted must depend on food availability, feeding rates and flight performance (figure 3). In certain species the need for a range of flight speeds may be more important than adaptation for one single speed.

We used the model of Rayner (1986, 1987) to calculate characteristic flight speeds V_{mp} and V_{mr}, the minimum flight power, $P_{\mathrm{mp}} = P(V_{\mathrm{mp}})$ and the minimum cost of transport, $C_{\mathrm{mr}} = P(V_{\mathrm{mr}})/MgV_{\mathrm{mr}}$ for the range of bat flight morphology, reflected by the mean morphology of each of the 16 bat families for which we have sufficient morphological data. Expressions for speed, power and cost as a function of morphology were then obtained by log-linear regression. All the multiple regression models we derived provided an extremely close fit to the estimated values ($r > 0.9999$); the formulae may be used to estimate performance for any bat. The strength of the expressions here lies in their ability to estimate how performance – as indicated by speed, mechanical power and cost of transport – might alter as the wing morphology of any individual bat lineage evolves. We derived the following expressions:

$$V_{\mathrm{mp}} = 8.96\ M^{0.214} = 6.58\ M^{0.422}\,B^{-0.479}\,S^{-0.148}; \tag{4}$$

$$V_{\mathrm{mr}} = 11.75\ M^{0.211} = 8.71\ M^{0.423}\,B^{-0.498}\,S^{-0.144}; \tag{5}$$

$$P_{\mathrm{mp}} = 10.87\ M^{1.185} = 24.01\ M^{1.555}\,B^{-1.794}\,S^{0.314}; \tag{6}$$

$$C_{\mathrm{mr}} = 0.105\ M^{-0.036} = 0.319\ M^{0.108}\,B^{-1.264}\,S^{0.468}. \tag{7}$$

If wing shape and relative wing size in bats are constant (that is if wingspan, wing area and other dimensions vary isometrically with body mass so that, for example, $B \propto M^{\frac{1}{3}}$ and $S \propto M^{\frac{2}{3}}$) the multiple regressions in equations (4) to (7) may be rearranged to correspond closely to the expected scalings $V \propto M^{\frac{1}{6}}$, $P \propto M^{\frac{7}{6}}$ and $C \propto M^{0}$; these predicted results are derived either from similarity models or from (3) with the assumption that there is no systematic size variation in p_{i}, p_{par} and p_{pro} (von Helmholtz 1874; Pennycuick 1969, 1975; Lighthill 1974). With the further assumption that lift coefficient is constant, speed is expected to be proportional to the square root of wing loading, Mg/S, a result that may also be derived from (4) and (5) on assuming isometry.

In these equations, the deviations from isometry of the expected scalings of speed, power and cost against body mass alone result from departures from isometry within the Chiroptera. The predicted rise in aerodynamic power with mass or size between different bats ($M^{1.185}$) is considerably steeper than that ascribed to other components of energetics, which vary approximately as $M^{0.75}$ (McNab 1982). This implies that surplus energy available for enhanced flight activity falls off as size increases, so that smaller bats have greater reserves of power, relative their requirements for activity, than larger bats. Therefore, constraints on adaptation and behaviour imposed by flight energetics should be stricter in larger bats, in which the energy demands of flight might substantially limit activity (e.g. *Pteropus poliocephalus*, p. 416). We propose that, in most smaller bats, factors other than power or energy may be the dominant influences on wing adaptations, with power becoming more critical as size increases.

These equations show that with variation of body mass in an individual without change in wing dimensions (e.g. during feeding, pregnancy or extended flight) performance does not scale isometrically, and the $M^{\frac{1}{6}}$ and $M^{\frac{7}{6}}$ rules for scaling of mechanical performance do not apply. Furthermore, the apparent $P \propto M^{0.70}$ rule for interspecific scaling of metabolic flight power in bats (see, for example, Carpenter 1986, S. P. Thomas 1987), is not valid within an individual bat or within a species. Instead, in an individual bat, speed is predicted to vary as $M^{0.42}$ and mechanical power as $M^{1.56}$; these results are close to the 0.5 and 1.5 indices derived by Pennycuick (1975, p. 21).

A limitation of this analysis is our use of the mechanical energy consumption in flight (calculated as the mean rate of increase of the kinetic energy of the air surrounding the animal) as a measure of flight power. Selection could be more influenced by a bat's total fuel use or by metabolic flight power, which is usually obtained from mechanical power by assumption of constant efficiency (Pennycuick 1969, 1975; Tucker 1973). This is not justified by our present knowledge of flight physiology (above relations; see also Rayner (1986)) but because there are few metabolic measurements on bats (see, for example, S. P. Thomas 1975, 1987; Carpenter 1985, 1986) we have had to accept that mechanical and metabolic flight powers are directly proportional.

Equations (4)–(7) predict no direct relation between flight speed and aspect ratio, except in the sense that bats with a high aspect ratio are likely to be more efficient in flight and therefore, at a given size, to have greater power in reserve for acceleration. Several authors (e.g. Findley *et al.* 1972) have claimed that such a relation should be expected, but this must occur indirectly because the wings of the fastest flying bats (e.g. molossids) not only have high aspect ratio but are also unusually short, and therefore have high wing loadings. We will ascribe this to selection for good rolling acceleration.

Narrow wings always have small wing areas and high wing loadings unless they are also long; a bat with high wing loading (but with short or average-sized span) must fly fast to obtain sufficient weight support; by flying fast it reduces the induced power but increases parasite and profile powers. Because profile power is much larger than induced power at high speeds, and increases slightly with length of wing (Rayner 1979), fast-flying species should have short wingspans (equations (4) and (5)). Bats with long wings of high aspect ratio usually have low or average wing loading (e.g. some emballonurids, mormoopids and vespertilionids; see below) and fly slowly, whereas bats with short or medium-length wings of high aspect ratio (e.g. *Taphozous* and molossids) have a high wing loading and must fly fast. Long wings should be advantageous also for migratory bats, whose goal is to minimize the energy consumed covering a given distance. Migratory bats do not necessarily have to fly fast and their wing loadings are rather low. Bats requiring to make extended flights when time is at a premium benefit from both high aspect ratio and high wing loading; possible examples would include long-distance commuting to and from a colonial roost by refuging species. So long, narrow wings of high aspect ratio are favoured for slow forward flight economy, and short, narrow wings of high aspect ratio are appropriate for economic fast flight. However, long wings increase the static and inertial loads on the wing skeleton, and these loads may be limiting at the high wingbeat frequencies necessary with short wings or at very slow flying speeds (Norberg 1979, 1981*b*; Rayner 1987). Bats could counter these loads by evolving a stronger, and heavier, skeleton, but this would in turn raise flight energy demands. Bats with a low aspect ratio (short, broad wings) and low wing loading (large wing area) can fly slowly within vegetation. A large tail membrane and broad wings enable the bat to make rapid changes of direction in slow flight, and permit the use of the membrane to catch insects.

Although overall wing shape is critical for determining flight power and preferred flight speed, forward flight performance has little obvious relation to wingtip shapes. Our mechanical model treats the wing as an integral surface, and does not distinguish between the functions of the hand- and arm-wings in weight support or thrust generation. However, two factors may influence wingtip shape. First, in fast forward flight the noctule *Nyctalus noctula* and the megachiropteran *Rousettus aegyptiacus* generate lift continuously during both downstroke and upstroke, and minimize retardation during the upstroke by flexing the elbows and drawing the wingtips in towards the body while retaining the leading edge of the wing more or less straight (Rayner 1986, 1987; Rayner *et al.* 1986). Evidence from wingbeat kinematics suggests that these observations are representative of many bats. The bat wing permits little flexure or folding of the hand-wing without serious loss of lift; flexure can be greatest (retardation least) with relatively long arm-wings or short hand-wings. Thus, in fast-flying bats, the tip length ratio (T_l) might be rather low.

Second, the wingtip ratios are also related to the distribution of lift across the wingspan (Rayner 1986), but the importance of this is harder to assess because of two conflicting influences. Thrust is obtained most efficiently from a flapping wing with a distally skewed distribution of lift; for this reason, steady flapping flight is favoured by rounded wingtips, and hence by large tip shape index, I. But if wing strength or wing mass is critical, maximum lift with given bending moment along the wing axis is obtained when most lift originates from the inner portion of the wing; in this case the wingtips should be small (low T_S) and I should be relatively low. This constraint on wing mass is presumably more important when the wings are narrow and the aspect ratio is large, but it could also be relevant when the wingspan is short and wingbeat frequency is high.

Together these pressures form a plausible explanation for the particularly high aspect ratio and slightly pointed wingtips (I just greater than unity) in fast-flying molossids (but see also below) and for the low tip-shape index in some small-winged pteropodids. Closely analogous factors are responsible for the pointed wings in fast-flying birds, such as ducks and alcids, which have little requirement for slow-flight manoeuvrability. Other than these factors we find no mechanical grounds to support the suggestion of Findley *et al.* (1972) that fast-flying bats should have long wingtips (high T_l), although we find a non-significant correlation between these quantities in our analysis of flight speeds (§4.5).

For the reasons outlined here, power, speed and cost optimization may represent strong pressures on morphological adaptation. Power, or some measure of it (e.g. power per unit mass, P/M, or the ratio $P/M^{0.75}$, of mechanical flight power to an index of metabolism), could be used as currency for modelling the overall energy demands of flight. Cost of transport might be a more realistic currency for migrants or for long-range foragers. The size and shape of the wings of aerial-foraging bats should ensure that the most economic foraging speed is compatible with the typical flight characteristics (speed, predictability, habitat) of their prey. For such animals it is possible that intermediate, rather than extreme, wing loading and flight speeds might be favoured. The importance of flight speed and energy as constraints on the adaptive radiation of bats is wider than this narrow mechanical context, however, because morphological adaptations must ensure that the overall component of flight energy in the energy budget is most economical, and also that the bat's behavioural and ecological plasticity (the range of flight patterns and environmental conditions it can accommodate) is sufficient that the risk of failing to survive and reproduce is acceptably small.

3.3. *Hovering and slow flight*

For bats foraging in confined spaces, the abilities to fly slowly, to manoeuvre and to hover are important and are essential for some gleaning insectivores and for hover-feeding nectarivores. We have identified three major mechanical constraints on slow flight and hovering performance, namely power, wing inertia and lift generation. Power is probably the most important, for at low speeds it is large owing to the dominant induced power component. Induced power to fly slowly at a fixed speed is proportional to M^2/B^2 (equation (3)); in hovering, it is proportional to $M^{1.5}/B$ (Pennycuick 1969; Rayner 1979). Hovering should be more prevalent in smaller bats, and is favoured by relatively long wings. Aerofoil stall may also be a problem, as in slow flight and in hovering the arm-wings travel slowly and the lift they generate is relatively small. Effective lift generation demands relatively large wingspan and low wing loadings; because profile drag is relatively unimportant, there is no reason to expect a high aspect ratio. However, wing inertia and the proximity of obstacles prevent excessive wing lengths. Most of the wing mass is located in the arm-wing and at the wrist joint; to reduce wing inertia the arm-wing should be short (Norberg 1979, 1981*b*), i.e. T_l should be large. Lift in hovering is proportional to the second moment of wing area (Rayner 1979); hovering bats should have relatively large (high T_l and T_S) and rounded wingtips (high I). Relatively high wingbeat frequency and amplitude also optimize lift in hovering (Rayner 1979), but the wingbeat in hovering is complex and the necessary anatomical correlates (Norberg 1970*a*, *b*, 1976*b*) are beyond the scope of this paper.

3.4. *Mass variation and load-carrying ability*

Bats sometimes have to carry heavy loads; some species are more capable of this than others. Because, in an individual bat, power rises with mass or with 'all-up' load approximately as $M^{1.55}$ (equation 6), flight energy can be a severe constraint on load transport. There are three major sources of enhanced loading, namely the transport of food items, the transport of foetuses or of young by (possibly lactating) females, and natural seasonal and daily mass variations; in some circumstances the changes in weight related to loads can be considerable. The largest single food items are carried in flight by carnivores: the megadermatid *Macroderma gigas* ($M = 0.12$ kg) can fly with single rodents up to half of its own mass in its teeth (Kulzer *et al.* 1984). Frugivores and sanguivores may ingest large quantities of food in a single bout, and frequently fly back to the roost to refuge food; vampires may take on as much as half of their normal mass as blood, although this impairs their flight ability (Wimsatt 1969; Crespo *et al.* 1970; McNab 1973). Similar loads are associated with pregnancy; pregnant *Leptonycteris nivalis* may fly with body mass enhanced by as much as one third compared with normal mass, and the total mass carried by bats flying with young may be as much as double that of the adult female (R. Davis & Cockrum 1964). It is not clear whether bats regularly or consistently carry young in flight, or do so only when moving roost or when disturbed (R. Davis 1970). Flight during the later stages of pregnancy or with young probably represents the most critical loads carried by bats, and may be one of the reasons why bats' wing areas are large compared with those of birds of similar mass, and why many bats show reversed sexual dimorphism. Many insectivorous species are able to carry considerable loads. Of a number of species tested by R. Davis & Cockrum (1964), the best load-carrying ability was found in a female *Plecotus townsendii* ($M = 0.010$ kg) which carried a load equivalent to 73 % of its own mass; like many other plecotines (p. 397) this species has an unusually low wing loading. This ability is not required directly by predation (food items of insectivorous bats are usually small) but reflects rather that temperate bats must enhance body mass before hibernation and to cope with periods of food shortage.

Mass-carrying ability will be linked most closely with wing loading. As wing loading increases, the bat must fly faster and expend more energy, and the range of accessible flight behaviour is reduced until flight is no longer possible. Because they habitually fly with substantial loads, we expect carnivores to have relatively low wing loading. Large wingspan will convey power economy, and large wing area and large wingtips ensure sufficient thrust and weight support when loaded, without risk of stall. Large wing area also permits a slow controlled approach to prey and facilitates easy take-off under load; this feature, shared also with owls, appears essential for nocturnal carnivores. However, bats may have low wing loadings for reasons other than carnivory; the load-carrying ability of plecotines (which are insectivorous) reflects their large wings suited for gleaning or for slow flight in clutter. Relatively large wings also allow bats more readily to tolerate some degree of natural mass variation.

Because power increases steeply with load (as $M^{1.55}$), smaller bats, which have relatively more power in reserve, can carry additional weight more readily than larger ones. It may be ecological factors, such as food size and availability, which preclude carnivory or frugivory with large prey items in very small bats. For the same reasons, the pressures on morphology associated with load-carrying, hovering, forward flight, take-off, landing and manoeuvrability in smaller bats should also be somewhat weaker than in larger-sized animals.

3.5. *Manoeuvrability, agility and turning*

Many bats live or forage in cluttered environments, and some pursue active, agile and unpredictable prey. These two factors have strongly influenced flight adaptation. In the Microchiroptera, successful foraging, particularly in clutter, is also influenced by echolocation; some species use calls which are clutter-resistant, whereas some do not (see, for example, Neuweiler 1984); others forsake echolocation while hunting (Fenton 1984). In some cases foraging success may be more limited by echolocation than by flight performance, but data on this point are lacking.

Manoeuvrability has been understood by many authors in a general sense as a bat's ability to exploit its environment other than by steady flight or hovering; however, the term has not been properly defined. Central to the concept is the ability to change flight direction, but we draw mechanical distinctions between turning in a small space, turning without loss of speed or momentum, and initiating a turn rapidly. These different aspects of performance conflict to some extent; a fast turn with small turning radius is rarely possible, and a tight turn must necessarily be slow. Although many authors (e.g. Struhsaker 1961, Dwyer 1965, Vaughan

1966, Strickler 1978*a*) have equated low aspect ratio with low speed and good 'manoeuvrability', there is no direct relation between these quantities. For example, low aspect ratio acts against rapid changes of direction unless, as in rhinolophids and nycterids, it is linked with low wing loading, when it becomes an adaptation for turning in slow flapping flight.

To clarify this problem we define two terms. Manoeuvrability refers to the space required by a bat to alter its flight path while flying at a fixed speed; it is inversely proportional to the minimal radius of turn which the bat can attain, and also to wing loading. The lower the turning radius (the higher the manoeuvrability), the smaller the space in which a bat can fly effectively, and the greater the chance of catching close prey or of flying in cluttered environments. Agility is the maximum roll acceleration during the initiation of a turn, and measures the ease or rapidity with which the flight path can be altered. Agility has a more complex relation with morphology than does manoeuvrability.

(*a*) *Turning flight manoeuvrability*

In a level, steady turn the animal must generate a transverse or lateral force to provide centripetal acceleration, while still supporting the weight and flapping the wings to give thrust. This is achieved by banking the body and wings so that lift has a component towards the centre of curvature of the flight path. The theory of turning in powered flapping flight has been discussed by R. Å. Norberg & Norberg (1971). The thrust generated by the flapping wings may permit the animal to turn without net loss of height, provided that the bank angle is not too large. In a powered turn, wingbeat kinematics are dictated by the balance between weight support, thrust and the lateral force required for equilibrium, all of which must be obtained from the lift force on the flapping wings. Because flight speed is determined by wing loading, bats have the greatest opportunity to enhance the lateral force when the wing loading is low. The radius of turn, r, is also determined by the wing loading ($r \propto Mg/S$). Rayner & Aldridge (1985) analysed a slow flapping turn by *Plecotus auritus*, and found that lateral acceleration (V^2/r) rises to a peak at the sharpest and slowest point of the turn; at this stage performance is limited by the total force lateral to the flight path (weight plus thrust plus the effect of lateral acceleration). Aldridge (1985, 1986) demonstrated that similar constraints apply to the sharpest turns (highest manoeuvrability) in seven British species.

A bat of given wing loading and mass can turn tightly at a low speed, or can make a wider turn at higher speed. In either case optimal performance is obtained with maximal lift coefficient at the peak of the turn, and both flight speed and manoeuvrability are determined by wing loading, Mg/S. Manoeuvrability is optimal in bats with low wing loading and with the ability to enhance mean lift coefficient significantly above its comparable value in straight flight. Additional correlates of this may include both high wing camber (fore–aft curvature across the wing chord) and the ability to control camber by flexing the fifth digit or by depressing the hindlimb (Vaughan 1970*b*; Norberg 1972*b*; Baagøe 1987; Rayner 1986).

Turning may be most important in cluttered environments, where a large wingspan could be a disadvantage. For high manoeuvrability, wings should have large wing area (low wing loading), reduced wingspan and low aspect ratio. This means also large tip shape index, I; if the tip area index (T_S) is average, the tip length index (T_l) must be small. The rhinolophids and hipposiderids we examined have these characteristics.

(*b*) *Agility and the initiation of turns*

To initiate a turn from steady flight, a bat introduces asymmetry into the distribution of lift across its wingspan to produce a net rolling moment. Asymmetry can be achieved in at least four ways: (1) by flexing one wing differentially; (2) by pronating or supinating part of the wings; (3) by stalling part or all of one wing; and (4) by introducing negative camber on one wing to produce a negative angle of attack so that lift is directed ventrally. To retain momentum a bat must simultaneously maintain enough lift to balance both thrust and weight. Bats approaching a turn commonly gain height, which is a means of slowing to obtain a tighter turn (for any bat V^2/r is fixed, so that r is least when V is least), and temporarily transfer kinetic energy to potential energy during the turn (Rayner & Aldridge 1985).

When the total horizontal and vertical forces are in equilibrium, the aerodynamic rolling torque τ across the wingspan is equal to $MgB\lambda_1$, where λ_1 is the first spanwise moment of the distribution of lift across both wings. In straight flight λ_1 is normally zero. Andersson & R. Å. Norberg (1981, equation (14)) suggest that in initiating a turn this quantity may be proportional to BS; if this is true, flight speed must fall as the bat rolls, but we have assumed that in the early stages of a turn the bat does not alter its speed, but simply controls the moment of lift by adjusting wing plan-form and/or wing area. The maximum angular acceleration, $\alpha_{\max}$, available to a bat, and hence the fastest entry into a turn and the greatest agility, is then obtained as

$$\alpha_{\max} = \tau/J = MgB\lambda_1/J, \tag{8}$$

where J is the total roll moment of inertia of the body (J_b) and wings (J_w). The relation between λ_1 and J_w and wing morphology is not clear, but we indicate below some likely trends affecting roll performance.

The total roll moment of inertia comprises two components, the inertia of the body and of the wings about an axis parallel to the flight path passing through the centre of the body. Both have been measured for a small sample of insectivorous microchiroptera (Norberg 1976*a*; Aldridge 1985); the data suggest that body and wing inertia are broadly comparable in magnitude. In *Plecotus auritus* the measured wing inertia, J_w, about the humeral joint was 1.1×10^{-6} kg m^2 (Norberg 1976*a*), and Aldridge (1985) estimated the roll moment J_b of the body to be 0.84×10^{-6} kg m^2. We assume therefore that, in bats, wing- and body-roll moments of inertia are comparable, with wing inertia probably slightly larger. A decrease in either or both could favour agility by permitting enhanced maximum roll acceleration, thus reducing the time taken to enter and complete a turn. Bats adapted for fast rolling turns should have relatively thin or narrow bodies. Wing inertia is determined by the spanwise distribution of mass on the wing, which is controlled predominantly by the size and location of the components of the wing skeleton. Mass distribution decreases distally along the wing, with peaks corresponding to the elbow and to the carpal joint and fifth digit, which make the dominant contribution to inertia (figure 17 in Norberg 1976*a*).

Here we have to model wing inertia in relation to the dimensions of the wing. On dimensional grounds it can be argued that wing inertia will be proportional to $M_w B^2$, with the constant of proportionality being related to wing shape, that is to aspect ratio and the wingtip indices. In this analysis we cannot suppose that wing mass, M_w, is proportional to body mass, M (although this could be a good approximation in bats as a whole). Wing mass is dependent on wing dimensions and will rise with wingspan and wing area unless there is unusual thinning of the skeleton, apparently precluded for mechanical reasons. Although there are insufficient data to relate wing mass directly to wingspan, wing area and the other wing measurements, it seems reasonable to suppose that wing mass will increase at least in proportion to wing area or to wingspan squared. This means that J_w will vary with wingspan and/or wing area at least as fast as SB^2, and possibly as fast as SB^3; both have similar implications for adaptation of wing morphology for agility.

Inertia should fall with rising tip length index, T_l, as this corresponds to a more proximal location of the carpal joint (Norberg 1979, 1981*b*). To enhance roll agility it is advantageous to have relatively pointed wingtips, so that the tip shape index, I, should be low and the aspect ratio high; this ensures that wing mass is not concentrated towards the wingtips.

Agility depends also on the magnitude of the first moment of lift λ_1 which can be generated by distorting the wings. The most natural mechanism for initiating a roll in fast flapping flight is to pronate one wing and supinate the other (see, for example, Norberg 1976*c* on *Nyctalus noctula*). The moment λ_1 is dimensionless and is independent of wing size, but it is influenced by wing shape. When pronation is confined to the hand-wing, λ_1 will be greatest on wings with large, rounded tips (high T_S, high I and low aspect ratio). Roll movements are often accompanied by flexure of the wings to reduce wing area and inertia, J_w (*Nyctalus noctula* and *Otomops martiensseni*) (Norberg 1976*c*); flexure is most readily achieved with relatively long arm wings (low T_l).

These three possible pressures on wingtip shape for increased agility conflict. For low inertia, T_l and aspect ratio should be large but I should be small. Large wingtips (large T_S and I and low aspect ratio) can provide a large moment of lift. For maximum wing flexure and the greatest possibility of controlling inertia, T_l should be small; however, few bats with low T_l are reported as highly agile, and we think that this third pressure is probably weak. The other two are important. For instance, compared with other vespertilionids, noctules have small wings with long, thin tips corresponding to reduced roll inertia, and their habit of hawking for flying insects at high flight speeds demands high agility (Norberg 1976*c*). On the other hand, high roll rates as high as 450 rad s^{-2} have been recorded by Aldridge (1985) in horseshoe bats (Rhinolophidae) compared with values between 130 and 275 rad s^{-2} in other British microchiropterans (excluding *Nyctalus*). The wings of horseshoe bats have unusually small but rounded tips, which should tend to maximize inertia, but their relatively low wing loadings and highly cambered wings permit them to increase lift on the hand-wing to maximize λ_1. Taken together, these features allow rhinolophids to outweigh their high wing inertia and increase agility in slow flight. By comparison, the relatively long or pointed wingtips of the genera *Taphozous*, *Nyctalus* and molossids give good agility in fast hawking flight.

Agility can be achieved by fast or slow turns, which correlate with the different foraging environments used by noctules and horseshoe bats. Furthermore, morphological differences can be linked to differences in turning behaviour. Wing loading is the main factor distinguishing fast and slow turns. The small wings and high wing loading in noctules and molossids (linked to their high flight speeds; see below) may preclude enhancing λ_1, so for high agility they must reduce inertia as far as possible. Because they fly fast, the aerodynamic rolling torque (proportional to V^2) is large; their small wings are apparently dictated by the requirements of flight speed during foraging. On the other hand, horseshoes fly slowly, and make tight, slow turns with high manoeuvrability. With their larger, more cambered wings and much lower loadings they can readily increase lift and hence obtain good agility without wings specialized for low inertia.

3.6. *Acceleration, take-off and landing*

These aspects of flight behaviour seem to have less direct relation to morphology than do steady flight, agility and manoeuvrability. To a large extent acceleration and take-off performance are improved more by physiological adaptations that permit short-term anaerobic metabolism than by morphological specialization. Economical acceleration is favoured in streamlined bats with long and high aspect ratio wings (leaving more power for acceleration). Take-off is most straightforward when a bat can fall initially to gain momentum and flight speed. Take-off from the ground is more demanding, especially when loaded; as in birds, it forms a major constraint on flight, particularly for larger bats and for species with high wing loading (some molossids cannot take off from the ground (Strickler 1978*a*)). The vampire bats feed on foot; they are markedly agile in terrestrial locomotion, with specialized musculature permitting a rapid jumping take-off (Altenbach 1979). Many smaller insectivorous bats move well on the ground and can take off from a level surface (Lawrence 1969); some species swim and can take off from water (Kolb 1975, 1984; Kingdon 1974).

Landing can be a greater problem for bats that roost hanging upside down. Some bats land directly on vertical surfaces or branches and adjust their posture while clinging to the surface. Others, however, adjust posture in flight by performing a half roll while slowing to approach the perch (e.g. *Cardioderma cor* (Vaughan 1976); *Hipposideros commersoni* (Vaughan 1977); *Anoura geoffroyi* (G. G. Goodwin & Greenhall 1961); *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis nattereri*, *Barbastella barbastellus* (Barrett-Hamilton 1910; Kulzer & Weigold 1978)). These species all have rounded wings, which favour this form of landing because they allow roll at low speeds without loss of either momentum or lift. Bats with smaller or more pointed wingtips may be unable to use a rolling landing, but it seems essential for roosting beneath a horizontal surface or a small branch.

3.7. *Migration and commuting flight*

Much of our discussion concerns the ways in which bats use flight to locate and acquire prey, for we consider this to be the dominant influence on bat wing morphology. However, many species need to fly considerable distances, either in seasonal migrations or in nightly commuting flights, and because long sustained flights represent considerable drains on energy and time they may also influence morphology.

Many bats from a number of families migrate (§7), but with a few exceptions records for most migrating species are incomplete and conjectural. In the absence of other pressures on morphology, we expect migrants to have high aspect ratio and pointed wingtips giving low cost of transport. Since cost of transport falls slightly with increasing size (equation (7)), migration may be more common in larger bats. There is no obvious constraint on wing loading, but high wing loading gives fast flight and therefore reduces the time invested in migration. Only if migration flights are sustained for considerable distances are they likely to influence morphology significantly; we have insufficient information to test this fully.

In nightly commuting, however, the situation is rather different. Roosting in groups or colonies (refuging) can have many advantages, and has important consequences for foraging patterns and home range distributions (Bateman & Vaughan 1974; Kunz 1974; Heithaus & Fleming 1978; Fleming 1982). One advantage is that bats are familiar with, and regularly forage over, a wide area, but this can mean that they have to fly long distances nightly to locate food. For this reason we expect high aspect ratio (low cost of transport) and high wing loading (high flight speed) both to be beneficial for commuting species, but they may be outweighed when manoeuvrability or hovering are required to obtain food.

3.8. *Prey capture and foraging*

We have set out a range of basic patterns of flight (steady flight, acceleration, hovering, rolling, turning, take-off, landing) and have predicted how each should correlate with morphology. Perhaps the most demanding of flight tasks is the pursuit and capture of flying insect prey. Movements during prey capture must be synthesized from these components, but relatively little is known about the capture behaviour of flying insects by wild bats. Webster & Griffin (1962) and others have demonstrated that airborne insects are usually caught in the wing or tail membranes, and transferred to the mouth while in flight, without obvious serious impairment of flight performance while the wing is unavailable for lift (see also Schnitzler & Henson 1980). We have defined five basic prey capture techniques in insectivorous bats (§2.3). Here we discuss briefly how foraging behaviour should be reflected in morphology.

(*a*) *Insectivores*

Fast, long-range hawking. Bats which fly quickly in pursuit of flying prey rely primarily on speed to catch insects, and they must be agile at high speeds. These 'fast-hawking' species should therefore have high wing loading and long and pointed wingtips. They should have short, high aspect ratio wings to reduce cost of transport and permit high flight speeds.

Slow hawking. Many bats hawk insects while flying slowly, and usually detect prey at relatively short range; like fast-hawking species, they rely on rolling to initiate turns. Species foraging in open spaces may have long wings with a high aspect ratio, which reduce cost of transport and allow slow flight. Species feeding among clutter have greater need for manoeuvrability than agility, and should therefore be rather small; flight in clutter imposes short wings, and to provide sufficient manoeuvrability the wing area should be high, aspect ratio low, and the wingtips should be relatively short and rounded.

Trawling. This category refers to bats that 'gaff' insects from water surfaces, generally with their hindlimbs. Many other hawking species, particularly slow fliers in open spaces, feed opportunistically over water and may take aquatic insects. The main requirement for trawling is relatively slow flight (and hence low wing loading); because the foraging space is uncluttered, the wingspan may be long. High aspect ratio would give economic flight, but is not essential.

Gleaning. Many bats take resting or non-flying prey, by hover-gleaning or by ground-gleaning. Hover-gleaning consists of picking insects from surfaces while hovering or flying slowly. It shares many of the characteristics of slow hawking, and because of the use of confined space it is restricted to small bats or to species with a very low aspect ratio. Hovering is generally favoured by long wingtips, but this pressure could be outweighed by the advantages of short, rounded wingtips for manoeuvrable flight in clutter. Ground-gleaning bats may land to catch their prey; they require above all low wing loading permitting slow approach to prey and an easy take-off. Otherwise they share characteristics with bats using slow hawking in clutter and/or hover-gleaning. Some specialized species (mainly molossids, but also *Mystacina tuberculata*) also forage on the ground for flightless or resting arthropods; we do not consider how this might affect flight adaptations in these species.

Flycatching and perch-hunting. These are specialized capture modes in which the bat spends much of the time perched and seeking prey, and only flies when prey is located. Flycatching bats obtain insects in the air, and will therefore need high manoeuvrability (low wing loading). To ambush prey they may need good acceleration (large wingtips).

(*b*) *Other food sources*

The prey-capture modes of other animalivorous bats (carnivores and piscivores) can be compared directly with those of insectivores: piscivores 'trawl' for fish over water, and

TABLE 3. PREDICTED MORPHOLOGICAL CORRELATES OF FLIGHT PERFORMANCE

(The table shows how morphology is expected to vary with various indicators of performance and flight patterns. It therefore also shows the flight behaviour(s) for which a bat of particular morphology might be adapted. The plus symbols (+) indicate where a high value is more advantageous, and minuses (−) where a low value is expected. Indirect correlations (such as between aspect ratio and flight speed), which we did not predict in §5.3 but which are recorded owing to morphological allometry within bats, are not shown. Relations shown in square brackets are weak or uncertain. Isometric scaling is the trend of variation with size or mass if all morphological and kinematic parameters vary geometrically: because it is low power and cost that are important, these quantities decrease with size, and act more weakly on smaller bats. Selection for low flight speed is not shown: this is the obverse of selection for high speed. All characteristic flight speeds (V_{mp}, V_{mr}, etc.) are approximately proportional. Pressure for fixed flight speed (dictated, for instance, by prey flight speeds) corresponds to fixed wing loading; wingspan and wingtip shape are determined by other considerations.)

		isometric scaling	calculated or predicted morphological dependence M, B, S	A	Mg/S	T_l	T_S	I	notes
high flight speed	V	$M^{\frac{1}{6}}$	$M^{0.42}\,B^{-0.50}S^{-0.14}$	·	+	[−][a]	·	−	
low flight power									
forward flight power	P	$M^{-\frac{7}{6}}$	$(M^{1.56}\,B^{-1.79}S^{0.31})^{-1}$	+	·	·	·	+[b]	
hovering power	P_{hov}	$M^{-\frac{7}{6}}$	$(M^{1.5}\,B^{-1})^{-1}$	[−]	−	+[c]	+	+[b]	
low cost of transport	C	M^{0}	$(M^{0.11}B^{-1.26}\,S^{0.47})^{-1}$	+	·	−?[a]	·	−	
load-carrying		$M^{-\frac{1}{3}}$	$(Mg/S)^{-1}$	·	−	+	+	·	d
turning									
avoidance of clutter		$M^{-\frac{1}{3}}$	B^{-1}	·	·	+[c]	·	[+]	
manoeuvrability		$M^{-\frac{1}{3}}$	$(Mg/S)^{-1}$	[−]	−	[−]	[−]	+	d
agility	α	$M^{-\frac{1}{3}}$	$MgB\lambda_1/(J_b+J_w)$	·	·	·	·	·	f
low wing inertia	J_w	$(M^{-\frac{5}{3}})$	$1/(MB^2)_w$	+	+	+	[−?]	−	
high lift moment	λ_1	M^{0}	·	−	[−]	[−]	+	+	
insectivore feeding strategies									
fast hawking				+	+	+	·	−	
slow hawking				−	−	−	·	+	g
trawling				[+]	−	·	·	·	
hover-gleaning				−	−	[−]	·	+	
ground-gleaning				·	−	[−]	·	·	

Notes:

[a] Low T_l is expected on the basis of maximum upstroke flexure; the importance for steady high-speed flight is conjectural, but it is valuable for good acceleration.

[b] Rounded wingtips give optimal lift distribution.

[c] Long wingtips for optimal kinematics in slow flight (Norberg 1979, 1981*a*; Altenbach 1979).

[d] Also high chordwise wing camber or good ability to control camber (compare phyllostomids) for additional lift when loaded or in steeply-banked turns.

[e] Wing inertia modelled as MB^2, SB^2 or SB^3.

[f] The relation of agility to wing morphology depends on the magnitudes and variation of λ_1, J_b and J_w. Lift moment, λ_1, is more important in low speed rolls (that is in slow-flying bats) and in rolling landings (e.g. rhinolophids, hipposiderids), while the wing moment of inertia, J_w, is more critical in fast rolls in short- or small-winged bats (e.g. *Taphozous*, *Nyctalus*, molossids). See figure 9 and discussion in §3.5.

[g] Aspect ratio may be high in species hawking slowly away from clutter.

carnivores glean small vertebrates (usually from the ground) and sometimes hunt from perches. Many feed opportunistically on insects by using similar flight patterns. They should therefore have similar morphological characteristics. Nectarivores and some frugivores may hover while feeding and are predicted to have relatively long wingtips, but there are conflicting pressures on the wingspan: long wings reduce power and give easier lift generation, while short wings give agility and easier manoeuvrability in clutter. Other aerodynamic pressures on vegetarian species are weak, but bats feeding on patchily distributed food (this category also includes the sanguivores) may need to fly fast and so may have high wing loadings (see §3.7).

3.9. *Morphological correlates of flight behaviour: a summary*

A complex mosaic of characters influences the flight morphology of bats. In the above discussion we have selected stylized aspects of performance, determined the most favourable morphological adaptations correlated with them, and from these predicted how differing foraging techniques will be reflected in morphology. We have not compared the strength of the various performance influences acting on bats of different taxa or diets; nor have we tried to assess the importance of adaptational plasticity in determining the breadth of accessible flight performance for any bat. The various influences and their predicted morphological responses are summarized in table 3. In the remainder of the paper we consider the flight behaviour of individual species, families and groups of bats in the light of these conclusions. We use principal-components analysis to display the size and shape of wings in different bats to assess the importance of the mechanical constraints on different taxonomic and ecological groups of bats. To this end, in §4.3 we present the conclusions of the preceding discussion of flight mechanics in a form compatible with this analysis.

4. RESULTS

4.1. *Flight morphology and bivariate correlations*

Morphological data from our measurements and from the literature are given in table 1. The sources of these data are given in the legend to the table.

Bivariate correlations (RMA lines) between wing morphology (wingspan, wing area, aspect ratio and wing loading) and mass expressed as power functions are shown in table 4. Relations which are significantly allometric (in the sense that they differ significantly from the isometric design or geometric similarity hypothesis) are indicated by the symbol *. These relations are also plotted in figures 4–7; in each, part (*a*) is a scatter plot of all available data, and part (*b*) shows the RMA line for the individual families. Symbols used to distinguish the various families in these and subsequent figures are shown in the legend to figure 4.

These calculations and illustrations update the findings of Norberg (1981*a* (table 3 and §3.1)) with a considerably larger data set. In that paper, Norberg discussed the major trends both within and between the bat families and compared bat and bird wing morphology; the majority of the conclusions remain valid, and there are no significant differences between the regression calculations given there and the regressions associated with the RMA lines derived here.

The plots of aspect ratio (figure 6*a*, *b*) reveal an unusual phenomenon, which is not clearly understood. With mass, aspect ratio rises slightly, but non-significantly. In families consisting largely of smaller bats (e.g. Emballonuridae, Vespertilionidae, Molossidae) aspect ratio tends

TABLE 4. CORRELATIONS BETWEEN WING MORPHOLOGY AND BODY MASS IN BATS

(The relations shown below are the reduced major axes for the relevant sample, calculated on the basis of the mean species wing morphologies given in table 1. All quantities are expressed in units of metres, kilograms and seconds. The first column gives the number of records available for each class; sample sizes for each correlation are generally slightly smaller. Correlation coefficients for these relations are consistent; the significance of the majority of those between wingspan, wing area or wing loading and mass is at least 5%, non-significant values occurring for some families or subfamilies with very small sample sizes or narrow ranges of mass. Most correlations between aspect ratio and mass are not significant at the 10% level. For sample sizes greater than 2, deviations from isometry significant at the 5% level are indicated by an asterisk. There are insufficient data to determine scalings for primary piscivores; sanguivores vary as Desmodontinae.)

class	n	wingspan, B/m	wing area, S/m^2	aspect ratio, $A = B^2/S$	wing loading, $(Mg/S)/(\mathrm{N\ m^{-2}})$
isometry	—	$M^{0.333}$	$M^{0.667}$	M^0	$M^{0.333}$
all bats	257	$1.200M^{0.322*}$	$0.203M^{0.639*}$	$12.44M^{0.148}$	$67.16M^{0.444*}$
Pteropodidae	51	$1.230M^{0.350}$	$0.239M^{0.715*}$	$8.63M^{0.110}$	$45.37M^{0.327}$
Pteropodinae	37	$1.207M^{0.332}$	$0.238M^{0.717}$	$5.40M^{-0.111}$	$45.94M^{0.339}$
Nyctimeninae	6	$1.036M^{0.298}$	$0.174M^{0.581}$	$4.27M^{-0.107}$	$64.88M^{0.465}$
Macroglossinae	7	$1.544M^{0.423}$	$0.234M^{0.725}$	$15.42M^{0.234}$	$46.34M^{0.302}$
all microchiroptera	208	$1.262M^{0.332}$	$0.183M^{0.614*}$	$17.10M^{0.209*}$	$104.6M^{0.541*}$
Rhinopomatidae	2	$1.093M^{0.331}$	$0.069M^{0.436}$	$17.39M^{0.225}$	$142.9M^{0.564}$
Emballonuridae	13	$1.005M^{0.267}$	$0.075M^{0.401}$	$18.45M^{0.202*}$	$171.0M^{0.664}$
Nycteridae	4	$0.920M^{0.254}$	$0.142M^{0.477}$	$7.58M^{0.088}$	$71.98M^{0.533}$
Megadermatidae	3	$1.542M^{0.398}$	$0.361M^{0.764}$	$7.69M^{0.089}$	$28.11M^{0.248}$
Rhinolophidae	11	$1.439M^{0.352}$	$0.159M^{0.549}$	$11.14M^{0.128}$	$91.41M^{0.541}$
Hipposideridae	7	$1.371M^{0.331}$	$0.249M^{0.640*}$	$10.28M^{0.096}$	$43.08M^{0.381*}$
Noctilionidae	2	$2.676M^{0.538}$	$0.442M^{0.867}$	$16.21M^{0.209}$	$22.21M^{0.133}$
Mormoopidae	5	$1.329M^{0.325}$	$0.220M^{0.641}$	$3.04M^{-0.205}$	$96.90M^{0.529}$
Phyllostomidae	35	$1.290M^{0.355}$	$0.254M^{0.709}$	$3.64M^{-0.151}$	$52.47M^{0.372}$
Phyllostominae	9	$1.147M^{0.300}$	$0.233M^{0.646}$	$3.76M^{-0.165}$	$48.64M^{0.395}$
Glossophaginae	9	$1.428M^{0.378}$	$0.262M^{0.719}$	$13.32M^{0.160}$	$63.13M^{0.398}$
Carolliinae	2	$13.90M^{0.956}$	$5.276M^{1.457}$	$36.60M^{0.455}$	$75.86M^{0.457}$
Sturnirinae	2	$1.176M^{0.341}$	$0.157M^{0.610}$	$10.19M^{0.107}$	$62.54M^{0.390}$
Stenodermatinae	9	$1.253M^{0.358}$	$0.242M^{0.708}$	$5.21M^{-0.050}$	$60.54M^{0.400}$
Desmodontinae	3	$4.676M^{0.732}$	$0.064M^{0.343}$	$412.6M^{1.178}$	$453.3M^{0.975}$
Thyropteridae	2	$3.638M^{0.493}$	$0.937M^{0.836}$	$14.12M^{0.150}$	$10.51M^{0.165}$
Vespertilionidae	93	$1.520M^{0.370*}$	$0.324M^{0.729}$	$16.83M^{0.198*}$	$110.3M^{0.547*}$
Vespertilioninae	83	$1.494M^{0.367*}$	$0.304M^{0.718}$	$16.30M^{0.191*}$	$108.1M^{0.540*}$
Miniopterinae	3	$0.584M^{0.153}$	$0.096M^{0.470}$	$38.35M^{0.362}$	$803.0M^{0.985}$
Nyctophilinae	4	$1.374M^{0.332}$	$0.587M^{0.820}$	$2.44M^{-0.217}$	$24.05M^{0.261}$
Mystacinidae	2	$1.050M^{0.312}$	$0.0218M^{0.163}$	$50.65M^{0.461}$	$450.8M^{0.837}$
Molossidae	25	$1.384M^{0.362}$	$0.130M^{0.611}$	$21.11M^{0.218*}$	$103.7M^{0.476}$
primary insectivores	175	$1.295M^{0.334}$	$0.160M^{0.583*}$	$20.37M^{0.239*}$	$135.0M^{0.596*}$
primary carnivores	4	$1.239M^{0.319}$	$0.306M^{0.695}$	$4.40M^{-0.112}$	$32.12M^{0.305}$
primary frugivores	61	$1.231M^{0.350*}$	$0.235M^{0.702*}$	$8.36M^{0.092}$	$45.81M^{0.332}$
primary nectarivores	15	$1.290M^{0.361}$	$0.191M^{0.657}$	$12.68M^{0.163}$	$61.62M^{0.388}$
all insectivores	198	$1.282M^{0.334}$	$0.187M^{0.618}$	$17.37M^{0.211*}$	$103.7M^{0.539*}$
all carnivores	9	$1.312M^{0.353}$	$0.295M^{0.717}$	$10.23M^{0.202}$	$49.07M^{0.430}$
all piscivores	4	$1.802M^{0.399}$	$0.240M^{0.644}$	$14.19M^{0.168}$	$55.98M^{0.443}$
all frugivores	81	$1.226M^{0.341}$	$0.234M^{0.691}$	$4.72M^{-0.107}$	$47.16M^{0.349}$
all nectarivores	60	$1.232M^{0.349}$	$0.238M^{0.713*}$	$8.65M^{0.091}$	$44.99M^{0.318*}$

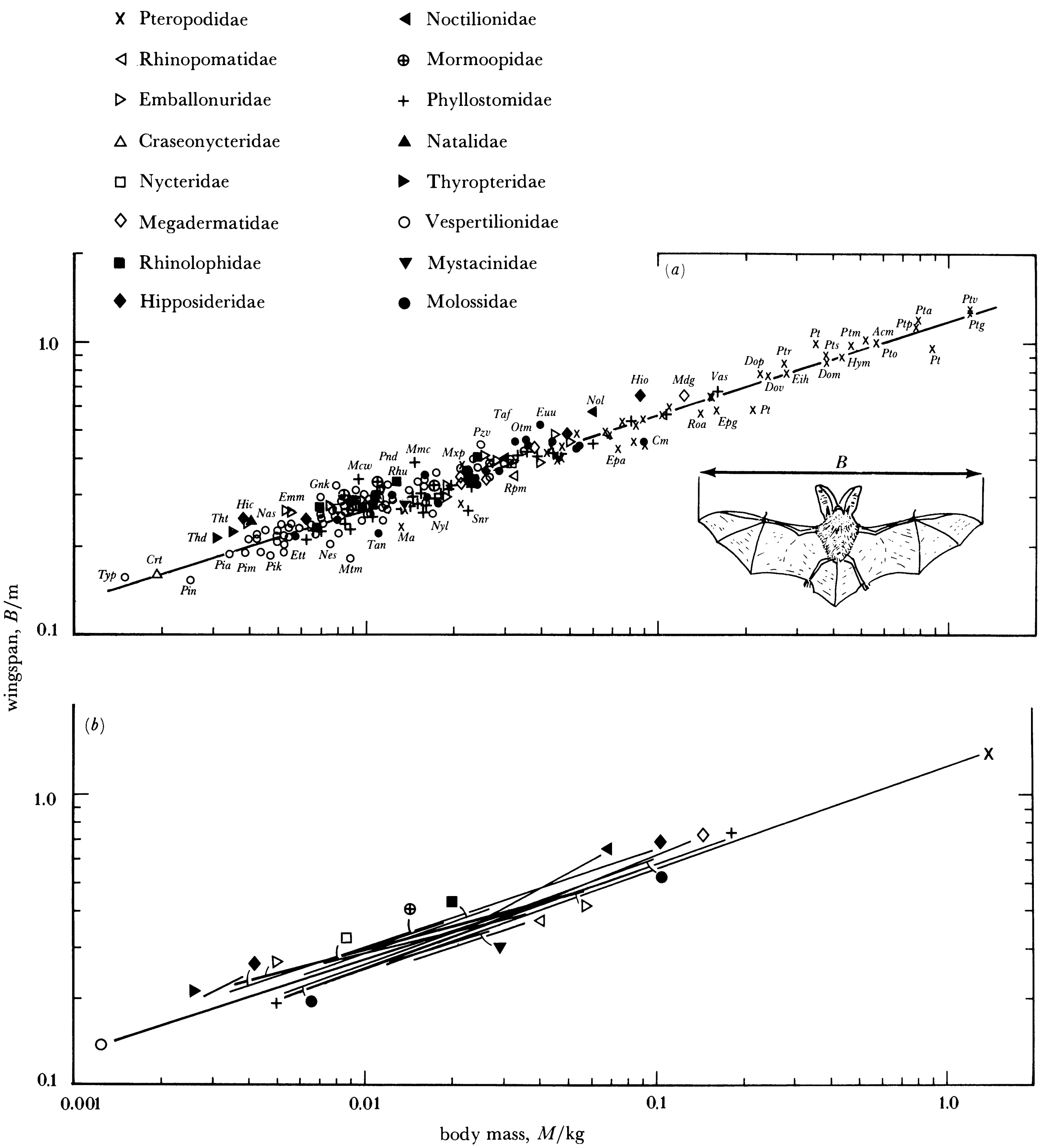


FIGURE 4. Wingspan, B, plotted on logarithmic coordinates against body mass, M, for bat species. (*a*) Scatter plot of wingspan against mass, together with symbols used in all figures to identify the different bat families; (*b*), mean variation of wingspan with mass for each family. Lines shown are reduced major axes; equations are given in table 4.

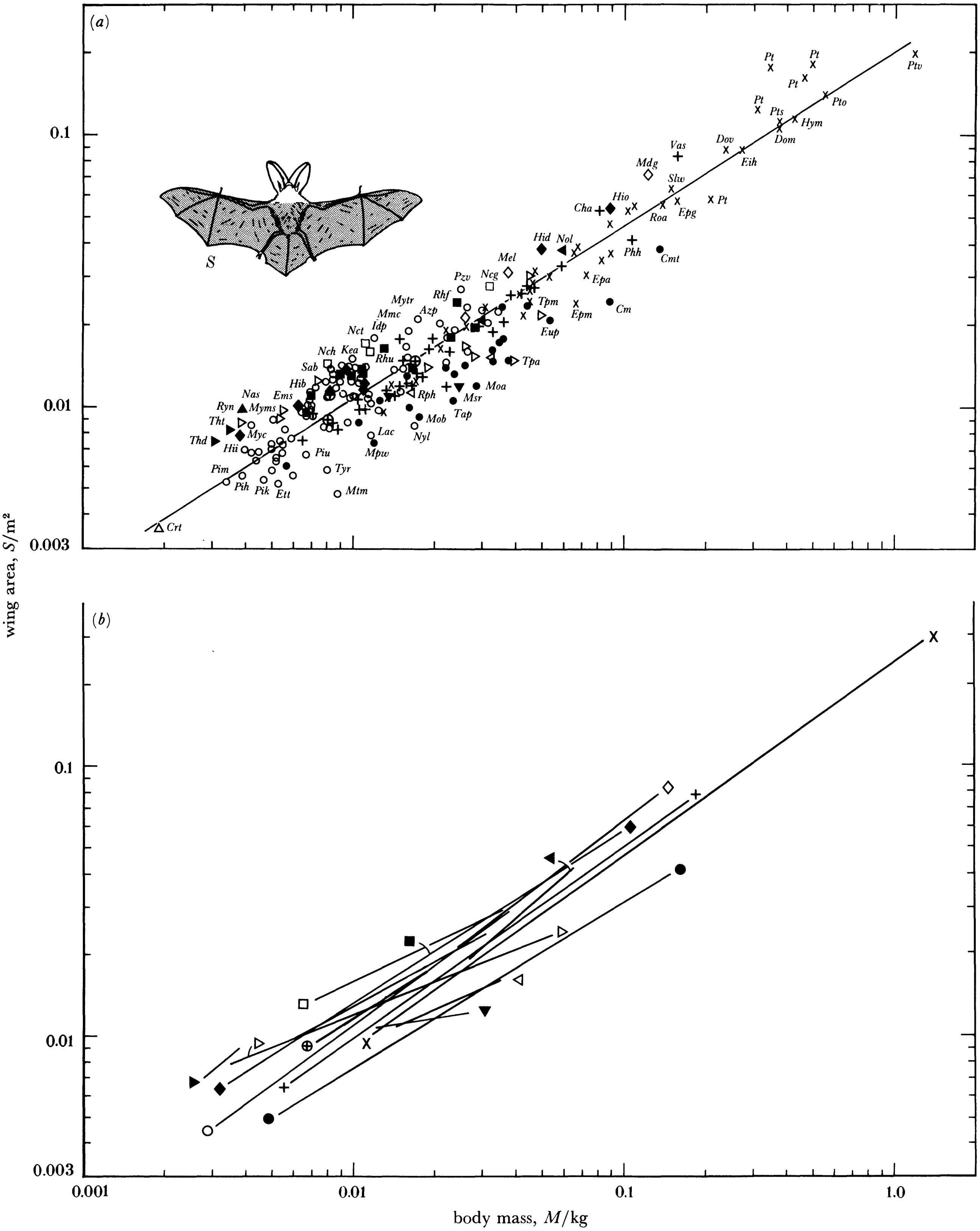


FIGURE 5. Wing area, S, plotted on logarithmic coordinates against body mass, M, for bat species. (Details as figure 4.)

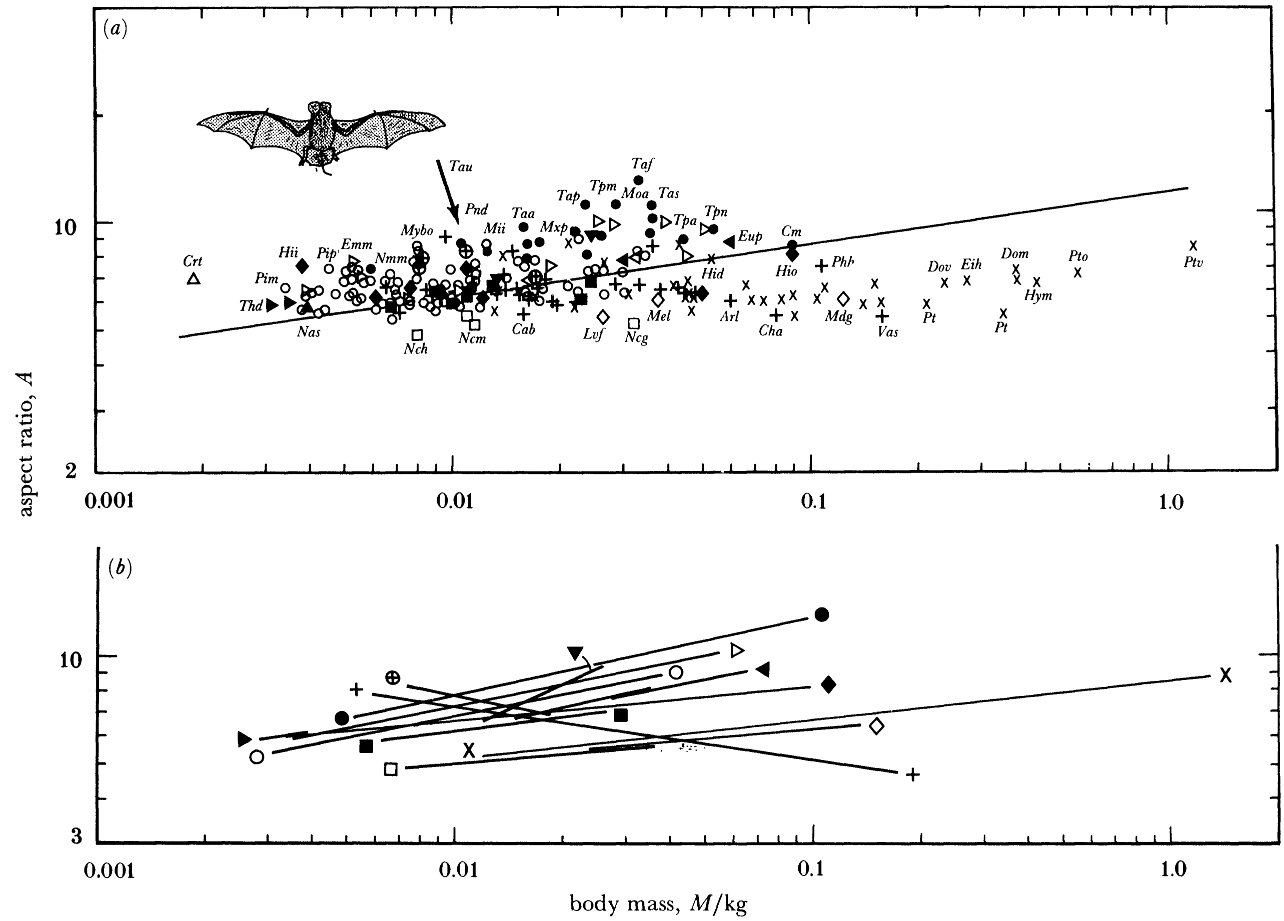


FIGURE 6. Aspect ratio, A, plotted on logarithmic coordinates against body mass, M, for bat species. (Details as figure 4.)

to rise more steeply with size, but this is not maintained into the larger size range represented largely by frugivorous pteropodids and phyllostomids. The result is that bats of body mass between 0.01 and 0.05 kg have a wide range of aspect ratios; the highest wing loadings relative to size are also found in this mass range (figure 7*a*). The species with unusually high aspect ratio (greater than 8.0) and wing loading include molossids as well as emballonurids of the genus *Taphozous*; the reasons for the small wings in these species can be traced to niche adaptations (§5), but this alone does not account for the concentration of high aspect ratios in a narrow size (mass) range. We conjecture that a combination of mechanical and ecological factors are responsible: fast-flying bats with a high aspect ratio rely on high-altitude hawking of flying insects. A balance between prey size, activity and availability, bat flight speed and flight behaviour and the problems of locating a small fast-flying insect may make this form of feeding behaviour uneconomical for both lighter and heavier bats. The only larger insectivorous genus, *Cheiromeles* (Molossidae), has near average aspect ratio.

4.2. *Principal-components analysis*

The principal-components analysis was performed on data from 215 species of bat from 16 families, the missing families being Furipteridae and Myzopodidae. Because body mass, wingspan and wing area are closely correlated, the first principal component, Q_S, was

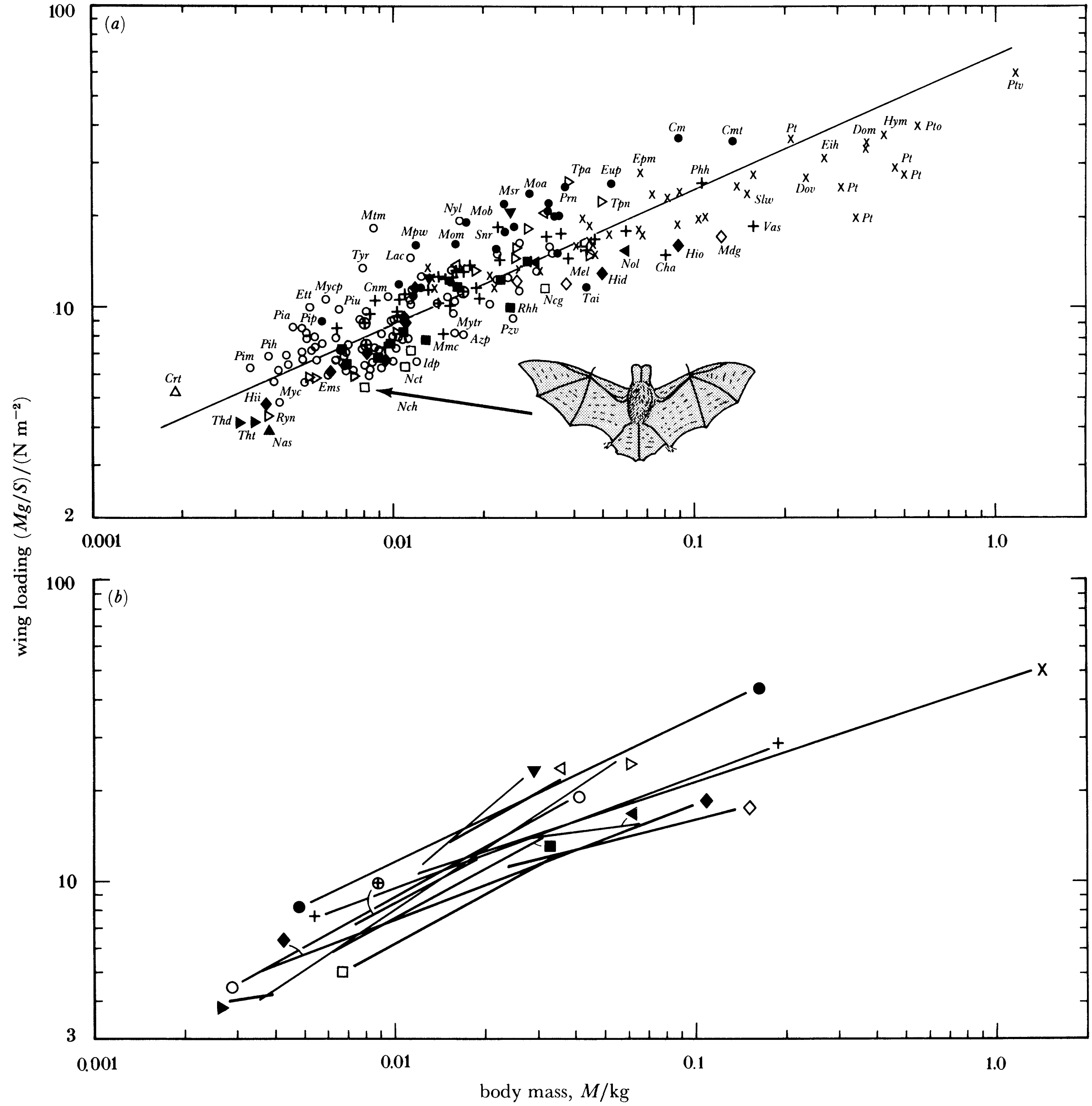


FIGURE 7. Wing loading, Mg/S, plotted on logarithmic coordinates against body mass, M, for bat species. (Details as figure 4.)

responsible for a significant proportion (97.4 %) of the overall variation, and we interpret this as a measure of size. Our discussion concentrates on components Q_1 and Q_a, which account for 1.8 and 0.8 %, respectively, of the variation. The small percentage variation explained by these components emphasizes the close scaling of wing proportions with size in bats, and implies that mechanical constraints responsible for this scaling are tight. Although statistically unimportant, these components effectively describe size-independent or shape variation between bats. The values assigned to them measure the deviation of any species from the 'average' morphology represented by size variation in Q_s alone ($Q_l = Q_a = 0$). The components were calculated as

$$\left.\begin{aligned} e^{Q_s} &= 77.0 \quad M^{0.31} \; B^{0.97} \; S^{0.49}; \\ e^{Q_l} &= 3.77\times10^{-3} M^{3.02} \; B^{-2.08} S^{-3.71}; \\ e^{Q_a} &= 1.81\times10^{-5} M^{-1.47} B^{14.6} \; S^{-5.12}. \end{aligned}\right\} \qquad (9)$$

Each component is expressed in standardized form so that the components have zero mean and unit standard deviation. The algebraic form of the second and third components gives them their interpretation as loading and aspect components: from equations (9) it is evident that Q_l is close in form to wing loading Mg/S and Q_a to aspect ratio $A = B^2/S$, each being corrected to ensure mutual statistical independence. In the remainder of this section the terms 'loading' and 'aspect' refer to principal-component values rather than to wing-loading and aspect-ratio values shown in table 1.

A limitation of this analysis derives from expressing components in standardized form. Because errors are size-dependent, in larger bats a small error in measured wingspan or wing area can produce a noticeable error in calculated shape components. This may explain the scatter in the aspect-ratio components of larger pteropodids.

Our calculated loading and aspect components are plotted in different ways in figure 8*a*–*g*. We show all species together (figure 8*a*), and separate them by superfamily (figure 8*b*–*e*) to facilitate some comparisons; figures 8*f* and *g* show the means of the various families and feeding classes as well as the mean value of Q_S for each group. In these figures, species with relatively small wings (high loading) and high aspect ratio are located in the upper right quadrant, those with large wings and low aspect ratio in the lower left quadrant, and so on. Species with a short span tend to have high loading but a range of aspect ratios, but species with long span have low or average loading and high or average aspect ratio. Our morphological comparisons refer usually to relative measurements, independent of body mass, or of size in the case of the principal components. An 'average' character of a species is average when compared with the mean for the entire sample, where necessary independent of size. The correlation lines in figures 4–7 and the axes in the principal-component diagrams in figures 8 and 11–15 mark the size-corrected means of the various quantities.

Our analysis reveals obvious differences between the bat families studied. Of the three families with particularly small members, two (Natalidae and Thyropteridae) have remarkably low loading but average aspect ratio, while the still smaller *Craseonycteris thonglongyai* has near-average wing dimensions. As the largest family, it is not surprising that most vespertilionids are near-average, although some species have disproportionately small wings. Four families have particularly high mean aspect ratio (mean $Q_a > 1$ in Emballonuridae, Noctilionidae, Mormoopidae and Molossidae) but none shows a correspondingly low mean aspect ratio. The wings of heavier bats tend to be relatively close to the average dimensions (Pteropodidae, Megadermatidae) although noctilionids have particularly high aspect ratio, coinciding with their specialized piscivorous habits. In terms of wing adaptation the molossids are the most specialized, reinforcing earlier studies (e.g. Vaughan 1966, Norberg 1981*a*). In general, however, size in molossids is average (first component $Q_S = 0.09$; figure 8*g*); this result supports our suggestion in §4.1 that extreme flight adaptations are precluded toward the extremes of the size range by a combination of mechanical and ecological factors. We discuss the wing adaptations and flight behaviour of individual species in detail in §5, and consider specializations associated with feeding classes in §6.

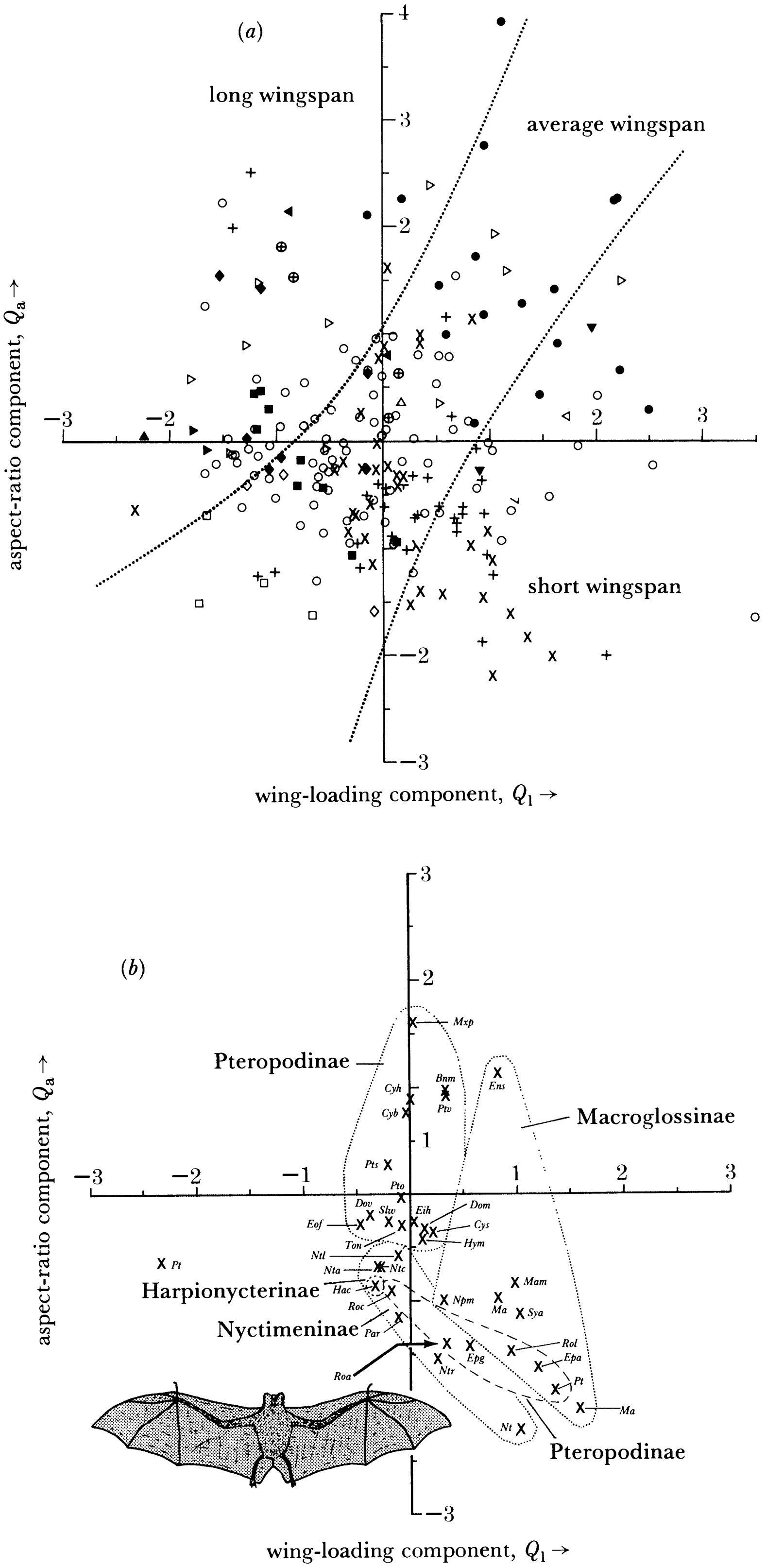


FIGURE 8(*a*,*b*). For description see p. 375.

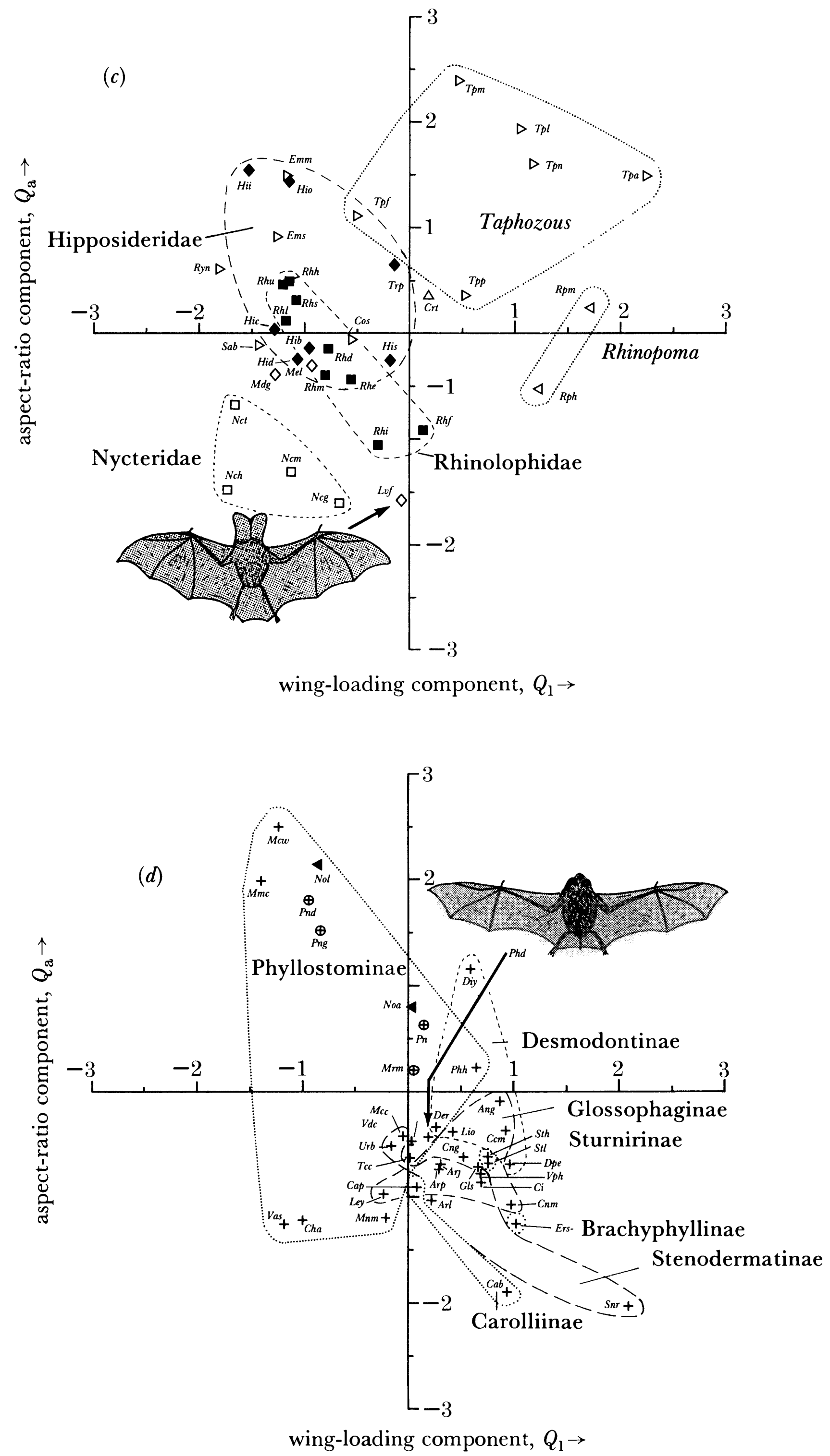


FIGURE 8 (*c*, *d*). For description see p. 375.

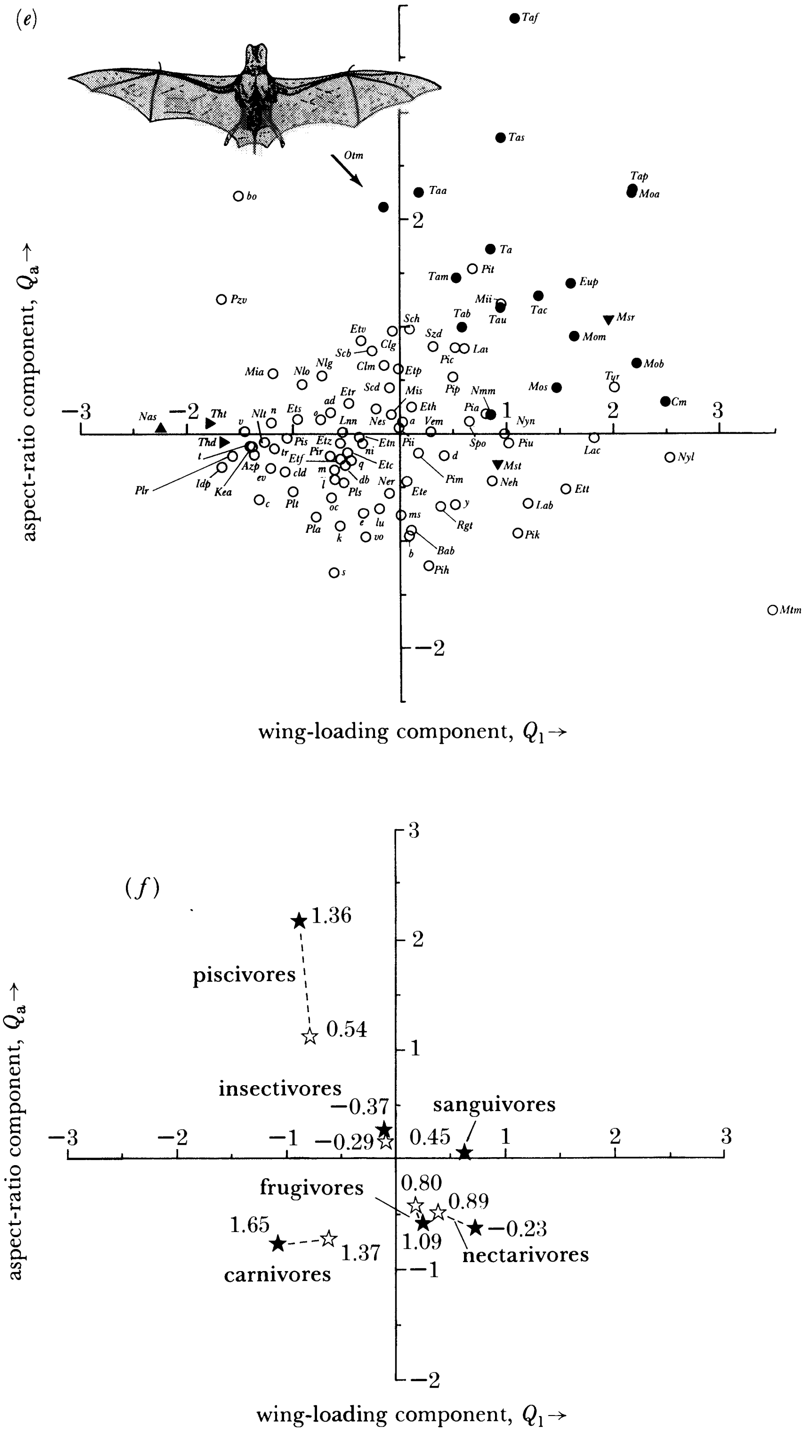


FIGURE 8 (*e*, *f*). For description see opposite.

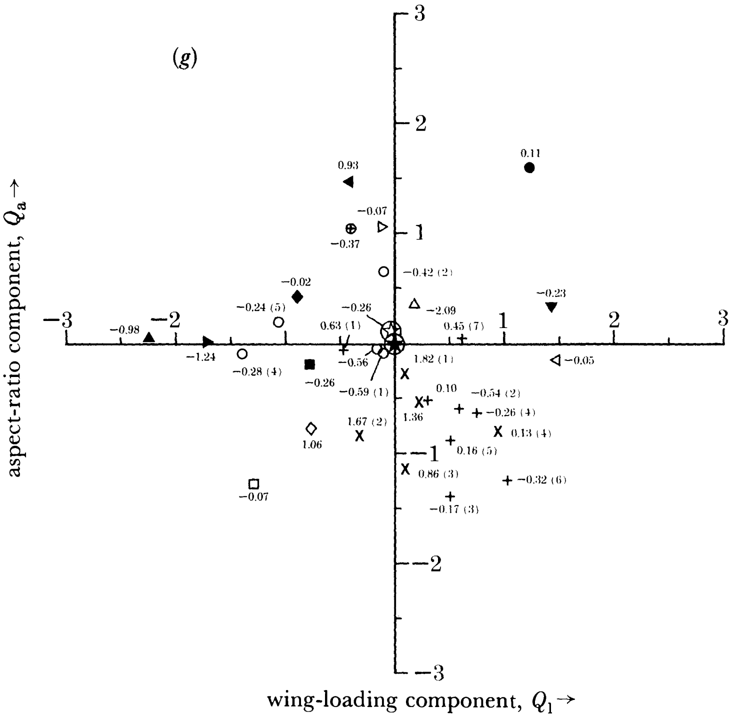


FIGURE 8. Scatter plot of second and third principal components of wing morphology in bats. The second component is identified as a size-independent wing size or loading, and the third component as wing shape or aspect ratio. The symbols used to identify families are shown in figure 4*a*. For convenience the figure has been divided into separate portions corresponding to the Chiropteran superfamilies, as follows: (*a*), all bat species; (*b*), Pteropodoidea (Pteropodidae); (*c*), Emballonuroidea (Rhinopomatidae, Emballonuridae, Craseonycteridae) and Rhinolophoidea (Nycteridae, Rhinolophidae, Hipposideridae, Megadermatidae); (*d*), Phyllostomoidea (Noctilionidae, Mormoopidae, Phyllostomidae); (*e*), Vespertilionoidea (Natalidae, Thyropteridae, Vespertilionidae, Mystacinidae, Molossidae); (*f*), means of principal components of bats grouped into different feeding classes; (*g*), means for each family and subfamily. In (*g*) the closed star is the mean for all bats, and the open star the mean for all microchiroptera, the numbers (1)–(7) indicate subfamilies for the respective families in the order in which they are given in table 1. In (*f*) the closed stars refer to the means of primary feeding classes, and the open stars to the mean for all bats taking that food. The numbers adjacent to each point in (*f*) and (*g*) are the values of the first (size) principal component; larger figures correspond to larger, generally heavier, bats.

4.3. *Principal components and flight performance*

In §3 we demonstrated how certain patterns of wing morphology favour particular flight tasks, and summarized the discussion in table 3. Now we recast our conclusions about the adaptation of relative wing size and shape to make them compatible with the principal components analysis.

If flight morphology evolves in response to pressure to perform a single flight task, then (at least as far as other constraints permit) wing morphology will change so that adopting a particular style of flight makes the greatest possible contribution to fitness. The predicted morphological responses to the tasks listed in table 3 are illustrated in figure 9, in a form compatible with the principal-component scatter plots of figure 8. For each pressure, the direction shown represents the way in which the morphology of a bat should change to maximize (or, where appropriate, to minimize) the relevant quantity, assuming that only that one selective pressure has a significant effect on morphology. These directions are calculated by converting the formulae (table 3) relating performance to body mass, wingspan and wing

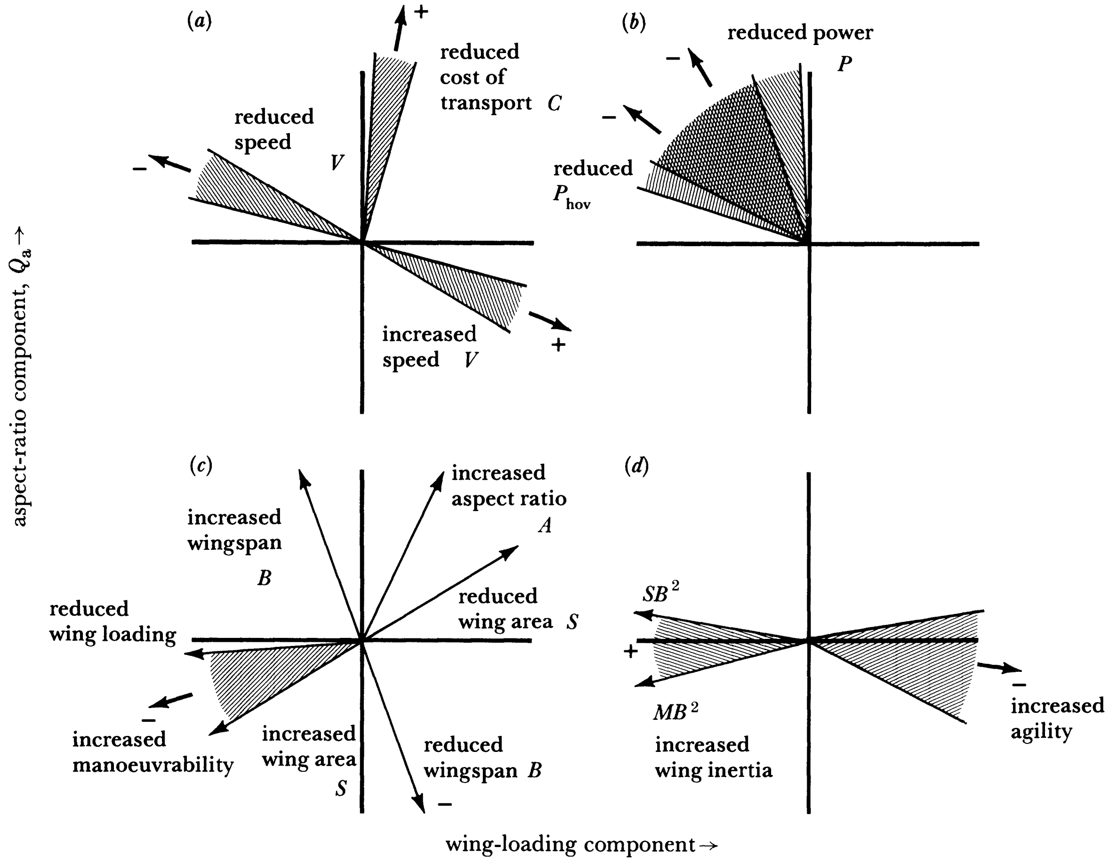


FIGURE 9. Predicted trends of variation of wing morphology in response to strong selection for particular aspects of flight performance. (*a*) Selection for flight speed and for reduced cost of transport; selection for *fixed* speed represents a constraint on the wing loading (see (*c*)). (*b*) Selection for reduced power in forward flight (*P*) and in hovering (P_{hov}); there is a greater premium on low wing loading for power economy in hovering and slow flying bats, and aspect ratio becomes more critical for forward flight where speed is less critical. (*c*) Effect on components of varying wingspan, wing area, aspect ratio, and wing loading while maintaining other parameters and body mass constant, together with predicted result of selection for improved manoeuvrability and load carrying. (*d*) Selection for improved agility; lower wing loading component corresponds to increased wing inertia, and therefore the most agile bats should have relatively small wings. In each case the shaded region denotes the area of uncertainty associated with whether body mass is held constant or is allowed to vary to best favour the particular aspect of performance; the signs indicate a predicted tendency for increased (+) or reduced (−) size or body mass to improve this aspect of performance. Adaptation to more cluttered environments may be linked with pressure for small wingspan (*c*).

This analysis supposes that only one aspect of flight performance is selected. The predicted tendencies for morphology to adapt are purely diagrammatic. Because the contribution of flight performance to fitness cannot be quantified, we have made no attempt to compare the relative magnitudes of morphological change associated with a given change in performance or fitness; the importance of different pressures will vary with trophic role, and depends also on overall size, so that some features (e.g. agility, manoeuvrability) are important in smaller bats, while others (e.g. power, cost, load-carrying) are more critical for larger species. Adaptation must compromise between different factors, and this can be indicated by the proximity of individual species and families in figure 8 to different regions on these diagrams.

area into principal-component form by using equations (9). In figure 9 the shaded areas represent regions of uncertainty about whether such adaptive changes are associated with constant body mass or with constant size (first principal component Q_S). In figure 9*d* the shaded areas illustrate different models of wing roll moment of inertia and magnitudes of body inertia. The signs alongside each arrow indicate the sense of changes in the first size component which most favour that aspect of performance, so a plus sign implies that larger body size is more suitable. The directions associated with change of a single morphological parameter are shown in figure 9*c*, and the correlates of various possible models of wing inertia (see §3.5*b*) in figure 9*d*.

Many of these possible pressures conflict; it is not possible to evolve simultaneously the potential for extreme low power and high agility, or for low cost of transport and high manoeuvrability. However, in addition to wing size and shape, wingtip adaptations (considered in §4.4) can contribute to specific aspects of performance by reducing the unfavourable effects of certain gross wing forms, and can permit compromise between apparently conflicting pressures. It is also possible that bats have evolved to compromise between different pressures without optimizing any one factor, and indeed this kind of adaptation may be essential if an animal is to avoid excessive specialization. For instance, some fast-hawking species (such as molossids) in the upper right quadrant may have compromised between low cost of transport (large third principal component) and high speed and high agility (large second component) at the expense of manoeuvrability, so they can forage only in open areas away from obstacles. Similarly, bats with low aspect ratio but low or average wing loading in the lower left quadrant (e.g. rhinolophids and many vespertilionids) should have good turning performance (both manoeuvrability and low-speed agility are high) and with short wings they should fly well in clutter; these are the features we predict for slow-hawking and/or hover-gleaning bats. Flight in these species might be relatively expensive because power and cost are high; this adaptation is restricted to smaller bats, for which high power is not a serious penalty when hunting abundant, accessible and often stationary prey.

Frugivores and nectarivores responding to pressures for high-speed commuting flight and for flight within clutter should fall in the lower right quadrant, but if hovering performance is more dominant they may adapt for low hovering power and fall in the upper left quadrant. We have predicted that trawling insectivores and piscivores should have high aspect ratio and low wing loading, and should fall in the upper left quadrant.

4.4. *Wingtip shapes*

Scatter plots of wingtip length and area indices (figure 10) have been divided into separate portions based on superfamilies for ease of interpretation. The solid line shows the relation $T_S = \frac{1}{2}T_l$, that is triangular wingtips with wingtip shape index $I = 1$. Species below this line are primarily pteropodids (with long or very long wingtips) or have particularly thin wingtips, including *Macroderma gigas*, *Phyllostomus hastatus*, *Mimetillus moloneyi*, *Nyctalus noctula* and *Tadarida teniotis*. The majority of bats have more rounded wings with $I > 1$, and there is considerable consistency within families. The most rounded wings are found in Nycteridae, Rhinolophidae, Hipposideridae, Noctilionidae, Natalidae and some Phyllostomidae. The highest values of I occur in *Hipposideros speoris* and *Chrotopterus auritus*; most hipposiderids also have relatively small wingtips. *Rhinopoma hardwickei* has the shortest wingtips ($T_l = 0.9$); the hand-wings are also short in other rhinopomatids, and the three other species in which the hand-wings are shorter than the arm-wings ($T_l < 1$) are all hipposiderids.

4.5. *Flight speed measurements*

The correlations between measured open-field flight speeds and morphology (table 5) form a means of testing some of our predictions and of assessing their comparative importance.

The prediction that flight speed scales with body mass as $M^{\frac{1}{6}}$ and with wing loading as $(Mg/S)^{\frac{1}{2}}$ (§3.2) is familiar; based on isometry, speed should rise as wingspan $B^{\frac{1}{2}}$ and as wing

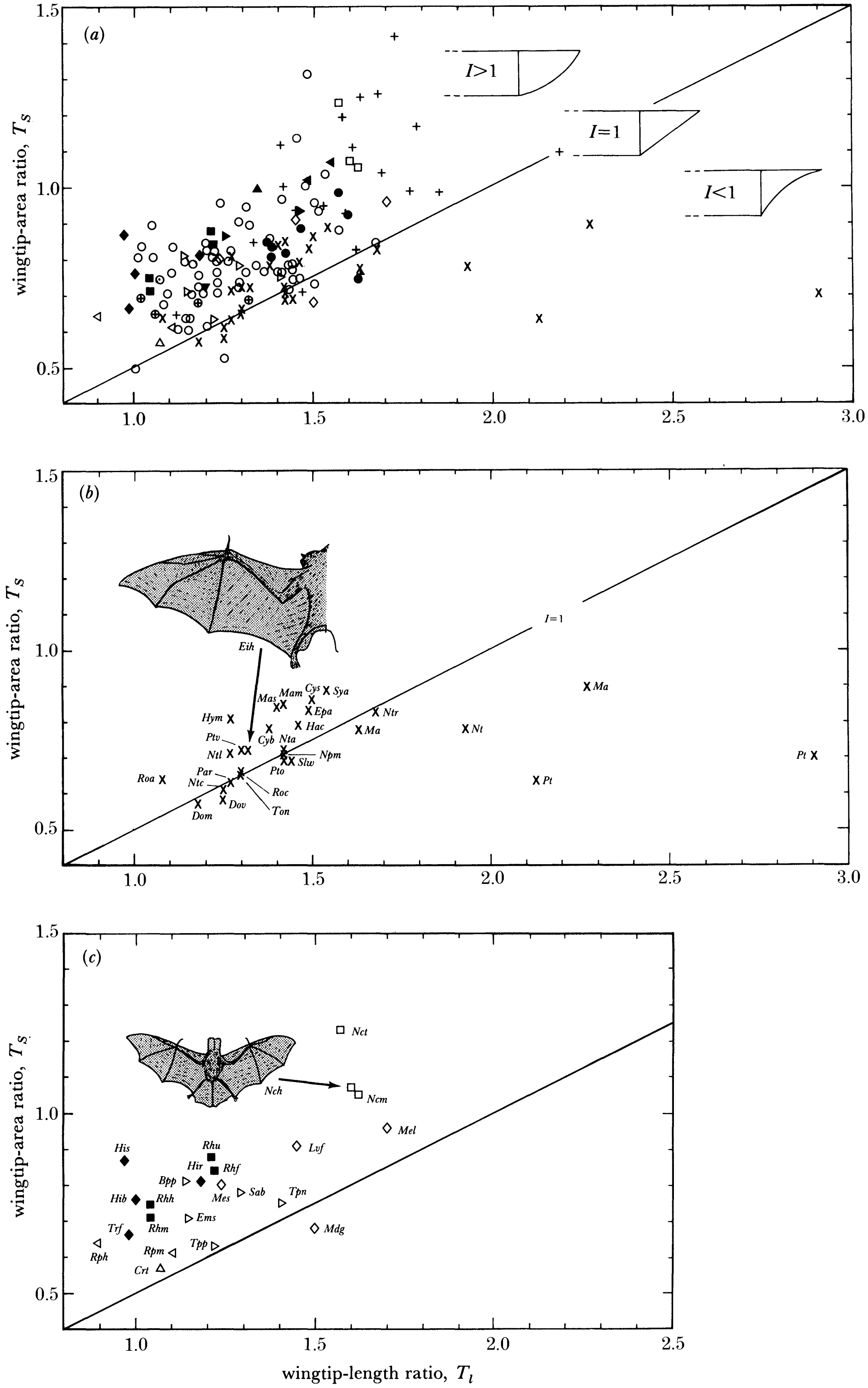
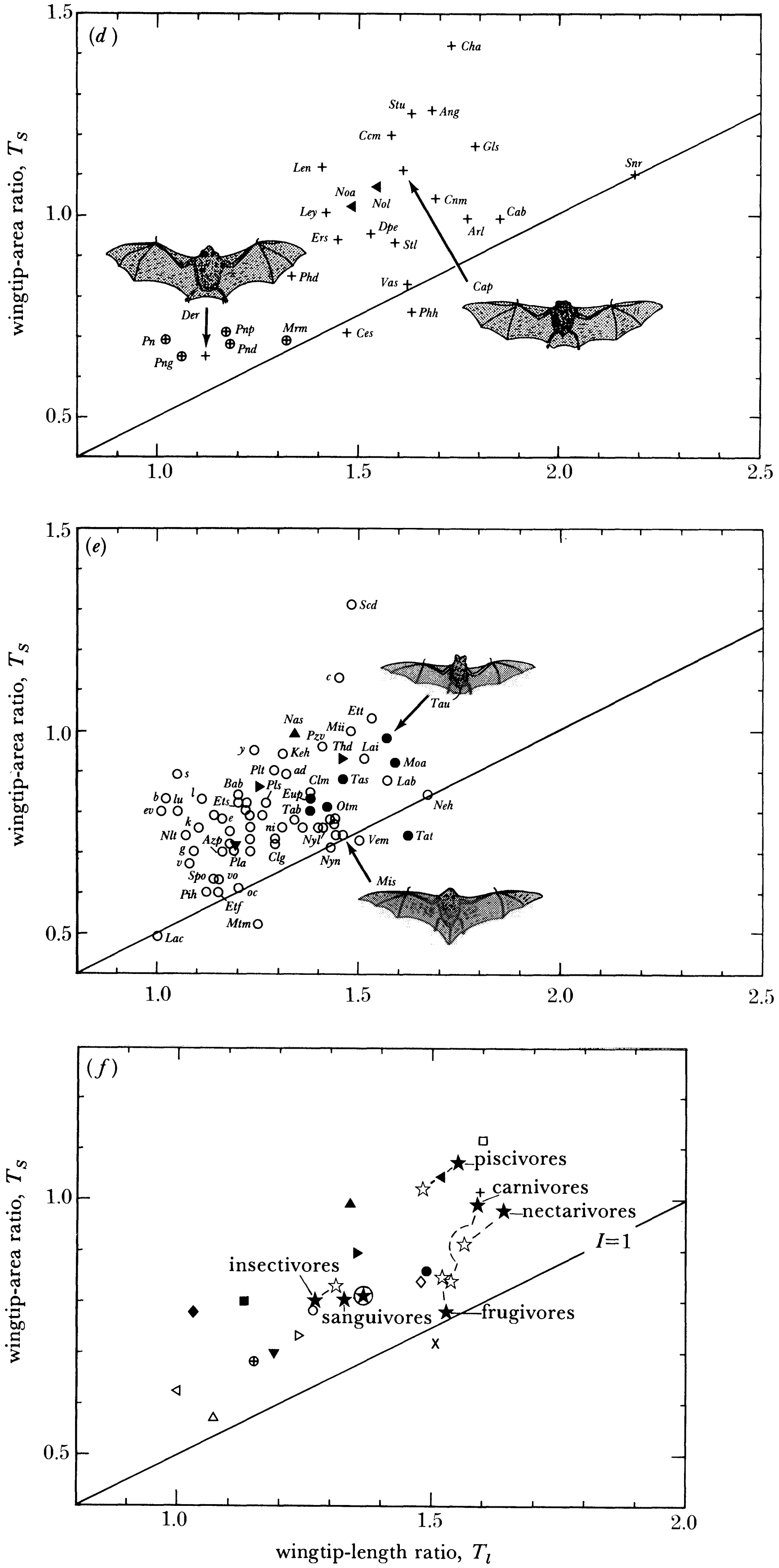


FIGURE 10. Scatter plot of wingtip length ratio, T_l, and wingtip area ratio, T_S, in bats. For convenience we have divided the figure into separate portions, similar to those in figure 8, as follows: (*a*), all bat species; (*b*), Pteropodoidea (Pteropodidae); (*c*), Emballonuroidea (Rhinopomatidae, Emballonuridae, Craseonycteridae) and Rhinolophoidea (Nycteridae, Rhinolophidae, Hipposideridae, Megadermatidae); (*d*), Phyllostomoidea (Noctilionidae, Mormoopidae, Phyllostomidae); (*e*), Vespertilionoidea (Natalidae, Thryopteridae, Vespertil-



ionidae, Mystacinidae, Molossidae); (*f*), means of each family and means of principal components of bats grouped into different feeding classes. The solid line represents triangular wingtip shape $T_S = T_l$ or $I = 1$; above this line the value of I is higher than 1. In (*b*)–(*e*) species are identified by the codes listed in table 1; in (*e*) the '*My*' for *Myotis* species is omitted to save space. The symbols used to identify families are shown in figure 4*a*.

TABLE 5. CORRELATIONS BETWEEN FLIGHT SPEED AND MORPHOLOGY IN BATS

(The equations shown are bivariate and multiple logarithmic–linear regressions for measured open-field flight speed V (m s^{-1}) on morphology for the 26 species for which data were available (§2.3), together with the appropriate correlation coefficients or variance ratios. Sample size, n, is 26 for correlations with wing morphology (M, B, S and principal components) and 24 for correlations with wingtip ratios. Relations that differ significantly at the 5 % level from the expected variation of speed against mass based on isometry or on our predictions of equation (5) and §3.2 are indicated by an asterisk.)

independent variable(s)	equation for V	expected scaling	correlation coefficient
bivariate regressions			
body mass, M/kg	$26.2M^{0.316}$*	$\frac{1}{6}$	0.677
wingspan, B/m	$19.8B^{0.896}$	$\frac{1}{2}$	0.629
wing area, S/m^2	$44.1S^{0.437}$	$\frac{1}{4}$	0.559
wing loading, $(Mg/S)/(\mathrm{N\ m^{-2}})$	$1.44(Mg/S)^{0.673}$	$\frac{1}{2}$	0.704
aspect ratio, A	$0.474A^{1.393}$*	0	0.483
tip length ratio, T_l	$5.43T_l^{0.847}$	possibly <0	0.360 (n.s.)
tip area ratio, T_S	$6.48T_S^{-0.110}$	0	-0.038 (n.s.)
tip shape index, I	$7.81I^{-0.302}$	< 0	-0.367 (n.s.)
multivariate regressions			
M, B, S	$5.36M^{0.46}B^{0.89}S^{-0.76}$	see eqn (4)*	$F(3,22) = 7.9$,
principal components	$7.35\mathrm{e}^{(0.29Q^{\mathrm{S}}+0.16Q_1+0.06Q_{\mathrm{a}})}$	see fig. 9	$P < 0.001$

area $S^{\frac{1}{4}}$. With mass, wingspan and wing area varying simultaneously, the predicted relation is given in equations (4) and (5) (see also table 3). For aerodynamic reasons we also conjectured that high flight speed might correlate with short wingtips (low T_l), and with low wingtip shape index, I (pointed wings), which is related to low wing inertia and to good agility in fast flight. To some extent these pressures could conflict, and so few bats have markedly short but pointed wingtips (§4.4). We did not expect a direct relation between speed and aspect ratio or wingtip area index T_S.

There are definite limitations with our flight-speed data sample. First, flight speed is notoriously difficult to determine reliably in any flying animal; for small, nocturnal animals like bats the problems are compounded. Second, the data were obtained by different workers using various methods, often with no indication of accuracy. For instance, although Baagøe (1987) gives ranges for his measurements, even the maxima are generally lower than mean speeds obtained for the same or comparable species by other workers. Third, our predictions for the relations between speed and mass or wing loading and between mass and body mass, wingspan and wing area are based on the assumption that aerodynamic conditions on the wing are the same in all bats and that all fly at the same characteristic speed, V_{mr}. However, different species operate in different situations, selecting their speed accordingly; for instance, bats flying among vegetation may fly more slowly than V_{mr}, whereas bats foraging at high altitude may forage most efficiently at speeds higher than V_{mr}. We do not know whether the flight-speed data represent foraging bats, commuting bats, or agitated individuals. Finally, the samples of species for which open-field speeds are available is heavily biased, containing few large bats, no pteropodids and no species with relatively high wing loading; of the 26 species analysed, 19 are vespertilionids, and 18 have body mass less than 0.015 kg.

In spite of these caveats, it is remarkable that correlations (table 5) between speed and morphology are as close as we have calculated. Correlations with mass, wingspan, wing area and wing loading are all significant, and none of the calculated scaling indices differ from our predictions at the 1% level. Furthermore, the agreement between measurements and the predicted multiple regression for V_{mr} (equation (5)) is also significant at the 1% level.

As predicted, low flight speed is correlated with large wingtip shape index, I ($p < 0.05$), and although speed decreases with wingtip area ratio, T_S, the variation is weak and not significant. Contrary to our prediction, speed increases with wingtip length ratio, T_l, but not significantly. Because the two expected tendencies for speed to increase with short and with pointed wingtips conflict, the pressure for short wingtips to favour wing flexure and acceleration is evidently outweighed by pressures favouring pointed wingtips to optimize wing inertia.

Also contrary to our prediction, speed increases significantly with aspect ratio ($p < 0.05$), as noted by Findley *et al.* (1972). Although we found no aerodynamic reason to expect a direct correlation between speed and aspect ratio, the correlation is not unduly surprising because high aspect ratio is correlated with pointed wingtips, and because bats with high aspect ratios tend to have higher than average wing loadings (§4.2). We suggest that the correlation arises indirectly owing to these factors.

The multiple regressions between speed and wing morphology support this conclusion; the relations of speed to mass, wingspan and wing area suggest that speed will increase, rather than decrease, with wingspan when mass and wing area are constant, but this is unimportant and non-significant because the three morphological quantities are closely intercorrelated. It is easier to visualize the relation with principal components of morphology (table 5), for it shows that speed increases weakly with size, Q_s, fairly strongly with wing loading, Q_l, and also with aspect ratio, Q_a. The highest speeds should tend to correlate with lower values of Q_a (figure 9), implying that measured flight speed varies more closely with Q_l than predicted by equations (4) and (5). This discrepancy may indicate a breakdown in the predictive model, but could also be explained by the limitations inherent in the data sample; it is also consistent with our suggestion that, to optimize feeding, bats with wings of low aspect ratio will tend to fly relatively slowly compared with their size and to V_{mr}, whereas bats with wings of high aspect ratio (and also with high wing loading) may fly nearer to, or even faster than, V_{mr}. For the purposes of this paper we have identified high wing loading or high second principal component, Q_l (e.g. in figure 8) and long, pointed wingtips as the most critical morphological correlates of high flight speed; low wing loading and rounded wingtips correlate with low speed. Short wings, low aspect ratio and rounded wingtips are important for slow flight in clutter, and we interpret this as the main significance of the aspect ratio, Q_a.

5. COMPARISON OF FAMILIES

In the next stage of our analysis we combine the results from our morphological analysis and our aerodynamic models to predict the likely flight behaviour of individual species, taxonomic groups and feeding classes of bats. We compare our predictions with observations reported in the literature. Unfortunately, these observations are frequently imprecise, are rarely consistent and use erratic terminology, and descriptions from different sources may not be comparable; for several species we have been unable to locate descriptions of natural flight behaviour. In spite of this, the observations consistently agree with our predictions, and resoundingly support our view that links between morphology, flight behaviour and feeding ecology in bats are moulded by constraints rooted in flight aerodynamics.

Below, aspect ratio and wing loading refer both to the absolute values of these quantities (tables 1 and 4; figures 6 and 7) and to the size-independent measures of these quantities (Q_l and Q_a) derived from our principal components analysis (figure 8). 'Average' refers usually to the average value for bats taken as a whole; the value of the appropriate component is close to an axis in figure 8. Wingspan, wing area and wing loading are described as small, average or large relative to the size (or mass) of the bat concerned rather than to the magnitude of the absolute value. Values of aspect ratio, wingtip size and shape indices should be read as absolute. In this discussion we have subdivided the larger families and subfamilies according to the magnitude of aspect ratio.

5.1. *Pteropodidae*

Pteropodids in our sample range in body mass from 0.01–0.015 kg in some nectarivores to about 1 kg for the largest frugivores. The family is the only one in the suborder Megachiroptera, and is disturbed throughout the Old World tropics and subtropics. Most pteropodids are frugivores, but some, principally in the subfamily Macroglossinae, are primarily nectarivorous. Wingspan and wing area in pteropodids increase slightly faster with body mass than would be predicted from isometry ($B = 1.2\ M^{0.35}$, $S = 0.24\ M^{0.71}$). Aspect ratio rises slightly with rising body mass, and wing loading is close to isometry ($A = 8.6\ M^{0.11}$, $Mg/S = 45\ M^{0.33}$) (table 4). Most pteropodids (fruit and/or nectar feeders) have below-average aspect ratio (figure 8*b*), and also have average or high wing loading. High wing loadings are found mostly in vegetarian bat species in the Pteropodidae and Phyllostomidae, few of which have below-average wing loading.

Fruit-eating Megachiroptera may fly long distances nightly between roosting and feeding places; Marshall (1983) quotes typical distances up to 20 and 50 km. Members of several genera (e.g. *Eidolon*, *Epomophorus*, *Pteropus*, *Rousettus*, *Myonycteris*, *Nanonycteris*) also migrate, at least in parts of their range, to maintain access to optimum food sources; total distances up to 750 km have been recorded (Marshall 1983; D. W. Thomas 1983). Most pteropodids use flight to reach food sources and do not feed while foraging; they usually fly straight and relatively fast, but some species have good manoeuvrability and slow flight in clutter and hover while taking fruit or nectar.

Species with high aspect ratio

Pteropodids with high aspect ratio include the frugivorous *Pteropus vampyrus* and *Balionycteris maculata* and the nectarivorous *Eonycteris spelaea* with high wing loading, and *Micropteropus pusillus*, *Cynopterus brachyotis* and *C. horsfieldi* with average wing loading. *P. vampyrus* and *C. brachyotis* have slightly rounded wingtips which are shorter than average; together with the low wing loading, these features are typical of slow, manoeuvrable flight. *E. spelaea* is noted to hover close to flowers before feeding while clinging to the plant, and is adept at flying in clutter (Gould 1978). *Micropteropus pusillus* is very small, and has rapid, agile and erratic flight resembling that of some insectivorous bats; it flies beneath, between and through clumps of fairly dense vegetation (C. Jones 1972), and is manoeuvrable but does not hover (Kingdon 1974). All five species have about average wingspan and wing area for their size (figures 4 and 5).

Species with average aspect ratio

Eidolon helvum, *Pteropus scapulatus*, *P. tonganus*, *Styloctenium wallacei*, *Dobsonia moluccense*, *D. viridis*, *Epomops franqueti*, *Hypsignathus monstrosus*, *Cynopterus sphinx* and *Thoopterus nigriscens* are about average-sized in wing dimensions, and all belong to the Pteropodinae. They have average wingtip lengths, although the wingtips are pointed in *P. tonganus* and *D. viridis*, slightly pointed in *E. helvum*, *S. wallacei* and *T. nigrescens*, and rounded in *D. moluccense*, *H. monstrosus* and *C. sphinx*. The rounded wingtips (figure 10*b*) are characteristic of the manoeuvrable flight described in *C. sphinx* by R. E. Goodwin (1979); this species hovers while feeding on fruit or nectar, and is more agile than larger pteropodids (T. J. Roberts 1977). *D. moluccense* is described as unusually slow compared with *Pteropus* species (which generally have higher aspect ratio), and to be able to hover before landing owing to its unusual wing articulation in which the wings join along the mid-line of the back (L. S. Hall, in Strahan 1983). *E. helvum* has slow, straight and relatively non-agile flight, sometimes making short glides between wingbeats (Rosevear 1965, Kulzer 1968). *Epomops franqueti* has slightly longer wingspan and lower wing loading than the others, and its flight is appropriately slow and manoeuvrable; it changes course quickly and frequently, and commonly flies in and out of the crowns of trees and close to the ground (C. Jones 1972); it also scavenges fallen fruits (Kingdon 1974). One (unidentified) *Pteropus* species has a long wingspan and very low wing loading, and should fly slowly, but this individual ($M = 0.347$) differs so much from the rest of the family that it may represent an error.

Species with low aspect ratio

Aspect ratio is low in all Nyctimeninae, in all but one (*Eonycteris spelaea*) Macroglossinae, in *Harpyionycteris celebensis* (Harpyionycterinae) and in *Rousettus* and *Epomophorus* species of the Pteropodinae; we interpret this primarily as an adaptation for flight within clutter.

The combination of low aspect ratio, relatively short wingspan and high wing loading is characteristic of species that fly fast within vegetation, including *Rousettus leschenaulti*, one *Pteropus* sp., *Epomophorus anurus*, *E. gambianus*, two *Macroglossus* sp., one *Nyctimene* sp. and *Syconycteris australis*. All have short or average wingspan. Wingtips are generally average in length, and are rounded in *E. anurus*, *Macroglossus* and *S. australis*. Epomophorines occur in open savannah and riverine forest (Fenton *et al.* 1985); at least some species (e.g. *Epomophorus gambianus* (Marshall & McWilliam 1982) and *E. wahlbergi* (M. B. Fenton, personal communication)) hover before or during feeding. *Epomophorus wahlbergi* roosts close to its feeding site and flies slowly, seldom rising above the forest canopy (Kingdon 1974; Wickler & Seibt 1976). *E. gambianus* is agile even among thick vegetation (Marshall & McWilliam 1982). Of these bats, all but *Nyctimene* sp. are at least partly nectarivorous. *S. australis* hovers while feeding (G. C. Richards, in Strahan (1983)). According to van der Pijl (1956), *Macroglossus* species are not very manoeuvrable, and do not hover but sit on flowers while feeding; this is typical of the majority of nectarivorous pteropodids (Dobat & Peikert-Holle 1985).

Rousettus aegyptiacus (figure 1*a*), *Notopteris macdonaldi* and *Nyctimene robinsoni* have wing loading slightly above average, and are predicted to fly more slowly than the previous species. The wingtips are short and somewhat rounded in *R. aegyptiacus*, but are longer and more pointed in *Notopteris macdonaldi* and *Nyctimene roinsoni*. *R. argyptiacus* has rather slow, straight flight with low manoeuvrability (Walker 1964; Kingdon 1974).

Rousettus celebensis, *Nyctimene aello*, *N. albiventer*, *N. cephalotes*, *Paranyctimene raptor* and *Harpyionycteris celebensis* all have average wingspan and low aspect ratio, but average or slightly below-average wing loading. We predict that they are slower fliers than species in the former group. The wingtips are rounded in *N. albiventer* and *H. celebensis*, but more pointed in the other four species; they are average in length in all but *H. celebensis*, in which the wingtips are relatively long.

5.2. *Rhinopomatidae*

The rhinopomatids are insectivorous bats of the Old World tropics, found mainly in deserts and steppes. Of the three species we have data for two: *Rhinopoma hardwickei* ($M = 0.016$ kg) and *R. microphyllum* ($M = 0.032$ kg). Both have rather short wingspan and high wing loading (figure 8*c*), correlating with the high flight speeds reported in *R. hardwickei* by Habersetzer (1981). In this species, the aspect ratio is below average, whereas it is about average in *R. microphyllum*. In both the wingtips are extremely short (figure 10*c*) and there is no tail membrane; this contributes to the low wing area and high wing loading. Rhinopomatids are swift fliers, and are variously described as foraging for insects in open country, often at relatively high altitude and away from obstacles (Kingdon 1974; Smith & Starrett 1979), and as flying at intermediate levels of forests in open spaces around the canopy, and below the high- and fast-flying *Taphozous nudiventris* (= *T. kachhensis*), *T. melanopogon* (Emballonuridae) and *Tadarida aegyptiaca* (Molossidae) in the same habitat (Neuweiler 1984; Habersetzer 1986). Simmons *et al.* (1984) describe the hunting flight of *R. hardwickei* as similar to that of the molossid *Tadarida brasiliensis*, which also forages away from clutter (*T. brasiliensis* has comparable wing loading to rhinopomatids (figure 8*c*, *e*), although it has higher aspect ratio and lacks their abnormally short wingtips). Habersetzer (1986) relates the wingtip design to the absence of hovering in *R. hardwickei*, and we would expect this from its wing morphology. Harrison (1964, p. 62) described the flight of *R. hardwickei* as '...a series of alternating flutters and glides, with a rising and falling motion...' (see also Kingdon 1974); the flight of *R. microphyllum* is similar (T. J. Roberts 1977). This undulating pattern contributes to energy saving in steady, level flight (Rayner 1985*c*), but although common in pteropodids undulating flight is more rare in microchiropteran bats, of which few species commonly glide.

The Rhinopomatidae have tentatively been described as the least derived of extant microbats (see, for example, Revilliod 1916; Vaughan 1970*b*; Kingdon 1974; Hill & J. D. Smith 1984; Simmons *et al.* 1984), at least morphologically. Part of the evidence for this is the short and small wingtips. This proposal is consistent with the hypothesis that the ancestors of bats were arboreal gliders (Smith 1977; Norberg 1985, 1986*a*; Padian 1987; Rayner 1986; Scholey 1986), and is further supported by the gliding habits of the family and their lack of hovering flight. However, the apparent similarity in feeding behaviour with molossids (usually considered the most specialized microchiroptera) may indicate that the Rhinopomatidae are not primitive in wing morphology, and that their small wingtips are associated with other factors.

5.3. *Emballonuridae*

Emballonurids are a diverse pantropical group of insectivorous bats with high diversity in wing size and shape. Wingspan and wing area increase more slowly with body mass than predicted by isometry ($B = 1.0\ M^{0.27}$, $S = 0.08\ M^{0.40}$) (figures 4 and 5); Norberg (1981*a*) found that the exponent for forearm against mass in this family was 0.26, similar to our scaling of wingspan. Aspect ratio and wing loading range widely and show strong positive allometry against body mass ($A = 18\ M^{0.20}$, $Mg/S = 171\ M^{0.66}$) (figures 6 and 7), implying that larger emballonurids have relatively shorter, but narrower, wings than smaller ones.

Species with high aspect ratio

Bats in the genus *Taphozous* have high aspect ratio; wing loading is much higher than in other emballonurids (figure 8*c*), and is comparable with that of molossids. The wingtips are relatively short in *Taphozous perforatus*, somewhat longer in *T. nudicentris*, and are rather pointed in both. Like most molossids, *Taphozous* species are fast fliers, and hawk insects at high altitudes. *T. georgianus*, *T. mauritianus*, *T. melanopogon*, *T. nudiventris* and *T. peli* forage high above ground and trees in the same low-clutter space as the sympatric *Tadarida aegyptiaca*, and fly fast with great agility but poor manoeuvrability (Lang & Chapin 1917; Fenton 1972; Kingdon 1974; Fenton *et al.* 1980; Neuweiler 1983, 1984; Habersetzer 1986). We predict that *T. flaviventris*, which has below-average wing loading, may be somewhat slower than these species, and that *T. perforatus*, a rather smaller animal with more average wing loading and aspect ratio, will be slower and less agile, but more manoeuvrable, than other *Taphozous* species and may fly at lower, more cluttered levels; Kingdon (1974) reports that it lives in forests.

Emballonura species and *Rhynchonycteris naso* have low wing loading and above average aspect ratio and long wingspan, and have slow, enduring and manoeuvrable flight. *R. naso* forages slowly in straight lines close over moving water (Hall & Dalquest 1963; Bradbury & Emmons 1974; Bradbury & Vehrencamp 1976). The wingtips are short and rounded in *E. semicaudata* and *Balantiopteryx plicata*. Data on wing loading and aspect ratio are lacking for *B. plicata*, but it has been described as flying slowly and erratically (Walker 1964), as pipistrelle-like (W. B. Davis & Russell 1952), as highly manoeuvrable (Strickler 1978*a*) and as commuting more than 20 km nightly; this suggests average wing loading and slightly above-average aspect ratio, resembling some *Pipistrellus* species.

Species with average aspect ratio

Coleura seychellensis and *Saccopteryx bilineata* have rather long wingspan, average aspect ratio and low wing loading. The wingtips in *S. bilineata* are rounded and of average length; its morphology suggests slow and manoeuvrable flight in open or semi-open spaces. There are conflicting observations of this bat. Hall & Dalquest (1963) describe *S. bilineata* as resembling *Myotis*, but slower and more deliberate, and flying erratically as it hawks insects over water; morphologically it resembles some 'trawling' *Myotis* species of the *Leuconoe* subgenus (§§6.2*c* and 6.4). However, Bradbury & Emmons (1974) report that it forages just above the forest canopy, and that although flight is faster than *S. leptura* (which flies close to the ground) it is slower than in the sympatric *Pteronotus* species (Mormoopidae) and molossids which flew at higher levels. Fenton (1982*b*) described *S. bilineata* as usually flying at the lower levels of the forest. This bat can hover, and is swift and acrobatic (Findley *et al.* 1972; Strickler 1978*a*). Its foraging habitat shows considerably greater seasonal fluctuation than other sympatric emballonurids (Bradbury & Vehrencamp 1976); this factor may have some influence on its rather lower aspect ratio.

5.4. *Craseonycteridae*

The single species *Craseonycteris thonglongyai* is one of the smallest bats ($M = 0.0019$ kg, range 0.0017–0.0020 kg) (Hill & S. E. Smith 1981). If our arguments are correct and mechanical constraints on flight performance in very small bats are weak, then other factors may be crucial in this species in dictating morphological specialization. The wings of *C. thonglongyai* are slightly smaller and narrower than average, and the wingtips are short and rather pointed. It is reported to hover frequently and to forage around the stems of bamboo plants with high agility and manoeuvrability (Nabhitabata *et al.* 1982). Hill & S. E. Smith (1981) predicted that these bats would glean insects; given their small size, this is not inconsistent with their morphology.

5.5. *Nycteridae*

Nycterids are confined to Africa and tropical South East Asia; they are relatively small and mainly insectivorous. They have particularly low aspect ratio and wing loading (figure 8*c*), and long (*Nycteris thebaica*) or average wingspan, but they have large tail membranes, large ears and long and very rounded wingtips. Their flight is particularly slow and manoeuvrable. *N. hispida* flutters around vegetation hawking slow-flying moths or hovering and gleaning (Brosset 1966; Kingdon 1974); Rosevear (1965) noted that it turns abruptly, and sometimes flies close to water. *N. thebaica* is also a foliage gleaner (O'Shea & Vaughan 1980), and is also reported to glean the ground for scorpions (Kingdon 1974) and other prey (Fenton *et al.* 1983*a*); this behaviour is similar to that of *Antrozous pallidus* (Vespertilionidae) (Kingdon 1974; Bell 1982), which is morphologically comparable. The largest nycterid, *N. grandis*, takes a variety of prey including insects, fish, frogs, bats and birds (Fenton *et al.* 1981), and is a gleaner, hunting from a perch and taking prey from the ground (Fenton *et al.* 1983*a*, 1987). Each bat can consume two frogs each night and can carry prey up to 50% of its own mass (Fenton & Rautenbach 1986; M. B. Fenton, personal communication).

5.6. *Megadermatidae*

This family is confined to the Old World and Australian tropics, and includes some of the largest Microchiroptera; of its four genera, three are carnivorous, the exception being *Lavia frons*. All megadermatids have long ears and long or average wingspan. *Megaderma lyra* and *Macroderma gigas* have low wing loading and average aspect ratio; *L. frons* has average wing loading but differs from the other species in its very low aspect ratio and rounded wingtips. Wingtip shape varies among the four species we studied: in *Megaderma* the wingtips are rounded, but in *M. lyra* they are very long and in *M. spasma* they are average in length; in *Macroderma gigas* the wingtips are pointed, mainly because of the unusually short fourth digit. *M. gigas*, *Cardioderma cor* and *L. frons* have rather long wingtips (figure 10*c*). We predict that the flight of megadermatids is slow and manoeuvrable, and that these bats are adapted to flying in heavy clutter. Taken with their long ears, the wing morphology indicates slow flight and perhaps gleaning (the long ears in *M. lyra* coincide with listening for acoustic cues from prey (Fiedler 1979)). Low wing loading also provides the capacity for increased lift, which is essential for bats taking large animal prey. Two foraging patterns have been noted in these bats, gleaning and 'flycatching'. *Megaderma lyra* usually flies close to the ground, gleaning small vertebrates and some large insects; it can rise readily from the ground even with a substantial load of at least 50% of body mass (Walker 1964; Neuweiler 1983, 1984; Habersetzer 1986). The behaviour of *Cardioderma cor* resembles that of *Megaderma lyra*, both often hunting from a perch to ambush prey on the ground (Vaughan 1976). *Macroderma gigas* feeds mainly on birds (taken while at rest in vegetation) and mammals, although it may be more opportunistic; all food is obtained by gleaning, generally after a flycatcher-like sally from a perch (Douglas 1967; Kulzer *et al.* 1984; Tidemann *et al.* 1985). *L. frons* is primarily insectivorous and mainly hunts insects as a flycatcher (Shortridge 1934; Wickler & Uhrig 1969; Kingdon 1974; Vaughan &

Vaughan 1986); its flight is erratic and fluttering, and it flies in clutter with precise manoeuvrability (U.M.N., personal observations; Kingdon 1974). This flight pattern is consistent with its extremely low aspect ratio wings. However, the foraging behaviour of *L. frons* is plastic, the bat sometimes using 'towering' flights, similar to those of neotropical tyrannid flycatchers, to catch large, high-flying insects (Vaughan & Vaughan 1986).

5.7. *Rhinolophidae*

The horseshoe bats (Rhinolophidae) are relatively small, insectivorous species of the Old World; although they are primarily tropical they are found throughout Africa and in Europe as far north as central Britain. Rhinolophids have low to average wing loading and aspect ratio (figure 8*c*). Wingspan is about average and increases geometrically with mass ($B = 1.4\ M^{0.35}$); wing area is large in *R. fumigatus*, *R. hildebrandtii*, *R. landeri* and *R. swinnyi* but is more average in the others, and increases with mass more slowly than isometry ($S = 0.16\ M^{0.55}$). Wing loading rises above isometry ($Mg/S = 91\ M^{0.54}$); aspect ratio increases as $A = 11\ M^{0.13}$, but this is not significant.

Rhinolophids are specialized for flycatching and in some cases for gleaning. Prey is usually sought close to foliage; *R. ferrumequinum* is believed to take prey from the ground (Barrett-Hamilton 1910; Stebbings 1977; Schnitzler *et al.* 1985 and references therein). In all species the wingtips are very rounded and short, but they are especially short in *R. hipposideros* and *R. megaphyllus* (figure 10*c*). Flight is slow and manoeuvrable with some hovering, often within clutter. The temperate species *R. ferrumequinum* and *R. hipposideros* have butterfly-like flight with glides (Barrett-Hamilton 1910; Stebbings 1977); the low aspect ratio of these bats would suggest that their cluttered habitat is a severe constraint on their wingspan. Despite their short wingtips, many rhinolophids fly slowly and can hover (see, for example, Barrett-Hamilton 1910; Wallin 1969). The African species *R. hildebrandtii* alternates between continuous flight and short flights from perches, foraging just above the ground in woodland or riparian forest (Fenton & Rautenbach 1986), and the Australian *R. megaphyllus* also hunts flying insects by flycatching (Fenton 1982*b*). Muller & Baldwin (1978) suggest that *R. megaphyllus* makes short bursts of rapid flight interspersed with periods of rest or more steady flight; the pectoral muscles are adapted for intense anaerobic metabolism. The combination of low aspect ratio and/or low wing loading in these species suggests them to be more manoeuvrable than other rhinolophids in our sample. *R. aethiops* and *R. rouxii* (for which we have no data) also hunt from perches (Shortridge 1934; Schnitzler *et al.* 1985); we predict that this flight pattern is typical of many rhinolophids.

5.8. *Hipposideridae*

Hipposiderids have a more confined tropical distribution than the closely related rhinolophids, which they resemble with their large wing area, low wing loading (figure 8*c*) and very short, rounded wingtips (figure 10*c*). Aspect ratio is high in *Hipposideros cineraceus*, *H. commersoni* and *Triaenops persicus* and average in *H. bicolor*, *H. caffer*, *H. diadema* and *H. speoris*. The flight of some hipposiderids is slow and close to the ground (Findley *et al.* 1972) and butterfly-like and delicate (Kingdon 1974). Some, but not all, species can hover (Pirlot 1977; *H. bicolor* but not the shorter-winged *H. speoris* (Habersetzer *et al.* 1984)). Adaptation for hovering could explain the long wings of hipposiderids, but the unusually short wingtips are surprising in this context. *H. speoris* flies in more open areas than *H. bicolor* but has shorter wings and extremely rounded wingtips. Both fly slowly and only a few metres above the ground; *H. speoris* forages often in circles around vegetation but never into foliage, whereas *H. bicolor* has a more erratic flight, often forages within foliage and sometimes hovers or lands on the ground to pick up prey (Habersetzer 1986). The large *H. diadema* is described as straight and swift (R. E. Goodwin 1979). *H. caffer* is noted to fly rapidly and continuously while foraging, making quick turns, and taking fluttering prey in a range of flight patterns, which include gleaning from the ground and attacks on flying prey in the open (Kock 1969; Bell & Fenton 1984). The largest hipposiderids, *H. commersoni* (Vaughan 1977) and *H. diadema* (Brown & Berry 1983), hunt flying prey from a perch, as also does *H. armiger* (Shortridge 1934).

Triaenops persicus has less rounded wingtips than the *Hipposideros* species, and should be less manoeuvrable though more agile; its longer but smaller wings suggest flight in more open clutter. It flies low over ground and bushes with a delicate, butterfly-like flight (Harrison 1964).

5.9. *Noctilionidae*

The two noctilionid species of the rivers and coasts of the New World tropics are known primarily as piscivores, but both also take insects. *Noctilio leporinus* eats mainly fish; the smaller *N. albiventris* takes more insects. Both species forage over open water, but may also feed on fruits (Strickler 1978*a*). The most striking flight adaptation in the family is the high aspect ratio of the wing, which is especially marked in *N. leporinus*. This species also has below-average wing loading (figure 8*d*). In both species the wingtips are long and rounded (figure 10*d*); these adaptations favour slow and sustained flight away from clutter. *N. leporinus* flies with constant, but relatively slow and shallow, wingbeats (to be expected from its high aspect ratio, low wing loading and long and rounded wingtips) and does not appear to be particularly fast (G. G. Goodwin & Greenhall 1961). Its long wings permit slow flight, and may also be essential to minimize power consumption and cost of transport during foraging flight. They also allow some advantage from the ground effect, which can represent a reduction in induced drag of perhaps 10 % owing to the proximity of the wing aerofoil to the plane water surface. *N. albiventris* is rather smaller than *N. leporinus*, and exhibits a fair degree of manoeuvrability in confined spaces (Smith & Starrett 1979); this and its insectivorous habits are consistent with its shorter, broader wings and more average aspect ratio.

5.10. *Mormoopidae*

Mormoopids are insectivores and are closely related to the phyllostomids, with which they share distribution in the New World tropics. But they have higher aspect ratio than most phyllostomids (figure 8*d*). *Pteronotus davyi* and *P. gymnonotus* have longer wingspan and resemble *Noctilio leporinus* and *Emballonura* species. The wing loading (and hence flight speed) is typically lower than in molossids. The wingtips are short in all species and are rounded like those of some emballonurids and rhinolophids (figure 10*d*). We predict mormoopids to have relatively slow or average flight speeds, to have average agility but rather low manoeuvrability, and to hawk flying insects in relatively open spaces. Owing to the low cost of transport, foraging flights may be sustained for long periods.

These predictions concerning flight speed appear to be confirmed. G. G. Goodwin & Greenhall (1961), Walker (1964) and Bonaccorso (1979) described the flight of *Pteronotus* species as straight, swift and low, often along streams in wooded areas. *P. davyi* is very agile (Hall & Dalquest 1963). *P. gymnotus* flies at lower levels of forests (Fenton 1972), and *P. parnelli* forages within 3.5 m of the ground (Bateman & Vaughan 1974); flight at low levels appears typical of the family (Walker 1964; Hill & J. D. Smith 1984). *Mormoops megalophylla* flies faster then *P. davyi* and *P. gymnonotus* (G. G. Goodwin & Greenhall 1961; Bateman & Vaughan 1974), and we would expect this from its higher wing loading.

Vaughan & Bateman (1970) have described mormoopids as having enduring, rapid and manoeuvrable flight and to forage for insects while on the wing. They base this conclusion on the morphology of the elbow, which they see as better suited to the demands of sustained flight than that of phyllostomids. This feature may compensate for the rather low manoeuvrability.

5.11. *Phyllostomidae*

The New World phyllostomids are a diverse group; they are primarily fruit-eaters, but some use nectar and pollen, others are purely nectarivorous, and a few are carnivores. Most species have short or average wingspan and low or average wing area; aspect ratio is low and wing loading above average in most species, and with two exceptions the family is clustered around the lower right quadrant of figure 8*d*. Wingspan, wing area and wing loading all increase more rapidly with body mass than isometry ($B = 1.3\ M^{0.36}$, $S = 0.25\ M^{0.71}$, $Mg/S = 52\ M^{0.37}$) (table 4); mean aspect ratio decreases slightly with size ($A = 3.6\ M^{-0.15}$) but the correlation coefficient (-0.13) is not significant. Wingtips are typically slightly longer and larger, and rather more rounded, than average.

Owing to the diversity in the family we consider the subfamilies of the Phyllostomidae separately. There is some uncertainty over the appropriate division, and we follow Hill & J. D. Smith (1984) and Corbet & Hill (1986). In our morphological classification there is considerable overlap between some of the subfamilies; our data are insufficient to explain all ecological and phylogenetic differences between phyllostomid subfamilies. Similar problems were experienced by Smith & Starrett (1979) in attempting to use a multivariate analysis of wing osteology to discriminate species between subfamilies.

(*a*) *Phyllostominae*

The phyllostomines are the least specialized phyllostomids, and are the most similar to the vespertilionids in wing size and shape. They are more or less omnivorous, and with the exception of *Phyllostomus discolor*, the larger species are all to some extent carnivorous. The group is characterized by lower wing loading than most other phyllostomids. The wingtips are relatively large but vary in shape, being more pointed in the larger *Vampyrum spectrum* and *Phyllostomus hastatus*.

(i) Species with high aspect ratio

Phyllostomus hastatus has aspect ratio and wing loading higher than average for all bats, and should be fast and rather agile. Although it has a high wing loading, this species is primarily a carnivore, but it also includes nuts, fruits and insects in its diet. It has rather long and pointed wingtips, and swift, powerful flight (G. G. Goodwin & Greenhall 1961).

Mimon crenulatum is unusual among phyllostomids in its very low wing loading and very high aspect ratio. It has relatively the longest wings in the family, and is similar to *Pteronotus davyi* of the Mormoopidae. If our data are representative, we predict it to have slow and enduring flight, probably foraging under or around, but not within, vegetation.

Macrotus waterhousei also has unusually high aspect ratio; it is possible that this record represents an error, as in most respects this species is reported to resemble *M. californicus*.

(ii) Species with low aspect ratio

Like some Megadermatidae, the carnivorous phyllostomids have average wingspan and low aspect ratio, associated with flight among clutter, and large tail membranes (and hence low wing loading) enabling them to fly readily with prey. *V. spectrum* and *Chrotopterus auritus* have very low wing loading and aspect ratio. *V. spectrum* can take off with prey almost as heavy as its own mass (Findley *et al.* 1972). It flies slowly and powerfully (Mortensen 1977), sometimes feeds on foliage-roosting birds (Vehrencamp *et al.* 1977) and has rather pointed wingtips; in these qualities it resembles *Macroderma gigas* (Megadermatidae; §5.6). *C. auritus* has the most rounded wingtips of any bat and, in addition to feeding on small mammals, gleans foliage for insects (Mortensen 1977). Both of these species have very slow and manoeuvrable flight and can fly within vegetation. *Trachops cirrhosus*, which has average wing loading and relatively low aspect ratio, is also carnivorous; it is slow and very agile (? manoeuvrable) (Mortensen 1977), can hover, and gleans insect and animal prey from tree trunks, foliage, the ground or from water (Barclay *et al.* 1981).

P. discolor differs from its congenor *P. hastatus*: it is smaller and has lower wing loading, an aspect ratio slightly below average, rounded wingtips, and the shortest hand-wing of all phyllostomids investigated (although the length of the wingtip is about the average for all bats). We predict that it should fly relatively fast and be a poor hoverer. *P. discolor* usually sits on a flower when feeding, emptying it of nectar in a single visit (Heithaus *et al.* 1975; Smith & Starrett 1979); it forages in flocks, has strong, rapid flight, faster than *P. hastatus*, and was not observed to hover in captivity (Brosset 1966; Mortensen 1977). *P. discolor* has a large home range and is migratory (Fleming *et al.* 1972, Heithaus *et al.* 1975); this behaviour is consistent with its high flight speed.

The smaller phyllostomines are primarily insectivorous. Most glean resting insects; a few, apparently confined to the genus *Macrotus*, hawk insects in flight (Wilson 1973; Gardner 1977). The data for *M. waterhousei* may be inaccurate; this species, which has average wing loading, probably resembles *M. californicus* in other measurements. Both are described as among the most alert and agile bats in flight, having slow flapping flight; they are highly manoeuvrable, can hover, and glean prey from surfaces (Hayward & R. Davis 1964; Barbour & W. H. Davis 1969). *M. waterhousei* flies within the crowns of trees (Humphrey & Bonaccorso 1979) but *M. californicus* gleans from the ground (Bell 1985). This observation is consistent with this species' relatively low wing loading and low aspect ratio. *Micronycteris megalotis* gleans insects from foliage (LaVal & LaVal 1980), and occasionally eats fruit which it 'picks' while hovering (G. G. Goodwin & Greenhall 1961, Bonaccorso 1979); Mortensen (1977) reported its flight to be slow and deft among dense vegetation. It has relatively short wings, very low aspect ratio and low wing loading.

(*b*) *Glossophaginae*

These relatively small bats are specialized for nectar feeding and parallel the Macroglossinae (Pteropodidae). We find (as did Smith & Starrett (1979)) that the group is morphologically distinct and shows rather little interspecific variation. The wing loading is high and aspect ratio is below average. Mean wingtip length is similar to that of other phyllostomids (i.e. larger than average) but wingtip area is very large and the wingtips are unusually rounded.

Despite their high wing loading, the broad wing and long wingtips fit glossophagines for hovering (§3.3); this is the normal feeding mode for most species (Vogel 1968; Strickler 1978*a*; Dobat & Peikert-Holle 1985); *Glossophaga soricina* (Heithaus 1982, Lemke 1984); *Leptonycteris nivalis* and *L. yerbabuenae* (= *L. sanborni*) (Howell 1979); *Anoura geoffroyi* (G. G. Goodwin & Greenhall 1961); *A. caudifer* (von Helversen & Reyer 1984)). The group also has other specialized adaptations for hovering: '... the exceedingly large volume proportion of the *serratus major* (*superior*) in *Choeronycteris mexicana* may be due to this bat's exceptional ability to hover' (Struhsaker 1961).

The availability of nectar is not constant; glossophagines adjust their diet and behaviour according to seasonal availability of food (Heithaus *et al.* 1975). They cannot always reach their food by hovering; Lemke (1984) has shown that the proportion of foraging time spent hovering in *G. soricina* is correlated with flower morphology, and that young (and presumably less experienced) bats hover less often. The *Leptonycteris* species in the southern United States are strong direct fliers and migrate (Barbour & W. H. Davis 1969) and they have lower wing loading than the other glossophagines, which usually have relatively small ranges. For instance, although it is a refuging species, mean recapture distances for the tropical *G. soricina* were only about 200 m (Heithaus *et al.* 1975). We have no data for *A. caudifer*, but this bat has narrower, more pointed wings and flies faster than *Glossophaga* species; these characters correlate with its more extended range (von Helversen & Reyer 1984).

(*c*) *Carolliinae*

The two species of the genus *Carollia* have longer and more rounded wingtips than most phyllostomids; wingspan is short or average, wing loading is average to low for the family, and aspect ratio is very low. We predict that these bats fly relatively fast within clutter, but have low endurance. *Carollia* species have been described by G. G. Goodwin & Greenhall (1961) as rapid fliers, making sudden swerves. They differ from *Artibeus* species, which have similar wings but are rather larger, by feeding at lower levels of forests on a wider range of fruits (Bonaccorso 1979). A detailed study of foraging behaviour in *C. perspicillata* (Heithaus & Fleming 1978) revealed high flight speeds for forest bats (4.5–6.7 m s^{-1}) and short distances (mean 1.2 km) in commuting, with few exploratory flights during commuting.

(*d*) *Sturnirinae*

Hill & J. D. Smith (1984) do not distinguish this group from the Stenodermatinae, but unlike the stenodermatines, which have pointed wingtips, we find sturnirines to have rather rounded wingtips; they also have unusually short wings. The two *Sturnira* species we analyse are very small and have high wing loading and a typical aspect ratio for phyllostomids. We predict them to resemble glossophagines, that is to be relatively fast, to fly well in clutter, and to hover. The major component of the diet is fruit (Gardner 1977).

(*e*) *Stenodermatinae*

This subfamily is composed of a range of species, most of which are frugivorous. Morphologically it is the most diverse of the phyllostomid subfamilies (see also Smith & Starrett (1979)). Aspect ratio is consistently low, but although mean wing loading is slightly above average for the family, it varies from just below average in *Uroderma bilobatum* and *Vampyrodes caraccioli* to very high in the short-winged *Stenoderma rufum*. The group is comparable in behaviour and morphology to the smaller members of the Pteropodinae, except that the wingtips, although equally pointed, are much longer and larger than in the megachiropterans.

Eight stenodermatine species studied by Bonaccorso (1979) in Panama (including *Artibeus phaeotis*, *A. jamaicensis*, *A. lituratus*, *Vampyrops helleri*, *Vampyrodes caraccioli* and *Chiroderma villosum*) were all canopy-foraging frugivores, and this appears typical of the group. There was some vertical stratification in flight levels, with *A. jamaicensis* flying relatively close to the ground although it still foraged in the canopy. All of these species could carry sizeable single fruits weighing as much as 40% of their own mass, despite their rather high wing loading.

Artibeus species and other stenodermatines have unusually broad wings, with a large dactylopatagium which could increase chordwise wing camber (Vaughan 1970*c*), permitting them to reduce flight speeds while flying among vegetation. Heithaus *et al.* (1975) found that *Artibeus phaeotis* flies relatively short distances, but *A. jamaicensis* may cover up to 10 km in its foraging flights (Morrison 1978). *A. jamaicensis* has near-average morphology, but has breast-muscle enzymes resembling those of burst-flying birds (Valdivieso *et al.* 1978); it flies in and out among vegetation, darting up and down repeatedly and hovering while tearing at a fruit (Quelch 1892). It is not a swift flier (G. G. Goodwin & Greenhall 1961), but manoeuvres well (Hall & Dalquest 1963) and, unlike others in the subfamily, does not roost in foliage (Morrison 1980). *A. lituratus* and *Vampyrodes caraccioli* both hover while searching for fruit and insect prey (Morrison 1980); this is consistent with the relatively large wingtips of *A. lituratus* and the average wing loading of both.

Centurio senex, for which we have no wingspan or wing area measurements, has particularly pointed wingtips compared with other stenodermatines; its habits are unclear but it appears to scavenge for fallen fruits (Strickler 1978*a*; Bonaccorso 1979). The flight is wobbling and jerky, resembling a butterfly (G. G. Goodwin & Greenhall 1961). It is unlikely to be able to hover.

Stenoderma rufum differs somewhat from other stenodermatines. The wingtip is extremely long and pointed, and the wings are among the shortest in all bats, giving it higher wing loading and lower aspect ratio than other phyllostomids. It should fly in dense clutter and may be able to hover.

(*f*) *Brachyphyllinae*

The Brachyphyllinae (= Phyllonycterinae) are largely nectarivorous and are allied to the Glossophaginae. We have measurements only for *Erophylla sezekorni*, which has very short and small wings giving it high wing loading and low aspect ratio, and small, rounded wingtips. Little has been reported of the foraging habits of this species, but in a cave its flight was rather slow and deliberate (R. E. Goodwin 1970). Valdivieso *et al.* (1978) found that like *A. jamaicensis* (which it resembles morphologically) *E. sezekorni* has flight muscles suited for flying only occasionally and in short bursts. We predict it to be similar to glossophagines, but to fly faster, and perhaps to sit or perch while feeding in preference to hovering.

(*g*) *Desmodontinae*

The sanguivore sub-family includes only three genera, each with a single species: *Desmodus rotundus*, *Diaemus youngi* and *Diphylla ecaudata* have wing dimensions rather similar to other phyllostomids. They have short (*D. ecaudata*) or average wingspan and relatively high wing loading. However, aspect ratio differs noticeably among the species, being high in *Diaemus* *youngi*, average in *Desmodus rotundus* and somewhat lower in *Diphylla ecaudata* (figure 8*d*). As in many phyllostomids, the wingtip in *D. ecaudata* is relatively long and rounded, but in *Desmodus rotundus* it is very short and only slightly rounded, and more resembles that of the mormoopids.

We predict vampires to fly relatively fast, and *Diphylla ecaudata* to be more manoeuvrable than *Desmodus rotundus*. *Diphylla ecaudata* has a somewhat shorter wingspan than the other two species, and is rather similar in aspect ratio and wing loading to the short-spanned *Sturnira* species, *Glossophaga soricina* and *Vampyrops helleri* but, like the other vampires, has markedly smaller wingtips. *D. ecaudata* is presumed to feed on avian blood and to make short flights within vegetation. Walker (1964) reported that searching vampires fly along fairly straight courses low over the ground. The high wing loading in desmodontines gives fast flight with moderate power consumption, and may be related to extensive commuting flights from a communal roost. Because feeding is relatively slow, long commuting distances (3.4 km in *Desmodus rotundus* (Wilkinson 1985)) could make time an important factor limiting total blood intake (Wimsatt 1969; McNab 1973). If our data are representative, *Diaemus youngi*, with higher aspect ratio, might travel further while foraging than the other two species; it is reported to be swift and deliberate in flight (G. G. Goodwin & Greenhall 1961).

(*h*) *Comparison of Phyllostomidae and Vespertilionidae*

The Phyllostomidae and the Vespertilionidae (§5.14) are the dominant families in the Microchiroptera. Vespertilionids are almost entirely insectivorous, many catching flying insects, whereas many phyllostomid species are frugivorous or nectarivorous or are diverse or opportunistic in diet. With the possible exception of *Macrotus*, none of the insectivorous phyllostomids feeds on flying insects, and all animal prey is obtained by gleaning (Wilson 1973; Humphrey *et al.* 1983). In general, phyllostomids have shorter wingspan and higher wing loading than vespertilionids, and longer (and in some species broader) wingtips correlating with good hovering performance. Hovering is most important for the nectarivores, but some frugivorous phyllostomids hover while feeding.

In addition to the shorter wings, a further reason for the higher wing loading in phyllostomids is the small size of their tail membranes compared with those of vespertilionids. Many insectivorous bats catching flying prey use the tail membrane to trap food (§3.8) and the tail also adds to manoeuvrability. Because phyllostomids rarely hawk, they have little need for a large tail. However, in comparison with other phyllostomids, the animalivorous species (mostly phyllostomines) have a relatively large tail membrane adding to manoeuvrability and giving low wing loading and hence the ability to fly with heavy prey. On the other hand, a reduced tail is less of a hindrance in climbing and clinging among vegetation. Therefore, vegetarian phyllostomids might be expected to have a reduced or absent tail membrane, as is also the case in pteropodids. The higher wing loadings in the family associated with small tail membranes are most characteristic of vegetarian species, which also have short wingspan and low aspect ratio. These bats typically make rapid and short flights among vegetation. If nectar is sparse or if there are long distances between fruits or flowers, morphology would favour high flight speed allowing the greatest opportunity of foraging during a single night (von Helversen & Reyer 1984; Lemke 1984). This evidently outweighs any pressure for low wing loading to fly better with larger single fruits or with greater nectar loads. The same argument may also be appropriate to explain the rather small wings in the blood-feeding desmodontines.

5.12. *Natalidae, Furipteridae, Myzopodidae and Thyropteridae*

The Natalidae are small insectivorous bats from the New World tropics, and of the eight species our sample includes only *Natalus stramineus*, which has long wingspan, very large wing area, average aspect ratio and extremely low wing loading (figure 8*e*). The wingtips are average in length and very rounded (figure 10*e*). We predict its flight to be extremely slow and manoeuvrable. It was described by Walker (1964) as fluttering and almost moth-like, and by Strickler (1978*a*) as highly manoeuvrable. In larger bats this wing shape is associated mainly with gleaning from the ground and with flight in open, uncluttered spaces; however, natalids are very small, and with good manoeuvrability can inhabit dense clutter.

The Furipteridae (two species and genera from tropical South America) and Myzopodidae (one species from Madagascar) are allied to the Natalidae, but we have no morphological measurements of them. Both are relatively small; the Furipteridae are insectivorous (LaVal & Fitch 1977) and the same is presumed for the Myzopodidae.

The two *Thyroptera* species within the Thyropteridae resemble the Natalidae in all wing dimensions (long wingspan, very large area, average aspect ratio and very low wing loading) (figure 8*e*). Their wingtips are rounded and slightly longer than average. We predict that their flight will be slow and manoeuvrable in clutter, like that of *Natalus*. Findley & Wilson (1974) described the flight of *T. tricolor* as agile and manoeuvrable, and confined to near the forest floor; they thought that it gleaned insect prey from vegetation. However, the species was described as an aerial insect feeder by LaVal & Fitch (1977).

5.13. *Vespertilionidae*

This is the largest bat family; it has worldwide distribution and includes more than 300, mainly insectivorous, species. The vespertilionids are diverse in wing dimensions, and include bats with a wide range of wing loadings, although most have average or low aspect ratios. Some species have a very low aspect ratio (e.g. the unusually short-winged *Mimetillus moloneyi*) but the majority cluster around the average wing proportions for all bats and show a slight displacement toward lower wing loading (figure 8*e*). The largest genus, *Myotis*, shows considerable variation, but tends to be concentrated in the low wing loading, low aspect ratio category typical of manoeuvrable and slow-flying bats. On average, wing loading is lower in vespertilionids than in phyllostomids (although the variation is greater in the former group), reflecting the stricter flight demands associated with aerial insect catching. Wingspan and wing area in vespertilionids increase with body mass more steeply than predicted by isometry ($B = 1.52\ M^{0.37}$, $S = 0.32\ M^{0.73}$) (table 4; figures 4 and 5); aspect ratio and wing loading increase sharply with increasing mass ($A = 16.8\ M^{0.20}$, $Mg/S = 110\ M^{0.55}$; figures 6 and 7). Most vespertilionids have rounded wingtips which are shorter than average, but the variation in wingtip size and shape is considerable (figure 10*e*).

Species with high aspect ratio

Most vespertilionids have average wingspan and aspect ratio, although there is large variation. Species with high aspect ratios include *Pipistrellus ceylonicus*, *P. pipistrellus*, *P. tasmaniensis*, *Lasiurus cinereus* and *Miniopterus inflatus* with relatively high wing loadings, *Scotophilus borbonicus*, *S. heathii*, *S. dinganii*, *Scotozous dormeri*, *Chalinolobus gouldii*, *C. morio*, *Eptesicus pumilus* and *E. vulturnus* with about average wing loading, and *Myotis bocagii*, *Pizonyx vivesi*, *Miniopterus australis*, *Nyctophilus gouldii* and *N. geoffroyi* with low wing loading and longer wings than the others (figure 8*e*). Wingtips are pointed in the pipistrelles and *E. vulturnus*, and rounded in the other species. The wingtips in *S. dinganii* are long, and are the most rounded of all vespertilionids (indeed in our sample only *Hipposideros speoris* has more rounded wingtips). We predict that bats with high aspect ratio have enduring flight away from clutter, and that those with high wing loadings will fly faster than others. The flight of the pipistrelles is described characteristically as erratic and butterfly-like (see, for example, Barrett-Hamilton 1910; Brosset 1966; Stebbings 1977; R. E. Goodwin 1979; Ahlén 1981) and they should be agile and fast owing to their rather high wing loading and slightly pointed wings. *P. ceylonicus* is faster than *P. mimus* (T. J. Roberts 1977), as expected from its higher wing loading. *Scotophilus heathii* is fast and direct (T. J. Roberts 1977); *S. dinganii* (*S. nigrita*) flies strongly and forages above the canopy (Kock 1969; O'Shea & Vaughan 1980). *L. cinereus* flies rapidly along straight line paths in open areas (Barclay 1985), sometimes making rapid swoops near the ground (U.M.N., personal observations); it is migratory, in accord with its high aspect ratio. *Myotis bocagii* and *Pizonyx vivesi* are specialized trawling and piscivorous species, which are considered below.

Species with average aspect ratio

Species with average aspect ratios and short or rather short wingspans have small wing areas and high wing loadings. These include *Nyctalus leisleri*, *N. noctula*, *Tylonycteris robustula*, *Lasiurus borealis*, *L. castaneus*, *Pipistrellus nanus*, *P. nathusii* and *Scotorepens orion* (figure 8*e*). *P. nanulus* is a short-winged species with average-length wingtips, but we lack data for wing area. All but *L. borealis* have rather pointed wingtips; *L. castaneus* shows the shortest wingtips among vespertilionids. We predict that species in this group will have fast, but not enduring, flight and poor manoeuvrability, and should fly primarily away from clutter, relying on agility to hawk flying insects. All the short-winged species are observed to fly rapidly and straight, usually at relatively high altitudes above or along the tree canopy (e.g. *L. borealis* (U.M.N., personal observations), *L. castaneus* (Barbour & W. H. Davies 1969), *N. leisleri* and *N. noctula* (Barrett-Hamilton 1910; Stebbings 1977; Ahlén 1981; personal observations)). *N. noctula* often makes rapid half-rolls when diving for insects (§3.5*b*) (Norberg 1976*c*).

Species with average aspect ratio, wingspan and wing loading include *Myotis albescens*, *M. dasycneme*, *M. nigricans*, *Miniopterus schreibersi*, *Vespertilio murinus*, *Eptesicus hottentotus*, *E. nilssonii* (figure 1*e*), *Pipistrellus mimus*, *P. rusticus* and *Nycticeius schlieffenii* (figure 8*e*), most of which have short and rounded wingtips (the wingtips are long and straight in *V. murinus*), and *Myotis dasycneme*, which has somewhat longer wingtips. We predict that these bats should have fairly generalized flight patterns, ranging from slow and manoeuvrable flight in clutter to hawking in semi-open areas. *M. dasycneme* and *M. nigricans* fly over water, often at some height (Hall & Dalquest 1963; Nyholm 1965; Sluiter *et al.* 1971). *Miniopterus schreibersi* appears very swift (Harrison 1964; Kingdon 1974) although its wings are not unusually small; these observations may reflect agile flight in high-altitude hawking.

Species with relatively long wingspan, and hence rather low wing loading, include *Eptesicus capensis*, *E. fuscus*, *E. regulus*, *Myotis adversus*, *M. daubentoni*, *M. grisescens*, *M. myotis*, *M. occultus*, *M. oxygnathus*, *Pipistrellus rueppelli* and *Lasionycteris noctivagans*. *M. grisescens* has short and rounded wingtips, whereas *E. fuscus* and *M. occultus* have short but rather pointed wingtips. In *E. regulus* and *M. adversus* the wingtips are average in length, but whereas they are only slightly rounded in the former they are very rounded in the latter. The long wings and low wing loading indicate flight in uncluttered habitats. In fact, most vespertilionids with relatively long wings fly slowly away from clutter, for instance around treetops (examples include *E. fuscus* (Hall & Dalquest 1963; van Zyll de Jong 1985), and *Lasionycteris noctivagans* (Barbour & W. H. Davis 1969; Barclay 1985; van Zyll de Jong 1985)). A number of *Myotis* species, including *M. adversus* (Dwyer 1970), *M. bocagii* (Fenton *et al.* 1977) and *M. daubentonii* (with slightly lower aspect ratio) (Nyholm 1965) skim over water surfaces trawling for aquatic insects; these bats usually have long wings associated with slow flight away from clutter, and rather short and less rounded wingtips than other *Myotis* species. The piscivorous bats *Noctilio leporinus*, *N. albiventris* and *Pizonyx vivesi* have longer, but comparably shaped, wingtips. (See §§6.2*c* and 6.4 for discussion of trawling and its relationship to piscivory.)

Vespertilionids with yet longer wings have still lower wing loading. This group includes *Myotis evotis*, *M. nattereri*, *M. thysanodes*, *M. tricolor*, *M. velifer*, *Pipistrellus subflavus*, *Eptesicus sagittula*, *Plecotus rafinesquii*, *Idionycteris phyllotis*, *Chalinolobus dwyeri*, *Kerivoula argentata*, *Antrozous pallidus* and *Nyctophilus timoriensis* (figure 8*e*). Most long-winged vespertilionids have short and rounded wingtips which allow large second moment of lift (and hence potentially high roll acceleration) and maximum wing flexure for greatest possible reduction of wing inertia. We predict that these bats will fly slowly and be relatively agile, and will fly around, but rarely within, clutter. This is supported by observations of, for example, *P. subflavus* (Hall & Dalquest 1963). The flight of *M. velifer* is stronger and more direct than that of other species of the genus (Barbour & W. H. Davis 1969). However, species such as *M. evotis*, *M. thysanodes* and *P. rafinesquii* forage among trees and close to vegetation, and may be hover-gleaners (Barbour & W. H. Davis 1969; Findley 1972; van Zyll de Jong 1985). *Idionycteris phyllotis* flies very slowly and also forages among clutter, but it shows a wide behavioural repertoire, including hover-gleaning (like some other plecotines) and high-altitude hawking (Czaplewski 1983), features consistent with its low wing loading but otherwise rather generalized morphology. *Antrozous pallidus* is also a gleaner, commonly landing on the ground to take insects and other arthropods (Bell 1982); it can hover for brief periods and makes short glides (Orr 1954), but is not very manoeuvrable (van Zyll de Jong 1985). *Nyctophilus* species are also gleaners (Strahan 1983). *L. noctivagans*, *M. leibii* and *Pipistrellus subflavus* are migratory, and this correlates with their long wings.

Species with low aspect ratio

The species *Pipistrellus kuhli*, *Eptesicus tenuipinnis*, *Nycticeius humeralis* and, in particular, *Mimetillus moloneyi*, have short wingspan, high wing loading and very low aspect ratio. *Myotis yumanensis*, *Rhogeessa tumida* and *P. hesperus* have relatively short wingspan, rather high wing loading and low aspect ratio. We predict that these species will have fast but not enduring flight. *M. moloneyi* has short and very pointed wingtips; *P. hesperus* and *N. humeralis* have short and rather pointed wingtips, whereas those of *M. yumanensis* are average in length and very rounded. *N. humeralis* has the longest wingtips among our sample of vespertilionids; *M. moloneyi* has the most extreme wing morphology and its flight habits are hard to predict. It should undoubtedly be fast, but with the very high wing loading the low aspect ratio confers neither good agility nor manoeuvrability. The foraging flight of *M. moloneyi* is fast, with rapid wingbeats, and the bat pursues fast-flying insects (termites) in open spaces above the forest canopy and along rivers and pools. It makes regular pauses during foraging flights and cannot make sudden turns (Lang & Chapin 1917; Kingdon 1974). These pauses and the high wingbeat frequency are consistent with the high mechanical flight power associated with its low aspect ratio. It may owe its small wings to its habit of roosting in narrow crevices (Brosset 1966). In contrast to our predictions, *Nycticeius humeralis* is migratory, and Walker (1964) describes its flight as slow and erratic. *Myotis yumanensis* forages in open areas, often low over flowing water (Herd & Fenton 1983; van Zyll de Jong 1985). The flight of *Rhogeessa tumida* is described as fast (Hall & Dalquest 1963); this is consistent with its high wing loading.

Bats with average wingspan and low aspect ratio include many *Myotis* species (e.g. *M. bechsteinii*, *M. californicus*, *M. emarginatus*, *M. keenii*, *M. leibii*, *M. lucifugus*, *M. mystacinus*, *M. occultus*, *M. sodalis*, *M. volans*), *Eptesicus serotinus*, *Plecotus auritus* (figure 1*c*), *P. austriacus*, *P. townsendi*, *Nycticeius rueppellii* and *Barbastella barbastellus*). These all have average or low wing loading and, apart from *M. californicus* and *M. volans*, short and rounded wingtips. The wingtips are more pointed in *M. volans*, but relatively long and extremely rounded in *M. californicus*. We predict that these bats fly rather slowly, usually close to or within clutter. Species with rounded wingtips (which correlate in this group with lower wing loading) should be more manoeuvrable than the others. *N. rueppellii* is slow and direct in flight (G. C. Richards, in Strahan (1983)). *M. californicus* flies slowly and erratically, usually close to the grounds, *M. lucifugus* forages over water and among trees, but *M. volans* has rapid and direct flight high in the open, usually at treetop level, although it also forages closer to the ground and occasionally under the canopy (Barbour & W. H. Davis 1969; van Zyll de Jong 1985). *M. keenii* is reported to forage high, but rather slowly, along forest edges and over ponds and clearings (Cowan & Guiget 1965). Many of this group hover to glean insects from surfaces (e.g. *M. bechsteinii*, *M. emarginatus*, *M. keenii*, *P. auritus* and some (but not all) other plecotines) (Barrett-Hamilton 1910; Brosset 1966; T. J. Roberts 1977; Stebbings 1977; Bell 1980; Ahlén 1981; Swift & Racey 1983; van Zyll de Jong 1985). Most species in this category fly only short distances; surprisingly, considering its relatively low aspect ratio, *M. lucifugus* is migratory.

Summary of vespertilionid wing adaptations

Vespertilionids usually have slow and manoeuvrable flight, and most have average wingspan and average or slightly below-average wing loading, lower than that of frugivorous bats. Their tail membranes contribute to larger total wing area and lower wing loading. Many insectivorous bats use the tail membrane to trap flying prey (§3.8) and the tail enhances manoeuvrability. The wingtips are usually short and rounded, but some species (e.g. *Scotophilus dinganii* and *Myotis californicus*) have long, large and extremely rounded wingtips, some (e.g. *Nycticeius humeralis*, *Vespertilio murinus*, *Nyctalus noctula*, *Lasiurus cinereus*, *L. castaneus* and *Mimetillus moloneyi*) have unusually pointed wingtips, and in some myotids (e.g. *Myotis bechsteinii*, *M. evotis*, *M. lucifugus* and *M. sodalis*) the wingtips are very short and rounded.

Many species are hoverers and/or gleaners, and most (but not all) of these have long ears, low wing loading and low aspect ratio. The large genus *Myotis* has been divided into three subgenera with characteristic morphology and behaviour (Tate 1941; Findley 1972): *Myotis* (including *M. bechsteinii*, *M. emarginatus*, *M. evotis*, *M. keenii*, *M. myotis*, *M. nattereri*, *M. thysanodes*), most having large wings and long ears and gleaning both from vegetation and the ground; *Selysius* (including *M. californicus*, *M. leibii*, *M. mystacinus*, *M. nigricans*, *M. sodalis*), which have broad wings and are slow-hawkers; and *Leuconoe* (including *M. adversus*, *M. albescens*, *M. bocagii*, *M. daubentonii*, *M. grisescens*, *M. occultus*, *M. velifer*, *M. volans* and *M. yumanensis*), which are heavily built, have longer wings and large feet, and trawl for aquatic insects. Our data do not have sufficient resolution to distinguish these groups fully, but the *Selysius* (slow-hawking) bats have larger and more rounded wings and the *Leuconoe* (trawling) bats have longer and more pointed wings than the more average *Myotis* (hover-gleaning) subgenus. These trends are in accordance with our predictions.

Short-spanned vespertilionid species, such as *Mimetillus moloneyi*, *L. borealis*, *L. castaneus*, *Nyctalus noctula*, *N. leisleri*, *Tylonycteris robustula*, *Scotozous dormeri*, *Scotorepens orion* and several *Pipistrellus* and *Nycticeius* species, have high wing loading and are fast fliers. Species with relatively high or average aspect ratio and pointed wings (e.g. *Nyctalus* species) are particularly agile in fast flight and hawk fast-flying insects away from clutter. This group parallels the adaptations of some emballonurid and molossid species, but lacks their very high aspect ratio. Longer-winged bats, such as *Nyctophilus* and *Eptesicus* species, *Antrozous pallidus* and some *Myotis* (*Selysius*) species, usually have low wing loading and high or average aspect ratio. They fly slowly, often close to the ground in open areas or around or within vegetation, and may glean from the ground. The shortest and most rounded wingtips (indicating agility in slow flight) are found in this group.

5.14. *Mystacinidae*

Mystacina tuberculata, a forest species in New Zealand, eats a diet of insects, fruit and nectar and has been reported to scavenge at fallen fruits and at vertebrate carcasses. *M. tuberculata* has exceptional running ability and can burrow, but it is not particularly threatened by terrestrial mammal predators; much, if not all, of its food is taken on (or even under) the ground (Daniel 1979) and it seems to parallel some New Zealand birds in that its wings are reduced. Our data do not fully support the implication that its flight is impaired; although the wingspan is shorter than average, *M. tuberculata* has only moderately high wing loading (figure 8*e*) and short and slightly rounded wingtips. Its flight is slower and less agile than that of the other endemic New Zealand bat, the vespertilionid *Chalinolobus tuberculatus* (Daniel 1979). Slow flight in *M. tuberculata* would be surprising in view of its unusually small wings.

Earlier in this century a second species of *Mystacina* became extinct because of predation by introduced carnivores (M. J. Daniel, personal communication). *M. robusta* was rather larger than *M. tuberculata* and had much higher wing loading and aspect ratio. This indicated faster flight with less manoeuvrability and greater agility than in *M. tuberculata*.

5.15. *Molossidae*

Molossids are widely considered to be the most highly adapted bats, and are characteristically specialized for hawking of high-flying insects. Wingspan increases with mass slightly faster than isometry, and wing area slightly slower ($B = 1.38\ M^{0.36}$, $S = 0.13\ M^{0.61}$). Aspect ratio and wing loading are relatively high in larger molossids ($A = 21.1\ M^{0.22}$, $Mg/S = 104\ M^{0.48}$); although in the whole family aspect ratio and wing loading are unusually high, extremely small wings occur only in smaller molossids. If wing loading in the largest molossids were relatively as high as in the smaller species, flight speeds would be unacceptably high and hawking of aerial insects would become energetically too expensive and/or behaviourally impractical. The wingtips are typically slightly larger than average and are slightly rounded (figure 10*e*).

Molossids are unusual in having relatively small wing area, and the high wing loading of most species (figure 7) implies fast flight relative to other bats of comparable size and an inability to manoeuvre within clutter. Descriptions of molossids consistently refer to their flight at altitude, their high flight speeds and their considerable agility. In this they parallel some insectivorous birds; the wing loading of bats is typically rather lower than that of birds of similar size, but the wing loading of insect-hawking molossids is similar to that of swifts and hirundines, which have relatively large wings and slow flight (Norberg 1981*a*, 1986*b*). Swifts and hirundines are the diurnal ecological counterparts of molossids; the two groups are adapted primarily for hawking flying insects away from clutter. The flight of molossids is rapid, enduring and agile, but not particularly manoeuvrable. The rather long and rounded wingtips indicate that the main mechanical constraint influencing the family has been the need for high rolling acceleration for adept hawking of insects in open spaces. The high wing loading may be an important adaptation to confer high flight speeds and thereby to save time during regular long-distance flights to foraging areas and distant water holes. However, this high speed can be achieved only at the expense of reduced manoeuvrability; power output and cost of transport are also increased unless aspect ratio is also high. In the larger molossids, for which the energy margin is perhaps more critical, wing loading is rarely as large as in the smaller species. In relation to its body size the large *Otomops martiensseni* has lower wing loading and flies more slowly than other molossids, but its actual flight speed is comparable to that of other, smaller, molossid species.

Species with high aspect ratio

Bats of the genera *Otomops*, *Tadarida* and *Eumops* and *Molossus ater* have very high aspect ratio. *Otomops martiensseni* (figure 1*d*) and *T. aegyptiaca* have the largest wings and the lowest wing loading of all molossids (figure 8*e*), and are hence predicted to fly more slowly. *T. aegyptiaca* and *T. fulminans* also have long wingspan, and *T. fulminans* has the highest aspect ratio of any bat in our sample. The flight of these animals is inexpensive and enduring (low power and cost of transport) compared with most other bat species, and they are confined to foraging in open spaces. *O. martiensseni* has relatively slow and straight flight in open country, and so differs from other molossids (Kingdon 1974). It makes dives and rapid glides during prey capture and at landing, and performs side-slips with partly folded wings to lose height rapidly (Norberg 1976*c*).

The average-spanned bats (most *Tadarida* species, *E. perotis*, *Neoplatymops mattogrossensis*, *M. ater*) have high wing loading and should have rapid, straight and sustained flight in open areas. Any lack of manoeuvrability owing to their unusually high wing loading and aspect ratio is compensated by high agility. *T. brasiliensis* is one of the most gregarious of all bats. The Mexican free-tailed bats (*T. b. mexicana*, the subspecies included here) leave their caves in huge numbers as a serpentine undulating column of bats stretching for many kilometres across the sky before the bats spread out in several directions (Barbour & W. H. Davis 1969). The bats increase speed as they reach the open sky; R. B. Davis *et al.* (1962) recorded speeds of more than 18 m s^{-1}, with a top speed of at least 27 m s^{-1}. The flight is straight and, from Carlsbad Caverns in New Mexico, the bats travel about 65 km to reach their feeding area; they also migrate (Barbour & W. H. Davis 1969). These long distance flights are in accord with their high aspect ratio. *T. midas* is noted to fly high and continuously during foraging, and to travel up to 10 km from their day roost (Fenton & Rautenbach 1986). *M. ater* flies high, fast and erratically (G. G. Goodwin & Greenhall 1961). *E. perotis* has strong and fast flight, and makes dives and rapid glides during insect catching and landing (Vaughan 1959), like those of *O. martiensseni*. Although they are characteristically fast-hawking bats, certain molossids also forage on the ground, running about with some agility (e.g. *T. australis*) (G. C. Richards, in Strahan (1983)). This may allow the bats to compensate for periods of low abundance or activity of high-flying insects, as these morphologically specialized species are unable to adopt other modes of aerial feeding.

Freeman (1981*a*) noted that aspect ratio is generally higher in New World than Old World molossids, and she suggested that this could be linked with migration or with cliff roosting. We propose that it may also be associated with differential character displacement with respect to otherwise comparable bats (e.g. *Taphozous* and *Diclidurus* species of the Emballonuridae).

Species with near-average aspect ratio

The short-winged *Molossus* and *Cheiromeles* species have average or slightly large aspect ratio, and lie at a similar place in the wing loading and aspect ratio diagram to the rhinopomatid *Rhinopoma microphyllum* (figure 8*c*) and short-spanned vespertilionids such as *Tylonycteris robustula*, *Lasiurus borealis*, *L. castaneus* and *Nyctalus leisleri* (figure 8*e*). We predict that these molossids will fly fast and hawk insects in semi-open spaces. We have already noted that flight in rhinopomatids and some emballonurids is similar to that in some molossids.

6. Comparison of feeding classes

We have defined feeding classes based on the main food items taken by bats (§2.3). Our principal-component analysis reveals important morphological differences between these classes. Figures 8*f* and 10*f* show the mean morphology of feeding classes defined in two ways: open stars are primary food classes (representing the sole or dominant diet component); filled stars are the mean of all bats taking that class of food. The addition of species from other feeding classes dilutes the statistics and in each case the latter group is closer to average morphology than the corresponding primary class (see also correlation equations in table 4).

Insectivores dominate the Chiroptera (representing approximately 70% of species), and inevitably are close to the morphological average, but there is considerable variation within the class (§6.2). Carnivores and piscivores have low wing loading and low and average aspect ratio, respectively; both have relatively large, rounded wingtips, and are relatively large bats. Frugivores and nectarivores have below-average aspect ratio, slightly above-average wing loading and large but pointed wingtips. Primary frugivores are large, nectarivores are generally small. We have considered the sanguivores (Desmodontinae) in §5.11 (*g*).

6.1. *Size differences between feeding classes*

Although the size range of bats is large, it is much smaller than the range of birds. In bats, body mass spans about three orders of magnitude, from less than 0.002 kg (*Craseonycteris thonglongyai*, *Tylonycteris pachypus*) to about 1.5 kg (*Pteropus giganteus*, *P. vampyrus*), whereas flying birds span four orders of magnitude, from 0.0015–0.0020 kg to about 15 kg, so the largest flying birds weigh ten times as much as the largest bats. Size limits in bats are discussed in §9.1, where we compare morphological and metabolic constraints on maximum size in bats with those in birds. Still, size variation in bats coincides with diet for both mechanical and ecological reasons, as all the largest bats are frugivores and all the smallest are insectivores.

Differences in diet (as measured, for instance, by our feeding classes) are influenced by geographical range. Temperate bats are mostly small and insectivorous, but tropical communities enjoy a greater variety of food habits, reflecting greater food availability (McNab 1982). The mobility of bats permits exploitation of patchily distributed food resources (see, for example, McNab 1971; many species feed opportunistically and/or display seasonal duality in diet (Gillette 1975). The greater diversity in tropical bat communities appears to be determined not by tighter packing of ecologically and/or morphologically neighbouring species but by the addition of more outlying and variable species (Findley 1976; Findley & Wilson 1982; Findley & Black 1983; Schum 1984). All these factors permit tropical bats to attain larger sizes and more extreme morphology; in our analysis all outliers in all size and shape components are tropical, and often have distinctive habits. Variation in size is usually correlated with variation in food-particle or prey size (see, for example, Ashmole 1968): large fruit bats eat larger fruits than small bats (J. R. Baker & Z. Baker 1936; van der Pijl 1957); small animal-eating bats take small insects, whereas larger ones may take larger insects or small vertebrates. We identify here mechanical factors which delimit size in the feeding classes. These act in tandem with physiological factors, which we cannot consider here. We do not attempt to assess the relative importance of mechanical, physiological and ecological constraints on body size.

Taking flying insects by hawking or flycatching and attacking non-flying prey by hovering and gleaning in clutter imposes large demands on manoeuvrability, which exceed comparable demands on vegetarian species because of the potential response of the prey. We have shown that smaller bats are more manoeuvrable and agile and can fly more slowly. They also enjoy a larger energy margin because the demands of flight are low compared with other components of metabolism. Small bats therefore display a broader repertoire of flight behaviour, and this may be reflected in more generalized flight adaptations. At the other extreme, larger bats cannot fly in dense clutter, and the fall-off in manoeuvrability and their tighter energy margin may prevent them from acquiring sufficient insects. For these reasons, insectivory is restricted to relatively small bats, ranging from around 0.002 kg (e.g. the genera *Craseonycteris*, *Thyroptera*, *Furiptera*, *Tylonycteris*, *Pipistrellus*) to about 0.14 kg (*Cheiromeles torquatus*), but of 175 insectivores in our analysis only seven (*Taphozous nudiventris* (Emballonuridae), *Hipposideros commersoni*, *H. diadema* (Hipposideridae), *Tadarida congica*, *Eumops perotis*, *Cheiromeles* sp. and *Cheiromeles torquatus*, (Molossidae)) are heavier than 0.05 kg, and all are either perch hunters or high-altitude fliers relying on speed and agility rather than manoeuvrability to catch insect prey. Bats dominate the 'niche' of small nocturnal insectivores, we think, because of constraints on manoeuvrability, agility and flight energetics. However, Fenton (1980) has pointed out that echolocation is a relatively short-range operation, and this factor also determines a maximum size for bats actively hunting animal prey.

Hovering flower-visitors are also restricted in size for aerodynamic and mechanical reasons. Taking fruit or nectar and/or pollen while hovering may be more costly than flight-hunting, and demands a reliable food source (see, for example, von Helversen & Reyer 1984). These bats range from 0.0065 kg (glossophagine phyllostomids) to about 0.045 kg (macroglossine pteropodids). The larger macroglossines perch rather than hover while feeding, so pressures for small mass to improve hovering performance are weaker than in the glossophagines. Some macroglossines (e.g. *Megaloglossus woermanni*, *Macroglossus minimums*) are among the smallest pteropodids and are comparable in mass to the smallest glossophagines, and we have predicted they will hover readily.

Frugivores are usually larger than insectivores, although the size ranges overlap extensively.

Species examined that feed mainly on fruit range in size from about 0.01 kg (*Artibeus phaeotis*) to about 0.06 kg (*A. lituratus*) in the phyllostomids and from about 0.014 kg (*Balionycteris maculata*) to about 1.5 kg (*Pteropus giganteus*) in the pteropodids. Only the larger species can handle large fruits, which they often carry to feeding roosts, although the largest pteropodids will defend trees laden with ripe fruit (e.g. *Pteropus vampyrus* (Gould 1977*a*)). Frugivores may have difficulty in obtaining sufficient protein from fruit. Phyllostomids resolve this problem by eating some insects, but pteropodids must take larger quantities of fruit than their energetic requirements (D. W. Thomas 1984). Thomas has suggested that frugivorous pteropodids may dispose of energy from excess fruit intake by flying; if this is so, flight economy is unlikely to be a significant factor influencing wing morphology in frugivorous pteropodids.

Larger animal-eating bats are able to take larger prey, and so carnivores are larger than most insectivorous species. Carnivorous bats range from about 0.035 kg (*Nycteris grandis*) to about 0.16 kg (*Vampyrum spectrum*). Fishing bats range from 0.025 kg (*Pizonyx vivesi*) to 0.06 kg (*Noctilio leporinus*). The three vampires (0.028–0.036 kg) feed solely on blood, a nearly pure protein diet. These bats ingest almost their own weight in blood each night but concentrate the food intake (and reduce the load they must carry) by passing plasma from the blood while they feed (McNab 1973). Larger bats might take too much blood from their victims and hence impair their own means of livelihood, might be unable to carry the load involved, or might have insufficient feeding time in a night. Moreover, the necessity of subtle landing or climbing on a victim may also preclude larger size. We see no obvious mechanical factors constraining the lower range of size in these bats.

6.2. *Insectivores*

Most bats feed mainly on insects, but use different foraging techniques. We have distinguished the following broad foraging strategies in insectivores: (*a*), fast, long-range hawking; (*b*), slow, short-range hawking; (*c*), trawling; (*d*), hovering and/or gleaning; and (*e*), flycatching. These categories may overlap or intergrade; few species belong uniquely to any one. Most bats are opportunistic and feed in various ways. But observations in the literature (discussed in §5) are generally consistent, and we feel justified in assigning the majority of insectivorous species to one dominant category. Other authors (for example, Brosset 1966; Neuweiler 1983; Hill & J. D. Smith 1984) have discussed broadly similar definitions of feeding strategies and of the use of habitat space. Simmons *et al.* (1979) and Bell (1980) distinguished long- and short-range hawking (short-range including trawling) and gleaning, and discussed the consequences for echolocation. Bonaccorso (1979) used comparable categories to study neotropical foraging guilds, but his species sample contained a narrow range of insectivorous species (no vespertilionids) and some strategies were not represented.

(*a*) *Fast hawking*

This group comprises bats which rely on speed and agility to catch insects away from clutter; they often fly at considerable altitudes, above canopy level or within clearings or pathways, and typically in wide circles or on regular straight-line beats. These species use echolocation to detect prey at relatively long range (about 3–5 m or more) (Simmons *et al.* 1979; Bell 1980). We have predicted (§3.8) that fast-hawking bats should have high wing loading for fast flight, and relatively long, pointed wingtips for low wing inertia and hence good agility at high speeds. High aspect ratio results in low cost of transport, and this could be important if foraging flights are sustained.

Characteristic species in this group include molossids, emballonurids of the genus *Taphozous*, and noctules (*Nyctalus*) and lasiurines in the Vespertilionidae. All these species forage at high speeds and altitude. Rhinopomatids are similar, but generally do not fly as high or as strongly. As predicted, fast-hawking bats have above-average loading and aspect ratio and pointed wings, and fall in the upper right quadrant in figure 8. Molossids and noctules have, as expected, small hand-wing areas and only slightly rounded wingtips (low T_S and I) but the wingtips are relatively long (relatively high T_l). Rhinopomatids and lasiurines have rather short wingtips, and should be less agile in flight.

A few insectivores with high wing loadings have low aspect ratios, including *Pipistrellus kuhlii*, *Eptesicus tenuipinnis*, *Nycticeius humeralis* and (the most extreme) *Mimetillus moloneyi*. Flight in these short-winged bats is very expensive, and is relatively straight with very low manoeuvrability, which results from the high wing loading. *N. humeralis* and *M. moloneyi* have pointed wingtips and hence good agility, whereas *E. tenuipinnis* has very rounded wingtips and hence better manoeuvrability. Insectivorous bats need good manoeuvrability and agility and relatively low flight power, because many are on the wing for long periods seeking and catching prey. This may explain why so few insectivorous bats have the apparently unfavourable combination of high wing loading and low aspect ratio.

(*b*) *Slow hawking*

This is a more diverse group, dominated by sustained flight in or around clutter. These bats locate their prey by echolocation at short range, and require slow speed manoeuvrability and agility to catch it in flight. For this reason these are mainly rather small bats. Some species (in for example the genera *Saccopteryx*, *Pipistrellus*, *Eptesicus*, *Miniopterus* and *Vespertilio*) probably fall between the fast- and slow-hawking categories, flying slowly and relatively undisturbed by clutter.

Low-flying insectivores with high aspect ratio and long wings, such as the emballonurid genera *Emballonura* and *Rhynchonycteris*, many hipposiderids and mormoopids, *Macrotus* (Phyllostomidae) and some vespertilionid genera (e.g. *Lasionycteris*, *Nyctophilus* and *Eptesicus*), have low wing loadings. Hence they have slow, manoeuvrable and inexpensive flight, and can afford to be on the wing for long periods. Their long wings may confine them to more open areas. Mormoopids and some hipposiderids forage close to the ground, but usually fly away from clutter. Short and rounded wingtips are further adaptations for low-speed agility (maximum wing flexure for reduction of wing inertia and large roll moments of lift). Prey capture movements are often similar to those of the faster, higher-flying bats described above, but slow-flying species may be attracted to predictable insect swarms.

Most insectivorous species in the Nycteridae, Megadermatidae, Rhinolophidae, Natalidae, Thyropteridae and Vespertilionidae (e.g. the *Myotis* sub-genus *Selysius*) have low wing loading and low or average aspect ratio. The wingtips are usually short (except for *Nycteris*), broad and rounded, as we have predicted for slow-hawking bats (§3.8). The low wing loading and the relatively short, cambered wings permit highly manoeuvrable flight and the slow tight turns which are essential for insect hawking near to vegetation. Many of these bats may also glean resting insects.

(*c*) *Trawling*

Many insects swarm over water and regularly attract feeding bats. This mode of feeding is used opportunistically by many slow-speed hawking species, and prey location and capture techniques are similar, but foraging over water is particularly favoured by longer-winged animals. The related behaviour pattern of trawling for aquatic insects on the water surface is more specialized. Trawling is characteristic of myotids of the *Leuconoe* sub-genus (Findley 1972), and has been reported in *M. capaccinii*, *M. dasycneme* and *M. daubentonii* in the Palearctic (Nyholm 1965; Stebbings 1977; Wallin 1969), *M. albescens*, *M. grisescens*, *M. lucifugus*, *M. velifer* and *M. yumanensis* in North America (Barbour & W. H. Davis 1969; Belwood & Fenton 1976; Fenton & Bell 1979; Herd & Fenton 1983; van Zyll de Jong 1985), *M. macrotarsus* in south east Asia (M. B. Fenton, personal communication), *M. adversus* in Australia (Dwyer 1970; Thompson & Fenton 1982) and *M. bocagii* in Africa (Fenton *et al.* 1977). Trawling is also used in insect catching by *Nycticeius sanborni* (L. S. Hall, in Strahan (1983) and by the piscivorous bats *Noctilio albiventris*, *N. leporinus* and *Pizonyx vivesi* (§6.4), and it has been deduced in *Macrophyllum macrophyllum* (Phyllostomidae) from morphology and faecal samples (Brosset 1966; Gardner 1977). Most trawling species have average or slightly high aspect ratio, low wing loading and rather long, pointed wings (figure 11), giving them slow, economic and manoeuvrable flight in accordance with our predictions (§3.8). They resemble piscivorous species in their well-developed hind feet, which are often free of the wing membrane.

(*d*) *Gleaning and hovering*

Many bats hover briefly while searching for food or while gleaning from vegetation. Insectivorous and nectarivorous bats which are known to be gleaners and/or hoverers are shown in figure 12. We distinguish two forms of gleaning: from vegetation and surfaces such as walls and tree trunks, requiring hovering flight, and from surfaces like the ground, requiring the ability to handle prey on the ground and often to fly off with it.

Hover-gleaning is characteristic of many small myotid (sub-genus *Myotis*) and plecotine vespertilionids (including *Myotis auriculus*, *M. bechsteini*, *M. evotis*, *M. keenii*, *M. myotis*, *M. nattereri*, *M. thysanodes*, *Plecotus auritus*, *P. austriacus*, *P. rafinesquii*, *P. townsendii* and *Idionycteris phyllotis*). The strategy is also used by some nycterids and hipposiderids, and by many of the smaller insectivorous phyllostomids. As we predicted (§3.8), hover-gleaning bats have average lengthed wings, low wing loading and rounded wingtips, so that they achieve good manoeuvrability at the penalty of relatively expensive flight. Hover-gleaning can probably be used opportunistically by virtually all small and manoeuvrable insectivorous bats; from wing morphology we predict it to be adopted by *Craseonycteris thonglongyai*, natalids and thyropterids. For energetic reasons hovering bats should benefit from long wings, but hovering sequences are rather short, and selection forces favouring manoeuvrability in clutter seem to have acted against long wings in hover-gleaners. On the other hand, microchiropterans have proportionately longer wings than passeriform birds of similar mass, and, in the lower mass range, insectivorous bats have nearly the same wingspan as hovering hummingbirds, which have longer wings than other birds of similar size (Norberg 1981*a*).

Ground-gleaning enables bats to obtain flightless insects and other terrestrial arthropods or to catch flying insects before they can take flight. Like hover-gleaners, these bats need slow and manoeuvrable flight, and may have longer wings where their habitat is less cluttered. Bats known to take insects in this way include *Nycteris thebaica* (O'Shea & Vaughan 1980), *Cardioderma cor* (Vaughan 1976), *Megaderma lyra* (Fiedler 1979), *Macroderma gigas*, *Macrotus californicus* (Bell 1985), *Antrozous pallidus* (Bell 1982) and the larger insectivorous phyllostomids (Wilson 1973; Gardner 1977; Bonaccorso 1979). Wing morphology is rather varied: the

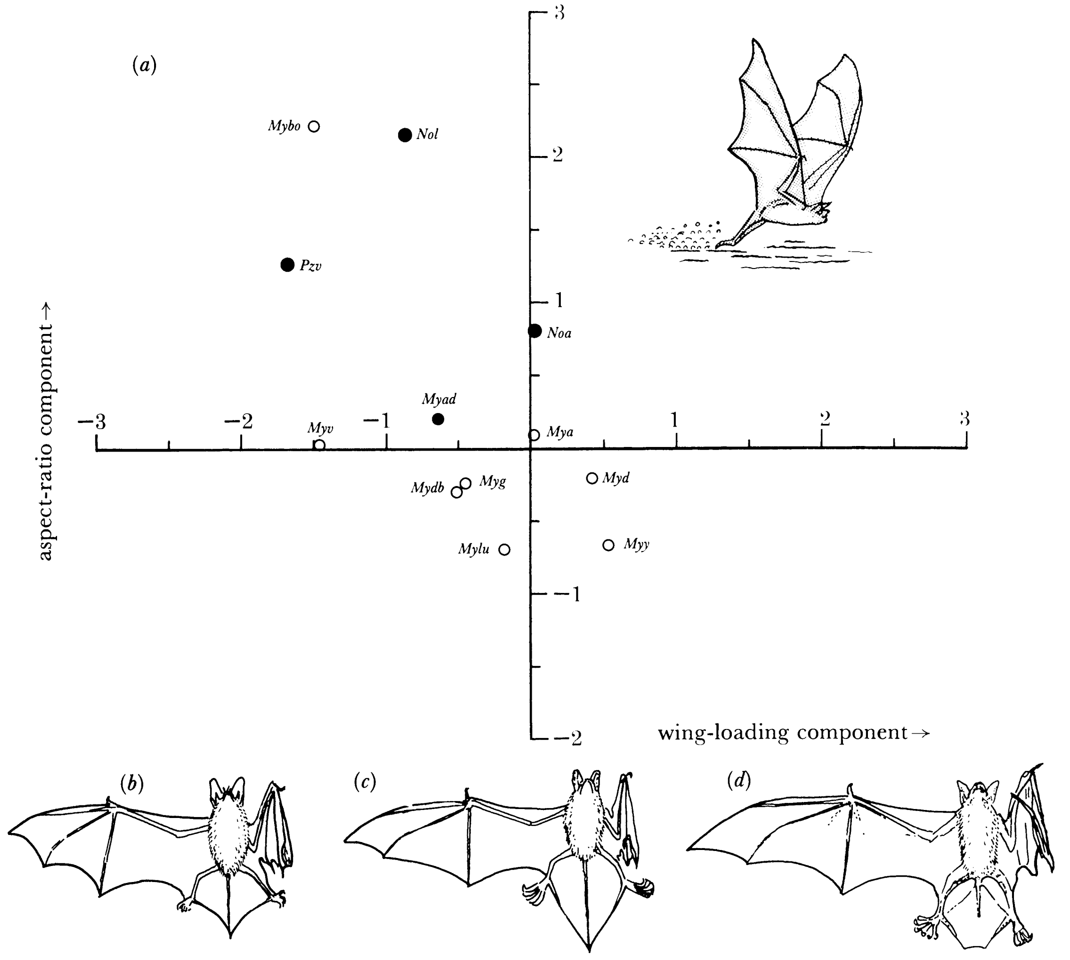


FIGURE 11. (*a*) Scatter plot of second and third principal components of wing morphology in trawling insectivorous bats (open circles) and in piscivores (closed circles). (Details as in figure 8.) The inset bat is drawn from a photograph given by Leen & Novick (1969). (*b*) Wing outline of *Myotis myotis*, a typical slow-hawking insectivorous vespertilionid. (*c*) Wing outline of *Pizonyx vivesi*, a piscivorous vespertilionid. Note the enlarged wingtip and long claws on the feet, which are free from the tail and wing membranes. (*d*) Wing outline of *Noctilio leporinus* (Noctilionidae); the adaptations for piscivory seen in *P. vivesi* are more marked in this larger bat. (Parts (*b–d*) from Eisentraut 1951.)

majority fulfil our predictions in that aspect ratio is average, wing loading is low and the wingtips are rounded; in ground-gleaning phyllostomids the aspect ratio tends to be below average.

Many bat biologists have identified large ears as the acoustic accoutrement of gleaning; many of the species we list do indeed have large ears. Some gleaners need large ears to enable them to use low-intensity echolocation calls or to hear sounds from prey (see, for example, Fenton 1984), but detection and localization of prey on surfaces requires the capacity to fly slowly and to manoeuvre among vegetation. For slow-flying bats the drag of large ears is small (Norberg 1981 *a*) and selection is unlikely to act against their appearance, especially in view of the sensory benefits they confer. And, as we have argued, many slow-flying bats glean when prey is available. Note, however, that some bats with long ears do not glean (e.g. *Euderma maculatum* (Woodsworth *et al.* 1981; Leonard & Fenton 1983) and *Otomops martiensseni*).

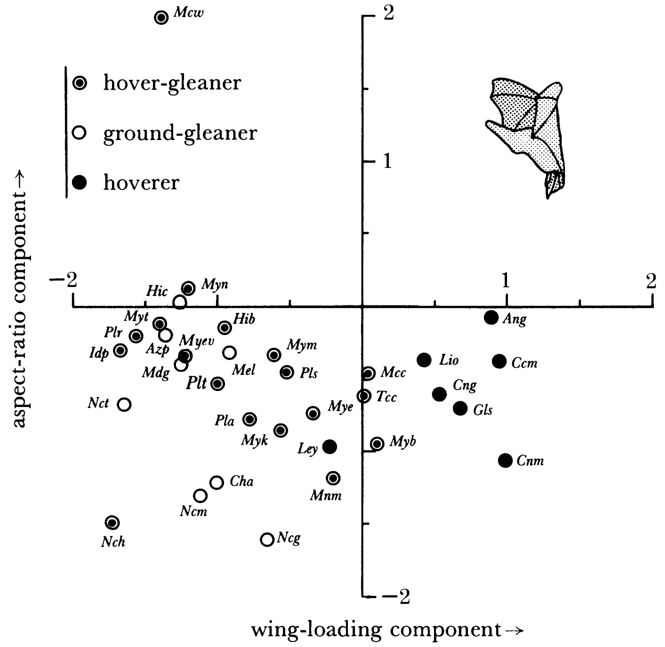


FIGURE 12. Scatter plot of second and third principal components of wing morphology in bats adopting hovering and/or gleaning feeding strategies. (Details as in figure 8.)

(*e*) *Flycatching and perch hunting*

Some bats hawk flying insects by making short flights from a perch; others use a perch while seeking non-flying prey. This strategy was likened to the behaviour of flycatching birds by Shortridge (1934), and has been termed 'flycatching' in bats; it is particularly important for the large megadermatids *Megaderma lyra*, *M. spasma* and *Macroderma gigas* in which flight costs are high, but it is used also by other species including *Cardioderma cor* (Vaughan 1976) and *Lavia frons* (Vaughan & Vaughan 1986), some *Rhinolophus* and larger hipposiderids. In vespertilionids flycatching has been noted only in *Nyctophilus bifax* (Fenton 1982*b*) and juvenile *Myotis lucifugus* (Buchler 1980). Of the flycatching megadermatids only *Lavia frons* relies on catching flying insects; the others usually, but not exclusively, glean prey from the ground.

Flycatching was considered by Hill & J. D. Smith (1984) to be primitive, and it resembles the use of feeding roosts by frugivores (Kunz 1982). But flycatching has some definite advantages. By using a 'sit-and-wait' strategy while seeking food (whether in the air or on the ground) the bat is inconspicuous and can 'ambush' its prey. As flights are infrequent and brief and the bat flies only for capture it uses less energy than in sustained hawking; a *C. cor* flew for a total of less than 11 minutes in a single night, and mean sally distance was less than 24 m (Vaughan 1976). Flycatching also enables the prey spectrum to be broadened (Vaughan & Vaughan 1986), and allows capture of larger prey items (Kunz 1982). Bats that use a flycatcher style commonly remain close to or among vegetation, and have short wings. Flycatcher bats have relatively large wingtips and low aspect ratio, giving good manoeuvrability, large roll moments of lift and increased agility; like many gleaners, they often have large ears. In some species the rapid acceleration needed to fly from a perch is reflected in flight-muscle biochemistry specialized for short, brief flights (pp. 387, 392).

A variation on 'flycatching' has been reported for *Artibeus jamaicensis* by Tuttle (1968), who observed that while hanging from a perch by one leg the bat used its wings to catch passing insects that came within reach. This behaviour does not demand any specialized wing form, but would be favoured by long wings and large wingtips.

6.3. *Carnivores*

We consider carnivorous bats to be those eating vertebrates other than fish. This class (figure 13) comprises only a few species, some of which are only partly carnivorous. Bats known to take vertebrates (chiefly frogs, small birds and small terrestrial mammals, but also reptiles and occasionally other bats) include *Nycteris grandis* (Nycteridae), *Megaderma lyra*, *M. spasma*, *Cardioderma cor* and *Macroderma gigas* (Megadermatidae) and *Phyllostomus hastatus*, *Trachops cirrhosus*, *Chrotopterus auritus* and *Vampyrum spectrum* (Phyllostomidae). There are isolated records of *Antrozous pallidus* flying with a small mouse (Bell 1982), and of *Nycticeius rueppellii* (M = 0.03 kg) feeding on small vertebrates (G. C. Richards, in Strahan (1983)) and other bats (Woodside & Long 1984).

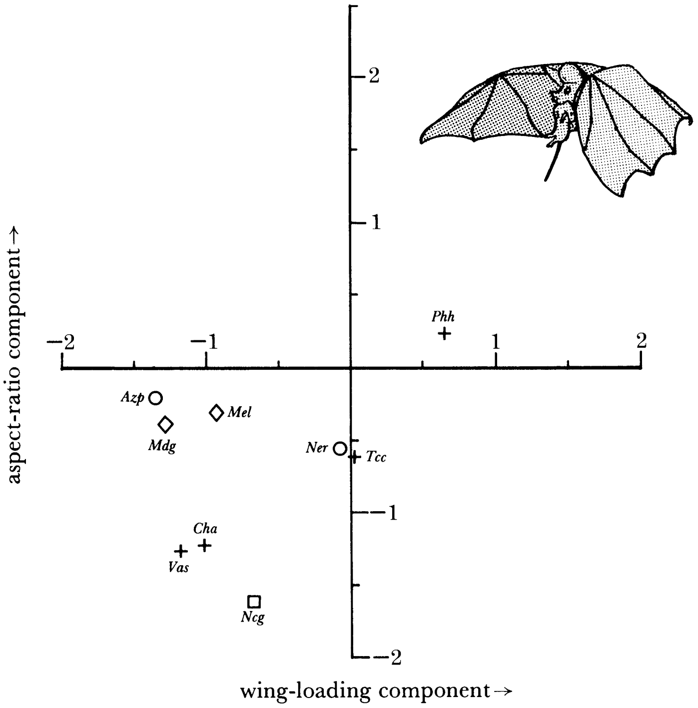


FIGURE 13. Scatter plot of second and third principal components of wing morphology in carnivorous bats. (Details as in figure 8.) The inset bat is drawn from a photograph given by Leen & Novick (1969).

Most carnivorous bats use a mixture of ground- or foliage-gleaning and perch-hunting; carnivory probably evolved as a result of insectivores' using these foraging techniques (Gillette 1975). Our predicted morphological correlates are similar to those of comparable insectivores, but carnivorous bats also have specialized adaptations of the jaws and teeth (Freeman 1984). Because they need to take off and fly with considerable loads, carnivores should have low wing loading (§3.4); they may also have low aspect ratio, as short wings allow flight within clutter during foraging. The wingtips should be relatively long for slow flight, for the short hovering bouts which may precede prey seizure, and for take-off. In all carnivores for which data are available, the wingtips are average in length or long (figure 10*f*); most species have low or average aspect ratio, and all but *P. hastatus* have low wing loadings. All but *N. rueppellii* have large or rather large ears, which together with slow flight aid auditory location of prey within vegetation much as they do for gleaning insectivores; many carnivores hunt without active echolocation to avoid alerting their prey (see, for example, Fiedler 1979; Kulzer *et al.* 1984).

6.4. *Piscivores*

Three bats, *Noctilio albiventris*, *N. leporinus* (Noctilionidae) and *Pizonyx vivesi* (Vespertilionidae) regularly eat fish or crustacea. *N. albiventris* is primarily insectivorous, but fish form a significant proportion of its food, and it catches insects by trawling (Suthers & Fattu 1973; Hood & Pitochelli 1983) (§6.2*c*). The noctilionids predominantly take freshwater fish, but *P. vivesi* apparently relies on marine prey (Walker 1964; Carpenter 1968). All piscivores have longer wings with higher aspect ratio than most other bats, but they do not have the high wing loadings typical of most other species with a high aspect ratio (figure 11). The wings are adapted for economic flight away from clutter, in this case over open water. The high wing area permits slow flight (which is advantageous, as the bats have to localize prey in the water, usually by the disturbances and ripples on the water surface) and also help the bats to benefit from ground effect (§5.10). The wingtips in the noctilionids and in *P. vivesi* are long and rounded, much more so than in trawling insectivores, probably as an adaptation for slow flight and for turning at the extremes of the foraging flights (§3.5).

We have identified a 'trawling' flight pattern in insectivores (§6.2*c*); fishing behaviour in noctilionids and *P. vivesi* closely resembles this strategy. There are isolated reports of 'trawling' myotids (*M. adversus* (Robson 1984), *M. albescens* (Whitaker & Findley 1980), *M. daubentonii* (Brosset & Deboutteville 1966), *M. macrotarsus* and *M.* (*Rickettia*) *pilosa* (Brosset 1966)) feeding on fish and ostracods. It is believed that piscivores evolved from trawling insectivores (Eisentraut 1951; Wallin 1969; Dwyer 1970; Novick & Dale 1971; Suthers & Fattu 1973; Gillette 1975). All trawling and piscivorous bats have greatly enlarged hind feet, and piscivores have sharp claws (figure 11). Some carnivorous bats (*Megaderma lyra*, *Nycteris grandis*) have been reported to eat fish, but it is not known how they are obtained.

6.5. *Frugivores*

Frugivores belong primarily to the Pteropodidae and Phyllostomidae, although species of a few other families (e.g. Noctilionidae (*Noctilio albiventris*, Vespertilionidae (*Antrozous pallidus*, *Rhogeessa tumida*) and Mystacinidae (*Mystacina tuberculata*)) take fruit as an alternative food. Many frugivores are relatively large. Frugivory makes little demand for highly agile or manoeuvrable flight, but some feeding strategies demand long commuting flights.

Many pteropodids and phyllostomids have reduced tail membranes or lack tails altogether (§5.11*h*). Frugivorous phyllostomids have higher wing loading than pteropodids. Most frugivores have high or average wing loading and low aspect ratio, and fall close to average in the lower right quadrant of figure 8 (*a*, *d*, *f*); this morphology is characteristic of fast but not enduring flight. The small tail membrane reduces total wing area, and wing loading tends to be higher in frugivores than in most insectivores. Wing loading is further increased in phyllostomids because the wings are usually shorter than in vespertilionids. Short wings are advantageous for bats flying in clutter, as the frugivores often do, but do not necessarily imply poor manoeuvrability if, in compensation, the wing area is large, producing low aspect ratio. Wingtip morphology varies among the species, but the wingtips are, on average, longer than in insectivores (figure 10*f*). Some wingtips in pteropodids are particularly long.

Frugivores, particularly refuging species, must commute long distances between foraging and roosting places. They can feed for longer periods by flying faster, and as most species cling or perch while feeding the mechanical pressures favouring hovering or manoeuvrability and agility are weak. Frugivores will benefit from high wing loading, which enables them to fly fast with moderate power consumption. For scaling reasons (§§3.2, 6.1), large size, especially in pteropodids, implies enhanced flight speed.

Bonaccorso (1979) classified frugivorous Panamanian phyllostomids in three foraging guilds, with the majority of species being 'canopy frugivores', foraging in trees above 3 m tall. Two species, *Carollia castanea* and *C. perspicillata*, were 'groundstorey frugivores' feeding on low bushes and shrubs, and one specialized species (*Centurio senex*) appeared to be a 'scavenging frugivore' feeding on fallen and rotting fruits. Within the arboreal frugivore guild, differences in food habits reflect diverging foraging, commuting and refuging habits and different patterns of use of foraging space (Heithaus *et al.* 1975). In view of the direct relation of these factors to flight behaviour, we expect that these differences will make a major contribution to segregation within the guild and will therefore also be reflected in flight morphology. Although even less is known of the foraging behaviour of Old World frugivores, we anticipate that parallel factors dictate the structure of pteropodid foraging guilds. Currently there are insufficient data on flight behaviour or wing morphology in frugivores for us to explore this hypothesis reliably, but with further field observations it could form a useful means of testing our predictions.

6.6. *Nectarivores*

Macroglossines (Pteropodidae) and glossophagine and brachyphylline bats (Phyllostomidae) feed primarily on nectar and pollen, but most of them also eat fruit and insects. The interrelations between bats and flowers have been reviewed by Dobat & Peikert-Holle (1985), and foraging ecology and energetics have been studied in three glossophagines by Howell (1979), von Helversen & Reyer (1984) and Lemke (1984). Glossophagine bats are excellent hoverers (§5.11*b*) and typically, but not exclusively, hover while feeding. Macroglossines perch on flowers when feeding (van der Pijl 1956) but they sometimes hover in front of flowers before landing (Gould 1978). The comparison between New and Old World flower bats parallels that between their diurnal ecological counterparts, the hummingbirds (Trochilidae), virtually exclusive hoverers, and the Old World sunbirds (Cinnyridae) and honeyeaters (Melophagidae) which both hover and perch. We do not know why hovering is more prevalent in flower-visiting birds and bats in the New World.

We have predicted that hovering bats (both gleaning insectivores and nectarivores) should be small, and should have low wing loading, long wings and long wingtips (table 3); there are no selection pressures for high aspect ratio. Long wings and low wing loading reduce mechanical power during hovering, but long wings may be impractical in dense vegetation because of interference with clutter and because they decrease manoeuvrability and increase inertial energy losses (§3.3). So there are conflicting selection forces acting on wingspan. Hovering nectarivores have rather short wingspan and low aspect ratio (in many species reflecting relatively large wing area) (figures 8*d*,*f*, and 12), so environmental pressures appear to outweigh energetic advantages from longer wings. (The same is true for hover-gleaning insectivores.) At the relatively small size of hovering nectarivores the energy margin is wide, and so would dilute any selective effect attributable to flight power. Nectarivores have less need for manoeuvrability than do insectivores, and have higher wing loadings.

Given that the wingspan must be short, the wingtips in nectarivores should be long, broad and rounded (giving large wingtip area) to improve hovering lift and manoeuvrability within clutter (table 3). In glossophagines the wingtip is indeed long and very rounded (figure 10*d*) although it is equally long in the macroglossines (figure 10*b*); *Macroglossus minimus* and *M. sobrinus* have rounded wingtips, but in *Notopteris macdonaldii* the wingtips are rather pointed. The wingtips are longer in nectarivores than in most frugivores (figure 10*f*).

The high wing loading in nectarivores is an adaptation for fast flight rather than for hovering. Many glossophagines are refuging species and may have to fly long distances nightly; *Anoura caudifer* is estimated to cover 50 km per night (von Helversen & Reyer 1984) (§7). When nectar supplies are sparse or there are long distances between suitable flowers, rapid flights might be necessary to ensure appropriate rates of food collection. Low wing loading should be preferable for good hovering performance, as it permits greater intake of food per flight; but high wing loading permits fast flight, and enhanced feeding time at flowers could outweigh the higher energy costs of faster flight (compare the frugivores above) and the high energy cost of hovering (*cf.* R. Å. Norberg 1981).

7. Migration, commuting and refuging

7.1. *Migration*

Several species of bat migrate long distances when dry or cold seasons begin, and although it may perhaps have a less significant influence on adaptation than do diet and foraging strategy, migration may also be reflected in bat wing morphology. We have predicted (§3.7) that for flight economy long-range migrants making extensive flights should have high aspect ratio and pointed wingtips, and that if time is a significant constraint they should also have high wing loading.

Records of migration by bats are reviewed by, among others, Griffin (1970), Yalden & Morris (1975), Fenton & Kunz (1977), R. R. Baker (1978) and Aellen (1985). However, many species have not been studied or reported, and in others the information available seems anecdotal or conjectural. We do not know whether all long migration flights are made in one go, and because some species migrate only in parts of their range our data may not be representative of migrating populations; so a test of our predictions cannot be reliable. In figure 14 (comparable to figure 8) we show the species for which we have information. We have distinguished species which make short-distance migrations over 200 km to hibernate or to ensure adequate food supplies, but it is unlikely that we have identified all the short-range migrants in our data simple.

As predicted, migrants tend to have wings with a high aspect ratio; all larger or heavier species and most of the long-distance migrants have relatively high aspect ratio and average wing loading. Many also have pointed wingtips. However, a number of species that make short-distance or facultative migrations have a lower aspect ratio than average. These species are relatively small insectivorous bats in which individual migration distances are low, and for which energy economy during opportunistic short migrations may well be outweighed by pressures on morphology associated with activity during feeding.

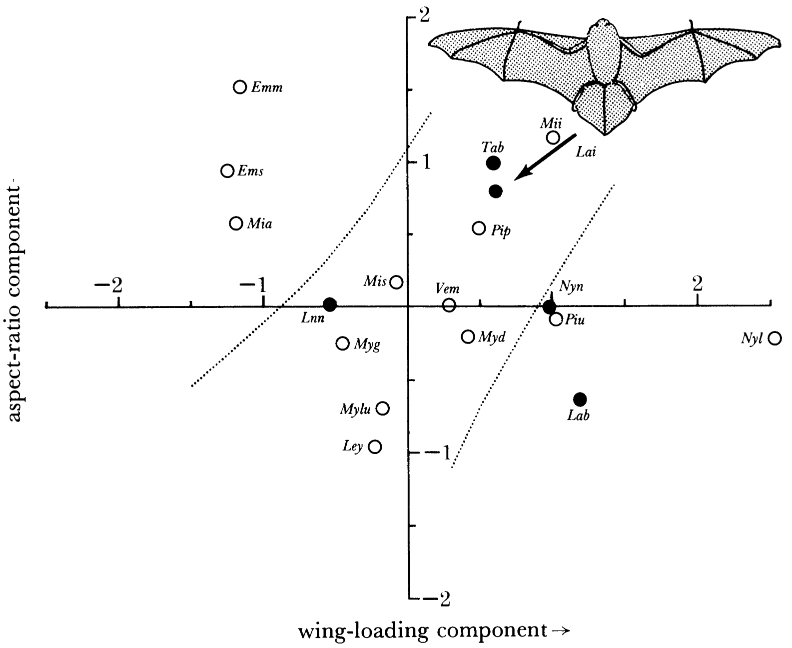


FIGURE 14. Scatter plot of second and third principal components of wing morphology in migratory bat species. (Details as in figure 8.) Filled circles indicate bats which migrate more than 1000 km, open circles, those which migrate between 200 and 1000 km. The dotted lines separate bats that have short or long wings (differing from average by over 8 %).

The longest migrations (at least 1000 km) are reported in *Lasiurus borealis*, *L. cinereus*, *Lasionycteris noctivagans*, *Nyctalus noctula* and *Tadarida brasiliensis* (see, for example, Yalden & Morris 1975; R. R. Baker 1978). *Lasionycteris noctivagans* has a long wingspan, whereas wingspan is short or average in *Lasiurus* species, *N. noctula* and *T. brasiliensis*; all have above-average aspect ratio and the wingtips are relatively pointed. *Lasiurus borealis*, *L. cinereus*, *N. noctula* and *T. brasiliensis* are relatively fast-hawking, high-altitude species, and have appropriate morphology. We do not know if migration or foraging has been the dominant influence on these bats, as high aspect ratio and high wing loading are appropriate for both; but because there are tropical molossids and emballonurids with similar wings but which do not migrate, we suspect that adaptation for fast hawking represented preadaptation for efficient migration. Only long-distance fliers are able to colonize isolated islands. This is certainly the reason why such islands have only a few bat species; for instance, *L. cinereus* is the only bat species on Hawaii, and is one of the only two species on the Galapagos Islands (the other is the endemic *L. brachyotis*, which may be a subspecies of *L. borealis*).

7.2. *Commuting and refuging*

Bats which roost in colonies (refugia) and fly out to feed may need to fly long distances to find adequate food resources. This is particularly important in frugivorous and nectarivorous bats (Fleming 1982), but some insectivores (e.g. emballonurids, rhinolophids, vespertilionids and molossids) (Kunz 1974, 1982) also roost colonially. We have identified a number of cases (in particular in phyllostomids and molossids) in which high flight speed may be important to permit sufficient foraging time during a night, and many of these bats have the expected high wing loading. Fleming (1982) argues that larger bats, which should fly faster, should have larger ranges. Just as it may have favoured the appearance of migration in bats, adaptation for fast hawking may have aided the commuting and refuging behaviour of species such as *Tadarida brasiliensis*. On this basis we predict that foraging strategies and use of refugia should form a mechanism of community structuring, and should be reflected in wing morphology.

8. ECHOLOCATION CALL STRUCTURE, FORAGING STRATEGY AND WING MORPHOLOGY

Our main argument is that flight mechanics impose significant constraints on behaviour, which are responsible for shaping the ecological roles of bats, and we have shown how the influence of these constraints may be traced in wing adaptations. Echolocation is also a fundamental component of the hunting and feeding behaviour of the majority of bat species. Associations, between the acoustic structure of echolocation calls and hunting behaviour and foraging-zone utilization, have been treated in detail in many bat species by several authors; the results have been summarized by Novick (1971), Simmons *et al.* (1979), Fenton & Bell (1979), Fenton (1980, 1982*a*, *b*, 1984, 1985), Ahlén (1981), Fenton & Fullard (1981), Neuweiler (1983, 1984) and Simmons and Kick (1983). These findings indicate that echolocation calls are specialized for particular tasks, and suggest that echolocation may have equal significance to flight in determining the foraging patterns a bat may adopt. Here we consider how flight and echolocation may interact, by demonstrating that associations between echolocation and foraging behaviour (primarily in animalivorous bats) are reflected also in flight speed and in wing morphology (figure 15). Most of the descriptions of echolocation calls are taken from the sources mentioned above.

8.1. *Relations between call structure and foraging strategy*

(*a*) *Fast hawking in open areas*

Echolocation call structure. Open-area foragers mainly use long, narrowband echolocation calls when cruising or searching for prey. These calls appear to be well suited for detection of prey, but give little information about target structure and are not clutter-resistant (Simmons & Stein 1980). However, on approaching a detected target the bats switch to calls of broader bandwidth, which provide more information about target detail. Because the amount of sound energy absorbed in air increases with increasing frequency, these species emit lower-frequency sounds at frequencies where they hear best (Neuweiler 1984).

Flight performance and wing shape. After detecting a prey, insectivorous bats must manoeuvre to catch it. Even though the time between detection and initiation of the manoeuvre is short, fast-flying species will travel farther than slow-flying bats before they are able to react. Further, fast-flying species have high wing loading and are agile, but have a large turning radius (§3.5). Therefore, long-range detection is essential for fast-flying bats. Narrowband echolocation calls of low frequency are thus related to high wing loading and high aspect ratio. They are found in fast-flying, open-area foraging species (marked with crosses in figure 15) such as molossids (Simmons *et al.* 1978; Fenton & Bell 1981; Neuweiler 1984; Fenton & Rautenbach 1986) and *Taphozous* (Emballonuridae) and *Rhinopoma* (Rhinopomatidae) species (Fenton *et al.* 1980; Habersetzer 1981; Simmons *et al.* 1984). These species are characterized by high wing loading, high aspect ratio and pointed wingtips (§6.2*a*).

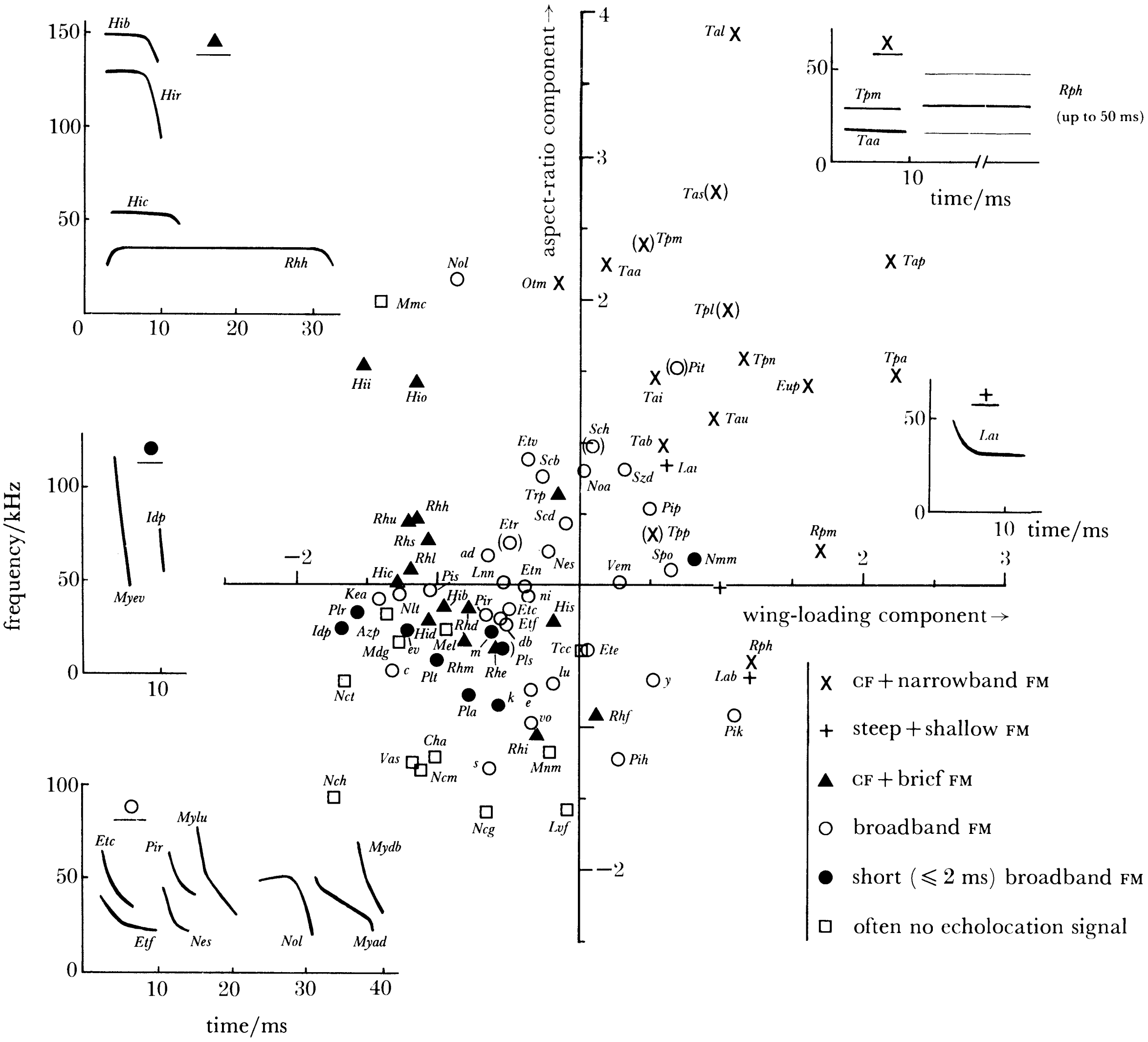


FIGURE 15. Scatter plot of second and third principal components of wing morphology in bats with different echolocation calls while in search of prey. The sonagrams are based on Simmons *et al.* (1979), Fenton & Bell (1981), Thompson & Fenton (1982), Fenton *et al.* (1983*b*) and Neuweiler (1984). (Details for the principal components as in figure 8.) Symbols shown in brackets identify calls predicted for the species concerned. As before, species are characterized by codes (see table 1); for *Myotis* species, the '*My*' has been omitted.

(*b*) *Fast hawking relatively close to obstacles*

Echolocation call structure. Some vespertilionids (plus signs in figure 15) fly in relatively open spaces, which may be close to vegetation. They use echolocation calls which include both steep and shallow frequency modulated (FM) sweeps, and include species like *Lasiurus borealis* (Fenton *et al.* 1983*b*), *L. cinereus* (Barclay 1985) and *Nyctalus noctula* (Vogler & Neuweiler 1983).

Flight performance and wing shape. All these species have high wing loading and are relatively fast fliers, and should thus benefit from long-range prey detection, they also have above average aspect ratio. *N. noctula* has pointed wingtips, whereas *L. borealis* and *L. cinereus* have slightly rounded wingtips, more like those of molossids.

(*c*) *Slow hawking*: *short range detection of fluttering insects*

Echolocation call structure. Pure or constant frequency tones (CF) combined with a brief FM sweep, at a high frequency range, are used by some emballonurids, rhinolophids, hipposiderids and the mormoopid *Pteronotus parnellii* to detect fluttering targets (see, for example, Goldman & Henson 1977; Barclay 1983; Brown & Berry 1983; Schnitzler & Ostwald 1983; Volger & Neuweiler 1983; Bell & Fenton 1984; Habersetzer *et al.* 1984; Fenton & Rautenbach 1986). A long call, or a close series of shorter calls (as in *Hipposideros*) that spans on insect's wingbeat cycle, means that in the echoes from one call a bat receives a blend of weak and strong signals at different Doppler shifts. These 'glints' may significantly increase the range at which a bat can detect and identify a target (Schnitzler 1987). This echolocation strategy permits bats to operate in dense clutter. Short broadband calls apparently do not permit bats to exploit this feature.

Flight performance and wing shape. Bats using CF and FM calls are shown by triangles in figure 15. Wing loading is generally low in these bats, presumably reflecting their value in clutter. The same call pattern is used also by bats hunting by flycatching (Schnitzler *et al.* 1985) and are therefore found in bats with a range of values of aspect ratio.

(*d*) *Slow hawking*: *detection of prey among clutter*

Echolocation call structure. Broadband (FM) signals are used for discrimination of target structure and for range finding (Simmons *et al.* 1975). These signals include a variety of combinations of short or long, steep or shallow calls and are used for short-range prey detection among clutter. Broadband calls are found in noctilionids and many vespertilionids (Fenton & Bell 1979; Miller & Degn 1981; Thompson & Fenton 1982; Fenton *et al.* 1983*b*; Herd & Fenton 1983; Barclay 1985) in species marked by open circles in figure 15. Trawling and piscivorous species also belong to this group (for instance *Myotis adversus*, *M. dasycneme* and *M. daubentoni*), and use short, broadband FM signals which typically lack the terminal CF phase found of some other myotids (Fenton & Bell 1979; Ahlén 1981; Miller & Degn 1981; Thompson & Fenton 1982). The significance of this call pattern for bats foraging over water is not fully understood (Thompson & Fenton 1982). While hunting over water, the noctilionids *Noctilio albiventris* and *N. leporinus* use short CF–FM calls to locate prey on the water surface, probably by the movement of the prey or by disturbances on the surface caused by the prey, but while catching prey switch to broadband FM calls similar to those of trawling myotids (Brown *et al.* 1983; Suthers & Fattu 1973; Wenstrup & Suthers 1984).

Flight performance and wing shape. From these characteristics, we expect broadband signals to be used by bats with low wing loading, and hence with slow flight and high manoeuvrability.

(*e*) *Gleaning*

Echolocation call structure. Surface gleaners often use very short (less than 2 ms) FM calls of low intensity, which might be an adaptation to fine texture discrimination of targets on a surface by spectral differences in the echoes (Habersetzer & Vogler 1983); the very short signals allow the gleaning bat to receive echoes from close targets without overlap with emitted echolocation sounds. But ground-gleaning bats need not use echolocation to find prey; they can listen to and localize the sounds produced by the prey and they may also rely on vision. In this way they avoid the problem of noise in the echoes owing to clutter, and reduce the risk of alerting their prey.

Flight performance and wing shape. Short FM signals are found in some plecotines and myotids (see, for example, Simmons *et al.* 1979; Fenton & Bell 1979; Neuweiler 1983), nycterids, megadermatids and phyllostomids (Fenton & Fullard 1979); these species are marked with solid circles in figure 15. Most of these bats have the low wing loading, low aspect ratio and rounded wingtips which we have identified as adaptations for slow and manoeuvrable flight within clutter.

Carnivorous gleaners. Gleaning carnivorous bats often switch off echolocation. Silent, slow flight within vegetation and high load-carrying capacity are favoured by low wing loading and low aspect ratio (§6.3). These species would also benefit from rounded wingtips for high manoeuvrability among vegetation. Among the bats which sometimes give up echolocation and instead localize prey passively are the carnivorous megadermatids, nycterids and phyllostomids, and also the non-carnivorous species *Lavia frons* (Megadermatidae), *Micronycteris megalotis* and *Macrotus californicus* (Phyllostomidae) and *Antrozous pallidus* (Vespertilionidae) (Fiedler 1979; Tuttle & Ryan 1981; Bell 1982, 1985; Fenton 1984); these species are marked with open squares in figure 15. *A. pallidus* emits calls while searching for prey but never during the approach (Bell 1982). All these bats have low wing loading and low or rather low aspect ratio, and most have rounded wingtips.

(*f*) *Echolocation for orientation*

The discussion above has concentrated on animalivorous bats, which use echolocation to locate prey and to guide prey capture. Sanguivorous and many herbivorous species use echolocation for spatial orientation and food location, and do not experience the problems associated with tracking moving prey items. For this reason we would expect correlations between echolocation call and flight morphology to be somewhat weaker in these species.

The sole megachiropteran genus in which echolocation is known is *Rousettus*; the signals consist of very short broad-band calls covering a wide frequency range, and permit these frugivorous bats to do little more than evaluate their proximity to obstacles. The calls of most phyllostomid bats are more complex, usually consisting of low-intensity, rather broadband FM sweeps (Howell 1974; Gould 1977*b*; Joermann 1984) which fulfil the same role as comparable calls in insectivorous species in permitting location of obstacles and texture discrimination in clutter. We have associated the high wing loading of vegetarian phyllostomids in part to the problems of seeking food and hovering within clutter.

8.2. *Relations between call structure and flight morphology*

Figure 15 summarizes how different call structures are associated with different wing morphologies. In most cases wing shape and echolocation calls may have responded independently to the requirements of the various foraging patterns of the bats, so that correlations between wing shape and the acoustic structure of the calls are secondary effects of adaptation to particular foraging niches. But the interactions between flight and echolocation performance are so close, at least in bats actively hunting prey, that it is hard to determine which, if either, is the dominant constraint on feeding activity. In one case, however, there is a direct relation between echolocation sounds and flight morphology. The narrowband, low-frequency echolocation call for long-range detection is a necessary adaptation for fast-flying, aerial-hawking bats with correspondingly high wing loading and high aspect ratio; here, wing and echolocation characteristics are coadapted. Slow foraging flights, on the other hand, enable the bat to manoeuvre and to catch prey detected at short ranges. However, there is a variety of foraging habitats, and also a variety of echolocation calls designed for clutter resistance. These various calls or combinations of calls may be adaptations to different habitat use and to the choice of prey or foraging site within the vegetation. Slow foraging within or near to clutter also requires specific wing shapes. But the echolocation calls and wing shapes found in bats foraging among clutter do not seem to be very closely related, and may thus have evolved independently of each other. Different combinations of wing characteristics and echolocation call structure may represent a range of solutions of the problems of exploiting vegetation of different density and structure.

9. Discussion

9.1. *Size scaling of performance and the size range of bats*

Our analysis has been concerned primarily with the interpretation of mechanical correlates of flight performance in size-independent form, and we have concentrated on principal components corresponding reasonably well to wing loading and aspect ratio. Deviations in wing size and shape in bat taxa and feeding classes, relative to the average for their size, have been shown to be related to the predictions of mechanical models of flight performance and foraging behaviour. We have tended to ignore the first principal component, representing overall size, but the predictions of §3 concern also the size-scaling of flight performance. This aspect of flight adaptation is important, as mechanical constraints delimit the extreme sizes reached overall by bats and the range of mass (or size) of individuals. The relative importance of the various mechanical constraints on flight performance are also size-dependent, and this was reflected in the differential size ranges of chiropteran feeding classes discussed in §6.1.

The first column in table 3 shows how various components of flight performance vary supposing that other quantities (wing morphology, etc.) vary isometrically. Similar results for these scalings were obtained by Andersson & R. Å. Norberg (1981). Of these mechanical quantities, the only one favouring large size is high flight speed (rising as $M^{\frac{1}{6}}$); cost of transport, C, and first moment of lift, λ_1 are expected to be independent of scale. In practice, cost of transport falls slightly with increasing mass (equation (7)) owing to allometry of wing dimensions. Some quantities, in particular wing inertia and flight power, rise dramatically as mass increases. This rise in inertia explains the poor agility of larger bats, and with the matching fall in manoeuvrability (both manoeuvrability and agility fall off isometrically as $M^{-\frac{1}{3}}$) may be one of the reasons why aerial hawking of flying insects is restricted to smaller species; similar difficulties associated with hovering and gleaning and flight in clutter probably explain why all insectivorous and nectarivorous bats are relatively small.

The particularly unfavourable scaling and mechanical flight power also imposes an upper limit to size in bats. Pennycuick (1975) has argued that the imbalance between mechanical power required for flight (scaling as $M^{\frac{7}{6}}$) and that available from the muscles (varying approximately as $M^{\frac{2}{3}}$ or $M^{\frac{3}{4}}$) prevents powered flight in birds above about 15 kg. The largest pteropodid is considerably smaller than this, and the basic similarity of flight physiology in birds and bats (S. P. Thomas 1987) does not suggest a metabolic constraint on size in bats much stricter than that in birds. Nonetheless, the low endurance of *Pteropus poliocephalus* (Carpenter 1985) may indicate a restriction on performance, in particular inability to sustain flight at V_{mr}, in larger pteropodids. Behavioural and ecological factors may also impose an upper limit to size (Rayner 1981). In an individual bat, the variation of performance with size, above all the increase of flight power as $M^{1.56}$ (equation 6), is the strictest restriction on the accessible range of body mass (§3.4).

At the lower end of the size range most mechanical aspects of performance improve considerably. This allows smaller bats greater scope to fly in different ways and greater plasticity in their flight behaviour, and opens the possibility of more energy-intensive modes of flight, such as hovering. Smaller size also confers greater agility and manoeuvrability. Moreover, because the wings are smaller, constraints related to environmental clutter and flight in confined spaces are weaker. The broader energy margin at small size suggests also that flight evolved in bats from small, insectivorous arboreal mammals, and subsequent radiation produced larger chiropteran forms able to take a range of diets (McNab 1982; Rayner 1980*a*; Scholey 1986). The only performance factor deteriorating significantly as mass becomes smaller is flight speed, but since many small bats feed on stationary or slow-moving food and do not travel far from their roosts, high speed is not always advantageous. Insects considerably smaller than bats can fly, and this suggests that, if mechanical factors impose a lower limit to size in bats, they are related to wing anatomy and skeletal strength rather than to aerodynamics. Other mechanical constraints may, however, impose a limit to the smallest size of an individual (see, for example, Andersson & R. Å. Norberg 1981). There is ample evidence that the problems of obtaining sufficient food and maintaining body temperature without impossibly long periods of foraging restrict the smallest mass of any individual flying bat (McNab 1982).

9.2. *Community ecology and ecological morphology of bat flight*

Central to our argument in this paper is the idea that mechanical constraints imposed by flight performance influence the flight morphology of bats. To us this relation appears axiomatic, because flight influences many facets of a bat's life. The relations, however, may be vague because they are determined by a broad range of factors, and they encompass many diverse features of the animals' biology. Although flight morphology and feeding behaviour are related, flight alone cannot be the sole mechanism by which bat species avoid competition. Considering different bat faunas, many authors (including Tamsitt 1967; Krzanowski 1971; McNab 1971; Fenton 1972, 1975; Fleming *et al.* 1972; Kunz 1973; Black 1974; Heithaus *et al.* 1975; Findley 1976; Bonaccorso 1979; Fenton & Bell 1979; O'Shea & Vaughan 1980; Findley & Black 1983; Humphrey *et al.* 1983; Schum 1984; Habersetzer 1986; McKenzie & Rolfe 1986; Baagøe 1987; and reviews by Humphrey & Bonaccorso 1979; Fenton 1982*a*; Findley & Wilson 1982) have demonstrated that communities are structured and that there are strong correlations of certain aspects of morphology with food selection and feeding behaviour. These studies imply that food resources are partitioned among the bats in a community, but the extent to which bats are specialized for particular foods is not known, and the mechanisms of faunal structuring in bats remain incompletely understood.

Similar conclusions have been reached in studies of avian faunas and communities (from an extensive literature; see, for example, Norberg 1979, 1981*b*; Miles & Ricklefs 1984; Sherry 1984) but many of these studies of birds have gone further in demonstrating how correlates of foraging strategy give rise to partitioning of dietary and habitat resources and to identifiable morphological specialization. Studies of bat faunal and community structures have hitherto lacked any clear understanding of the functional mechanisms underlying the apparent eco-morphological correlations (Findley & Wilson 1982). In this paper we have tried to fill this gap, by concentrating on the likely response of bat flight morphology to different evolutionary pressures associated with the known behaviour and ecology of different species of bats. It is premature to attempt to consider these relations at the community level; rather, we have defined our mechanical trends by looking at the entire range of bat species, without regard to faunal composition, zoogeographical variation or community structure, and therefore without the many complexities involved in detailed analyses of bat communities in individual habitats.

We have identified a range of pressures associated with different flight patterns, foraging strategies and diets, and have shown why bat flight morphology responds predictably to these pressures. But we see two major limitations in our approach. First, we are unable to test our predictions at the community level, since our morphological data are drawn indiscriminately from the literature, from museum and other collections, from captive animals and from field measurements. For our present purpose this was satisfactory, but this sample obscures intraspecific variation, with the result that (particularly in cases where a species' geographical range is large) apparent relations between species may not reflect relations between the morphology of bats in individual communities. Second, implicit in our supposition that ecology and flight morphology in bats are correlated is the assumption that flight behaviour (as evidenced by morphology) is a prime mechanism of niche separation in sympatric bats. Our analysis of families and feeding classes has demonstrated the validity of this expectation in bats *as a whole*, but its significance at the community level is less evident. Although some of the studies listed above have demonstrated morphological structuring within communities, other mechanisms of partitioning and segregation (see, for example, Fenton 1982*a*) may outweigh or parallel differences in flight performance or behaviour, and may not be reflected directly in flight morphology. For instance, Freeman (1981*b*, 1984) has shown that jaw morphology in animalivorous bats is closely correlated with food habits. And, as we have discussed in §8, echolocation calls are also correlated with foraging behaviour and they also can contribute to species separation (see, for example, Neuweiler 1983, 1984). That this acts in parallel with flight is to be expected, as presumably different forms of echolocation call, like different flight patterns, enable bats to find and obtain different prey in different habitats or microenvironments.

Despite these potential limitations, our conclusions that behavioural and ecological differences between related species correlate with specialization in flight morphology, and that these correlations are symptomatic of evolutionary selection within strict and identifiable aerodynamic constraints, suggest that, within bat communities, flight performance has a dominant influence on the evolution of adaptive specializations of bats.

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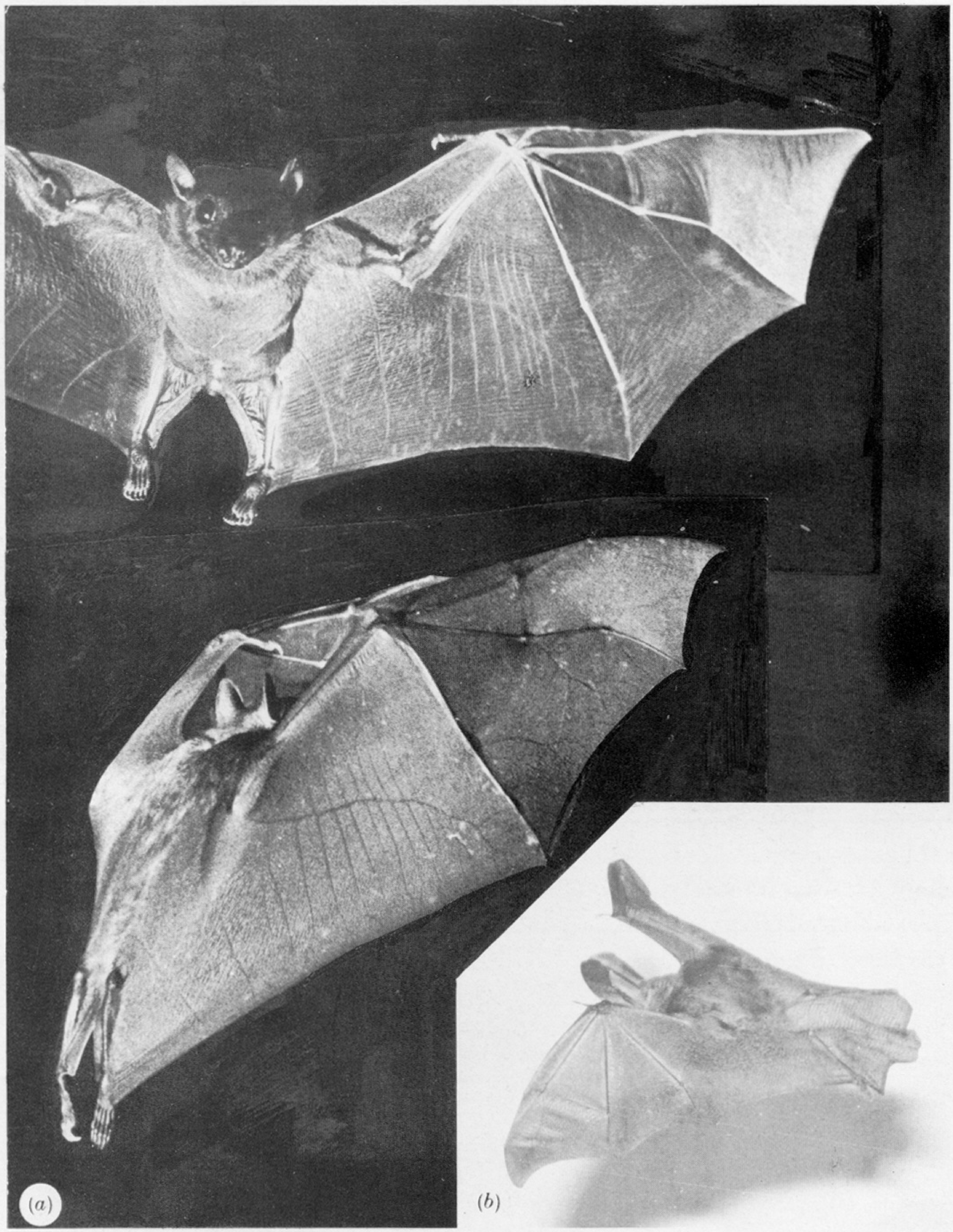

DESCRIPTION OF PLATES 1 AND 2

FIGURE 1. Photographs showing typical flying bats with different wing morphology. (*a*) *Rousettus aegyptiacus* (Pteropodidae) with low aspect ratio and average wing loading. (*b*) *Nycteris hispida* (Nycteridae) with very low aspect ratio and wing loading. (*c*) *Plecotus auritus* (Vespertilionidae) with low aspect ratio and low wing loading. (*d*) *Otomops martiensseni* (Molossidae) with very high aspect ratio and average wing loading. (*e*) *Eptesicus nilssonii* (Vespertilionidae). Photographs by U.M.N.

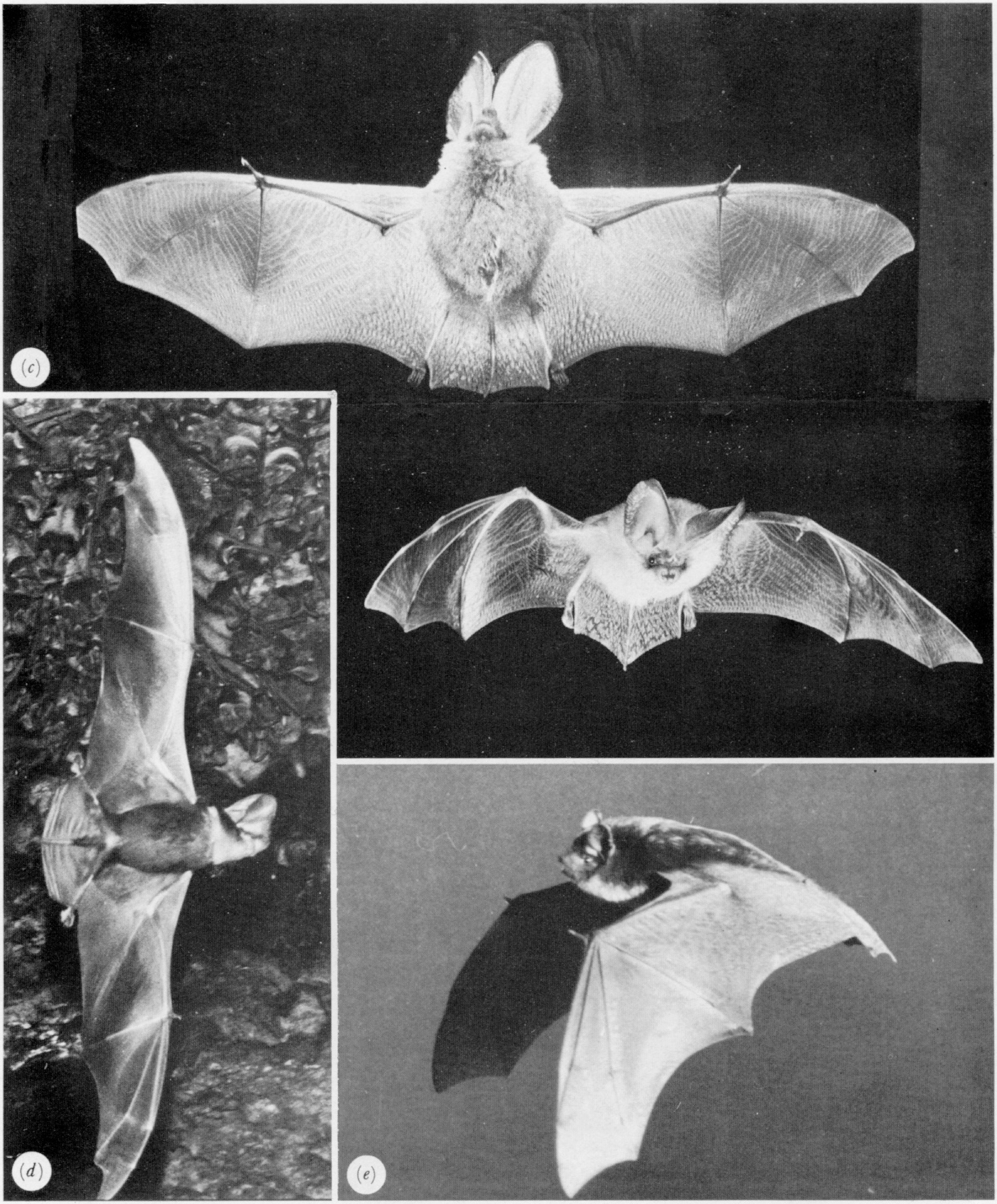

FIGURE 1*c*, *e*. For description see overleaf.