

# Does energy or calcium availability constrain reproduction by bats?

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## Synopsis

Bats are unusual mammals in being small but having long lives and small litters (typically only one or two young). I hypothesize that litter size is constrained by the need to raise young to near adult size before they can be independent. Our studies, and those of others, on a variety of species of bats indicate that juveniles typically start to fly at over 70% of adult mass and over 95% of adult skeletal size. This constraint appears to be associated with flight in vertebrates, since young birds also do not fly until fully grown. This means that each young is very costly and restricts the number that can be raised. Although energetic demands may be the proximate constraint, I argue that calcium is more important. For bats, calcium demand on reproductive females is high and calcium availability in most diets (insects, fruit, pollen) is low. Birds can at least partially overcome this by supplementing their diet with calcium-rich inanimate objects that are unavailable to bats because of their inability to forage on the ground and detect such items. This may help to explain why the reproductive output of birds exceeds that of bats. If the hypothesis is correct, bat foraging strategies may be based on the calcium content of prey in addition to energy content, and female and male foraging strategies may be based on different currencies. Vertebrate-pollinated and seed-dispersed plants may attract bats by offering high calcium rewards. In addition, however, it would mean that flight could only have evolved in bats in association with long lifespans, thereby constraining the possible life histories available to these mammals.

## Introduction

Amongst mammals, many life-history traits correlate with body size (Millar 1977, 1981; Harvey & Read 1988; Read & Harvey 1989). In general, large mammals live long lives and produce litters of few, large, slow-growing, late-maturing offspring. Small mammals live short lives and have litters of many, small, rapidly growing, early-maturing offspring. These correlations may simply result from common selective forces acting independently on

body size and life-history characteristics (Read & Harvey 1989; Promislow & Harvey 1990). Nonetheless, even when body size is factored out, life-history traits still correlate with one another (Read & Harvey 1989); some mammals produce litters of few, large, slow-growing offspring and live long lives for their body size, whereas others produce large litters of fast-growing young and die at an early age.

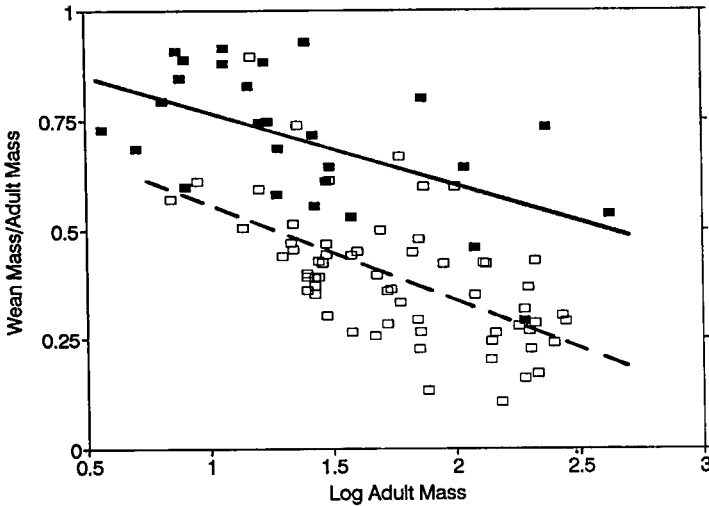
In the debate over the evolution of mammalian life-history variation, the second largest group of mammals, the Chiroptera, has been either completely ignored (Sacher & Staffeldt 1974; Western 1979; Millar 1981; Western & Ssemakula 1982), or severely under-represented (Millar 1977; Blueweiss, Fox, Kudzma, Nakashima, Peters & Sams 1978; Promislow & Harvey 1990). Bats can be used to argue against a simple allometric constraint on life-history variation. Despite the small size of bats (most have body masses under 100 g; Barclay & Brigham 1991), they are long-lived (Tuttle & Stevenson 1982) and have small litters. Most species produce only a single young and only eight are known regularly to produce more than two young (Tuttle & Stevenson 1982).

Recent laboratory and field studies on the growth, development and nutritional requirements of bats, and the availability of energy and nutrients in their diets, suggest that there are unique constraints on bat reproduction that may explain why this group of mammals has evolved the life-history pattern it has (Barclay 1994).

### **Pre- versus post-natal constraints**

Since bats are the only mammals to have evolved true flight, a reasonable assumption might be that small litters are somehow linked to the ability to fly. For example, litter mass may be constrained, thereby limiting the number of viable neonates that can be produced (Millar 1977). The mass of a near-term litter influences the ability of a female to fly and forage, since increased mass and wingloading increase flight costs and reduce the ability to fly slowly, manoeuvrably and with agility (Norberg & Rayner 1987). This could impair a female's foraging efficiency, especially for aerial insectivorous bats which rely on manoeuvrability to capture their prey. However, bats and similar-sized terrestrial mammals both produce litters with a mass averaging 25% that of the female (Kurta & Kunz 1987). Female bats thus carry as large a load as do other female mammals. The difference is that female bats put this mass into very few large offspring while terrestrial mammals divide it amongst many small neonates.

Flight may constrain litter size of bats, but for post-natal, not pre-natal, reasons. Young terrestrial mammals are weaned when they are on average 37% of adult body mass and some, such as lagomorphs, are weaned at 16% of adult mass (Millar 1977). In contrast, young bats begin to fly and become independent of the female only when they are at a mean of  $70.9 \pm$  (SD) 15.7%



**Fig. 1.** Ratio of mass at first flight or weaning to adult mass versus the log of adult body mass, for terrestrial mammals (open squares) and bats (closed squares). Lines were calculated using least squares (bats: ratio =  $0.94 - 0.17 \times \log \text{ adult mass}$ ; terrestrial mammals: ratio =  $0.78 - 0.22 \times \log \text{ adult mass}$ ).

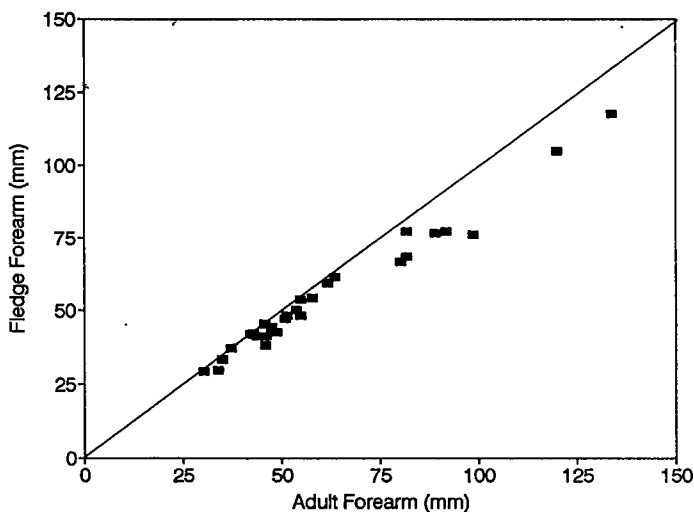
( $n = 27$ ; Appendix) of adult mass. In an analysis of covariance (ANCOVA) comparing the relative size at 'independence' for bats, and terrestrial mammals of the same size (<300 g; Millar 1977), with the log of adult mass as the covariate, both taxon ( $F = 62.4$ ,  $d.f. = 1, 86$ ,  $P < 0.001$ ) and log of adult mass ( $F = 43.5$ ,  $d.f. = 1, 86$ ,  $P < 0.001$ ) significantly influenced relative size at independence (the interaction term was not significant and was removed from the model). The relative size of young at first flight or weaning declines with adult size for both bats and terrestrial mammals, but bats start to fly at a significantly larger relative mass ( $\bar{x} = 70.9 \pm 15.7\%$ ) than that at which similarly sized terrestrial mammals are weaned ( $\bar{x} = 39.1 \pm 14.9\%$ ,  $n = 62$ ; Fig. 1). Even compared to other mammals with small litters ( $\leq 2$  young), bats raise their young to a significantly larger size (other mammals,  $\bar{x} = 38.3 \pm 17.5\%$ ,  $n = 13$  (data from Millar 1977);  $t = 5.66$ ,  $d.f. = 38$ ,  $P < 0.001$ ; arcsine squareroot transformed proportions). The difference in weaning mass between bats and other mammals is even larger, since female bats continue to nurse their young after they first fly while the young learn to fly, forage and echolocate (Jones 1967; Kunz 1973; Tuttle & Stevenson 1982; Brown, Brown & Grinnell 1983; Koehler 1991). In addition, maternal milk is the sole energy and nutrient source for non-volant bats, while nursing young of many terrestrial mammals obtain some of their nutrition by foraging for themselves. Each young is thus more expensive (in terms of energy and nutrients) to a female bat than is each young to an equivalently sized terrestrial mammal. I

suggest that this high cost of raising young restricts the number of young a bat can rear.

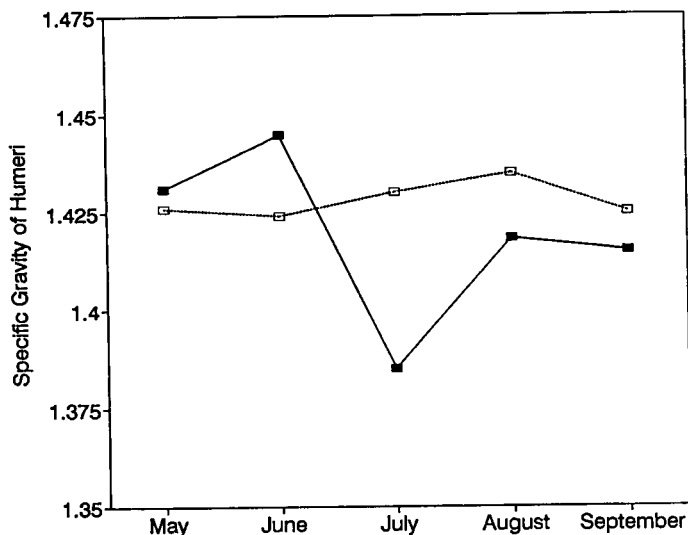
Birds also only fly when they reach adult size (Ricklefs 1979), which suggests that large size at independence is a requirement imposed by flight. In bats, and possibly birds, fully calcified wing bones may be required to withstand the unique torsion and shear forces placed on them during flight (Swartz, Bennett & Carrier 1992). In bats, the fifth finger provides wing camber necessary to generate lift and, again, may have to be ossified and stable before flight is possible (Kunz 1973).

### Energy or calcium constraint?

The large size of bats at independence means that each young requires a large parental investment, thereby restricting the number of young a female can raise. Energy is typically the currency used to measure the proximate cost of reproduction (Clutton-Brock 1991) and to model optimal foraging decisions (Stephens & Krebs 1986), but it is not likely to be the most critical resource restricting litter size in bats. At weaning, young bats are large not only in terms of mass, but also in terms of their skeletal system (Medway 1972; Kunz 1973). Forearm length, a standard measure of growth and size in bats, averages  $91.2 \pm 5.9\%$  ( $n = 30$ ) of adult size at first flight (Fig. 2; Appendix), and other skeletal elements are similarly large (Maeda 1972; O'Farrell & Studier 1973; Pagels & Jones 1974). Indeed, while relative mass at first flight varies (coefficient of variation (CV) = 22.1%), and females of



**Fig. 2.** Length of forearms of bats at first flight versus length of adult forearm. The line indicates a 1:1 relationship.



**Fig. 3.** Change in mean specific gravity of the humeri of adult male (open squares) and adult female (closed squares) little brown bats, *Myotis lucifugus*. Peak lactation occurs in July. Data from Kwiecinski *et al.* (1987).

some species start transferring the energetic costs of their young to the young themselves at 50–60% of adult mass, forearm length at first flight varies much less ( $CV = 6.4\%$ ). Females thus bear almost the entire nutrient cost of producing the skeleton of their offspring. Calcium demand is particularly stressful and causes significant structural changes in the bones of lactating bats (Kwiecinski, Krook & Wimsatt 1987). In the small (7–8 g) insectivorous little brown bat, *Myotis lucifugus*, for example, the specific gravity of the humeri of lactating females declines significantly, while no such decline is seen in males (Fig. 3; Kwiecinski *et al.* 1987). Females deplete their own calcium stores to meet the demand of their growing offspring. This osteoporosis is particularly evident in the mandible and the long bones of the wings and could reduce a female's fitness, owing to tooth loss or increased risk of wing-bone fractures (G. Kwiecinski pers. comm.). *M. lucifugus* bears only one young per year. The problems inherent in low calcium availability will be even greater for females of species that produce larger litters.

### Calcium availability

The problem that *M. lucifugus* and other insectivorous bats face is that insects have a low calcium content (Maxson & Oring 1980; Turner 1982 and pers. comm.; Ormerod, Bull, Cummins, Tyler & Vickery 1988; Studier & Sevcik 1992). A reproductive female relying on insects for calcium cannot obtain as

much as she needs. For example, a big brown bat (*Eptesicus fuscus*), which is a small (15-20 g) insectivorous species with litters of one or two, requires an estimated 11.56 to 23.12 mg of calcium per day during mid-pregnancy (Keeler & Studier 1992). If calcium is assimilated as efficiently as energy (75%; Barclay, Dolan & Dyck 1991), and a random sample of insects is consumed (1.62 mg/g; Studier & Sevick 1992), then between 9.48 and 18.96 g, dry weight, or 31.6 and 63.2 g, live weight, of insects is required per night to satisfy calcium demand. This is two to four times the bat's body mass! At an energy assimilation efficiency of 75% and an energy content of 7.25 kJ/g (live mass) of insect (Kurta, Bell, Nagy & Kunz 1989), the female would obtain between 171.7 and 343.2 kJ energy per night while obtaining sufficient calcium. This is 3.5 to 7.0 times her required energy (Kurta, Kunz & Nagy 1990). Compared to calcium, energy is relatively abundant for insectivorous bats.

Calcium availability is also low in the foods of the other two main groups of bats, frugivores and nectarivores. Vertebrate-dispersed fruits have a mean calcium content of  $2.91 \pm 2.74$  mg/g dry mass (Herrera 1987; see also Duke & Atchley 1986). Pollen is ingested by nectar-eating bats as a protein source, and has a mean calcium content of  $3.15 \pm 2.69$  mg/g dry mass (Stanley & Linskens 1974).

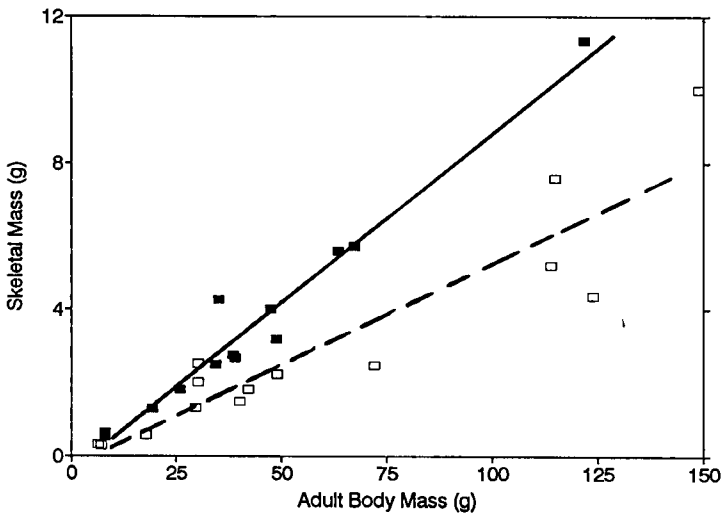
Nor can calcium be obtained in sufficient quantity by drinking fresh or salt water. Even fresh-water lakes classified as 'hard' contain only 25 mg Ca/l, or somewhat higher, and the surface water typically contains even less calcium (Reid & Wood 1976). At 25 mg Ca/l (= 0.025 mg/g), water contains 20 times less calcium than the average live insect does and a pregnant female *E. fuscus* would need to drink a minimum of 0.46 l/day to meet her requirements! Although seawater is richer in calcium, it still only averages 0.41 mg/g, or less than the average content of insects (Moran, Morgan & Wiersma 1986).

It could be argued that if bats have lighter skeletons than do terrestrial mammals, as an adaptation for flight, calcium demand on a reproductive female would be less than expected. I obtained mass data from museum-prepared skeletons of bats from 13 species (six families), ranging in adult body mass from 8 to 122 g (Barclay 1994). I compared these data with those from similarly sized terrestrial mammals (Prange, Anderson & Rahn 1979) which I supplemented with measurements from other rodents and insectivores housed in the University of Calgary Museum of Zoology (Barclay 1994). In an ANCOVA, with taxon as the main effect and the log of adult body mass as the covariate, only log of adult mass ( $F = 334.8$ ,  $d.f. = 1, 23$ ,  $P < 0.001$ ) significantly influenced skeletal mass (Fig. 4). Skeletal mass was not different between bats and terrestrial mammals ( $F = 0.93$ ,  $d.f. = 1, 23$ ,  $P > 0.3$ ) and skeletal mass changed relative to log of adult mass in a similar manner in the two groups ( $F = 0.07$ ,  $d.f. = 1, 23$ ,  $P > 0.7$ ). Thus, assuming that bats and other mammals have similar calcium content in their bones, the calcium

demand on female bats should not be lower than expected. A recent study by E. H. Studier and T. H. Kunz (pers. comm.) on mineral accretion in juvenile Mexican free-tailed bats (*Tadarida brasiliensis*) and cave bats (*Myotis velifer*), suggests that calcium requirements for growth are somewhat less than those for rodents. However, they conclude that, even in these species which produce only one young, calcium is the nutritional factor limiting growth and females are in calcium debt during lactation.

Although the difference in offspring size at weaning, and the associated calcium costs, may explain the difference in litter size between bats and small terrestrial mammals, it cannot explain the difference in reproductive output between bats and birds, since birds also fledge at adult size (Ricklefs 1979). Differences in calcium availability are the likely explanation. Most birds are relatively adept at terrestrial locomotion and are primarily visual predators. This allows them to locate and consume inanimate, calcium-rich items such as calcareous grit, eggshells, snail shells, bone fragments and ash, as well as calcium-rich invertebrates such as amphipods (Maclean 1974; Beasom & Pattee 1978; Mayoh & Zach 1986; Ficken 1989; Repasky, Blue & Doerr 1991; St. Louis & Breebaart 1991). Birds (and terrestrial mammals) can thus supplement their calcium intake.

Most bats are not adept at terrestrial locomotion. In addition, microchiropteran bats rely primarily on echolocation to detect prey. These features preclude bats from locating and/or obtaining the widely dispersed, inanimate



**Fig. 4.** Mass of adult skeletons in relation to adult body mass for terrestrial mammals (open squares) and bats (closed squares). Lines were calculated using least squares (terrestrial mammals: skeleton =  $-0.29 + 0.06 \times$  adult body mass; bats: skeleton =  $-0.46 + 0.09 \times$  adult body mass).

calcium-rich items consumed by birds. Even gleaning insectivorous bats rely on prey movement and/or sounds to detect insects on surfaces (Faure & Barclay 1992); they cannot distinguish inanimate objects from the substrate. Bats must thus rely on prey to provide calcium for reproduction and the low concentration in prey constrains reproductive output.

## Predictions

A number of testable predictions arise from the calcium-constraint hypothesis and positive results of such tests would lend support to it.

1. Female bats in species or populations to which more calcium is available should have larger litters, and/or more litters per year, and/or faster juvenile growth rates. Increased calcium intake could arise from consuming vertebrate prey, or by ingesting inanimate sources of calcium, as might be possible for bats roosting in limestone caves.

2. Reproductive females should base their foraging decisions on optimizing calcium intake while males and non-reproductive females would be expected to forage in a manner consistent with maximizing net energy intake. Since the calcium content of insects (Studier & Sevick 1992), fruit (Herrera 1987), and pollen (Stanley & Linskens 1974) varies, reproductive females could select prey on the basis of its calcium content rather than its energy content. Recent field experiments indicate that echolocating insectivorous bats do not make such fine-detailed discriminations between prey (Barclay & Brigham 1994). An alternative is that females select foraging areas where calcium-rich prey (e.g. stoneflies, Plecoptera) occur. There are data indicating that female and male insectivorous bats in the same area consume different prey (Belwood & Fenton 1976). Similarly, male and female short-tailed fruit bats (*Carollia perspicillata*) eat different fruits. The main one consumed by females, *Piper amalago*, has a high mineral (ash) content compared to those eaten by males (Fleming 1988), although no calcium analysis has been done.

3. Reproductive females should forage for longer than would be predicted if they were simply meeting their energy demands. Males and non-reproductive females should forage as predicted by models based on a currency of maximizing net energy intake. Determining energy intake of foraging bats is difficult, but there is support for this prediction from a radio-telemetry study of female *E. fuscus* (Aldridge & Brigham 1991). On the basis of mean attack rates and assumptions regarding attack success, it showed that lactating females foraged for longer than would have been expected if all they had been doing was meeting energy demand.

4. Females should have higher rates of tooth loss and bone fractures than males have. It is possible that the higher mortality rate amongst females of several species (e.g. Keen & Hitchcock 1980) reflects such differences between



the sexes, but less severe differences (finger bone fractures, tooth loss) might be evident in populations of captured bats.

5. Plants that compete for bats as pollinators or seed-dispersers should have higher calcium content in their pollen and/or nectar, and fruit, than invertebrate-pollinated plants do. Although protein content is often proposed as an important reward for pollinators and seed dispersers (Thomas 1984; Fleming 1988), for bats calcium may be even more important.

6. Bats that hibernate should have greater calcium constraints on reproduction than do bats that migrate. This prediction stems from the fact that hibernating bats resorb calcium from their bones and emerge from hibernation with depleted reserves (Kwiecinski *et al.* 1987). It is thus crucial that reproductive females replace the calcium lost during lactation prior to hibernation. Migrating bats, which are active all year, do not face this problem and may be able to cope with more severe or more prolonged calcium depletion, given that they can replenish their supply over the winter in preparation for the next litter. Among the Vespertilionidae, the only family of bats with a range of litter sizes, litters larger than one are more common amongst migrating species and those that are active all year round in tropical areas, than among hibernators (Koehler 1991).

There thus appears to be at least some support for the calcium-constraint hypothesis. Further field and experimental studies will be necessary in order to substantiate it more fully or refute it. If it is correct, however, it has broad implications for the biology of bats. Not the least of these is that if flight requires large size at fledging, the evolution of flight in mammals may only have been possible in conjunction with long life spans. The more typical life-history pattern of small mammals, involving short lives and large litters, is not one open to bats.

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## Appendix

Mean mass and forearm measurements of adult and juvenile (at first flight) bats from field (\*) and laboratory studies.

Species	Mass (g)			Forearm (mm)			Reference <sup>c</sup>
	Adult	Juvenile	%	Adult	Juvenile	%	
<b>Vespertilionidae</b>							
<i>Myotis lucifugus</i> *	7.7	6.5	84.4	37.4	37.1	99.2	1
<i>M. grisescens</i> *				43.0	42.1	97.9	2
<i>M. thysanodes</i> *				43.8	41.2	94.1	3
<i>M. velifer</i> *	11.6	10.6	91.4	46.1	41.3	89.6	4
<i>M. myotis</i> *	24.9	23.1	92.8	63.7	61.2	96.1	5
<i>Eptesicus fuscus</i> **	16.1	12.0	74.5	45.8	45.2	98.7	6
<i>E. fuscus</i> <sup>b*</sup>	19.2	13.2	68.8	47.6	44.1	92.6	7
<i>E. serotinus</i>	27.0	15.0	55.6	51.0	47.0	92.2	8
<i>Lasiurus cinereus</i> *	30.0	18.3	61.0	55.1	53.6	97.3	9
<i>Lasionycteris noctivagans</i> *	11.5	10.1	87.8	42.2	41.8	99.1	9
<i>Antrozous pallidus</i> *	17.4	13.0	74.7	53.9	50.0	92.8	10
<i>Nyctalus noctula</i>	26.5	19.0	71.7	51.5	48.0	93.2	8
<i>N. lasiopterus</i>				62.0	59.0	95.2	11
<i>Vespertilio superans</i>	18.9	11.0	58.2	48.9	42.5	86.9	12
<i>Pipistrellus subflavus</i> *	6.5	5.2	80.0	35.1	33.2	94.6	13
<i>P. pipistrellus</i> *	5.1	3.5	68.6	30.5	29.1	95.4	14
<i>Nycticeius humeralis</i>	8.0	4.8	60.0	34.0	29.5	86.8	15,16
<i>Tylonycteris robustus</i> *	7.4	6.7	90.5				17
<i>T. pachypus</i> *	3.7	2.7	73.0				17
<b>Rhinolophidae</b>							
<i>Rhinolophus cornutus</i> *	8.0	7.1	88.8				18
<i>R. ferrumequinum</i> <sup>c*</sup>						98.0	19

## Appendix (continued)

Species	Mass (g)			Forearm (mm)			Reference <sup>e</sup>
	Adult	Juvenile	%	Adult	Juvenile	%	
Molossidae							
<i>Tadarida brasiliensis</i> *	14.5	12.0	82.8	46.0	38.0	82.6	20
Phyllostomidae							
<i>Carollia perspicillata</i> <sup>d</sup>	17.0	15.0	88.2			93.4	21
<i>Phyllostomus hastatus</i> *	74.1	59.1	79.8	81.9	77.0	94.0	27
Noctilionidae							
<i>Noctilio albiventris</i> *	37.8	20.0	52.9	58.0	54.0	93.1	22
Pteropodidae							
<i>Micropteropus pusillus</i> *	31.0	20.0	64.5	55.0	48.0	87.3	23
<i>Epomops franqueti</i> *	109.0	70.0	64.2	89.3	76.4	85.6	24,25
<i>E. buettikoferi</i> * (female)	120.0	55.0	45.8	92.0	77.0	83.7	23
(male)	190.0	55.0	28.9	99.0	76.0	76.8	23
<i>Epomophorus</i>							
<i>wahlbergi</i> * (female)				80.4	66.4	82.6	25
(male)				81.9	68.2	83.3	25
<i>Hypsignathus</i>							
<i>monstrosus</i> * (female)	234.0	172.0	73.5	120.0	105.0	87.5	26
(male)	420.0	225.0	53.6	134.0	117.5	87.7	26
	$n=27 \bar{x}=70.9 \pm 15.7\%$			$n=30 \bar{x}=91.2 \pm 5.88\%$			

<sup>a</sup>From an eastern North America population in which twins are produced.

<sup>b</sup>From a western North America population in which single young are produced. <sup>c</sup>Based on wing span. <sup>d</sup>Absolute values not given.

<sup>e</sup>References: 1. Kunz & Anthony (1982); 2. Tuttle (1976); 3. O'Farrell & Studier (1973); 4. Kunz (1973); 5. de Paz (1986); 6. Burnett & Kunz (1982); 7. Holroyd (1993); 8. Kleiman (1969); 9. Kochler (1991); 10. Davis (1969); 11. Maeda (1972); 12. Funakoshi & Uchida (1981); 13. Hoying (1983); 14. Rakhmatulina (1972); 15. S. Steele (pers. comm.); 16. Jones (1967); 17. Medway (1972); 18. Yokoyama, Ohtsu & Uchida (1979); 19. Hughes, Ransome & Jones (1989); 20. Pagels & Jones (1974); 21. Kleiman & Davis (1979); 22. Brown *et al.* (1983); 23. Thomas & Marshall (1984); 24. Okia (1974); 25. Bergmans (1979); 26. Bradbury (1977); 27. A. Allgaier (pers. comm.).