Lactation and Postnatal Growth

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INTRODUCTION

The period following birth is critical for both mothers and their offspring, thus special attention should be given when caring for lactating and suckling bats. Mammary glands and milk production have largely evolved in mammals to facilitate the transfer of nutrients from females to their offspring. In addition to provisioning young with essential nutrients, milk provides other benefits, including the enhancement of immunocompetence in neonates and formation of maternal-offspring bonds (Jenness, 1985; Oftedal, 1984). When caring for female bats during lactation or of suckling young, several factors must be considered. First, one should avoid using terrestrial mammals as models for the dietary requirements of bats, both during reproductive and non-reproductive periods. The energy requirements of bats are generally higher than terrestrial species, especially associated with the high energetic cost of flight (Kurta *et al.*, 1989, 1990; Speakman and Thomas, 2003) and the relatively long periods of lactation (Kunz and Hood, 2000; Kunz *et al.*, 2009). Second, the energy and nutrient requirements of lactating females are substantially greater than those of non-reproductive and even pregnant individuals (Kunz, 1974; Kunz *et al.*, 1995a). This difference is most apparent in small species because the energy requirements of lactation scale negatively with body mass (Blaxter, 1961). With a 500-fold range in body mass, from the 2-g bumblebee bat (*Crasyonycteris thonglongyai*) to the 1,200-g Malayan flying fox (*Pteropus vampyrus*), strategies for provisioning offspring differ considerably among species. When possible, care givers should compare suckling patterns and postnatal growth rates from free-ranging or healthy captive populations, of the same or similar species, to evaluate their success in captivity (Kunz *et al.*, 2009). When it becomes necessary to hand rear bat pups, milk substitutes should mimic the predicted composition of the mother's milk as closely as possible (see Chapter 12).

Of the approximately 1100 bat species that have been described (Simmons, 2005), the composition of milk produced by mothers has been examined in less than 1% of the known species. Furthermore, rates of postnatal growth in young bats have only been examined in approximately 4% of the recognized species (Kunz *et al.*, 2009). Most published data on postnatal changes in body mass and length of forearm in suckling pups have been based on the analysis of 13 megachiropterans and 49 microchiropterans. Unfortunately, much of the published data on milk composition has been less valuable. The proximate composition of milk (i.e., macronutrient content) has been reported for only 7 species of megachiropterans and 12 species of microchiropterans (Hood *et al.*, 2001; Hood *et al.*, 2009; Kunz and Hood, 2000; Kunz *et al.*, 2009). Few of these studies, however, have examined changes in the composition of milk throughout the period of lactation.

Most studies on milk composition have focused on estimating the proximate composition of milk (i.e., the amount of protein, fat, carbohydrates, dry matter, and

energy), but only a handful of studies have evaluated mineral content (e.g., Hood *et al.*, 2001; Stern *et al.*, 1997; Studier and Kunz, 1995; Studier *et al.*, 1995) or the fatty acid content of milk (Hood *et al.*, 2001). Despite limited knowledge about the composition of milk from bats, the quality and type of data should be considered when adopting a feeding strategy for lactating mothers for assessing postnatal growth of suckling pups reared in captivity. The results of all studies on milk composition and postnatal growth in bats published prior to 2000 were summarized in Kunz and Hood (2000). In the present chapter, we focus on the most complete studies on milk composition and postnatal growth in bats. At present, there are no published studies on the transfer of immunoglobulins during lactation in bats. Bat workers are strongly encouraged to consult the primary literature when developing guidelines for the care of captive bats.

MAMMARY GLANDS AND NIPPLES

Monitoring the size, condition, and presence of expressible milk from a female's mammary glands can be a valuable method for determining if a female is currently lactating. Mammary glands of lactating female bats can usually be recognized by the whitish tissue that lies directly beneath the skin (Racey, 1988; 2009). These glands are usually flattened, disk-shaped structures, most commonly located in the anterior-lateral position (Kunz and Hood, 2000). Throughout the annual cycle, mammary glands progress from being undeveloped during the non-breeding season to well developed at peak lactation (the period of maximum milk output; Heideman, 1988). Mature female bats posses at least one pair of pectoral glands with nipples, although females in some genera, such as *Lasiurus* and *Otonycteris*, have two pairs of functional mammary glands and nipples.

Nipple morphology is highly variable in bats and can be used to help assess the reproductive status of both microchiropterans and megachiropterans (Racey, 1988; 2009; see also Racey, Chapter 3). However, nipple size alone can be ambiguous. Among microchiropterans, nipples of nulliparous females, and sometimes primiparous females, are rudimentary and are frequently accompanied by tufts of hair; whereas, the nipples of older, parous females are usually heavily cornified and darker in color, with none or few hairs (Racey, 1974, 1988; 2009). Milk can easily be expressed from most lactating bats, although in some cases it may be necessary to separate mothers and their young for 30 minutes or more to allow milk to accumulate before expression (Kunz *et al.*, 1983; Kunz *et al.*, 1995b; Racey, 1988, 2009). Recommendations for collecting milk from bats are summarized in Hood *et al.* (2009).

Some bat species have pubic or "false" nipples that should not be confused with functional nipples (Simmons, 1993). Reported for several families, false nipples, "holdfast" nipples, or so-called "pubic" nipples are generally located in the ventral, posterior-medial position, near the genitalia in females. These structures have been observed in the microchiropteran families Craseonycteridae, Megadermatidae, Rhinopomatidae, and Rhinolophidae, but they have not been reported for the megachchiropterans. False nipples are present ubiquitously in females among the

microchipteran families noted above, but only rarely occur in males. A lactiferous function of pubic nipples has been confirmed in females of some species of the Rhinolophidae and Rhinopomatidae based on the expression of milk and ductal branching pattern characteristic of mammary tissue (Simmons, 1993).

Functional mammary glands have been observed in males in at least two species of megachiropterans, *Dyacopterus spadiceus* (Francis *et al.*, 1994) and *Pteropus capistratus* (Bonaccorso, 1998; Kunz and Hosken, 2009). Reports of male lactation in *Cynopterus sphinx*, as suggested by Dobson (1878), have not been confirmed by recent observations. To date, no males have been observed nursing young, although such behavior can not be ruled out (Hosken and Kunz, 2009; Kunz and Hosken, 2009). Selection for lactation in male bats would most likely be observed in monogamous species where both sexes contribute to parental care; however, observed incidents may be by-products of male exposure to naturally occurring phytoestrogens from their plant (fruit and leaf) diets or xenoestrogens found in human-altered environments (e.g., breakdown products from organochlorine pesticides and similar compounds: Francis *et al.*, 1994; Kunz and Hosken, 2009).

NURSING

In many captive situations, the first indication that a mother has given birth is the presence of a newborn pup attached to its mother (Fig. 11-1). In many bat species, newborn pups attach themselves tenaciously to their mothers and appear to suckle from them on demand, especially during early lactation (Kunz and Hood, 2000).

In other species, mothers deposit their pups in maternity roosts and milk is provisioned on a regular schedule, as in *Tadarida brasiliensis* (Fig. 11-2) (Kunz *et al.*, 1995a; McCracken and Gustin, 1991). In these situations, mothers generally do not transport pups during foraging bouts. However, it is common for some megachiropteran species to carry their young while foraging (Gopukuman *et al.*, 2003), at which time they may continue to provision them with milk until they are fully weaned.

Most studies on free-ranging bats have supported the hypothesis that bats suckle their own young (see Kunz and Hood, 2000), except in cases of mistaken identity (McCracken, 1994) or when the

Fig. 11-1. Captive female *Pteropus vampyrus* with nursing pup. Photo © Dana LeBlanc, Lubee Bat Conservancy.
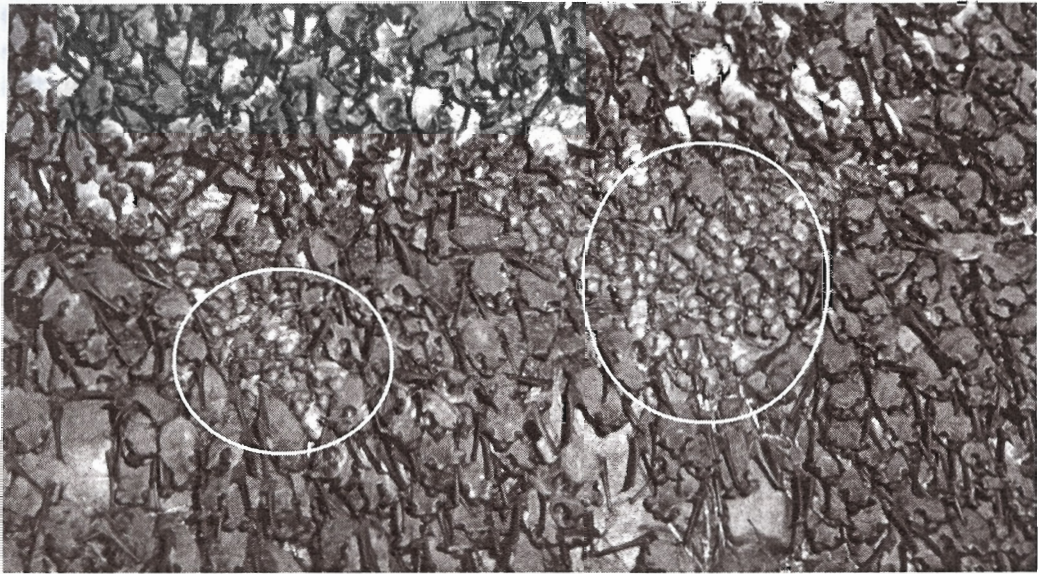
Fig. 11-2. Maternity cluster of *Tadarida brasiliensis* at Eckert James River Cave, Texas. Females suckle their own young, and when finished, they move away. The circled areas show spatially separated pups and adults. Photo by Thomas H. Kunz.

opportunities for reciprocity are high (Wilkinson, 1992). Evidence for indiscriminant communal nursing in free-ranging species, as postulated for the Brazilian free-tailed bat (*T. brasiliensis*) by Davis *et al.*, (1962), has been refuted based on behavioral and genetic analysis (McCracken, 1994). However, non-offspring nursing has been reported in some captive situations, especially following the death of a mother (Eales *et al.*, 1988). Communal nursing has been observed in common vampire bats (*Desmodus rotundus*) in both captive and free-ranging situations (Wilkinson, 1988).

MILK COMPOSITION

In cases where mother bats abandon their young or do not produce sufficient milk, it may become necessary to hand rear pups to ensure their survival. Formulas selected for hand rearing bat pups have generally been based on limited empirical data (Lollar and Schmidt-French, 1998). Many of these formulas have mimicked or been modified from human or cow's milk, which differ markedly from the composition of milk collected from both free-ranging and captive bats. As a consequence, nutritional deficiencies in hand-reared animals have been observed.

The proximate composition of milk has been examined in 18 species of bats (Kunz and Hood, 2000). Most early studies on milk composition of bats were based on small sample sizes and failed to consider the fact that milk composition may change over the course of lactation. The problem is also complicated by the small volumes of milk that can be collected from most lactating females, which often requires the pooling of samples for analysis (Kunz *et al.*, 1983). Lack of analytical methods for small sample volumes has made it nearly impossible to draw firm conclusions from the published literature (Korine and Arad, 1999; Kunz *et al.*, 1983, 1995b; Messer and Parry-Jones,

1997; Studier *et al.*, 1995). This and other biases in sampling have contributed to misleading conclusions about the milk composition of some species (Kunz *et al.*, 1995b).

More recent studies of milk composition and milk output of bats have been more informative, largely based on females captured at known stages of lactation, or assigned to different stages based on the age of an attached pup (Hood *et al.*, 2001; Hood, 2001; Kunz *et al.*, 1995b). New analytical methods now make it possible to measure the composition of milk from microliter quantities with high precision (W. R. Hood, unpubl.). Milk composition of bats from free-ranging or healthy captive populations can be used as models for comparison to other species under captive care. Notwithstanding, milk composition sampled from captive versus free-ranging bats may differ considerably. For example, milk collected from captive *Pteropus poliocephalus* contained almost one third less protein than milk collected from free-ranging animals (Messer and Parry-Jones, 1997).

Based on the data available to date, there is an apparent similarity between the macronutrient composition of a bat's diet and the composition of its milk. This relationship was first suggested by Huibregtse (1966) and corroborated by Kunz and Stern (1995). Although recent studies provide additional support for this hypothesis (Hood *et al.*, 2001; Korine and Arad, 1999; Stern *et al.*, 1997; Studier *et al.*, 1995), this generalization should be treated with caution, because the composition of milk is under endogenous control with the proximate components of milk synthesized within the mammary epithelia (Hood *et al.*, 2009). Milk macronutrients are not transferred directly from the intestinal lumen to the mammary ducts. Instead, this trend likely reflects similarly in diet within phylogenetic groups rather than the nutrient composition of the diet directly impacting milk composition. Most members of each family within the Chiroptera, with the exception of the family Phyllostomidae, have relatively similar, generalized dietary habits. When a milk replacer must be developed for a species with unknown milk composition, one should be able to mimic the proximate composition of a mother's milk by using published data from species of the same family with similar dietary habits (see Table 11-1). The authors recommend that multiple criteria be used, such as duration of parental care and body size-- factors that are broadly applicable, especially at the family level. The length of lactation (e.g., 1-month versus 6-month periods) should vary from high to low energy milk.

Among insectivorous vespertilionids (e.g., *Myotis lucifugus*, *M. velifer*, and *Eptesicus fuscus*) and molossids (*T. brasiliensis*), milk dry matter, fat, and energy content increased substantially from early to peak lactation. However, these trends were not statistically significant where sample sizes were relatively small (Kunz *et al.*, 1995b). Dry matter ranges from 22-25% in early lactation to 32-40% at peak lactation. Fat content of milk ranges from 9-17% in early lactation to 16-26% in late lactation, and the energy content of milk ranges from 5-17 kJ/g. Milk protein and carbohydrate content remains relatively constant throughout lactation and differs little between species, with protein content at 8-11% and carbohydrate content at 3.5-4.4% (Kunz and Hood 2000, Hood, 2001; Kunz *et al.*, 1995b).

Table 11-1. Proximate composition of bat milks

Unless otherwise noted, all values are expressed as percent composition (wet mass)

Species and lactation stage	Wild or Captive[a]	Diet[b]	Dry matter	Fat	Protein	Carbo-hydrate	Energy (kJ/g wet mass)[c]	Sample size[d]	Ref.[e]
Megachiroptera									
Pteropodidae									
Pteropus hypomelanus									
early	C	F	16.5	7.6	2.5	6.0	3.8	8-11	1
late			18.8	9.4	2.9	5.6	4.6	14-18	
Pteropus poliocephalus									
early	C	F	11.2	2.0	2.5	6.2	2.8	15	1
mid			10.8	1.7	2.4	6.3	2.3	31	
late			11.1	1.9	2.8	5.9	2.4	21	
early-mid	W	F	12.7	2.2	3.6	6.4	2.8	1-14	5
Pteropus pumilus									
early	C	F	17.2	8.1	2.7	5.7	4.2	13	1
late			21.9	9.7	2.9	6.2	5.0	6-9	
Pteropus rodricensis									
early	C	F	18.9	8.9	3.1	6.2	4.6	4-7	1
late			22.3	8.3	3.5	6.8	5.9	5-10	
Pteropus vampyrus									
early	C	F	16.2	6.3	3.1	5.8	3.3	16-17	1
late			17.4	7.9	2.6	5.5	4.6	7	
Rousettus aegyptiacus									
early	W	F	---	2.7	2.2	5.7	2.5	1(14)	3
mid			---	7.1	2.3	6.1	4.3	2(23)	
late			---	9.0	2.9	5.5	5.1	2, 6	
Microchiroptera									
Molossidae	W	I							
Tadarida brasiliensis									
early (1-21 d)			29.1	17.3	8.3	3.6	9.0	11(64)	4
peak (22-42 d)	C	F	36.5	25.8	7.7	3.4	12.1	21(71)	
Phyllostomidae									
Artibeus jamaicensis	W	F, I	17.8	9.0	3.6	6.1	5.3	21	6
Phyllostomus hastatus[f]									
early (10d)			19.7	9.1	7.8	4.0	5.9	31-32	7
mid (40d)			25.7	13.0	9.1	4.0	7.7		
late (70d)			31.7	16.9	9.7	4.0	9.5		
Vespertilionidae	W	I							
Eptesicus fuscus[f]									
early			27.3	12.8	9.5	3.6	6.7	36	2
peak	W	I	37.2	21.2	9.5	3.6	10.5		
Myotis lucifugus									
early			26.5	12.4	9.5	3.9	7.4	4(60)	4
peak	W	I	27.1	15.8	8.5	4.0	8.6	3(42)	
Myotis velifer									
early			25.4	11.6	9.2	4.0	7.1	3(28)	4
peak			32.4	19.9	10.7	4.4	10.6	3(11)	

Note: Compositions at early, mid, late and/or peak lactation are given when trends across lactation were significant.

[a] Indicates whether bats were wild caught (W) or in captivity (C) prior to milking.

[b] Indicates typical diet of species. Diets include insects (I) and fruit (F).

[c] Energy content calculated from the energy equivalents of fat (kJ/g), protein (kJ/g), and carbohydrate (kJ/g). In some cases these values were presented by the authors in kcal/g. Values are converted to kJ/g wet mass to facilitate comparison with other studies.

[d] Samples from individual bats were pooled for analysis. Values in parentheses are number of bats milked, if different from sample size. All analyses were not performed for some samples. In this case, sample size is presented as a range.

[e] References: 1) Hood *et al.*, 2001; 2) Hood, 2001; 3) Korine and Arad, 1999; 4) Kunz *et al.*, 1983; Kunz *et al.*, 1995b; 5) Messer and Parry-Jones, 1997; 6) Oftedal and Iverson, 1995; 7) Stern *et al.*, 1997.

[f] Composition at each stage of lactation is predicted from given regression equations.

In frugivorous pteropodids, including 5 species of *Pteropus, Epomophorus wahlbergi,* and *Rousettus aegyptiacus*, milk composition varied markedly among samples, and these differences generally did not contribute to significant trends across lactation (Hood *et al.*, 2001). Composition of bat milks (wet mass) ranged from 10.8-20.1% (dry matter), 1.7-10.2% (fat), 2.3-3.6% (protein), 5.7-6.4% (carbohydrate), and energy content ranged from 2.3-4.5 kJ/g. Significant changes in milk composition were observed from early to peak lactation in *P. pumilus* with an increase in dry matter and energy content (Hood *et al.*, 2001). An increase in energy and fat over the course of lactation was observed in *R. aegyptiacus* (Korine and Arad, 1999), whereas only fat content increased in *P. hypomelanus* during this period (Hood *et al.*, 2001). By contrast, a significant decrease in protein and carbohydrate was observed throughout lactation in *P. poliocephalus* (Messer and Parry-Jones, 1997).

Few studies have thoroughly examined milk composition in the Phyllostomidae. The most comprehensive studies include an omnivorous species, *Phyllostomus hastatus* (Stern *et al.*, 1997) and a frugivorous species, *Artibeus jamaicensis* (Oftedal and Iverson, 1995). The composition of milk in *P. hastatus* is similar to that of insectivorous vespertilionids, both in overall proximate (fat, protein, carbohydrate, dry matter) composition and trends in milk composition across lactation. Protein and carbohydrates appear to remain relatively constant. The milk composition at peak lactation in plant-visiting *A. jamaicensis* is nearly identical to the composition of milk in plant-visiting pteropodids (Hood *et al.*, 2001).

Several additional factors may contribute to within or between species variation in milk composition. Studies where milk samples have been analyzed individually suggest that the fat, dry matter and energy content can be highly variable, as in *Pteropus* spp. (Hood *et al.*, 2001) and *E. fuscus* (Hood, 2001). This variation may be influenced by several factors, including body condition, time of milk collection, and degree of gland evacuation (reviewed in Hood *et al.*, 2001). In a free-ranging population of another Old World plant-visiting species, *R. aegyptiacus*, time of day influenced milk composition, with dry matter of milk increasing significantly from morning until afternoon during late lactation (Korine and Arad, 1999).

Ben Shaul (1962) postulated that mammal species with frequent suckling schedules produce less concentrated milk than those that suckle their young infrequently. However, results from bats and other mammals do not consistently support this hypothesis (Hood *et al.*, 2001). Kunz *et al.* (1995b) suggested that the higher energy content of *T. brasiliensis* milk may be associated with pups suckling periodically during the day and night (McCracken and Gustin, 1991); whereas, female *Myotis velifer* and *M. lucifugus* produced less concentrated milk and allowed their pups to remain attached to their mothers teat throughout the day and suckle without restriction (Kunz *et al.*, 1995b). Recent studies on *E. fuscus* also suggest that pups suckle at leisure (Hood, 2001), but have milk energy and fat content similar to that of *T. brasiliensis*. A comparison of milk composition in four megachiropteran species (*P. hypomelanus, P. vampyrus, P. pumilus,* and *P. rodricensis*) found that the composition did not differ among these closely related species, despite a 6.5-fold difference in body size. These latter results fail to support Blaxer's (1961) hypothesis that the energy

requirements of lactation scale negatively with body mass, and although volume produced likely differs, total energy transfer should follow.

Mineral composition of milk has been examined in 12 species of Chiroptera, but even fewer studies have considered changes in mineral concentration throughout lactation (Table 11-2). Only half of these studies were based on sufficiently large sample sizes or known day of lactation to evaluate changes in mineral concentration over the course of lactation. Calcium content of bat milks, from these limited studies, ranged from 3.2 to 12.5 mg/g dry mass (DM) and magnesium content ranged from 0.25 to 1.2 mg/g DM. Concentration of calcium and magnesium decreased during lactation in *T. brasiliensis* (Studier and Kunz 1995), and *P. hastatus* (Stern *et al.*, 1997), but was not observed in other species. Concentrations of sodium and potassium varied substantially, with sodium content negligible to 9.9 mg/g DM and potassium 3.2 to 15 mg/g DM. Significant declines in sodium were found during lactation for *T. brasiliensis* (Studier and Kunz, 1995) and *A. jamaicensus* (Kwiecinski *et al.*, 2003), although no changes in potassium were reported. Iron and potassium concentrations have been less frequently noted. Several studies have suggested that calcium intake may be a limited nutrient for lactating females (Hood, 2001; Keeler and Studier, 1992; Kwiecinski *et al.*, 1987; Studier *et al.*, 1991). Thus, special consideration should be

Table 11-2. Mineral composition of bat milks
All mineral values expressed as mg/g dry matter

Species	Wild or Captive[a]	Diet[b]	Na$^+$	K$^+$	Ca^{2+}	Mg^{2+}	Fe	P	Sample size	Ref[c]
Megachiroptera										
Pteropodidae										
Pteropus hypomelanus	C	F	---	6.2	8.3	0.6	---	6.4	19	1
Pteropus vampyrus	C	F	---	5.3	7.6	1.2	---	7.3	13	1
Microchiroptera										
Molossidae										
Tadarida brasiliensis[d]										
early (10d)	W	I	1.6	3.5	6.8	0.57	0.13	---	56	5
peak (30d)			0	3.5	4.0	0.22	0.13	---		
Phyllostomidae										
Artibeus jamaicensis[d]										
early (10d)	C	F	3.0	15	3.2	1.3	0.33	---	64	3
peak (60d)			1.5	15	3.2	1.3	0.33	---		
Phyllostomus discolor[d]	C	F, I	3.0	9.3	3.3	1.0	0.18	---	40	3
Phyllostomus hastatus[d]										
early (10d)	W	F, I	9.9	5.4	12.5	0.85	0.23	---	23	4
mid (40d)			9.9	5.4	9.5	0.55	0.23	---		
late (70d)			9.9	5.4	5.9	0.25	0.23	---		
Vespertilionidae										
Eptesicus fuscus	W	I	---	6.2	8.8	1.2	---	---	5 (49)	2

Note: Composition at early, mid, late and/or peak lactation are given when trends across lactation were significant.

[a] Indicates whether bats were wild caught (W) or in captivity (C) prior to milking.

[b] Indicates typical diet of species. Diets include insects (I) and fruit (F).

[c] References: 1) Hood *et al.*, 2001; 2) Kunz and Hood, 2000; 3) Kwiecinski *et al.*, 2003; 4) Stern *et al.*, 1997; 5) Studier and Kunz, 1995.

[d] Composition at each stage of lactation is predicted from given regression equations. The dry matter content of the milk was estimated from the regression equation given by Kunz *et al.*, 1995.

given to providing reproductively active females with sufficient calcium, especially when they are nursing pups.

POSTNATAL GROWTH

Assessing postnatal growth of bats provides an indirect measure of a female's reproductive effort and can be valuable in captive situations for evaluating the relative health of pups. Low rates of postnatal growth may indicate that the mother is not producing sufficient milk or the young is not sucking successfully. To date, postnatal growth has been described for at least 62 species of bats (Cheng and Lee, 2002; Elangovan *et al.*, 2002; Hood *et al.*, 2002; Kunz and Hood, 2000; Rajan and Marimuthu, 1999; Swift, 2001); over half of these (n = 26) were based on captive animals. Among the 11 species of megachiroperans for which postnatal growth data are available, all but one study (*R. aegyptiacus*; Rajan and Marimuthu, 1999) was based on studies conducted in captivity. By contrast, among the 32 species of microchiroperans, 14 were based on captive animals (Kunz and Hood, 2000). The data summarized in Table 11-3 include those studies where body mass and/or length of forearm were measured repeatedly and sample sizes were sufficient to accurately and reliably describe rates of postnatal growth. Data summarized in this table include body mass and length of forearm at birth and adult size, as well as the daily rate of growth. These rates of growth may slow markedly, once an asymptote is reached at >65% adult body mass and >90% adult length of forearm.

Postnatal growth rates based on measurements from captive bats can be valuable for assessing responses to housing conditions (e.g., space and temperature) and health of the mother. Caution is advised when trying to generalize growth patterns if only a few animals are available or infrequent measurements are taken. Anomalous growth rates of pups may occur if mothers are overfed or underfed, pups are hand reared using questionable milk replacers, or inadequate housing fail to provide adequate flight space or suitable roost temperatures. Where postnatal growth patterns of captive versus free-ranging bats have been compared (Kunz, 1987; Kunz and Stern, 1995), growth trajectories are often more rapid, and the age at which growth rates reach an asymptote are often greater in captive animals (but see Elangovan *et al.*, 2002). More rapid growth rates in captive bats may, in part, reflect a greater nutritional plane for bats housed in captivity (Kunz and Hood, 2000), although there are exceptions when captive bats are undernourished (inappropriate diets), become physiologically challenged (response to low ambient temperatures), have little or no opportunity for exercise (lack of flight space), or become socially stressed (lack of opportunity for gregarious species to form clusters or solitary species to roost apart from others).

Postnatal growth rates of free-ranging bats may be affected by the availability of food, weather conditions (Hoying and Kunz, 1998), litter size (Koehler and Barclay, 2000), colony size, and social conditions (Tuttle, 1975, 1976). Temperature, rainfall, and food availability influenced the postnatal growth rates in *Perimyotis subflavus* (Hoying and Kunz, 1998) and *E. fuscus* (Hood *et al.*, 2002). In free-ranging conditions, cooler than normal temperatures are known to decrease the availability of insects and

Table 11-3. Body mass and length of forearm at birth, adult size and rates of postnatal growth in bats

Taxa	Wild or Captive[a]	Litter Size	Weaning (d)	Body Mass[b] Birth (g)	Adult (g)	Rate (g/d)	Sample size[c]	Length of Forearm[b] Birth (mm)	Adult (mm)	Rate (mm)	Sample size[c]	Reference
Megachiroptera												
Pteropodidae												
Cynopterus brachyotis	C	1.0	---	---	36.4	0.04	12 (81)	---	66.1d	0.06	12 (81)	Kunz and Hood, 2000
Epomophorus wahlbergi	C	1.0	81.1	16.1	129.6	---	---	30.9	---	0.03 M 0.04 F	(13) M (16) F	Sowler, 1983
Hypsignathus monstrosus	C	1.0	---	40.0	420.0 M 234.0 F	0.01 M 0.52 F	(8) M (17) F	---	134.0 M 120.0 F	0.03 M 0.01 F	(15) M (8) F	Bradbury, 1977
Pteropus hypomelanus	C	1.0	---	74.0	570.7	0.01	(417)	62.0	157.4	0.02	(419)	Kunz and Hood, 2000
Pteropus poliocephalus	C	1.0	---	76.0	639.5	0.02	1 (18)	---	149.1	0.03	1 (17)	Kunz and Hood, 2000
Pteropus pumilus	C	1.0	---	40.6	174.8	0.02	(95)	44.9	152.2	0.03	(102)	Kunz and Hood, 2000
Pteropus rodricensis	C	1.0	---	39.2	264.7	0.01	(166)	51.9	124.4	0.03	(180)	Kunz and Hood, 2000
Pteropus scapulatus	C	1.0	---	---	362.0	0.02	6 (81)	---	161.0	0.02	6 (69)	G. M. O'Brien, pers. comm.
Pteropus vampyrus	C	1.0	---	133.3	1132.6	0.02	(273)	79.5	224.7	0.03	(269)	Kunz and Hood, 2000
Microchiroptera												
Emballonuridae												
Peropteryx kappleri	W	1.0	---	1.5	12.8d	0.08	2 (18)	20.0	48.0d	0.07	2 (18)	Giral et al., 1990
Molossidae												
Molossus molossus	C	1.0	65	3.6d	15.1	0.08	14 (140)	17.0	38.1	0.05	15 (319)	Häussler et al., 1981
Tadarida brasiliensis	W	1.0	---	3.2	12.0d	0.17	49 (161)	18.5	43.0d	0.09	49 (161)	Kunz and Robson, 1995
Noctilionidae												
Noctilio albiventris	V	1.0	80.5	---	37.7d	0.06	20 (290)	---	65.0d	0.07	20 (293)	Brown et al., 1983
Phyllostomidae												
Artibeus jamaicensis	C	1.0	66.3	13.9	45.0d	0.04	22 (97)*	33.5	60.5	0.08	22 (96)	Taft and Handley, 1991
Carollia perspicillata	C	1.0	23.0	5.0	17.6	0.10	717 (21)*	24.2	43.6d	0.01	17 (21)*	Kleiman and Davis, 1979
Desmodus rotundus	C	1.0	285.0	7.0d	29.0d	0.01	4 (179)	---	59.0d	---	---	Schmidt and Manske, 1973
Phyllostomus discolor	C	1.0	---	7.0d	39.7d	0.05	6 (108)	---	62.4d	0.01	6 (108)	Rother and Schmidt, 1985
Phyllostomus hastatus	W	1.0	---	16.4	84.0d	0.06 M 0.06 F	21(197)M 18(168)F	34.4	81.9	0.07 M 0.07 F	20(172)M 18(200)F	Stern and Kunz, 1998
Rhinolophidae												
Rhinolophus ferrumequinum	C	1.0	60.0d	5.8d	22.9d	0.13	---	---	58.7d	---	---	Ransome et al., unpubl.
Vespertilionidae												
Antrozous pallidus	C	1.8	---	3.1d	18.8d	0.96	(377)	---	54.5d	0.10	(417)	Brown, 1976
Eptesicus fuscus	W	2.0	36.0d	3.5d	20.2d	0.14	(256)	---	45.2d	0.13	(254)	Hood, 2001
Eptesicus serotinus	C	1.5	24.0	5.8	23.5d	0.04	3 (28)*	---	53.0d	0.14	4 (22)*	Kleiman, 1969
Myotis lucifugus	W	1.0	25.0d	2.2	7.3d	0.22	(75)	---	37.6d	0.12	---	Maeda, 1976
Myotis macrodactylus	W	1.0	---	1.5d	7.1d	---	---	15.8	36.4d	0.27	(65)	Kunz and Anthony, 1982

continued

Table 11-3. continued

Taxa	Wild or Captive[a]	Litter Size	Weaning (d)	Body Mass[b] Birth (g)	Adult (g)	Rate (g/d)	Sample size[c]	Length of Forearm[b] Birth (mm)	Adult (mm)	Rate (mm)	Sample size[c]	Reference
Myotis myotis	W	1.0	31.5	6.2	24.9	0.09	53 (45)	23.7	63.7	0.15	53 (61)*	DePaz, 1986
Myotis thysanodes	W	1.0	21.0	---	8.0[d]	---	---	---	---	0.13	---	O'Farrell and Studier, 1973
Myotis velifer	W	1.0	43.0[d]	3.2[d]	8.9[d]	0.17	(280)	---	39.6[d]	0.12	(280)	Kunz and Robson, unpubl.
Nyctalus lasiopterus	C	1.7	---	5.3[d]	58.5[d]	0.12	(205)	22.1	62.0	0.14	5 (201)	Maeda, 1972
Nyctalus noctula	C	1.7	60.0	5.7	20.4	0.12	10 (30)	---	51.0[d]	0.11	10 (27)*	Kleiman, 1969
Nycticeus humeralis	C	2.1	30.0	2.0	10.2[d]	0.06	(63)	---	36.7[d]	0.09	28 (162)	Jones, 1967
Plecotus auritus	C	1.4	42.3	---	7.1[d]	0.25		---	38.0[d]	0.19	20 (109)	DeFanis and Jones, 1995
Pipistrellus mimus	W	2.0	52.0	0.5[d]	2.0[d]	0.11	20 (92)	---	27.0[d]	0.12	14-36(13)*	Isaac and Marimuthu, 1996
Pipistrellus pipistrellus	W	2.0	51.0	1.1	5.1	0.04	14-36(13)*	---	31.4[d]	0.12	(118)	Rakhmatulina, 1972
Pipistrellus savii	W	1.8	---	---	4.0[d]	0.19	(113)	---	---	0.16	50 (401)	Tiunov, 1992
Pipistrellus subflavus	W	2.0	---	1.6	6.4	0.13	50 (383)	13.2	34.9	0.15	20 (109)	Hoying and Kunz, 1998
Vespertilio murinus	C	2.0	28-36	---	---	---	---	14.8	45.1	0.17	8	Kozhurina, 1998
Vespertilio superans	W	2.0	35.0[d]	2.0[d]	18.4[d]	0.11	(64)	---	---	0.10	(71)	Tiunov, 1989

Note: Only those studies where the exact age of pups is known are included (adapted from Kunz and Hood, 2000).

[a] Indicates whether bats were wild caught (W) or in captivity (C) prior to milking.

[b] Mass and forearm measurements differentiated as male (M) and female (F) for sexually dimorphic species.

[c] Number of individuals (number of data points on which growth curve is based is given in parentheses; * published data represent means for each given age).

[d] Virginia Hayssen, pers. comm.

hence depress postnatal growth rates. As observed in free-ranging bats, prolonged periods of low ambient temperatures in captivity may lead to torpor in lactating females and thus reduce the amount of milk produced and hence available to suckling pups (Wilde *et al.*, 1999). Low cave temperatures and small colony size appeared to reduce the early postnatal growth and development of young *Myotis grisescens*, thus increasing energy demands on their mothers (Tuttle, 1975). Reduced postnatal growth rates and survival of newly volant, young *M. grisescens* may also reflect distances from maternity roosts that individuals must commute to reach productive foraging areas (Tuttle, 1976); although, this condition would not be relevant to captive bats.

Among the 33 species of bats in which postnatal growth rates were analyzed allometrically (Kunz and Stern, 1995), a significant negative correlation was found between postnatal growth rates and body mass, with the large pteropodids gaining as little as 0.01 g/d in body mass and forearm length increasing as little as 0.02 mm/d. By contrast, small vespertilionids may gain as much as 0.35 g/d in body mass, and length of forearm may increase by as much as 0.27 mm/d. Tropical species have the slowest postnatal growth rates among the bat species that have been analyzed. When the effects of diet, phylogeny, growth condition, and basal metabolic rate were removed from the analysis, climate was the only significant variable that affected postnatal growth rates (Kunz and Stern, 1995). These results suggest that tropical bat species have lower postnatal growth rate than those from temperate regions (Kunz and Stern, 1995; Kunz *et al.*, 2009). *D. rotundus* has the slowest growth rate of all tropical species, although this may largely reflect an exclusive diet of whole blood. Faster postnatal growth rates observed in temperate species may reflect selection for reduced time for growth in environments that are strongly affected by relatively cool and unpredictable summer temperatures. Presumably, bats from temperate regions also have evolved faster postnatal growth rates in response to selection pressures imposed by migration and hibernation (Kunz and Stern, 1995; Kunz *et al.*, 2009). Variation in the diets of insectivorous species may also account for observed differences in postnatal growth rates among different species (Kunz and Stern, 1995; Kunz *et al.*, 2009).

Recording and maintaining records of postnatal growth rates for captive young can provide valuable information needed to assess the condition of mothers and their pups. The effects of maternal condition on the size of pups and birth was reported for free-ranging populations of *P. hastatus*, with larger mothers giving birth to larger pups (Stern and Kunz, 1998). However, maternal effects on postnatal growth and development of young bats appear to be minimal in free-ranging populations of other species. In most situations, the condition of both pregnant and lactating females and pups should be monitored in captivity based on the uncertainty of dietary effects alone. Recommendations for developing postnatal growth curves are reviewed elsewhere (Kunz and Stern, 1995; Kunz and Hood, 2000; Kunz *et al.*, 2009). The most accurate method used for accessing rates of postnatal growth result from marking young animals shortly after birth and recording changes in body mass and wing dimensions on a regular basis (Baptista *et al.*, 2000). Caution is advised when assessing postnatal growth rates of free-ranging bats using date as the independent variable (e.g., Thomas and Marshall, 1984), as this approach can significantly bias postnatal growth

trajectories (see Baptista *et al.*, 2000). However, in captivity, when recording changes in body mass or linear measurements of known individuals, date of measurement can be converted to actual days. In free-ranging populations, when it is not practical to mark a sufficient number of newborn bats, growth curves can be quantified by evaluating the early linear segments of postnatal growth (Hood *et al.*, 2002).

CONCLUSIONS

Although steady progress has been made to characterize milk composition and patterns of postnatal growth in both free-ranging and captive bats, additional observations are needed to quantify milk composition and postnatal growth rates for species that are maintained in captivity. Ideally, bats hand reared in captivity should be fed milk replacers that reflect what is known from empirical studies on bat milk derived from free-ranging or captive bats, both in proximate composition and mineral content. To assist in calculating the nutrient content of milk replacers, an online nutritional calculator is available at http://www.ewildagain.org/Nutrition/calculatorlink.htm (see also Chapter 12). In addition, growth rates of pups should be monitored as an indication of relative condition so that necessary adjustments can be made to ensure their health and survival.

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BATS
IN CAPTIVITY

Volume 2: Aspects of Rehabilitation

edited by

Susan M. Barnard

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Front cover photo: Infant variable flying fox (*Pteropus hypomelanus*); photo © Dana LeBlanc, Lubee Bat Conservancy.
Back cover photo: Red bat (*Lasiurus borealis*) with radio tracking device; photo courtesy of NCRS, USDA Forest Service.