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ALLOMETRY OF LITTER MASS IN BATS: MATERNAL SIZE, WING MORPHOLOGY, AND PHYLOGENY

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We examine how litter mass in bats varies with respect to wing loading, an important aerodynamic aspect of flight. From geometric proportions, litter mass should scale to wing loading by an exponent of three. Conversely, analysis of aerodynamic consequences of carrying extra mass suggests that an exponent significantly less than three would be selectively advantageous. Our results show that Megachiroptera and Microchiroptera differ in the relationship between litter mass and wing loading. Litter mass in megachiropterans scales as expected by geometric proportions, whereas litter mass in microchiropterans, as a group, and for individual families, scales as expected if aerodynamic consequences of flight influence litter mass more than size constraints. Thus, selection pressures on reproductive traits appear to differ between the two suborders of bats.

Key words: Chiroptera, wing loading, allometry, litter mass, reproductive strategy

Several comparative studies have examined mammalian life-history strategies (Boyce, 1988; Charnov, 1991; Millar, 1981; Stearns, 1980), but few have included bats in their analyses. These relatively small volant forms are one of the most ecologically, morphologically, and reproductively distinctive groups of mammals and are second only to rodents in number of species. Although bats are the nocturnal ecological equivalent to birds, morphological adaptations of bats for flight and foraging are vastly different (Norberg and Rayner, 1987), and reproductive patterns of bats (O'Brien, 1993; Racey, 1982) are as distinctive as their ecology and morphology.

Reproductive specializations of bats include relatively long periods of gestation and lactation, small litter sizes, and large neonatal masses. The period from mating to conception is regularly extended by an assortment of timing delays, including storage of sperm (Racey, 1979), delayed implantation (Mutere, 1967), delayed development (Fleming, 1971; Heideman, 1988), and

slowed fetal growth (Racey, 1973; Racey and Swift, 1981). Lactation also is extended. Bats, like primates and marsupials, have lactation periods 50% longer (on a \log_{10} scale) than other mammals of similar body size (Hayssen, 1993). Parental investment of chiropterans is large, not only in terms of the long time devoted to gestation and lactation, but also because most neonates weigh ca. 25% of their mother's mass (Korta and Kunz, 1987). Bats are the only mammals that suckle their young until juveniles are nearly adult size (Kunz, 1987) and are also the only taxon of small mammals with predominantly singleton litters (Hayssen et al., 1993). These reproductive specializations often are assumed to be adaptations to a bat's volant mode of locomotion, but no direct analyses of reproduction with respect to flight have been made. Here we analyze neonatal or litter mass with respect to wing loading, an important aerodynamic aspect of flight.

Wing loading describes mass of a flying body relative to area of the airfoil that sup-

ports the mass in flight: mass \times gravitational constant/airfoil area (Nm^{-2}). Analyses on ecological morphology of flight in bats suggest that species with low wing loadings should be better able to carry extra mass (e.g., food or fetuses) than those with higher wing loadings (Norberg and Fenton, 1988; Norberg and Rayner, 1987). These studies present convincing evidence that frugivorous and carnivorous bats, which typically carry heavy loads when foraging, do, in fact, have low wing loadings. No analyses across species were conducted to examine wing loading and litter mass, although Norberg and Rayner (1987) predicted a negative correlation between these two variables for Chiroptera as a group. Aerodynamic and energetic consequences of additional mass that a female carries during gestation and lactation are clear. At some point, the additional mass will be too high for effective flight and this presumably imposes an upper limit on the size of offspring that females can transport unless females can compensate. Unfortunately, data on airfoil areas of reproductively active versus inactive female bats are lacking, however, some females do have larger wings than males (Myers, 1978; Williams and Findley, 1979) and morphology of wings in female *Eptesicus* changes over the course of pregnancy and lactation (Sevick and Studier, 1992).

Birds also fly and eggs of birds range from 2 to 25% of mass of females, with larger species having relatively smaller eggs (Olsen et al., 1994). In addition, birds with altricial young may produce smaller eggs than those with precocial young (Pettingill, 1985). Mass of eggs has not been systematically related to wing morphology across birds, although the small mass of eggs of swallows is presumed to result from selection pressures on flight (Brooke, 1991). Thus, the current literature on birds does not address the relationship between wing loading and parental investment.

Authors of studies on the allometry of mammalian reproduction have attempted to

understand the influence of body size on reproductive or developmental characteristics such as litter mass, age at eye opening, and duration of gestation or lactation (Hayssen, 1993; Jones, 1985; Kurta and Kunz, 1987; Martin and MacLarnon, 1985; Millar, 1981). Size can be defined in many ways. For mammals, the allometry of reproductive characters typically is examined using maternal mass or length of head and body. For bats, length of forearm is a common estimate of body size. The usual assumption is that larger animals will have larger offspring and that larger offspring will require longer lengths of gestation or lactation. However, because of surface-area-to-volume relationships and other factors related to economies of scale, larger animals may have relatively smaller offspring or relatively shorter developmental times.

Bats have achieved a range of body shapes and sizes, from the diminutive *Craseonycteris thonglongyai* at 2 g to the largest species, *Pteropus vampyrus*, at 1.2 kg (Kunz and Pierson, 1994). Not only are body sizes variable, but wing shape and size vary tremendously. Wing loading integrates three estimates of size in bats; length of forearm, length of head and body, and body mass (Ralls et al., 1982). Although wing loading is not independent of body mass, it may be an especially useful estimate of ecological size of a bat because it combines many aspects of size that are ecologically, behaviorally, and physiologically relevant to the biology of these volant mammals.

Allometric and aerodynamic considerations concerning the relationship of wing loading to litter mass generate different predictions. Because mass is proportional to length cubed, theoretically, litter mass should scale to lengths of head and body or forearm of adults by an exponent of three and to maternal body mass by an exponent of one. Similarly, as wing loading is essentially body mass (length cubed) divided by area (length squared), wing loading should scale to maternal body mass by an exponent

of one-third. Thus, from dimensional considerations of geometric similarity, wing loading should be positively correlated with litter mass by a scaling exponent of three. However, aerodynamics of flight suggest that animals with low wing loading should be better able to carry more mass, thus, an exponent significantly less than three would be selectively advantageous considering aerodynamic consequences of flight. Our analysis of reproduction and flight of bats has three goals; to provide systematic allometric analyses of litter mass as an index of the energetic cost of reproduction, to explore the interrelationship of flight and reproduction, and to investigate the relative importance of physiological constraints on the evolution of reproductive traits.

MATERIALS AND METHODS

Collection of data.—Reproductive (litter size, neonatal mass, lengths of gestation and lactation) and morphometric (length of head and body, length of forearm, body mass, wing area) data for >400 species representing 16 of the 17 families of bats were compiled either from study skins or specimen tags at the United States National Museum, the British Museum of Natural History, or from the primary literature (Hayssen et al., 1993). Study skins were used only for linear measurements. Masses of term or “large” embryos as well as smallest suckling young were used to estimate neonatal mass. Not all data were available for each species.

Individual species were chosen as the unit of analysis in part because the small size of the dataset and the lack of a complete phylogeny for bats makes use of recently developed comparative techniques (Harvey and Pagel, 1991) difficult or impossible. In addition, we used covariance analysis, which has some of the advantages of other techniques and is more amenable to interpretation. We also believe use of genera of other higher taxa essentially pools rather diverse lineages. Certainly, the ecological variability within the genus *Myotis* is as large or larger than that across genera of some other microchiropteran families (e.g., Megadermatidae). Because some *Myotis* are aerial feeders, some feed from the ground, and some are gleaners, members of the genus show a wide range of uncorrelated

traits. We suspect selection pressures that led to this divergence in foraging strategies also are manifested in wing design and reproductive characters. Although all members of a genus have similar phylogenetic roots, different species have been selected for and evolved in different environments. Thus, their adaptive patterns have been influenced by different competitive interactions, different mutualistic relationships, and different physical and climatic challenges.

On average, ancestral species with a highly variable and diverse genetic structure will diverge into numerous species with relatively independent adaptive trajectories (i.e., exhibit relatively little phylogenetic inertia), whereas ancestral gene pools of limited variability will produce species that are relatively constrained by history (Brooks and McLennan, 1991). Thus, for some clades, species-level comparisons will be useful, whereas, for other phylogenetic lineages, even familial or higher-level comparisons may be unproductive. Unfortunately, few data describe ancestral groups of bats. When possible, we performed our analyses at a number of taxonomic levels.

Wing loadings were calculated from wing areas given by Norberg and Rayner (1987), which included uropatagial and body areas. When wing and uropatagial area were unavailable they were predicted from regression equations (Table 1). For these predictions, airfoil areas from Norberg and Rayner (1987) were regressed against a hypothetical body-wing area. This area was modeled as a rectangle with a length four times the length of the forearm, and a width the length of the head and body. We considered incorporating wing shape into our analyses, but could not find sufficient data that were consistent across species for such an analysis.

We preferentially used morphometric data from females over those from males or from adults of unknown gender. For 436 species, 73% of morphometric data (length of head and body, length of forearm, and body mass) were available for females, 17% from adults of unknown gender, and 8% from males. The remaining 2% represent species for which one of the three measures of body size was not available.

Wing loadings calculated from published data and those from the above estimates showed nearly identical relationships with body mass (Table 2). Data on neonatal mass were available

TABLE 1.—Equations from least-squares regression for relationships between airfoil area (m^2) as presented in Norberg and Rayner (1987) and the area of a rectangle with a length of one head-body length (m) and a width of four times the length of the forearm (m). These equations were used to predict the area of an airfoil from lengths of forearm and head and body when the true area of the airfoil was not known. Common log-transformations of both wing area and rectangular area were used. All regressions were significant at $P < 0.0005$, except that for emballonurids and for the mixed-family grouping for which $P = 0.007$. n = number of species.

Taxon	Intercept (SE)	Slope (SE)	n	$R^2\%$	F (P)
Chiroptera	-0.186 (0.052)	0.862 (0.027)	108	90	1,001
Megachiroptera					
Pteropodidae	0.065 (0.085)	1.049 (0.060)	15	96	309
Microchiroptera	-0.291 (0.082)	0.808 (0.042)	93	80	377
Emballonuridae	-1.132 (0.116)	0.405 (0.061)	5	91	43 (0.007)
Rhinolophidae	-0.111 (0.148)	0.878 (0.076)	12	92	135
Phyllostomidae	-0.022 (0.202)	0.946 (0.109)	15	84	75
Vespertilionidae	-0.065 (0.137)	0.917 (0.066)	43	82	193
Molossidae	-0.224 (0.134)	0.888 (0.073)	8	96	150
Other families	-0.669 (0.322)	0.599 (0.168)	10	57	13 (0.007)

for 116 species. For these species, 94% of data of associated adult size and mass were from females, <5% were from adults of unknown gender, <1% were from males, and <1% were unavailable.

Statistical analysis.—Common log-transformations were performed to improve symmetry of distributions across species and uniformity of spread across orders (Hoaglin et al., 1983). For example, common log-transformations of litter mass reduced skewness of the distribution from 2.961 to 0.704 and kurtosis from 8.684 to -0.085. Similar changes toward normal distributions (skewness = 0, zero-centered kurtosis = 0—Wilkinson, 1988) were observed when the data were partitioned by suborder. Although untransformed data for 26 species of megachiropterans were not far from a normal distribution originally, transformation reduced skewness from 0.869 to -0.291, whereas kurtosis increased slightly from -0.501 to -0.853. Common log-transformation of masses for 90 litters of microchiropterans reduced skewness from 2.278 to 0.312 and kurtosis from 7.629 to -0.616.

We used t -tests to compare the ratio of litter mass to maternal body mass between suborders. Mass of litters at birth is the dependent variable, and characterization of its variance with respect to other variables is the major goal of this paper. Statistical treatment was by least-squares regression or analysis of covariance (Hayssen and

Lacy, 1985; Snedecor and Cochran, 1980). Least-squares regression was chosen over reduced major-axis analysis (Harvey and Mace, 1982) to maintain a constant dimensionality of slopes across different datasets and, thus, allow use of covariates such as body mass or wing loading for comparisons across families. In addition, slopes obtained using least-squares regression are not significantly different from those for similar comparisons done with reduced major-axis analysis (Kurta and Kunz, 1987).

Homoscedasticity of residual variances was tested by F -tests for suborder comparisons and by Bartlett's tests for familial analysis (Snedecor and Cochran, 1980). The small overlap in ranges of body size and mass for megachiropterans and microchiropterans restricts the usefulness of statistical comparison of regression coefficients because such comparisons would only be valid for the restricted region of overlap and, thus, would exclude most species. However, ranges of body size and mass across families of microchiropterans overlap extensively; thus, for families represented by five or more species, familial regression lines were tested for differences in slope and, if slopes were statistically homogeneous, for differences in elevation.

Differences in slope also were assessed by non-overlapping 95% confidence intervals (Sokal and Rohlf, 1981). For all taxa, regression coefficients (slopes) using true versus estimated wing loading were not significantly different.

TABLE 2.—*Relationship of wing-loading (N/m^2) to maternal body mass (kg) across bats, by sub-order, and for families using wing area data from Norberg and Rayner (1987) or including airfoil areas estimated with equations in Table 1 (estimated wing loading). Equations from least-squares regression of common log-transformed variables. All regressions were significant at $P < 0.0005$ except that for eight molossid species with a direct calculation of wing loading for which $P = 0.021$. The t -values for differences between regression slope and that expected from allometry (0.333) are given (ns = not significant, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$). n = number of species.*

Taxon	Intercept (SE)	Slope (SE)	t (P)	n	$R^2\%$
Chiroptera	1.799 (0.040)	0.430 (0.022)	4.41***	109	78
Estimated wing loading	1.787 (0.020)	0.420 (0.011)	7.91***	369	80
Megachiroptera					
Pteropodidae	1.598 (0.057)	0.256 (0.049)	-1.57ns	15	65
Estimated wing loading	1.591 (0.019)	0.259 (0.017)	-4.35***	50	82
Microchiroptera	1.944 (0.059)	0.505 (0.031)	5.55***	94	74
Estimated wing loading	1.982 (0.029)	0.521 (0.015)	12.53***	319	78
Emballonuridae	2.419 (0.077)	0.751 (0.041)	10.20***	5	99
Estimated wing loading	2.422 (0.025)	0.756 (0.013)	32.54***	22	99
Rhinolophidae	1.759 (0.079)	0.452 (0.040)	2.98*	12	92
Estimated wing loading	1.744 (0.058)	0.445 (0.030)	3.73***	40	85
Phyllostomidae	1.772 (0.103)	0.391 (0.064)	0.91ns	15	72
Estimated wing loading	1.809 (0.046)	0.407 (0.026)	2.85*	81	76
Vespertilionidae	1.891 (0.122)	0.475 (0.060)	2.37*	43	60
Estimated wing loading	1.870 (0.056)	0.467 (0.027)	4.96***	116	72
Molossidae	1.792 (0.197)	0.364 (0.117)	0.26ns	8	56
Estimated wing loading	1.879 (0.096)	0.406 (0.058)	1.26ns	34	60

The statistical package SYSTAT, version 4 (SYSTAT, Inc., Evanston, IL) was used to calculate most descriptive statistics and general-linear analyses.

Isometric expectations.—We used t -tests to compare derived constants of allometric rates (slopes) with those expected by geometric similarity (Sokal and Rohlf, 1981). If litter mass and wing loading scale isometrically with body size and mass, then with log transformations we predict litter mass should scale as follows: to length of forearm, length of head and body, or wing loading with a slope of three, to airfoil area with a slope of $3/2$ (1.5), and to maternal body mass with a slope of one. Similarly, wing loading should scale to length of forearm or length of head and body with a slope of one, to airfoil area with a slope of $1/2$ (0.5), and to mass with a slope of $1/3$ (0.333). Only wing loading versus body mass regressions are presented because similar patterns were observed with wing loading versus length of forearm, length of head and body, or airfoil area.

Scaling reflects the interaction of two variables, specifically, the rate at which one changes

relative to the other. For a given group, if scaling of litter mass and wing loading is steeper than that predicted by dimensional analysis, then litter mass in larger species of that group would be heavier than expected, whereas litter mass for smaller species would be lighter than expected. Conversely, differences in elevations of lines (intercepts as adjusted for the pooled slope) will reflect quantitative differences in the y -axis variable across groups. Thus, if two groups exhibit the same scaling relationship between litter mass and wing loading, but different elevations, then the litter mass of the group with the higher elevation will be larger than that of the other group for any given wing-loading value.

RESULTS

Wing loading and maternal mass.—Wing loading for bats scales to body mass more steeply than expected by geometric-dimensional analysis (Table 2). Microchiroptera, however, contribute unequally to this analysis and Megachiroptera and Microchiroptera differ in the allometry of

wing loading to body mass (Fig. 1a). For Megachiroptera, the regression slope is slightly lower than that expected from geometric similarity. The three largest pteropodids have high wing loadings and, thus, may overly influence regression coefficients. In fact, the relation of wing loading to mass in megachiropterans may be lower than calculated here and much lower than expected by geometric scaling. Conversely, the slope for microchiropterans is significantly larger than expected. Thus, for microchiropterans overall, the relationship between wing loading and body mass is steeper than expected by geometric scaling.

The allometric relationships between wing loading and body mass are similar across most families of microchiropterans (Fig. 1b), but elevations of these regression lines differ. The regression slope for emballonurids is steeper than that for other families, but also is based on the smallest sample. Molossids have the highest wing loading relative to body mass, followed by phyllostomids and vespertilionids, whereas rhinolophids have the lowest. These results follow from the fact that molossids have the smallest forearms and airfoil areas for their mass, whereas rhinolophids have the largest. Phyllostomids and vespertilionids are intermediate.

Litter mass and maternal mass or size.—

Litter mass in bats is highly correlated with maternal body size. This is true whether one considers length of head and body, length of forearm, or body mass (Table 3). The relationship with maternal body mass is strongest ($R^2 = 0.92$) and that for length of forearm the weakest ($R^2 = 0.83$). Allometries between litter mass and body size are slightly, but significantly, less than expected by geometric similarity (maternal body mass: 0.8-0.9 versus 1.0; length of forearm, length of head and body: 2.2-2.5 versus 3.0). Thus, litter mass is not an isometric proportion of maternal size.

The suborders of bats differ with respect to the allometry of litter mass (Fig. 2a). In general, litter mass appears more closely al-

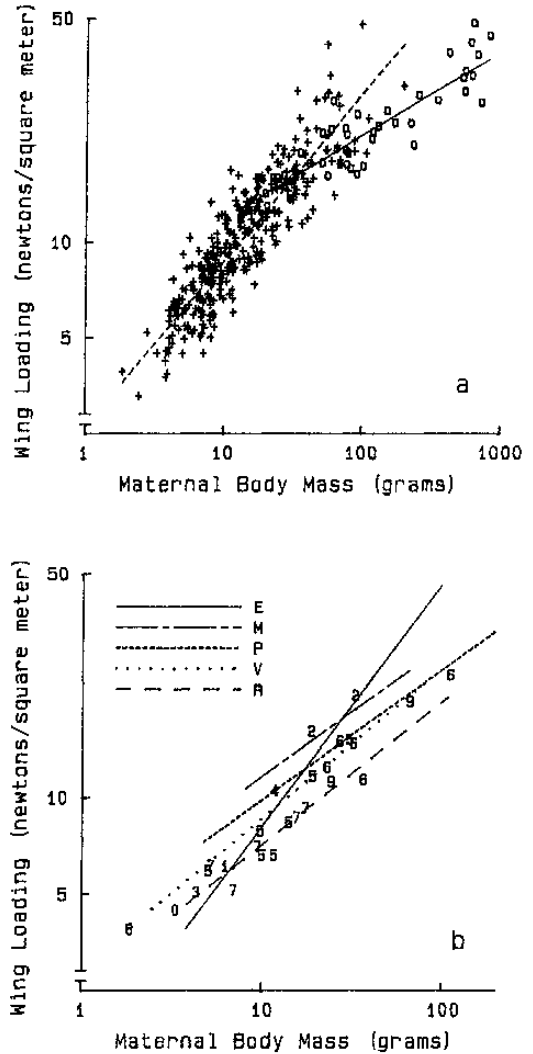


FIG. 1.—Relationship of wing loading (log N/m^2) to maternal body mass (log g) by suborder (A) and across microchiropteran families (B). Symbols for A: \circ Megachiroptera, $+$ Microchiroptera. In B, large samples for five families preclude plotting individual data points. These families are represented by regression lines only; Emballonuridae (E, $n = 22$), Molossidae (M, $n = 34$), Phyllostomidae (P, $n = 81$), Rhinolophidae (R, $n = 40$), Vespertilionidae (V, $n = 116$). Symbols for other microchiropteran families in E: 1) Natalidae, 2) Rhinopomatidae, 3) Thyropteridae, 4) Mystacinidae, 5) Nycteridae, 6) Megadermatidae, 7) Mormoopidae, 8) Craseonycteridae, 9) Noctilionidae, 0) Furipteridae.

TABLE 3.—Allometry of litter mass (kg) with respect to length of forearm (FA, m); length of head and body (HB, m); maternal body mass (MASS, kg); wing, uropatagial, and body area (airfoil area, m^2); estimated area of airfoil (estimated area, m^2); wing loading (N/m^2); or wing loading predicted from estimated area of airfoil (estimated wing loading, N/m^2). Equations from least-squares regression of common log-transformed variables for major taxa of bats. Area of airfoil and estimated area of airfoil equations not provided for individual families. F-statistics for regressions are significant at $P < 0.0005$ unless otherwise indicated and t-values comparing regression slope with that expected from geometric similarity ($slope_{exp}$) are given (ns = not significant, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$). n = number of species.

Taxon	Intercept (SE)	Slope (SE)	Slope _{exp}	t (P)	n	R ² %	F (P)
Chiroptera							
FA	0.767 (0.129)	2.379 (0.100)	3	-6.21***	115	83	561
HB	0.213 (0.083)	2.182 (0.072)	3	-11.36***	115	89	910
MASS	-0.896 (0.040)	0.829 (0.023)	1	-7.43***	115	92	1,318
AIRFOIL AREA	-0.069 (0.130)	1.254 (0.072)	1.5	-3.42**	69	82	305
Estimated area	-0.090 (0.085)	1.248 (0.048)	1.5	-5.25***	115	86	688
WING LOADING	-3.963 (0.144)	1.547 (0.133)	3	-10.92***	69	67	136
Estimated wing loading	-4.225 (0.104)	1.809 (0.095)	3	-12.54***	115	76	366
Megachiroptera (Pteropodidae)							
FA	0.823 (0.133)	2.416 (0.126)	3	-4.63***	25	94	370
HB	0.281 (0.125)	2.324 (0.145)	3	-4.66***	26	91	258
MASS	-0.895 (0.039)	0.861 (0.037)	1	-3.76***	25	95	549
AIRFOIL AREA	-0.238 (0.158)	1.128 (0.108)	1.5	-3.44*	12	91	109
Estimated area	-0.242 (0.085)	1.123 (0.063)	1.5	-5.98***	25	93	315
WING LOADING	-4.929 (0.867)	2.340 (0.655)	3	-1.01ns	12	52	13 (0.005)
Estimated wing loading	-5.170 (0.444)	2.564 (0.325)	3	-1.34ns	25	72	62
Microchiroptera							
FA	0.575 (0.265)	2.239 (0.197)	3	-3.86***	90	59	129
HB	0.641 (0.179)	2.521 (0.146)	3	-3.28**	89	77	298
MASS	-0.803 (0.083)	0.875 (0.044)	1	-2.84**	90	82	399
AIRFOIL AREA	0.015 (0.218)	1.300 (0.116)	1.5	-1.72ns	57	69	125
Estimated area	0.057 (0.185)	1.328 (0.098)	1.5	-1.76ns	90	67	182
WING LOADING	-3.748 (0.157)	1.318 (0.152)	3	-11.07***	57	57	75
Estimated wing loading	-3.866 (0.124)	1.430 (0.121)	3	-12.98***	90	61	139
Emballonuridae							
FA	0.328 (1.094)	2.166 (0.869)	3	-0.96ns	5	56	6 (ns)
HB	-0.247 (1.333)	1.806 (1.119)	3	-1.07ns	5	29	3 (ns)
MASS	-1.431 (0.679)	0.530 (0.371)	1	-1.27ns	5	21	2 (ns)
WING LOADING	-2.535 (0.832)	0.138 (0.752)	3	-3.81ns	3	0	0 (ns)
Estimated wing loading	-3.081 (0.530)	0.657 (0.496)	3	-4.72*	5	16	2 (ns)
Estimated wing loading ^a	-3.501 (0.292)	1.147 (0.288)	3	-6.43*	4	83	16 (ns)
Rhinolophidae							
FA	0.788 (0.580)	2.545 (0.447)	3	-1.02ns	15	69	32
HB	0.876 (0.537)	2.710 (0.429)	3	-0.68ns	15	74	40
MASS	-0.736 (0.214)	0.915 (0.109)	1	-0.78ns	15	83	70
WING LOADING	-4.041 (0.427)	1.806 (0.466)	3	-2.56*	7	70	15 (0.01)
Estimated wing loading	-4.219 (0.288)	1.942 (0.321)	3	-3.30*	15	72	37
Estimated wing loading ^b	-3.880 (0.364)	1.530 (0.421)	3	-3.49**	14	48	13
Phyllostomidae							
FA	0.611 (0.509)	2.162 (0.393)	3	-2.13*	20	61	30
HB	0.429 (0.504)	2.293 (0.442)	3	-1.60ns	20	58	27
MASS	-0.930 (0.213)	0.788 (0.133)	1	-1.59ns	20	64	35
WING LOADING	-3.896 (0.600)	1.486 (0.502)	3	-3.02*	10	46	9 (0.02)

TABLE 3.—Continued.

Taxon	Intercept (SE)	Slope (SE)	Slope _{exp}	t (P)	n	R ² %	F (P)
Phyllostomidae							
Estimated wing loading	-3.960 (0.484)	1.537 (0.415)	3	-3.53**	20	40	14 (0.002)
Estimated wing loading ^c	-4.020 (0.393)	1.613 (0.338)	3	-4.10***	19	55	23
Vespertilionidae							
FA	0.725 (0.407)	2.334 (0.291)	3	-2.29*	38	63	64
HB	0.530 (0.271)	2.446 (0.216)	3	-2.56*	38	78	128
MASS	-0.746 (0.145)	0.904 (0.073)	1	-1.32ns	38	80	154
WING LOADING	-3.894 (0.269)	1.456 (0.282)	3	-5.48***	27	50	27
Estimated wing loading	-4.051 (0.209)	1.590 (0.217)	3	-6.50***	38	59	54
Molossidae							
FA	1.208 (1.697)	2.583 (1.251)	3	-0.33ns	5	45	4 (ns)
HB	0.972 (1.097)	2.819 (0.946)	3	-0.19ns	5	66	9 (ns)
MASS	-0.510 (0.271)	1.043 (0.158)	1	0.27ns	5	92	44 (0.007)
WING LOADING	-4.838 (0.582)	2.143 (0.487)	3	-1.76ns	5	82	19 (0.022)

^a Without an outlier, *Taphozous longimanus* (3.0-g newborn, Krishna and Dominic, 1983).

^b Without *Hipposideros commersoni* (28-g term embryo, 111-g female, Brosset, 1969).

^c Without an outlier, *Sturnira tildae* (2.2-g large embryo, perhaps not near term, Goodwin and Greenhall, 1961).

lied to maternal body mass or size in megachiropterans ($R^2 = 0.92-0.95$) than in microchiropterans either as a group ($R^2 = 0.59-0.82$) or across individual families (length of forearm, $R^2 = 0.45-0.69$; length of head and body, $R^2 = 0.29-0.78$; maternal mass, $R^2 = 0.21-0.92$). Most megachiropterans are larger as adults than most microchiropterans, but they have relatively smaller young at birth. Regressions of suborders for litter mass versus maternal body mass cannot be statistically compared both because variances differ and because ranges of maternal mass overlap only slightly. However, the average ratio of litter mass to maternal body mass is significantly smaller ($P < 0.0005$) for megachiropterans (17.7%, $n = 25$ species) than microchiropterans (28.3%, $n = 90$ species). Within Megachiroptera, all five species with maternal body masses >400 g have litter masses $<15\%$ of maternal body mass, whereas no species with a maternal body mass <200 g has a relative litter mass that small, although *Haplonycteris* and small *Rousettus* are close. Within Microchiroptera (Fig. 2b), families do not vary significantly in litter mass relative to either maternal body mass or length of head and body, but they do

vary with respect to length of forearm (Table 3). Thus, megachiropterans have relatively small neonates whose mass and size are highly correlated to their mother's body mass, whereas the mass of the relatively larger neonates of microchiropterans is less related to maternal body mass or size. For microchiropterans, litter mass may be more influenced by other aspects of the animal's biology such as foraging habits, diet, seasonal energetics, or flight.

Litter mass and wing loading.—Wing loading incorporates three estimates of body size; length of forearm, length of head and body, and body mass. From geometric proportions, litter mass should scale relative to wing loading cubed. However, analysis of aerodynamic consequences of carrying extra mass suggests that a significantly smaller scaling exponent would be selectively advantageous. Our analyses show that for megachiropterans litter mass scales as expected from geometric similarity. However, for microchiropterans the scaling exponent for litter mass versus wing loading is significantly less than expected from geometric similarity (Table 3).

Overall, litter mass in bats is strongly and positively correlated with wing loading

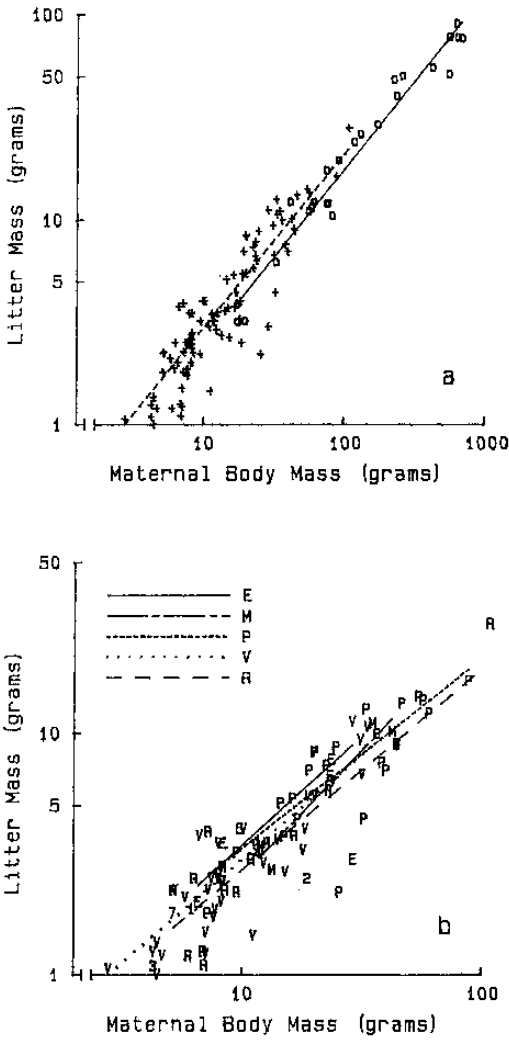


FIG. 2.—Relationship of litter mass (log g) to maternal body mass (log g) by suborder (A) and across microchiropteran families (B). Symbols are as in Fig. 1.

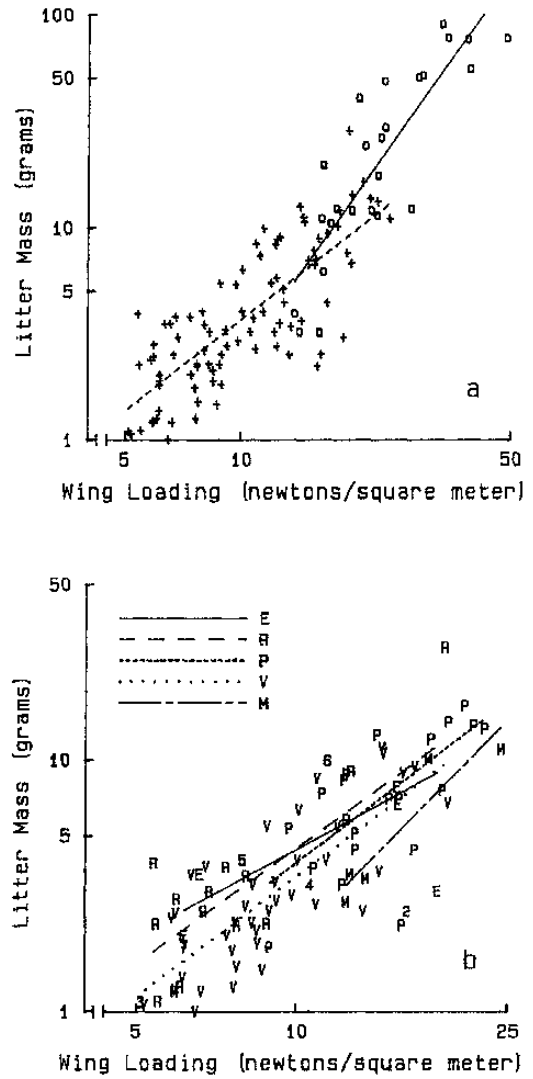


FIG. 3.—Relationship of litter mass (log g) to wing loading (log N/m²) by suborder (A) and across microchiropteran families (B). Symbols are as in Fig. 1.

(Fig. 3a). About 70% of the variation in litter mass can be explained by variation in wing loading. Litter mass is less tightly associated with wing loading than it is to any single body size variable. This is especially apparent in Megachiroptera for which 92–95% of overall variance in litter mass is correlated with individual size measures, but only 40–70% is correlated with wing loading. One could argue that as wing loading is a composite of three different vari-

ables, it will be subject to increased measurement error and therefore lower coefficients of determination (R^2). However, although the coefficient of variation for wing loading is twice as large as that for length of head and body or length of forearm (all log transformed), it is only one-half that for maternal body mass. Thus, the variability of wing loading is intermediate compared with single estimates of body size. In addition,

TABLE 4.—Allometry of litter mass (kg) with respect to wing loading from estimated wing areas (estimated wing loading, N/m^2) by genus for those genera with data for at least five species. Equations from least-squares regression equations of common log-transformed variables. The t -values comparing regression slope with that expected from geometric similarity ($slope_{exp}$) also are given (ns = not significant, * = $P < 0.05$). n = number of species.

Taxon	Intercept (SE)	Slope (SE)	Slope _{exp}	t (P)	n	$R^2\%$	F (P)
Rhinolophidae							
<i>Hipposideros</i>	-4.657 (0.292)	2.383 (0.321)	3	-1.92ns	10	85	55 (<0.0005)
<i>Hipposideros</i> *	-4.448 (0.462)	2.131 (0.536)	3	-1.62ns	9	65	16 (0.005)
Vespertilionidae							
<i>Myotis</i>	-5.250 (0.516)	2.893 (0.575)	3	-0.19ns	9	75	25 (0.002)
<i>Pipistrellus</i>	-4.147 (0.257)	1.587 (0.292)	3	-4.84*	6	85	30 (0.006)

* *Hipposideros* without *H. commersoni*.

estimated area of the airfoil should be subject to similar reasoning, but its coefficient of determination is not uniformly smaller than component variables; lengths of head and body or forearm.

The relationship between litter mass and wing loading differs between suborders. For Megachiroptera, the scaling of litter mass to wing loading is similar to that with respect to lengths of either forearm or head and body and not significantly different from that expected by isometry. For Microchiroptera, however, the exponent is much smaller than expected by geometric scaling. In fact, litter mass across species of microchiropterans appears to scale isometrically with area of the airfoil rather than single measures of length.

Within a given family, microchiropterans show similar scaling of litter mass to wing loading, but, for a given wing loading, families differ in their litter masses (Fig. 3b). Adjusted for wing loading, rhinolophids, and possibly emballonurids, have the largest relative litter masses, followed by phyllostomids and vespertilionids, with molossids having the smallest relative litter masses. Families with too few data points for regression analysis, but with known (rather than estimated) airfoil areas, also show differences with respect to litter mass. The megadermatid, *Megaderma lyra*, has a large litter mass relative to wing loading, whereas the rhinopomatid, *Rhinopoma*

hardwickei, has a small litter mass. The natalid, *Natalus stramineus*, the thyropterid, *Thyroptera tricolor*, and the mystacinid, *Mystacina tuberculata*, are intermediate.

Across families, families of microchiropterans with the largest wing loadings relative to maternal body mass have the smallest litter masses relative to wing loading. Thus, molossids with the highest wing loadings have the smallest litter masses and rhinolophids with the lowest wing loadings have the greatest litter masses. Even families with too few data for intrafamilial analysis conform to the trend. Rhinopomatids have high wing loadings for their maternal body mass, but small litter masses, whereas megadermatids with a large litter mass have low wing loadings for their size. In fact, multiple regression using means of the family for litter mass and wing loading shows that, after removing effects of maternal body mass, litter mass and wing loading are negatively correlated across families ($P = 0.11$, $n = 10$ families of microchiropterans).

Only three genera, one rhinolophid (*Hipposideros*) and two vespertilionids (*Myotis* and *Pipistrellus*), have sufficient data for analyses within a genus and each exhibits a different pattern (Table 4). Litter masses for species of *Hipposideros* are independent of wing loading, whereas those for both vespertilionid genera are positively correlated with wing loading. For species of *Myotis*, litter mass scales as expected by geo-

metric similarity; but for species of *Pipistrellus*, litter mass is a significantly smaller proportion of wing loading than expected by dimensional analysis.

Litter mass and lengths of gestation or lactation.—For bats, gestation ($n = 126$ species) is slightly, but significantly and positively, correlated with both mass of females ($P = 0.001$, $R^2 = 7.6\%$) and wing loading ($P < 0.01$, $R^2 = 4.6\%$), whereas lactation ($n = 86$ species) is not, although the relationship with mass of females nears significance (mass of females: $P = 0.07$; wing loading: $P = 0.26$). Litter size, neonatal mass, length of gestation, body mass of females, length of forearm, and length of head and body are known for 64 species of bats. Of these, litter mass and length of gestation are not correlated after removing effects of wing loading ($P > 0.3$), but may be related after removing the effects of body mass of females ($P = 0.14$). Thus, for females of equivalent mass, those with heavier neonates may have shorter lengths of gestation (negative coefficient).

The relationship of litter mass with length of lactation exhibits the reverse pattern. Statistical significance is nearly reached for the correlation of litter mass and length of lactation after removing effects of wing loading ($P = 0.14$), but not mass of females ($P > 0.6$) for the 51 species with appropriate data. Thus, mass of females does not affect the relationship between litter mass and length of lactation, but wing loading may. Females with similar wing loadings, but larger neonates, may have longer lengths of lactation (positive coefficient).

Analysis by suborder is hampered by much-reduced samples. For Megachiroptera, mass of litters is not related to length of gestation ($n = 11$ species) after removing effects of either mass of females ($P > 0.29$) or wing loading ($P > 0.5$), nor to length of lactation ($n = 8$ species; mass of females, $P > 0.4$; wing loading, $P > 0.5$). For Microchiroptera, mass of litters is not correlated with length of gestation ($n = 53$ spe-

cies; mass of females, $P > 0.3$; wing loading, $P > 0.3$), although mass of litters may be positively correlated with length of lactation ($n = 43$ species) when effects of wing loading are removed ($P > 0.1$), but not after removing effects of mass of females ($P > 0.6$).

Among families of microchiropterans, only rhinolophids and vespertilionids have sufficient data for analysis of mass of litters with length of gestation or lactation. For both families, litter mass is not correlated with length of gestation after removing effects of body size (rhinolophids: $n = 12$ species, $P > 0.6$; vespertilionids: $n = 22$ species, $P > 0.27$) or wing loading (rhinolophids: $P > 0.9$; vespertilionids: $P > 0.3$). Mass of females also has no effect on relationships between litter mass and length of lactation (rhinolophid: $n = 11$ species, $P > 0.5$; vespertilionid: $n = 19$ species; $P > 0.9$). However, wing loading may influence length of lactation and litter mass. For vespertilionids, species with large litter masses relative to wing loading may have shorter lengths of lactation ($P = 0.15$), whereas the reverse may hold for rhinolophids. Rhinolophids with large litter masses relative to wing loading have longer periods of lactation ($P = 0.06$).

DISCUSSION

Allometry of wing loading.—Although wing loading in bats scales to maternal body mass more steeply than expected by geometric-dimensional analysis, the suborders of bats exhibit opposite relationships between wing loading and maternal body mass. The overall trend reflects the disproportionate contribution of Microchiroptera to the analysis.

Scaling of wing loading to maternal body mass is lower for megachiropterans than for microchiropterans. Thus, for a given increment in mass, wing loading increases by a smaller amount in megachiropterans than in microchiropterans, either as a group or for individual families. Families of microchiropterans will have larger variation in wing

loading across an equivalent range of maternal body mass than will megachiropterans. Thus, differences in wing loading between small and large species will be less in pteropodids than in families of microchiropterans. This suggests that aerodynamic consequences of flight will be more homogeneous across species of pteropodids than across species within, for instance, Phyllostomidae. This may reflect similarities in diet and foraging strategies in pteropodids versus the highly diverse diets and foraging strategies found among phyllostomids.

The two families of microchiropterans with the highest wing loadings relative to body mass (molossids and phyllostomids) are also the two families for which wing loading scales more nearly as expected by dimensional analysis. Perhaps, these two families have the highest wing loadings possible and are therefore constrained by the physics of dimensional scaling, whereas other groups have lower wing loadings and, thus, are released from such physical constraints. Within Microchiroptera, rhinolophids have the lowest wing loadings relative to body mass and molossids the highest. Thus, rhinolophids would be expected to be able to carry a greater mass relative to body size or to carry the same mass at less energetic expense. For molossids, the reverse would hold.

Allometry of litter mass.—Mass of litters in most mammals is highly correlated with body size (Gittleman, 1986; Hayssen, 1985; Jones, 1985; Leitch et al., 1959; Martin and MacLarnon, 1985; Millar, 1981; Robbins and Robbins, 1979) and bats are no exception (Kurta and Kunz, 1987; this study). Litter mass in bats is not an isometric function of maternal body mass, but instead scales less steeply. Thus, larger species have relatively smaller offspring than predicted by isometry, whereas smaller species have relatively larger young. This trend is apparent within bats as a whole, as well as within suborders and families.

Not only do megachiropterans have rel-

atively small neonates, but mass and size of their offspring are more tightly correlated with that of their mothers than is the case for litters of microchiropterans. Thus, neonates of microchiropterans as a group and within families exhibit a greater range of relative masses and appear to be less constrained by maternal body size. Perhaps growth patterns of skeletal, organ, and muscle systems are more tightly integrated in megachiropterans than in microchiropterans.

The pattern of small size of adults and large variation in birth mass versus large size of adults and small variation in birth mass is not unique to bats. The same pattern is observed in ungulates and subungulates (Robbins and Robbins, 1979). Ungulates with maternal masses <400 kg have relative birth masses of 3–15%, whereas species >400 kg show a restricted range of only 4–8% of maternal mass. Thus, the trend toward higher correlations and smaller relative litter mass with increased body size is observed both within and between suborders of bats as well as in large mammals with predominantly single offspring. Rodents, which have a similar range of body sizes as bats, but larger litter sizes, may have litter masses that are not as highly correlated with maternal mass (Hayssen, 1985; Millar, 1981).

Mass of litters and reproductive investment.—Species with heavier than expected litters relative to maternal wing loading or maternal body mass do not have larger litters, nor do they have longer lengths of gestation or lactation. In fact, the regression coefficient for length of gestation, after removing effects of body mass, is negative, suggesting that shorter lengths of gestation are correlated with larger litter masses. The apparent independence of litter mass and duration of gestation may be a consequence of various timing delays associated with pregnancy in bats (Racey, 1982).

Among families of microchiropterans, relationships between different components of reproductive investment may simply be

idiosyncratic. For instance, relationships between litter mass and length of lactation differ between the only two families with sufficient data for analysis. Thus, vespertilionids and rhinolophids appear to have different patterns of reproductive investment. Rhinolophids with heavier offspring wean their offspring after a longer period of time, whereas, vespertilionids with heavier litters have relatively shorter lengths of lactation. Further, among vespertilionids, species with larger offspring have shorter periods of postnatal energetic investment, whereas, among rhinolophids, species with larger offspring have longer periods of investment. Most rhinolophids belong to only two genera (*Hipposideros* and *Rhinolophus*), whereas Vespertilionidae contains many genera. Rhinolophids and vespertilionids also differ greatly in body size, morphology, foraging strategies, etc. In addition, the quality of the data for rhinolophids and vespertilionids varies greatly with that for rhinolophids based on smaller samples and fewer studies (Hayssen et al., 1993). Conclusions regarding patterns of reproductive investment across families of bats are severely limited both by patterns of species richness and by the relative amount of available data.

Mass of litters and wing loading.—Bats are morphologically diverse, but their structural adaptations are constrained by flight, which is their most distinguishing characteristic. The additional mass that a female carries during gestation increases her wing loading (Davis, 1969) and, thus, the power she needs to sustain flight. Bats with high wing loadings should be less able to compensate for additional mass. These aerodynamic considerations predict a significantly smaller scaling exponent between litter mass and wing loading than considerations from geometric scaling, a result that we found for microchiropterans, but not for megachiropterans. Thus, geometric scaling may influence litter mass of megachiropterans more so than for microchiropterans. Alternatively, selection pressures may be

stronger on microchiropterans, perhaps because foraging for insects while flying is more aerodynamically demanding than searching for and carrying fruit, although New World fruit bats (phyllostomids) also conform to the pattern of microchiropterans. For microchiropterans, these results indicate that selection pressures in favor of a smaller litter mass with larger wing loading are operating in opposition to allometric constraints producing larger litter masses with larger body size.

The airfoil area of a bat in flight is not constant and wing loading probably varies moment by moment. If so, postural adjustments during flight might compensate for increased mass of offspring as gestation progresses. Measurement of airfoil areas from pregnant bats flying in wind tunnels over the course of gestation, or of non-pregnant females with offspring-sized masses appropriately attached, might provide data on dynamic aspects of wing loading. Investigations of large-eared bats that may hold their ears in different positions when carrying loads of different masses might be especially interesting. Some of these data may already be available (Hughes and Rayner, 1991). We would predict that bats carrying extra mass would increase their effective airfoil area by making postural adjustments during flight.

Bats have been excluded from most major analyses of reproductive patterns in mammals. They are a large, diverse, and an important group and, as we have shown, offer considerable challenges and potential insights into life-history theory and the evolution of reproductive patterns among mammals.

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