14

Methods for Assessing Size at Birth and Postnatal Growth and Development in Bats

THOMAS H. KUNZ
RICK A. ADAMS
WENDY R. HOOD

SIZE AT BIRTH AND POSTNATAL growth and development are important life-history traits (Case, 1978; Ricklefs, 1979; Ernest, 2003) because they reflect major components of parental effort (Millar, 1977; Oftedal, 1984; Kirkwood, 1985; Costa et al., 1986; Gittleman and Oftedal, 1987; Oftedal and Gittleman, 1988; Harvey and Read, 1988; Read and Harvey, 1989; Promislow and Harvey, 1990; Ernest, 2003). Although analyses of these and other traits have become increasingly incorporated into life-history analyses of bats (Kurta and Kunz, 1987; Kunz and Stern, 1995; Hayssen and Kunz, 1996; Kunz and Hood, 2000; Barclay and Harder, 2003), they have seldom been included in life-history analyses of other mammals (e.g., Millar, 1981; Western and Ssemakula, 1982; Martin, 1984; Martin and McLarnon, 1985; Wootton, 1987; Harvey and Read, 1988; Read and Harvey, 1989; Promislow and Harvey, 1990; Sterns, 1992; Ernest, 2003; Rolf, 2003; Charnov and Morgan, 2006; Bielby et al., 2007). Except for Kurta and Kunz (1987), Kunz and Stern (1995), Hayssen and Kunz (1996), Kunz and Hood (2000), and Barclay and Harder (2003), size at birth and postnatal growth in bats have seldom been considered in an ecological, evolutionary, or life-history context.

Despite the various published summaries of size at birth (Kleiman and Davis, 1979; Tuttle and Stevenson, 1982; Kurta and Kunz, 1987; Hayssen and Kunz, 1996; Kunz and Hood, 2000; Barclay and Harder, 2003) and postnatal growth in bats (Orr, 1970; Kleiman and Davis, 1979; Tuttle and Stevenson, 1982; Kunz and Stern, 1995, Kunz and Hood, 2000), few studies have considered intrinsic and extrinsic factors that could influence variation in these traits. In this chapter, we provide an overview of studies on size and developmental state at birth (Fig. 14.1A) and postnatal growth and development (Fig. 14.1B), review methods for assessing these traits, identify research needs, propose hypotheses, and suggest directions for future study.

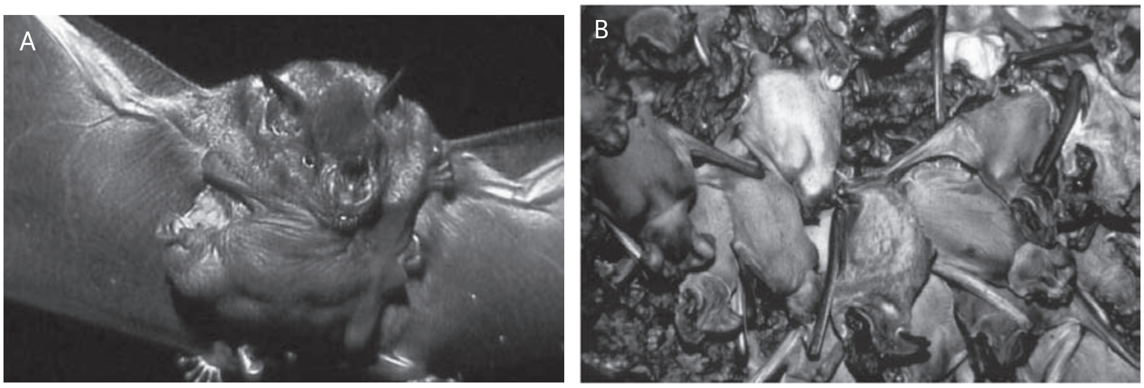

Figure 14.1. Bat pups. A, newborn *Artibeuus jamaicensis* attached to its mother. This and many other species of the family Phyllostomidae have well developed pelage at birth. B, maternity roost of *Tadarida brasiliensis*, showing several pups and one mother nursing a pup. *Tadarida* pups are born hairless and remain naked for approximately the first three weeks of life. *Photos by Peter V. August*.

SIZE AT BIRTH AND WEANING

One of the most striking life history traits of bats is the fact that single young are born at a relatively large size, ranging from 11% to 43% of their mother's body mass, with a mean of 23% (Kurta and Kunz, 1987; Barclay and Herder, 2003). These observations contrast with an average relative size at birth of 7.8% for terrestrial mammals (Kurta and Kunz, 1987). Another quite remarkable life history train in bats is that females typically suckle their young until they are nearly adult size (Kunz, 1987). On average, young bats are weaned at approximately 70.9±15.7% of adult body mass and 91.2±5.9% of adult length of forearm (Barclay, 1994). By contrast, young of terrestrial mammals are usually weaned at approximately 37% (range, 11–73%) of adult mass (Millar, 1977).

In Kurta and Kunz's (1987) analysis of the Chiroptera, body mass at birth, expressed as a percent of maternal mass, was highest in the Rhiniolophidae (28.8%), and smallest in the Pteropodidae (17.5%). Members of the Vespertilionidae (21.1%) and Phyllostomidae (26.6%) were intermediate in position with respect to relative mass at birth (Kurta and Kunz, 1987). As with other mammals, the relative size of chiropteran offspring at birth decreases with increasing maternal body mass (Kurta and Kunz, 1987; Barclay and Harder, 2003). Thus, relatively large species have smaller offspring at birth than small species (Kurta and Kunz, 1987; Hayssen and Kunz, 1996; Barclay and Harder, 2003).

Among bats, species that produce singletons produce young that average 23% of maternal mass, whereas pups from litters of two average about 17.7% of their mother's mass (Kurta and Kunz, 1987). Female bats that produce twins have litter masses that average about 35% of maternal mass. In their allometric analysis of litter mass and body mass in the mammals, Kurta and Kunz (1987) found no significant difference between litter mass and body mass in bats and other mammals, suggesting that litter mass is more influenced by foraging habits, diet, seasonal energetics, and mode of flight.

When litter masses of terrestrial mammals (25.3%) are compared to those of bats (26.2%), no significant differences have been detected (Kurta and Kunz, 1987; Barclay and Harder, 2003). However, Hayssen and Kunz (1996) found that litter mass in bats was strongly associated with wing loading. Their allometric analysis of 314 species from seven families revealed that the largest wing loadings are found among the microchiropterans, and the smallest occur among the megachiropterans. Molossids have the highest wing loadings and smallest litter masses, whereas rhinolophids have the lowest wing loadings and largest litter masses.

A reoccurring question has been whether offspring size and litter mass in bats is constrained by flight. Kunz and Kurta (1987) tested this hypothesis, and found that, when scaled to body mass, female bats produced litter masses comparable to other terrestrial mammals. When Barclay and Harder (2003) compared the relative size of litter masses in shrews and bats, they too found no significant difference, supporting the null hypothesis that litter mass of bats was not constrained by flight. However, in contrast to the findings of Hayssen and Kunz (1996) of no significant difference among bats and terrestrial mammals, Barclay and Harder (2003) found marginally significant effects of wing loading on litter mass. After accounting for variation associated with log (female) mass, litter size, and taxonomic affiliation, Barclay and Harder (2003) also concluded that relative to small species, larger species produced heavier litters. Bat species that produced singleton pups produced litters of higher relative mass than those that produced two young. They further concluded that wing loading had a limited affect on liter mass. While both Kurta and Kunz (1987) and Hayssen and Kunz (1996) reported that pteropodids produced litters that weighed less than other bat taxa, Barclay and Harder (2003) argued that Kunz and Hayssen's (1996) hypothesis of the effects of wing loading on litter mass failed to explain litter mass because it did not consider variation in flight requirements. They argued that natural selection should produce females with the same ability to carry additional mass independent of wing loading when they are not pregnant. In situations in which reverse sexual dimorphism has been described for bats (Myers, 1978; Williams and Findley, 1979), species with the largest litters also have the greatest size differences among the adult sexes. Barclay and Harder (2003) found that in species with reversed sexual dimorphism, females have larger wing areas than males.

Because bats wean their young at a larger size than most other mammals, each pup should be expensive to rear (Kunz, 1987; Kurta and Kunz, 1987; Barclay, 1994, 1995). Barclay and Harder (2003) suggested that the high cost of producing an offspring selects for a small, relatively invariable litter size in bats. They further suggested that the availability of calcium, rather than energy, might be the limiting factor affecting reproductive output (i.e., litter size) in bats. Moreover, they postulated that the evolution of polyovulation in bats was an important selective pressure that led to the observed dichotomy in birth mass among families (most notably distinguishing the vespertilionids and antrozoids from other taxa). This hypothesis is supported by the observation that the offspring of vespertilionids, in particular, have significantly smaller offspring at birth than observed in other families, and that offspring of the large-bodied pteropodids represent a smaller proportion of female mass than that of small-bodied species. This conclusion is consistent with the findings of Kurta and Kunz (1987) that as body mass of females increases, the relative size of offspring decreases.

When considered together, developmental conditions characteristic of bats can place enormous nutritional constraints on mothers, not only the need to transport a large litter mass during late pregnancy, but also to suckle their young well beyond the postnatal period that has been observed in most terrestrial mammals. Like primates and marsupials, bats have lactation periods that are 50% longer than mammals of similar body mass (Hayssen, 1993). This prolonged mother-infant association can potentially reduce valuable nutrient reserves in females (Barclay, 1994). At the same time, a relatively long association between mother and offspring also provides extended opportunities for young to develop social, foraging, and other skills from their mothers, and one could predict that these skills contribute to improvements in survival and thus increased individual and inclusive fitness. Thus, offspring size and litter size in bats is not likely to be constrained by cost of flight and the energy needed to support this activity, but rather by a combination of natal, postnatal, and postfledging demands placed upon mothers that reflect different mortality risks and the amount of time available for their offspring to attain adult size before they must migrate, hibernate, or again become reproductively active (Barclay and Harder, 2003).

Large birth size in mammals is generally associated with an advanced stage of physical development. For example, precocial mammals (e.g., ungulates) are typically larger and more developed at birth than altricial species (e.g., primates, carnivores). Although bats may be relatively large at birth and from the perspective of body size could be considered precocial, by most other criteria, neonatal bats are considered to be altricial (Kurta and Kunz, 1987). Apart from being born in an overall altricial state, bats appear to have evolved a relatively advanced neuromuscular system, especially in the hind limbs, which allows pups to cling tenaciously to their mothers or to a roost substrate shortly after birth (e.g., Kleiman and Davis, 1979; Kurta and Kunz, 1987; Hermanson and Wilkins, 1996; Adams and Thibault, 2000), and relatively advanced acoustic and olfactory senses that make it possible for pups to identify their mothers shortly after being born (e.g., Nelson, 1965; Gould, 1971; Schmidt, 1972; Vaughan and O'Shea, 1976; McCracken and Gustin, 1991; De Fanis and Jones, 1996; Jones, 2000). But despite their relatively large size at birth, relatively advanced olfactory and acoustic systems, and relatively well-developed hind limbs, newborn bats are for the most part functionally altricial based on their nearly complete absence of hair (in many species), inability to thermoregulate, poorly developed echolocation system, and poorly developed wing bones and flight musculature (Kunz and Pierson, 1994; Papadimitriou et al., 1996; Adams, 2000; Hermanson, 2000; Pederson, 2000; Vater, 2000).

The relatively longer postnatal period of dependency in bats can, in part, be explained by the fact that young bats cannot fly until they have nearly achieved adult size, and as a consequence, this means that females must nurse their babies until such time as they develop their wings and wing musculature and their sensory abilities (e.g., echolocation in microchiropterans) so that they can fly and feed independently of their mothers (Kunz, 1987; Barclay, 1994).

POSTNATAL GROWTH AND DEVELOPMENT

Among the 18 families and approximately 1,116 currently recognized species of bats (Simmons, 2005), studies on postnatal growth and development have been conducted on at least 60 species and 9 families, representing approximately 5% of the total number of species that have been described (Appendix 14.1). In the first comprehensive review of postnatal growth and development of bats, Orr (1970) summarized what was known at the time based on members of two families (Vespertilionidae and Molossidae). Nearly a decade later, Case (1978) conducted an allometric analysis of postnatal growth rates in terrestrial vertebrates and included 17 bat species, still representing the same two families. Case limited his analysis to the linear portion of the postnatal growth curve and overlooked potential confounding effects of body size in his analysis. Based on the available data, Case concluded that bats had intermediate growth rates when compared to other mammals. Tuttle and Stevenson (1982) summarized data on postnatal growth rates (length of forearm and body mass) for 24 species, representing five families. They concluded that successful pre- and postflight development was influenced by roost temperatures and the relative feeding success of nursing females (Tuttle, 1975, 1976). Kunz (1987) reviewed data on postnatal growth and energetics of suckling bats, discussed advantages and limitations of studying growth and development of free-ranging and captive bats, briefly reviewed methods for the study of postnatal growth and development, and discussed both intrinsic and extrinsic factors that may affect observed patterns. He suggested that growth and development of bats were mostly influenced by litter size, age of mother, milk output of mothers, and roost temperatures.

Kunz and Stern (1995) conducted an allometric analysis of postnatal growth in bats based on 33 species representing seven families. Their analyses suggested that food supply, climate, habitat, maternal factors, and the social environment of bats were the most likely factors that affected postnatal growth and development. Kunz and Hood (2000) evaluated interspecific and intraspecific patterns of postnatal growth in bats based on an analysis of 42 species, representing seven families, summarized data derived from a logistic growth model, and further considered intrinsic and extrinsic factors judged to be important selective forces that could influence observed growth patterns. Several chapters in Adams and Pederson (2000) included reviews of morphological and behavioral development of bats during the postnatal period, focusing mostly on the cranium, dentition, limb structure, ontogeny of flight, and foraging, and social behavior. Barclay and Harder (2003) reviewed life history traits of bats, and concluded that they fall along a fast to slow continuum, especially with respect to postnatal growth and development.

Since the most recent review of postnatal growth and development of bats (Kunz and Hood, 2000), several other studies have been published, including Rajan and Marimuthu (1999), Reynolds (1999), Koehler and Barclay, 2000; Swift, (2001), Elangovan et al. (2002), Hood et al. (2002), Cheng and Lee (2002); Reiter (2004); Sharifi (2004a, 2004b), Priya (2005), Krochmal and Sparks (2007). All told, these published studies include 14 megachiropterans and 49 microchiropterans (Appendix 14.1). Among the 87 different studies, 54 (ca. 58%) were conducted on natural populations, and 37 (ca. 42%) were based on captive animals. Of the 16 studies on postnatal growth of megachiropterans, only five have been based on free-ranging bat species: Krishna and Dominic, 1983 (*Cynopterus sphinx*); Sowler, 1983 (*Epomophorus wahlbergi*); Thomas and Marshall, 1984 (*E. gambianus*); Thomas and Marshall, 1984 (*Epomops buettikoferi*); and Thomas and Marshall, 1984, 1999 (*Micropteropus pusillus*). Appendix 14.1 does not include studies conducted specifically on postnatal changes in wing morphology, pelage, body composition, dentition, ontogeny of flight, echolocation, communication, or foraging behavior, although various authors may have used growth curves derived from their respective studies to provide additional insight into age-specific development in these and other traits.

Intrinsic and Extrinsic Factors

When conducting studies on postnatal growth and development, it is important to consider the effects of both intrinsic and extrinsic factors. In their analysis of 33 bat species, Kunz and Stern (1995), found a significant negative correlation between postnatal growth rates and body mass of adults (i.e., larger species had slower growth rates than smaller species; Fig. 14.2). Temperate species appear to grow faster than tropical species (Fig. 14.3A), however, and insectivorous species in temperate regions appear to grow faster than those in the tropics (Fig. 14.3B). Notwithstanding, these analyses found no significant effect of diet on postnatal growth rate when frugivorous and insectivorous species were compared (Fig. 14.4). Although not included in the allometric analysis, the common vampire bat (*Desmodus rotundus*) appears to have the slowest growth rates of all tropical species examined. Overall, these analyses suggested that tropical species have slower postnatal growth rates than those from temperate regions (Kunz and Stern, 1995). The faster postnatal growth rates observed in temperate species may reflect selection for reducing the amount of time needed to reach adult size and body condition and

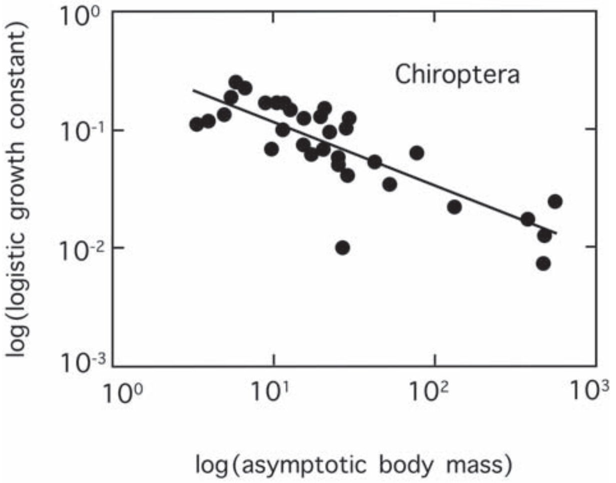

Figure 14.2. Allometric relationship between logistic growth constants and asymptotic body mass in the Chiroptera. *From Kunz and Stern, 2005.*

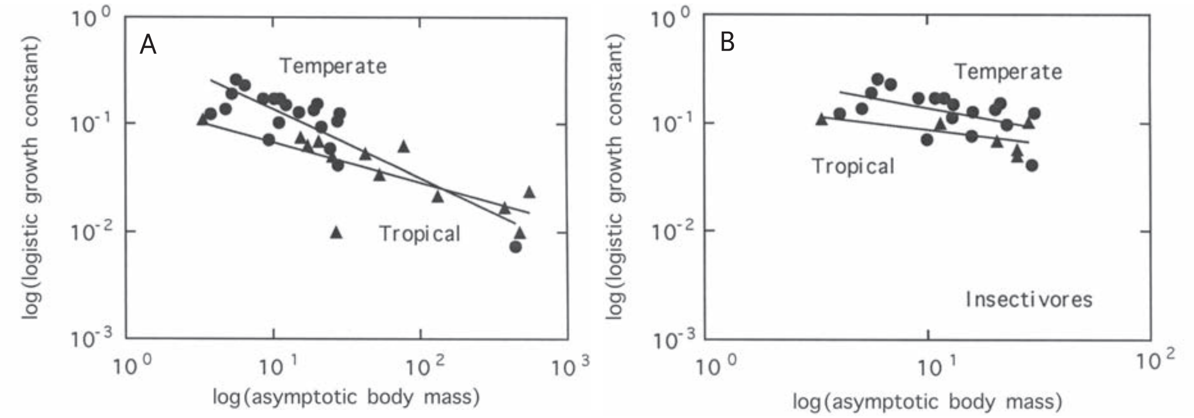

Figure 14.3. Allometric relationship between logistic growth constants and asymptotic body mass in temperate and tropical species. A, when the effect of body mass was removed, there was a significant effect of climate on growth constants. B, temperate insectivorous species have higher growth constants than their tropical counterparts. *From Kunz and Stern, 1995.*

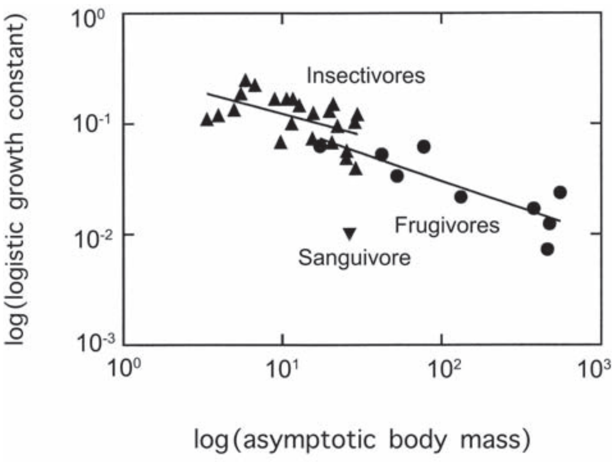

Figure 14.4. An allometric comparison of logistic growth constants of frugivorous and insectivorous species revealed no significant difference between these two feeding ensembles. Although not included in the allometric analysis, the sanguivorous vampire bat (*Desmodus rotundus*) has the slowest reported growth constant among the Chiroptera *From Stern and Kunz, 1995.*

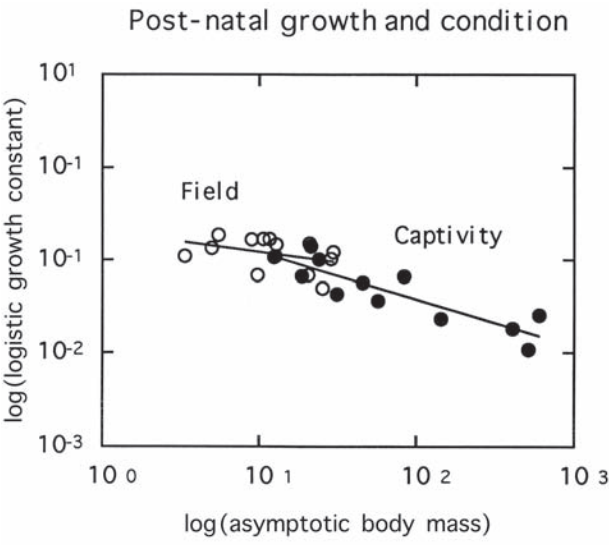

Figure 14.5. Allometric comparison of logistic growth constants between captive and free-ranging bats shows no significant difference among these two groups when effects of body mass were removed. *From Kunz and Stern, 1995.*

the deposition of fat stores needed for migration, reproduction, and hibernation (Kunz and Stern, 1995). Differences in the absolute and relative abundance and quality of insects in temperate versus tropical regions also may account for observed differences in postnatal growth rates (Kunz and Stern, 1995).

Growth and Development in Captivity

Potential biases may exist in studies on postnatal growth and development of bats in captivity, especially when they are based on small sample sizes or when the study includes lactating females of questionable nutritional status—either over fed or underfed, pups that were hand fed questionable diets, or bats housed in inappropriate conditions such as lack of flight space and unsuitable temperatures. Where postnatal growth rates of captive versus free-ranging bats have been compared (Kunz, 1987; Kunz and Stern, 1995), some growth trajectories of captive bats differed from free-ranging bats (Kunz, 1987); however, based on allometric analysis of growth rates, no significant difference was found (Fig. 14.5; also see Elangovan et al., 2002). In cases where more rapid growth rates have been observed in captive bats, this may reflect a higher nutritional plane (Kunz and Hood, 2000). In other situations, where reported postnatal growth of captive bats was slower than that of their free-ranging counterparts (reviewed in Kunz, 1987), factors such low temperatures (leading to torpor), little or no opportunity for exercise (lack flight space), and the possible effects of stress (lack of a normal social environment) may contribute to reduced postnatal growth rates.

QUESTIONS, RESEARCH NEEDS, AND HYPOTHESES

Interspecific Variation

Comparisons of postnatal growth rates among species are typically made using measurable variables (e.g., length of forearm, epiphyseal gaps, or body mass) and compared allometrically. Kunz and Stern (1995) found a significant negative correlation between postnatal growth rates and body mass. No significant phylogenetic effect (Megachiroptera versus Microchiroptera) on postnatal growth was found after removing the effect of body mass. The absence of a significant phylogenetic effect is not surprising given the small sample of megachiropterans (n=5) available for analysis.

The allometric analyses conducted by Kunz and Stern (1995) suggest a strong selection pressure for rapid growth rates in temperate climates compared to tropical climates. One hypothesis to account for higher growth rates of bats in temperate latitudes may be explained by increased selection pressures in response to a shorter growing season in temperate regions. Faster growth rates in temperate latitudes would allow individuals to achieve maximum somatic growth and to deposit important fat reserves before the onset of hibernation or migration (Kunz and Stern, 1995; Kunz et al., 1998b). This interpretation is consistent with Boyce's (1979) hypothesis that accelerated growth should occur among mammals living in highly seasonal, temperate environments. In this context, it would be interesting to compare postnatal growth rates of tropical species distributed over a wide range of altitudes and associated ambient temperatures.

Intraspecific Variation

Intraspecific variation in postnatal growth and development appears to be influenced by several factors. Temperature, rainfall, and food availability are among several extrinsic factors known to influence postnatal growth rates in free-ranging *Perimyotis* (*Pipistrellus*) *subflavus* (Hoying and Kunz, 1998), *Myotis lucifugus* (Reynolds, 1999) and *Eptesicus fuscus* (Hood et al., 2002). Low roost temperatures such as those observed in some caves, tree cavities, and small colonies may increase the energy costs incurred by lactating mothers, especially if they resist torpor during early postnatal growth and development of pups and as a consequence allocate less energy to milk production. Tuttle (1975) suggested that the high energy demands of lactating females contributed to slower growth rates in *Myotis grisescens* born in cool caves compared to warmer caves, and attributed this to increased thermoregulatory costs. Tuttle (1976) also suggested that reduced growth rates and survival of newly volant young *M. grisescens* may reflect increased energy costs associated with having to commute long distances to and from foraging areas. Low roost temperatures during lactation can lead to periods of torpor in mothers and pups, causing a reduction in postnatal growth rates (Hoying and Kunz, 1998).

Maternal condition also has been postulated as an important factor that may influence rates of postnatal growth and development of bats and other mammals. For example, Ralls (1976, 1977) suggested that bigger mothers should be more fit mothers. Stern and Kunz (1998) evaluated possible maternal affects (including body condition) on postnatal growth of young *Phyllostomus hastatus*, and found no relationships between growth rates in length of forearm and age or body mass of the mother. They did find, however, that males continued to grow to a larger size than females, and that there was a direct positive relationship between body mass of the mother and the body mass of pups. Stern and Kunz (1998) also found that males continued to grow to a larger size than females. Whether this continued growth reflects increased allocation of mothers to male offspring, or whether female in good condition allocate more energy to daughters than to sons as has been observed in roe deer (Hewison et al., 2005), remains to be determined for bats.

Because postnatal growth and development to maturity are influenced by a host of intrinsic factors—both genetic and social—it would not be surprising to find that the period of postnatal growth in both body mass and linear dimensions would be greater in males than in females, at least in species where sexual dimorphism has been reported. It is well known that a surge of estrogen at the onset of reproductive maturity in females accelerates fusion of the epiphyses of long bones, thus reducing growth of these elements, whereas testosterone facilitates increased bone density and muscle mass in males. Thus, in polygynous species in which males are larger than females, hormonal differences may be the basis for observed differences in postnatal growth rates and body size between males and females at maturity, independent of the condition of the mother. Where reverse sexual dimorphism has been observed in bats, Myers (1978) and Williams and Findley (1979) proposed that increased size in females might reflect selection on females to be able to carry larger litter masses.

When data on intraspecific variation in postnatal growth rates have been examined, both quantitative and qualitative differences are evident (Kunz and Hood, 2000; Barclay and Harder, 2003). Environmental (extrinsic) and biotic (intrinsic) factors both may affect intraspecific variation in postnatal growth rates in bats, thus we propose several hypotheses to test, including food supply and climate, latitude, diet (including water availability), gender, body condition, litter size, colony size, season, and growth conditions (captive vs. free ranging). Because many of these factors are interdependent, future studies should evaluate possible interactions among these variables to more effectively interpret observed intraspecific differences in postnatal growth rates. Given the various extrinsic and intrinsic factors known or postulated to influence postnatal growth and development, the following hypotheses were developed to encourage researchers to test them in both field and captive situations.

Extrinsic Factors

Local Climate and Food Supply Hypothesis

Growth rates of young animals should be higher if parents are subjected to higher planes of nutrition, either through natural abundance of food or through nutritional enrichment in captivity. Case (1978) postulated that feeding requirements of young mammals and availability of food to their parents were sufficient to account for much of the variability observed in postnatal growth rates in mammals. In free-ranging bats, meteorological conditions can directly affect the abundance and quality of food resources as well as the behavioral and physiological condition of mothers and their pups. The activity of flying insects may be reduced or altered by wind, moonlight, low temperature, and precipitation (Anthony and Kunz, 1977; Anthony et al., 1981; Richards, 1989; Rydell, 1989; Jones et al., 1995; Hoying and Kunz, 1998).

Field observations suggest that availability of food for lactating females is an important factor affecting growth rates in bats. In their study of postnatal growth of *Permyotis (Pipistrellus) subflavus*, Hoying and Kunz (1998) found significant interyear variation in postnatal growth rates (body mass increased at a slower rate in 1982 than in 1981). They attributed this difference, in part, to the contrasting abundance of insects during the two years of study. Births were delayed by nearly one week in 1982 and pups born during this inclement period experienced depressed growth. Not only were fewer flying insects available to lactating mothers, but unseasonably cool temperatures also caused daily torpor both in lactating females and their pups, thus contributing to the depressed postnatal growth rates. When ambient temperatures and levels of precipitation returned to normal conditions in subsequent days, the pups experienced compensatory growth (Hoying and Kunz, 1998). Reynolds (1999) reported marked interyear differences in growth rates of *Myotis lucifugus* and suggested that these differences reflected interannual differences in climatic variables that affected the availability of insect prey. Similarly, Reiter (2004) reported interyear differences in postnatal growth in *Rhinolophus hipposideros* and attributed this to differences in ambient temperatures and insect abundance. Dietz et al. (2006) also suggested that interyear differences in the size of young in three species of *Rhinolophus* at the time of weaning were manifestations of local insect variability.

Regional Climate and Latitude Hypothesis

Theoretically, populations of the same species occurring at higher latitudes should grow faster than populations at lower latitudes, thus ensuring that individuals at higher latitudes complete somatic growth and fat deposition before the onset of migration and hibernation (Fujita, 1986). Fujita found that postnatal growth rates (body mass and length of forearm) from a population of *Myotis lucifugus* in Alberta, Canada (54°56'N) were slower than those in New Hampshire (42°25'N). Although the general trend of higher growth rates in temperate versus tropical bats may hold in an interspecific allometric analysis (Kunz and Stern, 1995), Fujita's (1986) observation suggests that growth rate in the most northern part of a species' range may actually be slower, influenced by energetic considerations such as reduced availability of food and increased costs of thermoregulation. Cooler summer temperatures at northernmost latitudes may also directly affect availability of insects and the female's ability to convert energy and nutrients into milk.

If maintenance costs were higher for mothers and pups in colder, northernmost temperate latitudes, then less energy would be available for production. For species with a geographic distribution that extends from intermediate latitudes characterized by moderate temperatures into cool temperate latitudes, postnatal growth rates may indeed be slower at the highest latitudes. Thus, for species with geographic distributions that span from low to high latitudes, such as *Eptesicus fuscus*, we would predict a hyperbolic curve in growth rates, with the lowest rates occurring at the extremes and the highest rates at intermediate latitudes. Reduced postnatal growth rates, low fat deposition, and lower levels of fecundity at the northernmost latitudes of a species' range (Kunz et al., 1998b) may characterize the suite of life-history traits that limits the breeding distribution of a given species (also see Barclay and Harder, 2003). Few studies on postnatal growth and development of bats have considered life-history consequences of this variation (Reynolds, 1999).

Seasonal Variation Hypothesis

In tropical environments, female bats that produce two or more litters per year may experience marked differences in the availability of food and water at different times of year, which in turn may influence nutrient and energy transfer from mothers to pups. McWilliam (1987) showed that early postnatal growth rates in *Coleura afra* were higher during the short rainy season in Africa than during the long rainy season that followed an extended dry period. He attributed this difference to the poor condition of females following a pregnancy when food resources were low. In India, qualitative differences in postnatal growth rates were observed between spring and summer litters of *Cynopterus sphinx* (Krishna and Dominic, 1983), further suggesting that growth rates may vary seasonally, especially in polyestrous species.

Sex-specific Hypothesis

Sex-specific differences in postnatal growth rates should be most pronounced in sexually dimorphic species. Several species of insectivorous bats are weakly sexually dimorphic, with females being slightly larger than males (Myers, 1978; Williams and Findley, 1979), but for most species overall sex differences in postnatal growth rates appear to be correspondingly slight or nonexistent (Kunz, 1973; Kunz and Anthony, 1982; Burnett and Kunz, 1982; Reynolds, 1999; but see Kunz, 1974). Notwithstanding, at least two temperate species and several tropical species show sex differences in postnatal growth. In particular, we could expect sex differences in postnatal growth rates in species that exhibit high degrees of sexual dimorphism. Several highly polygynous species, including *Artibeus jamaicensis*, *Cynopterus sphinx*, *Epomophorus wahlbergi*, *Hypsignathus monstrosus*, and, *Phyllostomus hastatus*, and *Pteropus hypomelanus* show significant sexual dimorphism in adults that may be a consequence of sex-specific selection for different postnatal growth rates (Kunz and Stern, 1995). In *P. hastatus*, where reproductive variance is much greater for males, and where body size may affect reproductive success (Stern and Kunz, 1998), mothers should invest more in their sons than in their daughters (see Trivers and Willard, 1973). Such differential allocation of maternal resources to male pups often results in a high degree of sexual dimorphism in polygynous species (Bradbury, 1977b), suggesting that postnatal growth rates are greater or growth continues longer in males than in females in these species.

By contrast, sex differences in postnatal growth can be expected in temperate, hibernating species, where there is some evidence for reverse sexual dimorphism in adults (Myers, 1978; Williams and Findley, 1979). Reynolds (1999) found that young females *Myotis lucifugus* had higher growth rates than males in length of forearm during several years of a multi-year study, emphasizing the point that one year of study is not sufficient to characterize how environmental factors affect postnatal growth. Moreover, Reynolds (1999) postulated that because young females *M. lucifugus* have a greater chance of reaching sexual maturity in the year of their birth than females, mothers should invest more in females than males. The fact that young female *M. lucifugus* remained in maternity colonies longer during the summer than males, supports the hypothesis that females require higher levels of maternal investment than males (Reynolds, 1999). Kunz's (1974) analysis of postnatal growth of *Eptesicus fuscus* suggests that females may have grown faster than males in Kansas, although this pattern was not observed in a subsequent study on the same species in Massachusetts (Burnett and Kunz, 1982). Notwithstanding, both of the latter studies were single year studies, and thus from these it is not possible to explore how environmental factors may affect differential maternal investment to males and females. No sex-specific growth rates were observed in two other temperate species, including *Antozous pallidus* (Davis, 1969) and *Pipistrellus pipistrellus* (Hughes et al., 1995). However, lack of neonatal and adult size dimorphism in the former study, and the fact that the latter study was conducted in captivity, in which both males and females had ad libitum access to food, makes it impossible to draw definitive conclusions about factors that may or may not have affected sex differences in postnatal growth in this species.

Birth Timing Hypothesis

Bats born early in the parturition season should grow faster than those born later in the year. Young of *Rhinolophus ferrumequinum* born early experienced faster growth rates than those born later (Ransome, 1978; McOuat and Andrews, 1995). Similarly, early born *Perimyotis subflavus* showed faster growth rates than those born later (Hoying and Kunz, 1988). Reynolds (1999) also found that *Myotis lucifugus* born early in the parturition season had faster growth rates than those born later in this same period. Reiter (2004) also reported that young *Rhinolophus hipposideros* born early grew more rapidly than those born late. By contrast, Kunz (1973) found no differences in growth rates of *Myotis velifer* born early or late in the parturition season. Hoying and Kunz (1998) suggested that young born early in the growth period would benefit from the heat generated by clustered females, whereas those born late in the parturition period, as was the case of two late-born *P. subflavus*, would not have benefited from the warm thermal conditions experienced by the earliest cohort. Benefits derived from being born early in the parturition season, at least for temperate, hibernating species, is that these individuals would have more time to acquire adult body condition and fat reserves before migrating and/or entering hibernation. Although compensatory growth has been observed among individuals born late during the postnatal period, as in *P. subflavus* (Hoying and Kunz, 2998) and *Rhinolophus hipposideros* (Reiter (2004), these individuals may pay physiological and ecological costs in having a reduced life span (Metcalfe and Monaghan, 2001).

Litter Size Hypothesis

Postnatal growth rates of individuals in multiple litters should be slower than individuals from singleton litters. Most bats produce singletons, although a few species produce litters of two or more (Tuttle and Stevenson, 1982; Kurta and Kunz, 1987; Hayssen and Kunz, 1996; Barclay and Harder, 2003). Species in which twinning occurs can provide valuable information for testing the effects of litter size on postnatal growth rates. Among North American bats that have litter sizes greater than one, postnatal growth rates have been quantified for *Antrozous pallidus, Perimyotis) subflavus,* and *Eptesicus fuscus*. Existing data on postnatal growth rates of pups for species having varying liter size are available only for *A. pallidus* and *E. fuscus.*

Populations of *E. fuscus* in western North America typically produce litter sizes of one, whereas those in the east often produce twins (*E. fuscus*; Burnett, 1983; Holroyd, 1993); however, comparisons of postnatal growth rates between populations from different geographic regions may be confounded by differences in climate, food availability, or both. To avoid such geographic or other confounding effects on postnatal growth, when possible, singletons and twins should be sampled from the same population when possible. Bassett (1984) compared growth rates for length of forearm in singletons and twins of *A. pallidus* collected from the same captive population in California. He found that pups from both groups grew at the same rate, although singleton pups were larger at birth than those from litters with twins. However, because body mass generally is more sensitive to environmental effects during the postnatal period than is length of forearm (Hoying and Kunz, 1998), conclusions based on a comparison of length of forearm between singletons and twins may be less revealing than those based on body mass. Holroyd (1993) compared growth rates of twins versus singletons from a free-ranging population of *E. fuscus* in Alberta, Canada, and found that twin pups grew significantly slower in length of forearm and body mass than did singleton pups.

Colony Size Hypothesis

Postnatal growth of bats in large colonies (with warm temperatures) should be faster than those in small colonies (with cool temperatures). Conditions in the roosting environment of bats (Kunz, 1982; Kunz and Lumsden, 2003; Barclay and Kurta, 2007) potentially have important direct and indirect effects on intraspecific variation in postnatal growth rates (Tuttle and Stevenson, 1982). Tuttle (1975) compared preweaning growth rates in *Myotis grisescens* from several caves, each with contrasting roost temperatures, and found that postnatal growth rates of pups were highest in the warmest roosts. Tuttle postulated that females and pups from cooler caves would need to allocate more energy to maintenance, and thus less energy would be available for production (milk output by females and accretionary growth of pups). He also suggested that roost temperature was directly proportional to colony size, assuming that caves were of equal size and configuration, because large numbers of bats generated more heat and could more effectively increase the roost temperature of the cave (and thus reduce maintenance costs).

Postweaning growth and development also may be influenced by colony size (Tuttle, 1976), especially if individual bats from large colonies must fly greater distances to feed compared to bats from small colonies. Tuttle noted that bat pups born in large colonies experienced slower postweaning growth rates because they would need to allocate a greater amount of their nightly energy intake to support the added cost of flying long distances. These results suggest that interactions between roost locations (relative to suitable foraging habitats, colony size, and microclimate) should be considered when evaluating postnatal growth rates in bats.

Intrinsic Factors

After giving birth, a mother's direct biochemical influence on postnatal growth of pups is largely limited to the milk that she supplies. In addition, nonnutritional care may include sensory stimulation, thermal influence, pup retrieval, and transport. Maternal interactions with a developing infant can be considered as two major phases. The first phase of interactions occurs during pregnancy when hormones and antibodies regulate placental nutrients, oxygen, and waste exchange with the fetus (see Crichton and Krutzsch, 2000; Adams, this volume). The second phase occurs when the mother influences the newborn through sensory systems (e.g., tactile, olfactory, thermal, auditory, and visual), and the transfer of nutrients and energy in the form of milk. Combinations of these interactions are evident during the developmental period and are manifested by unique characteristics and the quality of parental care exhibited by each species.

Few studies have focused directly on parental care in free-ranging bats and how this care influences postnatal growth and development. Notable exceptions include studies by Nelson (1965), Thomson et al. (1985), McCracken and Gustin (1991), and Wilkinson (1985, 1992a). We suggest that mother-pup interactions, including nutritional and nonnutritional forms of care, be incorporated into studies of postnatal growth and development. Nutritional investment that mothers make in young bats, largely in the context of milk production and yield, are more thoroughly discussed in Kunz and Hood (2000) and Hood et al. (this volume). Acoustic communication and its role in mother-pup recognition and reunions have received moderate attention (Jones, 2000), but few studies have investigated the role of spatial, visual, and tactile cues in mother-pup interactions, and their implications for postnatal growth and development. This void in knowledge invites further study.

Because most newborn bats are functionally altricial at birth (Kunz and Kurta, 1987), they have a limited ability to regulate their body temperature. Thus, an important aspect of parental care in bats is the selection and maintenance of a thermal environment by the mother that facilitates rapid growth and development of young. Acoustic and olfactory responses also are important for promoting mother infant interactions, and tactile interactions are important for young to develop appropriate social and locomotor functions, including suckling behavior.

Sensory Facilitation Hypothesis

Early growth and development of bats is facilitated by sensory interactions between mother and pups. To a large extent, early postnatal growth and development of young bats depends on the interactions that develop between mother and young. Without the development of such interactions, young bats will be unable to secure milk during the suckling period, and in species that tutor their offspring by guiding them to food sources, normal sensory development may be delayed or impeded. For example, mother bats appear to rely on a combination of spatial memory, acoustic, olfactory, tactile, and/or visual cues to identify their young or to communicate with conspecifics. Early observations on bats that form very large colonies suggested that females suckle their young indiscriminately (*Tadarida brasiliensis*, Davis et al., 1962; *Miniopterus australis* and *M. schreibersii*, Brosset, 1962b). More recent studies on these and other species, however, have shown that nearly all female bats selectively nurse their own infants (*Antrozous pallidus*, Brown, 1976; *Desmodus rotundus*, Schmidt, 1972; *Eptesicus fuscus*, Davis et al., 1968; *Myotis velifer*, Kunz, 1973; *Pipistrellus pipistrellus*, Bishop et al., 1992; *Corynorhinus townsendii*, Pearson et al., 1952; *Rhinolophus condylura*, Kulzer, 1962; but see *Nycticeius humeralis*, Wilkinson, 1992a; and *Tadarida brasiliensis*, McCracken, 1984).

Selective nursing requires individual recognition, which ultimately is based on some form of communication. Except in rare circumstances, an infant suckling from its mother is more likely to survive and obtain adequate nourishment than if it was suckled by an adoptive mother. Thus, appropriate sensory cues are needed by both mother and young to facilitate mother-infant interactions that can lead to normal postnatal growth and development.

Although most animals rely on one form of communication over others (Scott, 1968), female bats use several cues to locate and identify their dependent young. Females of some species initially rely on spatial memory for locating their pups but subsequently use audition and olfactory cues for individual recognition (Gustin and McCracken, 1987). In these and similar situations, pups are accepted and allowed to suckle if recognized by their mothers (De Fanis and Jones, 1995b).

In some species, mother-infant communication may occur well past the onset of weaning (Bradbury, 1977a). Although we are unaware of any experimental evidence to support this claim, recognition of weaned young has been observed in *Desmodus rotundus* (Wilkinson, 1988), *Myotis adversus* (Dwyer, 1970), *Pteropus vampyrus*, and *P. hypomelanus* (W. R. Hood, pers. obs.). For species that are relatively long lived (Austad and Fischer, 1991; Brunet-Rossinni and Wilkinson, this volume) and highly philopatric (Lewis, 1995), we would expect roost mates to develop some form of individual recognition. The best candidates for long-term recognition include species that form small female groups based on matrilineal relationships. These and similar associations suggest that recognition cues are either learned or are genetically based on recognition of sensory cues similar to their own—so-called "phenotypic matching" (Beecher, 1982). Recognition of young by fathers has not been demonstrated in bats, although we would expect paternal recognition to occur in monogamous species, where males participate in the care of young (e.g., *Lavia frons*, Vaughan and Vaughan, 1987; *Cardioderma cor*, Vaughan, 1976; and *Vampyrum spectrum*, Vehrencamp et al., 1977) and where kin recognition functions as a mechanism to avoid inbreeding (Krebs and Davies, 1991).

Spatial Memory Hypothesis

Spatial memory appears to be the first sensory cue used by females for recognizing offspring in roost situations (Bradbury, 1977a; Mueller and Mueller, 1979). Spatial perception and memory may be especially important for species that leave their young in different roost locations at night, and in species that roost in large aggregations (Bradbury, 1977a; Mueller and Mueller, 1979). In *Tadarida brasiliensis*, lactating females associate with pups during scheduled nursing bouts, but they typically aggregate with other adults when they are not nursing their young. In an experiment to test for spatial memory in *T. brasiliensis*, McCracken (1993) marked females and removed their pups from known roosting areas in a maternity cave occupied by several hundreds of thousands, if not millions, of adults. Females returned to these roosting areas within the cave two or three times each night and searched for their young, which had been temporarily removed from the cave. Results from this experiment provided support for the spatial-memory hypothesis because visual, olfactory, and acoustic stimuli were absent. Use of spatial memory for locating young has also been suggested for solitary roosting *Lasiurus cinereus* (Koehler and Barclay, 1988) and in captive colonies of *Hipposideros speoris* (Habersetzer and Marimuthu, 1986).

Acoustic Stimulus Hypothesis

Acoustic communication appears to play an important role in facilitating interactions between females and their offspring. Exchanges of vocalizations are continually refined from birth until weaning, especially as the neonatal laryngo-nasal junction develops (Matsumura, 1979), where hearing is established in the young (Brown et al., 1978), and pups learn adult vocalizations and echolocation calls (e.g., Matsumura, 1981; Jones et al., 1992, Jones et al., 1993; Masters et al., 1995; Moss et al., 1997). Young bats of several species utter sharp, metallic "chirps" or "squeaks" during birth, as in *Nyctalus noctula* (Kleiman, 1969), or within hours of being born, as in *Corynorhinus townsendii* (Pearson et al., 1952), a behavior that most likely evolved to ensure that a pup is found and fed by its mother. *Tadarida brasiliensis* pups and their mothers vocalize almost continuously following parturition, presumably allowing each to learn the unique vocalizations on one another (Gelfand and McCracken, 1986). These single- and double-note vocalizations are termed "isolation calls" (Gould, 1971; Schmidt, 1972; Brown, 1976). Newborn *Antrozous pallidus* emit an almost continuous series of isolation calls when separated from their mother (Brown, 1976). Similarly, *Eptesicus fuscus* pups less than two weeks of age squeak continuously following a fall to the floor and until such time they are retrieved (Davis et al., 1968).

Isolation calls of *Tadarida brasiliensis* pups were distinguished by their mothers (60.4% classified correctly) in experimental trials, suggesting that similar recognition occurs in free-ranging populations (Gelfand and McCracken, 1986). In several species, pups produce individually distinctive calls that appear to attract mothers when they become separated (e.g., *Phyllostomus hastatus*, Rother and Schmidt, 1985; *T. brasiliensis*, Gelfand and McCracken, 1986; *Pipistrellus pipistrellus*, Jones et al., 1991; *Nycticeius humeralis*, Scherrer and Wilkinson, 1993; *Plecotus auritus*, De Fanis and Jones, 1995a).

Directive calls (i.e., attraction calls; Matsumura, 1981) are often emitted by mothers as they search for their young. This behavior is certain to ensure that a mother feeds a hungry suckling. In turn, mothers can be distinguished by their pups at distances up to one meter in extremely dense clusters of *T. brasiliensis* (Balcombe and McCracken, 1992). These directive calls are stereotyped and statistically discernible among individuals; a characteristic considered to be highly suitable for effective communication and for ensuring that the mother and young are united.

Vocal communication is also thought to be important when pups first become volant. A young *Saccopteryx leptura* was observed making short sallies from its roost during the day, and after a short period, its mother emitted several vocalizations, stimulating her pup to return to the roost (Bradbury and Emmons, 1974). As the pup approached its mother and climbed on her, both mother and pup emitted audible vocalizations, presumably verifying their identities. O'Shea and Vaughan (1977) reported "rallying" calls in *Antrozous pallidus*, which presumably promote contact between mother and pups upon return of the mother to the roost. Such contact is a form of maternal care that may facilitate growth and development of a bat pup.

Vocal communication between mothers and pups appears to be most complex early in the postnatal period. Infant bats that become separated from their mothers emit continuous broadband attractive calls, and mothers respond with "lead signals" [i.e., directive calls (Brown, 1976), antiphonal calls (Matsumura and Uchida, 1975), and search calls (Nelson, 1964)]. During the production of mutual, alternating signaling in *Rhinolophus ferrumequinum*, the acoustic character and pattern of infant vocalizations gradually changes until the high-intensity call precisely overlaps the call of its mother. Contact calls emitted by both mother and infant also appear to establish identity and facilitate mother-pup reunions in *Pteropus* (Nelson, 1965), *Eptesicus fuscus* (Gould, 1971), *Desmodus rotundus* (Schmidt, 1972), *Antrozous pallidus* (Vaughan and O'Shea, 1976), and *R. ferrumequinum* (Matsumura, 1981).

Acoustic recognition of offspring by mothers, and mothers by pups, has been verified experimentally in *Myotis lucifugus* and *Tadarida brasiliensis*. Turner et al. (1972) placed *Myotis* pups individually in a Y-maze and allowed a choice between its mother and another lactating female, and pups selected their own mothers in 75% of the tests. Despite the high error rate and overlap in duration of isolation calls of different infants, vocal cues may aid a mother in locating her own infant in a large maternity colony, with final recognition based on other cues such as olfaction, as in *Rousettus aegyptiacus* (Kulzer, 1961) and *T. brasiliensis* (Gustin and McCracken, 1987). Balcombe (1990) investigated call recognition in *T. brasiliensis*, and when lactating females were presented with calls of their own pup and an unrelated pup, mothers showed a significant preference for calls from their own pup. Similar observations were reported for *P. pipistrellus* by De Fanis and Jones (1996).

In some species, isolation calls have both genetic and learned components. Acoustic learning appears to be important in the development of isolation calls in *Phyllostomus discolor* (Esser and Schmidt, 1989). Mothers produce directive calls that are unique, especially in their patterns of frequency modulation. Isolation calls of pups gradually change to resemble the directive calls of their mothers, as both mothers and pups exchange isolation and directive calls. In a series of experiments, Esser (1994) demonstrated that when hand reared pups of *P. discolor* were isolated from conspecifics at birth, individuals that were subjected to playback calls of their mothers subsequently produced calls with more frequency minima and maxima than control pups which received no acoustic stimulation. Scherrer and Wilkinson (1993) argued that the isolation calls of *Nycticieus humeralis* had a strong genetic component, because pups were unable to learn isolation calls from mothers who did not emit equivalent sounds. However, both young and adult members of social groups in *P. hastatus* appear to learn calls that help coordinated foraging movements of other members in the same social group (Boughman, 1998).

Echolocation calls also may be used by some species for individual recognition, but these are probably less important in mother-pup interactions. Individual variation in FM (frequency modulation) calls has been described for several species of bats, including *Eptesicus fuscus* (Schnitzler et al., 1987; Thomas et al., 1987; Brigham et al., 1989; Masters et al., 1991, 1995; Fenton, 1994; Obrist, 1995; but see Rasmuson and Barclay, 1992) and *Myotis lucifugus* (Thomson et al., 1985). In *E. fuscus*, echolocation calls produced by adults were highly repeatable (>70%) compared to those produced by young (12% to 80%), but self-consistency increased with age (Masters et al., 1995). In trials with *Pipistrellus pipistrellus*, echolocation calls of pups were correctly discriminated in 82% of the trials by 6-day-old infants and in 91% of the trials by 15-day-old infants (Jones et al., 1991). Scherrer and Wilkinson (1993) found a high degree of repeatability in the calls of young *Nycticeius humeralis* (44% to 94%). Significant variation in echolocation calls exists among family members (38%) in *E. fuscus*, strongly suggesting a genetic basis to vocal signatures (Masters et al., 1995).

The structure of echolocation calls of young bats also appears to change with age: the calls of young bats are typically lower frequency than those of older individuals (*Rhinolophus hipposideros*, Jones et al., 1992; *R. ferrumequinum*, Jones and Ransome, 1993; *Asellia tridens*; Jones et al., 1993, *Myotis daubentonii*, Jones and Kokurewicz, 1994; and *M. lucifugus*, Pearl and Fenton, 1996; Moss et al., 1997). Jones and Ransome (1993) demonstrated that the resting frequencies (RFs) emitted by young *R. ferrumequinum* are highly correlated with the RF calls of their mothers, reporting that older females raise young with lower RFs than do younger females. Thus, age-related changes in echolocation calls of bats also appear to have both genetic and learned components (Jones and Ransome, 1993; Masters et al., 1995).

Females of *Hipposideros speoris* respond to the early FM calls of infants but are apparently unable to recognize individuals. It appears that because the calls of pups are dynamic, females are unable to rely on a single acoustic cue for pup recognition. As an alternative, females may resort to other forms of communication (Jones et al., 1991) or may respond to a changing template of their offspring's vocal signature. Individual isolation calls may be more ambiguous, and individual recognition may be less important in solitary species (Koehler and Barclay, 1988).

Olfactory Stimulus Hypothesis

Olfactory recognition of pups by their mothers and mothers by their pups facilitates rapid postnatal growth and development. Several investigators have suggested that female bats recognize their own roost and young using olfaction, although few studies have been conducted to test this hypothesis. Females of both *Pipistrellus pipistrellus* (De Fanis and Jones, 1995a) and *Eptesicus fuscus* (Bloss et al., 2002) are able to recognize odors from their own maternity roosts. The presence of odoriferous glands in females and their young and observations of maternal or mutual sniffing and apparent scent marking have been reported for several species (Altringham and Fenton, 2003). Females of *Nycticeius humeralis* possess a submandibular gland that increases in size by nearly 25% within 3 days of parturition. Immediately before departing to forage, females apparently use this gland to mark the faces of young bats less than or equal to 2 weeks of age (Watkins and Shump, 1981). Females of *Pteropus giganteus* have specialized glands in the tarsal, oral angle, muzzle, and perineal regions. Mothers may groom their infants in these regions, a behavior that may be important for sharing odors and for establishing a strong mother-infant bond (Jayaprakash and Alexander, 1993). Specialized skin glands become hypertrophied during lactation in *Megaderma lyra* (Begum and Alexander, 1993). Females of *Tadarida brasiliensis* actively produce odoriferous secretions from their muzzle and touch their chins to their own infants several times while selecting them and during nursing bouts (Gustin and McCracken, 1987).

Female bats of several species may initially locate their infants using auditory cues, but final recognition appears to be based on olfaction. Young of *Nycticeius humeralis* produce audible vocalizations when females return to their roost after foraging, but females apparently do not recognize their infants until olfactory cues are tested when they sniff the facial region of putative offspring (Watkins and Shump, 1981). This behavior has also been observed in *Plecotus auritus*, although whether the female sniffed a specific region is unclear (DeFanis and Jones, 1995a). When females of *Pipistrellus pipistrellus* return to their roost, they move through the cluster of young bats, shifting their heads side to side, apparently sniffing for their young (Rakhmatulina, 1972). Individual recognition was also apparent, but females needed more time to recognize odors of individuals from their own colony than females from different colonies.

Upon their return from foraging, females of *Pteropus poliocephalus* typically circle the camp where young pups are roosting, exchange calls with these infants, and finally land near their own young. Females sniff the chest of pups and either accept their own by opening one or both wings or reject the pup by pushing it away using her thumb and wing (Nelson, 1965). Although olfaction is extremely acute in *Desmodus rotundus* (Schmidt, 1973), no studies have examined the role of odors in individual recognition in this species (Wilkinson, 1985).

Only one study has unambiguously demonstrated that mothers recognize their own young using olfaction. Gustin and McCracken (1987) designed a double-blind test where lactating females of *Tadarida brasiliensis* were allowed to choose between the odor of their offspring and that of a randomly chosen, conspecific pup. Single females showed a preference for the odor of her own pup over that of a randomly chosen pup, and showed a significant preference for her own muzzle odor over that of a randomly chosen female. These observations suggest that females may use olfaction for phenotypic matching in pup recognition. Newborn pups, one to three days old, showed a preference for the scent of their mothers over a randomly chosen female, but this form of recognition was apparently abandoned by day four (Loughry and McCracken, 1991). Although *T. brasiliensis* pups recognized the auditory directive calls of females (Balcombe and McCracken, 1992), pups apparently shifted from olfactory to auditory modes once the auditory systems began to mature.

Several studies have shown that olfactory recognition is important in insectivorous bats, although we expect that olfactory recognition is even stronger in frugivorous, omnivorous, and sanguivorous species. Olfactory bulbs of bats with these latter food habits are more highly developed than those of insectivorous species (Mann, 1960; Stephan and Pirlot, 1970). The vomeronasal organ, an important site for olfactory and gustatory sensation, is rudimentary in many bats, but is well developed in phyllostomids, a family that consists largely of frugivorous and nectarivorous species (Bhatnagar, 1980). Although highly developed olfaction undoubtedly contributes to the location of food, the assumption that olfaction should play an important role in individual recognition is reasonable for these and related taxa, as has been suggested for frugivorous megachiropterans such as *Rousettus aegyptiacus* and *Pteropus* spp. (Kulzer, 1958; Nelson, 1965).

Visual Stimulus Hypothesis

Bats that have well-developed vision and rely on visual cues in their roosting environment (Suthers, 1970) can also be expected to use these cues in mother-pup recognition. Virtually nothing has been published on the interactions of mothers and pups based on visual stimuli. Most reports of visual communication involve interactions between conspecific roost mates associated with group formation, courtship, and mating displays. However, considering the relatively well-developed visual system in megachiropterans (Suthers, 1970), we would expect mothers and pups to communicate visually whenever possible, especially in species that roost in foliage and other places where sufficient ambient light is available. Some species, especially foliage roosting pteropodids and phyllostomids and some emballonurids, exhibit a rich array of visual displays, often produced independently of vocal and auditory signals. These include postural changes, wing flicking, wing shaking, hovering flight, baring of teeth, "boxing," head jerking, and erection of specialized hair patches (Fenton, 1985). Responses of bats to visual signals may be accompanied or followed by vocal or olfactory signals, but interpretation of visual signals can be ambiguous. For example, if a threat posture is accompanied by an audible vocalization or release of an odoriferous compound, the recipient's response may be to the combination of signals, not only to one. In this manner, each signal may reinforce the other, leading to an appropriate response by the recipient. Given the apparent occurrence of visual signaling among adult bats, it seems reasonable that mothers and pups should also rely on visual stimuli for recognition.

Tactile Stimulus Hypothesis

Physical contact between mother and young during the early period of postnatal growth and development can be expected to facilitate development. Tactile stimulation provided by the mother may be important in stimulating urination and defecation in pups, as reported for other mammals (see Hofer, 1981), and in facilitating the development of social relationships. Repeated tactile stimulation also may reduce the level of behavioral reactivity as has been observed in some terrestrial mammals (Matthews, 1969; Gubernick and Klopfer, 1981). In highly gregarious species of bats, there is often a high level of tactile stimulation among roost mates. To what extent this tactile stimulation is directed toward specific roost mates, including infants, or is an unintended consequence of contact clustering invites investigation.

Contact clustering appears to reduce metabolic rates in both young and adult bats (e.g., *M. thysanodes*, O'Farrell and Studier, 1973; *Tadarida brasiliensis*, Herreid, 1967; *Antrozous pallidus*, Trune and Slobodchikoff, 1976; *M. lucifugus*, Kurta et al., 1987), but whether this physiological response is a consequence of reduced behavioral anxiety or reflects other factors remains to be established. In maternity colonies of *Myotis lucifugus* and *Perimyotis subflavus*, adult females groom their young before departing on evening foraging bouts and again upon return from feeding (Burnett and August, 1981; Winchell and Kunz, 1996). Whether this type of tactile stimulation facilitates gut and bladder emptying of pups, reduces metabolic rates, or reduces ectoparasite loads invites further study.

Maternal Condition Hypothesis

Mammals are unique in their ability to produce milk from specialized mammary glands, which in turn provides the only source of energy, nutrients, and water available to dependent young (Hood et al., this volume). Ralls (1976) postulated that a bigger mother (in good condition) should be a better mother, thus, a mother in good physical condition should be a better provider of milk than one in poor condition. Because production of milk is generally considered the most costly aspect of mammalian reproduction (Millar, 1977; Oftedal, 1985; Gittleman and Oftedal, 1987; Hood et al., this volume), and likely the most important influence on reproductive success (Maynard Smith, 1977; Pond, 1977; Daly, 1979), a mother in good condition is likely to be a better mother, and thus raise more fit offspring.

Few studies have explored the possibility that nutritional factors (e.g., minerals) other than energy and nutrients derived from fat, protein, and carbohydrates influence postnatal growth of young bats (Barclay, 1994, 1995; Voigt et al., 2007). Studies that have examined the nutritional requirements of female bats and their young during lactation have largely focused on females and the proximate composition of milk (Hood et al., this volume). Available evidence suggests that female insectivorous bats are severely calcium limited during lactation (Kwiecinski et al., 1987, Studier et al., 1991, Keeler and Studier, 1992). As in other mammals, young bats are nutritionally dependent on their mothers until they are able to feed independently (Pond, 1977; Kunz, 1987; Barclay, 1994, 1995). While young of most terrestrial mammals are weaned at nearly 40% of adult body mass, young bats are not weaned until they reach about 70% of adult body mass (Barclay, 1994, 1995). This extension in the duration of dependency occurs because young bats are unable to fly and feed on their own until they have achieved adult dimensions (Kunz, 1987; Barclay, 1994, 1995), and mineralization of wing bones is nearly complete (Swartz et al., 1994; Papadimitriou et al., 1996).

Milk Yield Hypothesis

The amount and quality of milk produced by a mother represents the ultimate condition of a lactating female. For this reason, a reliable estimate of milk yield is an essential ingredient of assessing maternal condition of females. Milk yield has only been measured directly in four insectivorous and one omnivorous bat (Hood et al., this volume). However, these estimates of milk yield have not been linked to postnatal growth of individual bat pups. Based on isotope dilution, Kunz (1987) reported milk energy yield at peak lactation in *Myotis lucifugus* and *Eptesicus fuscus* as 18.5 and 22.87 kJ/day, respectively. These values were similar to those predicted from allometric equations of Hanwell and Peaker, 1977, and Oftedal, 1984. Using estimates of milk composition from Kunz et al. (1983) and data on metabolic rates of pups, Kurta et al. (1989, 1990) predicted milk energy yield at peak lactation in *M. lucifugus* and *E. fuscus* to be 19.3 and 29.7 kJ/day, respectively. To date, no studies have examined the relationship between milk yield of a mother and growth rates of her pups. At best, estimates of mean milk yield could be used to compare female condition and resultant growth rates of pups among colonies. Studies most likely to reveal effects of maternal condition, based on milk output and postnatal growth rates of bat pup, are those conducted in captivity.

Predicted mean values for milk yield are based on both the metabolic mass of females and their young (Oftedal, 1984). Females of *Nycticeius humeralis*, which typically produce twins, reportedly produce up to one-half their body mass in milk per day, and milk production apparently increases even further when litter size is three (Steele, 1991). By contrast, milk output in *E. fuscus* females as predicted by Oftedal's (1984) equation is less than the measured values (Kunz, 1987). Values of milk yield reported for captive *Plecotus auritus* (McLean, 1995) are based on Oftedal's (1984) predictive equation, and thus were not validated by empirical evidence. Stern (1995) found that free-ranging female *Phyllostomus hastatus* produced a maximum of 15.7 mL/day of milk at peak lactation. Until such time milk yield of individual bats can be related to postnatal growth of individuals pups, mean estimates of milk yield will provide limited insight into how milk production can be used as an index of maternal condition.

Regurgitation: A Special Case in Desmodus rotundus

The quantity of blood regurgitated by a female to its own or related offspring should influence rates of postnatal growth in vampire bats. In addition to provisioning vampire pups with milk, females of *Desmodus rotundus* regurgitate blood to their young. Within minutes of birth, this blood may inoculate the digestive tract of pups with symbiotic bacteria (Müller et al., 1980). However, females do not routinely feed blood meals to their young until they are about 3 months old, after which this behavior continues until the onset of weaning that occurs at approximately 7 months of age (Schmidt and Manske, 1973; Wilkinson, 1984, 1988).

During 400 hours of focal observations on the behavior of free-ranging *Desmodus rotundus*, Wilkinson (1984) reported 110 bouts of regurgitation, 75% of which occurred between mothers and their dependent young. The other 25% were between females and nondependent young, relatives, and unrelated individuals. Thus, food sharing in *D. rotundus* appears to be associated with the degree of relatedness and opportunities for reciprocity (Wilkinson, 1984). In this species, females belong to small, stable social groups of kin and non-kin where opportunities for reciprocation are high. Females that do not obtain a nightly blood meal are more likely to be fed by a female who has recently received a meal from another member of the group. If the amount of blood transferred from a female to a pup could be quantified, it may be possible to assess to fitness value of this behavior by comparing rates of postnatal growth among different individuals.

Thermal Regulation Hypothesis

Rapid postnatal growth and survival of young bats may be facilitated when females select roosting environments near thermal neutrality, and/or form dense clusters that promote efficient heat transfer to pups. The gregarious nature of young bats in many species also promotes conductive heat exchange, which is expected to facilitate digestion, increase assimilation efficiency (Twente, 1955; Davis et al., 1962), and facilitate rapid postnatal growth (Pearson et al., 1952; Dwyer and Hamilton-Smith, 1965; Kunz, 1973, 1974; Tuttle, 1975; Hoying and Kunz, 1998).

Ambient temperatures in the thermoneutral zone of bats not only provide favorable conditions for postnatal growth (Tuttle and Stevenson, 1982; Kunz and Stern, 1995), but also reduce thermal stress to lactating females (Huibregtse, 1966). High energetic costs experienced by females during lactation in *M. lucifugus* and *M. thysanodes* exceed levels that would allow bats to physiologically regulate their body temperature (Studier et al., 1973). Not unlike poikilotherms, bats may maintain their body temperatures behaviorally. Clustering of bats in temperate regions modifies the microclimate of maternity roosts by creating optimum roost temperatures (Licht and Leitner, 1967; Kunz, 1973; Hoying and Kunz, 1998).

Many temperate-zone bats form maternity colonies ranging from a few dozen up to several million individuals (e.g., *Eptesicus fuscus*, Davis et al., 1968; *Miniopterus schreibersii*, Dwyer, 1963). Within these colonies, mother-pup pairs aggregate in dense clusters, and maintain their body temperatures greater than those that roost singly (Twente, 1955). At ambient temperatures between 15°C and 35°C, mean rates of oxygen consumption are lower in clusters than in individuals and percent mass loss of body mass also decreases, giving cluster members a metabolic advantage (Herreid, 1967; Trune and Slobodchikoff, 1976).

A young bat that roosts in proximity to euthermic females in maternity roosts should grow faster than those isolated from heat generated by their mother and other females. This thermal influence is directly proportional to the amount of time a mother spends in contact with her young. Because newborn bats are functionally altricial, often lacking hair and with a limited ability to maintain euthermic body temperatures (Fujita, 1986; Kurta and Kunz, 1987), they often depend on their mothers to remain warm in a roost that otherwise may reach temperatures below thermoneutrality. McLean and Speakman (1997) noted that physical contact between mothers and pups in *Plecotus auretus* declined as the pups increased in age. At ambient temperatures of 10°C and 20°C, newborn *Myotis lucifugus* were unable to maintain their body temperature when they roosted alone (Fujita, 1986); however, when pups were allowed to form clusters, they maintained elevated body temperatures for longer periods at the same ambient temperatures as when they were housed alone.

If lactating females are exposed to prolonged cold temperatures during the maternity period, a decrease in body temperature can adversely affect milk protein synthesis and output (Wilde et al., 1999), and thus indirectly affect the growth rates of pups (Hoying and Kunz, 1998; Reiter, 2004). Because torpor is known to reduce the general level of activity, this could adversely affect the maturation of the brain, internal organs, and muscle, and lead to subsequent motor defects and reduced feeding efficiency (Gubernick and Klopfer, 1981). This postulated effect might not be relevant for bat species in which daily torpor is a normal aspect of their behavior and physiology.

Bats and other small mammals often enter torpor when ambient temperatures are too low to maintain an elevated body temperature or when food resources are scarce (Wang and Wolowyk, 1988; Hoying and Kunz, 1998). Because torpor slows physiological processes, including those required for milk production (Wilde et al., 1999), this form of energy conservation could be disadvantageous during lactation. However, some species, including *Antrozous pallidus* and *Myotis yumanensis* (Licht and Leitner, 1967), *Tadarida brasiliensis* (Herreid, 1967; Licht and Leitner, 1967), *Miniopterus schreibersii* (Dwyer, 1964), *Myotis nigricans* (Wilson, 1971), *Lavia frons* (Vaughan, 1977), and *Macrotus californicus* (Bradshaw, 1962), may remain euthermic during lactation and thus incur high energy costs during this period. Other species may enter torpor during lactation if ambient temperatures are low and food resources are scarce; such behavior has been observed in *Eptesicus fuscus* (Burnett and Kunz, 1982; Audet and Fenton, 1988; Hamilton and Barclay, 1994; Grinevitch et al., 1995), *Myotis lucifugus* (Studier and O'Farrell, 1972; Burnett and Kunz, 1982), *Myotis thysanodes* (Studier and O'Farrell, 1972), and *Perimyotis* (*Pipistrellus*) *subflavus* (Hoying and Kunz, 1998). Hamilton and Barclay (1994) examined differential use of torpor by *Eptesicus fuscus* during the reproductive season and found that torpor occurs less frequently in females when foraging conditions are poor (Grinevitch et al., 1995).

Pup Retrieval and Transport Hypothesis

Parents that retrieve young after they fall from roosts should reduce the probability of certain death caused by abandonment, predators, or scavengers. Retrieval of a flightless pup that has fallen from its roost is a relatively common occurrence in bats (Ansell, 1986; Davis et al., 1968; Davis, 1970; Fenton et al., 1976), and because this behavior may also involve females transporting young in flight, maternal effort may be high (Kunz, 1987; Barclay, 1995). For this reason, retrieval may help ensure that a pup survives and is further provisioned by its mother.

Transport of young bats by mothers is also considered a form of maternal care that can affect rates of postnatal growth, development, and survival. For species that regularly carry their young during foraging bouts or transport them to alternate roosts, the increased energetic costs of flight associated with this behavior may be substantial (Radhamani et al., 1990), but it ultimately can improve a pup's survival and a female's inclusive fitness if the pup survives to produce offspring of its own.

Transport of young by mothers during foraging bouts has been reported for several frugivorous and nectarivorous species (e.g., *Carollia perspicillata*, Pine, 1972; Bradbury, 1977a; *Artibeus lituratus* and *Glossophaga soricina*, Tamsitt and Valdivieso, 1963; *Pteropus poliocephalus*, Bartholomew et al., 1964; *Choeronycteris mexicana*, Mumford and Zimmerman, 1964; *Desmodus rotundus*, Schmidt and Manske, 1973), although this behavior is uncommon or rare among most small insectivorous species (*Pipistrellus pipistrellus*, Rakhmatulina, 1972; *Myotis velifer*, Kunz, 1974; *Myotis lucifugus*, Kunz and Anthony, 1996; *Hipposideros caffer*, Brosset, 1969; *Tadarida brasiliensis*, Davis et al., 1962, and *Nycticeius humeralis*, Watkins and Shump, 1981). Exceptions to this behavior among the insectivorous species include *Taphozous perforatus* and *T. melanopogon* (Brosset, 1962a).

Species that regularly move their pups among alternative tree roosts during the lactation period (Barclay and Brigham, 1996; Kunz and Lumsden, 2003; Barclay and Kurta, 2007; Carter and Menzel, 2007; Chaverri and Kunz, 2006) help sustain mother-pup contact, thus reducing the risk of predation. Females of some species (e.g., *Megaderma lyra*) move their young to night roosts while they are foraging (Marimuthu, 1988), but because of the high cost of flight associated with bats carrying extra loads (Hughes and Rayner, 1993), mothers are unlikely to transport their young on prolonged foraging flights unless this behavior reduces risks of predation on young bats and at the same time they learn important foraging skills (Radhamani et al., 1990). When mothers transport young on foraging flights, this may increase the fitness of pups if this behavior increases the ability of pups to forage successfully when they become volant and independent of their mothers (Gopukuman et al., 2003).

Allogrooming Hypothesis

Allogrooming may increase the growth and development of young bats when mothers groom their offspring. Observations of allogrooming in bats have been made mostly in captive situations (Kleiman, 1969; Kunz et al., 1994a; McLean, 1995; W. R. Hood, pers. obs.). The most thorough documentation of allogrooming in bats was reported for *Plecotus auritus* (McLean and Speakman, 1997), where it was observed that the relative amount of time that females spent allogrooming decreased over the course of lactation. Similar observations were reported by Kleiman (1969) for *Nyctalus noctula*, although the significance of such declines in allogrooming remains unclear.

Only a few studies have reported allogrooming activities in free-ranging populations. Female *Eptesicus fuscus* and *Perimyotis subflavus* have been observed licking, nuzzling, scratching, rubbing, or hanging in direct physical contact with their pups (Burnett and August, 1981; Winchell and Kunz, 1996). In *Desmodus rotundus* mutual grooming occurs between mother and offspring, but this reciprocity varies among individuals of different age groups (Wilkinson, 1986). Allogrooming in *D. rotundus* appears to be independent of roosts and ectoparasite levels, but may facilitate individual recognition in roosting situations and thus facilitate food sharing (Wilkinson, 1986).

Alloparental Care Hypothesis

Females (or possibly males) that assist in the care of offspring produced by other females should increase the fitness of the pups that are cared for and the inclusive fitness of the caregiver, particularly if the caregiver is related to or is the mother or the father of the infant. Alloparental care was observed at the time of parturition in captive *Pteropus rodricensis* (Kunz et al., 1994a). In this instance, a female roost mate assisted and tutored an unrelated female before, during, and after parturition. The helper female groomed the mother's anovaginal region, grasped her with partially outstretched wings, fanned her, "tutored" her in the feet-down birthing position, groomed the emerging pup, and physically nudged the pup toward its mother's nipple as it emerged from the mother's vagina, a behavior that has been observed on several occasions in this species (W. R. Hood, pers. obs.). Reports of "babysitting" have been reported for *Myotis thysandodes* (O'Farrell and Studier, 1973), based on the presence of a few adult females present in a maternity roost after other adults had departed. An alternative explanation for the latter observation is that some females in late pregnancy may have delayed their departure from the maternity roost when parturition was eminent (Kunz, 1973), which to a casual observer may have suggested that adults were babysitting. Alloparenting behavior, when it occurs, may facilitate the development of parenting skills, cohesion of groups, and socialization (Kunz et al., 1994a), but it may also improve the chances that a pup will develop to maturity.

Most females selectively nurse their own offspring, although misdirected nursing has been reported in captive groups of *Pipistrellus pipistrellus* (Kleiman, 1969; Eales et al., 1988; Hughes et al., 1989; DeFanis and Jones, 1996). In free-ranging populations of *Tadarida brasiliensis* (McCracken and Gustin, 1991), pups may engage in milk stealing, and in *Nycticeus humeralis*, mothers sometimes nurse unrelated offspring as they approach weaning age (Wilkinson, 1992a). On theoretical grounds, one could expect alloparental nursing to evolve through kin selection or reciprocity if the benefits of provisioning unrelated pups outweighed the costs, especially in colonies with high levels of relatedness. However, there is no evidence for reciprocity or kin selection in the food-sharing behavior of *T. brasiliensis* (McCracken et al., 1994) or in *Nycticeus humeralis* (Wilkinson, 1992b). Wilkinson (1992b) suggested that female *N. humeralis* may gain an immediate benefit by dumping excess milk to unrelated offspring, if foraging costs were lower with a reduced body mass. Alternatively, females may gain a deferred benefit if they nurse unrelated pups that return to the same colony in subsequent years and share information about feeding and roosting sites (Wilkinson, 1992b).

Paternal Care Hypothesis

Males of some species may share in the care and nurturing of young and thus promote postnatal growth and development. Because most bat species are polygynous, paternal care would not be expected in these species. But in monogamous species where paired males and females roost together, paternal care could be important if it facilitates postnatal development of offspring (Kunz and Hood, 2000). Evidence for a male's contribution to roost establishment, maintenance, and mate and pup guarding are known for only a few tropical species (Kunz, 1982; Kunz and Lumsden, 2003). In most temperate species, maternity roosts are inhabited largely by females and their young, while males assume little or no responsibility for parenting. In the New and Old World tropics, however, males of some species defend roosts or harems and in doing so invest in the care of young. In *Carollia perspicillata*, *Phyllostomus hastatus*, and *Artibeus jamaicensis*, males defend females and their pups from other males at roost sites, although such defense may occur independently of the presence of pups, especially if the primary motivation for doing so is to inseminate a female who undergoes a postpartum estrus (Porter, 1979; McCracken and Bradbury, 1981; Morrison and Morrison, 1981; Kunz et al., 1998a). In some monogamous species—*Lavia frons* (Vaughan and Vaughan, 1987), *Cardioderma cor* (Vaughan, 1976), and *Vampyrum spec-*

trum (Vehrencamp et al., 1977)—males may protect females and their young from predators by defending the foraging territories in which young bats learn to feed.

The investment that some males make in the construction of tents in foliage and other plant parts, and defense of the same, could be interpreted as paternal care, assuming that the investment made by males somehow benefits their progeny. In the short-nosed fruit bat (*Cynopterus sphinx*), males have been observed constructing tents and subsequently defend these structures and their female occupants during the pregnancy and lactation periods (Balasingh et al., 1995). Twice each year, males of *C. sphinx* sever and modify stems, leaves, and vines of selected plant species, forming tents (Kunz et al., 1994b; Balasingh et al., 1995; Bhat and Kunz, 1995). A single male may spend from 30 to 50 days constructing one tent and several additional months defending females and their pups that roost in these structures. Similar types of paternal effort can be expected for other tent-roosting species (Timm, 1987; Kunz et al., 1994b; Kunz and McCracken, 1996; Tan et al., 1998; Storz et al., 2000; Hodgkison et al., 2003, Dechmann et al., 2005; Campbell et al., 2006; Kalko et al., 2006; Chaverri and Kunz, 2006).

In monogamous species and in those polygynous species that form harems, and in species where the putative father is present during the developmental period of pups, paternal influence on the developmental of vocalizations (including echolocation) and early flight and foraging can be expected. For example, in the monogamous megadermatid *Lavia frons*, males and females typically roost near one another and hunt from perches as sit-and-wait predators (Vaughan and Vaughan, 1987). When pups accompany one or another parent to a shared feeding territory, they are likely to learn about their parent's foraging perches through direct observation.

In most species of mammals, including bats, the primary caregivers are females. However, males of at least two megachiropterans (*Dyacopterus spadecius* and *Pteropus capistratus*) develop active mammary glands at certain times of year (Francis et al., 1994, Bonaccorso, 1998). Whether these males suckle pups remains an open question, and additional research is needed to determine whether males of these species facilitate the growth and development of pups (Kunz and Hosken, 2009).

Development of Flight, Echolocation, and Feeding Behavior

Two important benchmarks for successful postnatal growth and development in bats are the attainment of flight (Jones, 2000) and independence from mothers (Kunz and Hood, 2000). Postnatal development of the neuromuscular system of bats establishes the crucial circuitry for specialized tasks such as flight, navigation, and feeding skills (Powers et al., 1991; Stern et al., 1997). For microchiropterans, development of echolocation is essential for feeding success, survival, and reproduction. Early development of the vocal and auditory systems appears to be important for the development of echolocation and social calls used by microchiropterans to capture prey and to locate and identify mates and offspring (McCracken and Gustin, 1991; Moss et al., 1997; Jones, 2000).

The extent to which either or both parents are involved in the development of communication and echolocation skills in bats has not been investigated. For most species, only a maternal influence is expected, because adult sexes of many species are segregated during the maternity period. Young bats of some species may accompany their mothers on foraging flights, including *Noctilio albiventris* (Brown et al., 1983), *Eptesicus fuscus* (Brigham and Brigham, 1989), and *Desmodus rotundus* (Wilkinson, 1985, 1987), but other species, such as *Myotis myotis* (Audet, 1990), *M. lucifugus* (Buchler, 1980; Kunz and Anthony, 1996; Adams, 1996a, 1996b), *Pipistrellus pipistrellus* (Racey and Swift, 1985), and *Rhinolophus ferrumequinum* (Jones et al., 1995) appear to develop foraging skills independent of their mothers. To determine what role mothers may assume in the development of echolocation and early foraging success of their pups will require long-term studies where both mother and pups are followed simultaneously.

Morphological Ontogeny and Shifting Feeding Niches

Juvenile bats face energetic and functional demands confronted by few other mammals (Adams, 2000). Young bats are nourished from their mother's milk until such time they are able to fly, and for variable periods of time during the weaning period. During this developmental period, young bats rapidly shift from a nonvolant stage, at which time they are suckled by their mothers to a volant stage that requires them to fly, capture prey, avoid predators, and gain sufficient body mass and fat reserves to sustain them during migration or hibernation. Not only must they be able to sustain flight, but they must also be able to make aerial maneuvers to pursue and capture evasive insects or navigate in clutter to search for flowers that produce nectar, distinguish ripe from unripened fruit, and other foods consistent with their dietary habits.

Changes in wing and hind limb morphology, muscular development, echolocation, and flight skills continue for some time after young bats become volant (Adams and Pederson, 2000). This postweaning developmental period is characterized by marked changes in the ossification of wing elements (Papadimitriou et al. 1996), wing shape (Adams, 1996a, 1996b, 2000), aspect ratio and wing loading (Adams, 2000), cranial morphology and dentition (Pederson, 2000), vocalizations (Gould, 1975, 1977; Moss et al., 1997), and the ability to hear and process echolocation calls that facilitates the ability to navigate in both open and cluttered environments (Vater, 2000). These ontogenetic changes, in turn, are generally paralleled by shifts in emergence times (Kunz, 1973; Kunz and Anthony, 1996), foraging behavior (Buchler, 1980; Adams, 1997, 1998), nightly activity budgets (Kunz, 1973; Buchler, 1980), and types and sizes of prey (Anthony and Kunz, 1977; Buchler, 1980; Rolseth et al., 1994; Adams, 1996a, 1997). Overall, ontogenetic changes in foraging behavior and diet are often manifested by a shift from simple to more complex habitats and increased dietary diversity (Adams, 2000). Adams (2000) presented a three-dimensional, adaptive landscape model that illustrates the relationships wing loading, aspect ratio, and dietary complexity beginning with the onset of flight through various stages of volancy. Early flight and volancy in bats has been frequently characterized by loss of body mass in juveniles (Tuttle and Stevenson, 1982, Kunz, 1987; Kunz and Stern, 1995; Hamilton and Barclay, 1998). This loss has been attributed to loss of prefledging body fat, poorly developed echolocation skills, and the inability to successfully capture evasive insects. Hamilton and Barclay (1998) suggested that the low body mass observed after weaning may reduce flight costs and further make it possible for young bats to avoid aerial predators during this critical developmental period.

EVALUATING SIZE AND DEVELOPMENTAL STATE AT BIRTH

Accurate and reliable estimates of size and developmental state at birth are needed to reliably set baselines for assessing postnatal growth rates. Obtaining such estimates, however, can be challenging. Access to newborn may not be easy and estimates based on aborted embryos or older young can bias results (Tuttle and Stevenson, 1982). Davis (1969) and Kunz (1973) used the presence of an umbilical cord as a criterion for establishing size at birth in free-ranging bats. This criterion has been subsequently used in many other studies on postnatal growth of free-ranging bats (e.g., Kunz and Anthony, 1982; Burnett and Kunz, 1982; Kunz and Robson, 1995; Hoying and Kunz, 1998; Stern and Kunz, 1998; Reynolds 1999; Hood et al., 2002; Chaverri and Kunz, 2006). For captive bats, determining size and developmental state at birth often can be determined by direct observation of parturition and by subsequently recording relevant measurements directly from pups.

Assessing size at birth requires criteria that can unambiguously make it possible to distinguish newborn from older young. Typically, bats are born with an attached umbilical cord (sometimes with the placenta still attached, as in *Tadarida brasiliensis*, Fig. 14.6). In most instances, the umbilical cord dries and falls off neonates within the first 24 hours of being born. If a neonate has an attached umbilicus at the time of capture, one can generally assume that this is the day of birth. This assumption has been confirmed by marking newly born pups and subsequently observing the presence or absence of an umbilicus (Kunz, 1973). At times, the umbilical cord falls off within a few hours of birth, and at other times, it may remain longer than one day. For this reason, using the presence of an umbilical cord as the sole criterion for newborn status could result in overestimating the true size at birth of a pup that prematurely lost its umbilicus. If a pup retains its umbilicus past the first day, this could lead to an overestimate of size at birth. From our experience, umbilical cords are more likely to dry and fall off sooner in arid roosting environments, than in humid roosting environments where the umbilicus sometimes remains attached beyond the first day. When this uncertainty exists, we suggest using the mean and standard deviation of the length of the forearm of pups with attached umbilical cords that show other characteristics of recent birth (e.g., wet skin or neonatal pelage), and then assign one-day-old status to pups that are equal to or less than one standard deviation of these bats.

Evaluating Postnatal Growth Rates

To thoroughly quantify rates of postnatal growth of pups, every effort should be made to identify and capture as many newborn bats as possible—using the criteria described above—and to make repeated recaptures and measurements of marked individuals. For most species and for questions being asked about postnatal growth and development, the best time to capture pups for measurements and for testing developmental stages (e.g., olfactory responses, flight ability) is soon after mothers depart from their roost to feed. This is the ideal time to capture and process pups because the marked bats are easier to find, and also because it causes little disturbance to adults and less disturbance to flightless pups that might be dislodged from their mothers. Once pups are able to fly, it may be necessary to enter the roost during the day to capture marked individuals. While this can cause some disturbance to mothers and pups, the level of disturbance at this time is considerably less because pups are able to fly and are less likely to be dislodged from their natal roosts.

To address questions related to the influence of maternal condition on postnatal growth rates of offspring, it is necessary to capture mother-pup pairs and monitor changes in postnatal growth rates and the body condition of both the mothers and their pups. To conduct such a study, it may be more appropriate to use captive rather than free-ranging bats to avoid disturbing the entire colony in efforts to capture mothers and pups together. Postnatal growth rates can be determined and developmental states assessed from the marked bats that are subsequently recaptured and measured (see below).

In situations where it is not possible to capture newborn bats to document size at birth and to monitor changes in body mass or linear dimensions, marking and measuring pups at some unknown age during the early linear period of postnatal growth and then recapturing and marking them several days later still makes it possible to calculate growth rates. If several bats can be captured, measured,

Figure 14.6. Newborn Brazilian free-tailed bat, *Tadarida brasiliensis*, with attached umbilical cord and placenta. *Photo by N. I. Hristov.*

released, and recaptured in this manner, longitudinal rate of postnatal growth R (e.g., mm/day or g/day) during the linear growth period can be calculated for each bat, using the equation proposed by McOuat and Andrews (1995):

$$R = \frac{(L_2 - L_1)}{(t_2 - t_1)}$$

where L and t are the size and date of capture (1) and recapture (2), respectively.

Based on data on individual growth rates derived in this manner, a mean growth rate during the linear period of postnatal can be calculated. While such data will not provide information needed to describe the complete growth trajectory from birth to asymptotic size, they can provide valuable information for comparing growth rates of different species during the linear period of postnatal growth (e.g., Tuttle and Stevenson, 1982), and for evaluating individual variation in growth rates of the same species at different colonies (e.g., Tuttle, 1975) or between years (Reynolds, 1999; Hood et al., 2002; Reiter, 2004).

Alternatively, when mothers carry their young on nightly feeding bouts, as do foliage-roosting phyllostomids and pteropodids, it may be possible to capture both mothers and newborn young in their day roost (Chaverri and Kunz, 2006). If one or more pups can be captured, marked, and recaptured multiple times, a reference curve can be determined during the linear growth period. Once a reference curve has been derived using linear regression, the initial length of forearm or body mass from other marked bats can be fitted to the reference curve and subsequent measurements of these individuals can be used to describe growth curve beyond the linear period. While this method has limitations, growth curves derived from such data often yield rates indistinguishable from those derived from data based on bats that were marked as new born, measured, and subsequently recaptured (T. H. Kunz, unpublished data).

Most studies on postnatal growth rates of bats have recorded changes in length of forearm and body mass (Fig. 14.7; Appendix 14.1), but other measurable variables have been recorded, including changes in the length of epiphyseal cartilages (e.g., Burnett and Kunz, 1982; Kunz and Anthony, 1982; de Paz, 1986; Kunz and Robson, 1995; Isaac and Marimuthu, 1996; Stern et al., 1997; Hoying and Kunz, 1998; Stern and Kunz, 1998; Rajan and Marimuthu, 1999; Reynolds, 1999; Baptista et al., 2000; Sharifi, 2004a, 2004b; Reiter, 2004; Krochmal and Sparks, 2007).

Kunz and Anthony (1982) quantified postnatal growth rates of free-ranging bats based on a combination of linear changes in the length of forearm and the cartilaginous epiphyseal gaps formed by fourth metacarpal and articulated first phalanx. This method was developed based on observations that the wing elements (primarily the length of forearm, metacarpals, and phalanges) increase linearly during the early period of postnatal growth, including the growth plates (epiphyseal cartilaginous gaps) of the metacarpals and phalanges (Rybár, 1969a, 1969b, 1971; Baagoe, 1977). The length of the forearm is easily measured in the field or laboratory with an acceptable degree of precision (±0.1 mm) using dial calipers. Measured in this manner, the length of the forearm provides the most reliable estimates of early postnatal growth, because it can be measured with a relatively high degree of precision and confidence. Recording the length of forearm repeatedly during the postnatal growth period yields the most reliable data to quantify growth of young bats, and for comparing growth rates with nonlinear models.

Changes in the length of the forearm should be measured until the asymptotic size (adult) is reached so these data can be used for analyses using nonlinear models. Measurements of body mass can also be used in this fashion for comparing growth rates, but because this trait is more variable than length of forearm, or other linear elements, it provides a less precise characterization of postnatal growth and for reliably predicting age from growth curves, owing to the inherent variability of body mass (Kunz and Anthony, 1982). Notwithstanding, changes in body mass during the postnatal period may be an appropriate variable for evaluating changes in body condition and how bats respond to extrinsic variables (e.g., Hoying and Kunz, 1998; Reynolds, 1999; Hood et al., 2002; Reiter, 2004).

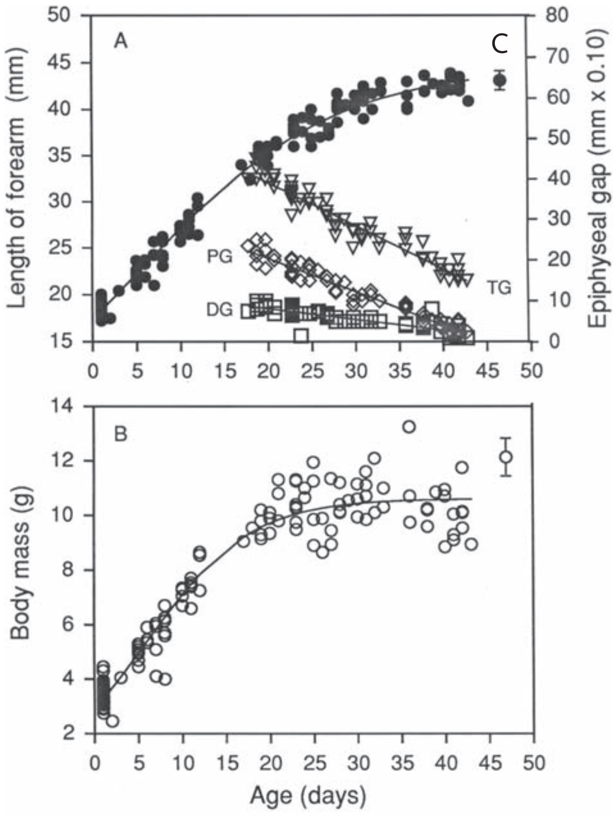

Figure 14.7. Postnatal growth curves of the greater spear-nosed bat, *Phyllostomus hastatus* based on changes in body mass (A), length of forearm (B), and lengths of epiphyseal gaps (C). PG=proximal gap; DG=distal gap; TG=total gap. *From Stern and Kunz, 1998.*

The epiphyseal growth plates of cartilaginous gaps in the long bones also increase linearly during early weeks of postnatal growth (Fig. 14.8), and can be measured with a dissecting microscope fitted with an ocular micrometer (5 mm) until such time as the bony epiphyses fuse with either the diaphysis of the metacarpal or the diaphysis of the first phalanx, respectively. As with length of forearm, growth curves derived from the early phase of linear changes in epiphyseal gaps also can be quantified, although it is often difficult to precisely measure the length of these growth plates or growth plates in very young bats. We recommend using the length of the forearm to characterize postnatal growth during the early linear growth pe-

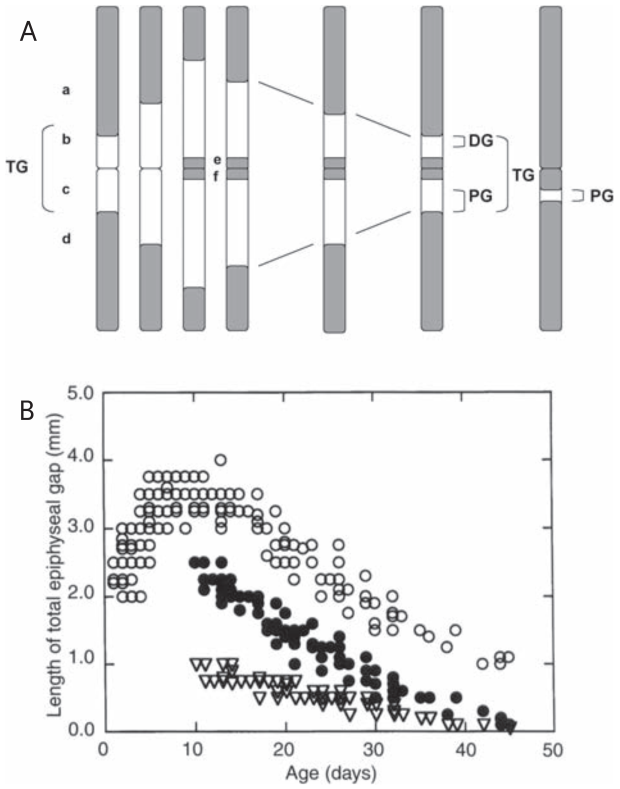

Figure 14.8. Changes in lengths of the total, proximal, and distal gaps (from *Perimyotis subflavus*). A, schematic diagram of total (TG), proximal (PG), and distal (DG) epiphyseal gaps in the fourth finger during the postnatal growth period. B, scatter plot of changes in epiphyseal gap lengths, showing increase in length during the first two weeks of the postnatal period and decreases in lengths in linear trajectories thereafter. *From Hoying and Kunz, 1998*.

riod until such time the growth trajectory becomes nonlinear. Once the length of forearm changes from a linear trajectory to a nonlinear trajectory and approaches adult dimensions, the decrease in length of epiphyseal gaps can be used to quantify growth rates and for developing age-estimation equations (see below).

Changes in the length of growth plates or cartilaginous gaps are quantified by measuring the transilluminated wing and measuring the length of these gaps. During the early linear phase of growth, before the bony epiphyses (the bony ends of long bones) begin to form, a single cartilaginous gap is present, which includes the cartilaginous ends of long bones. Once the bony epiphyses begin to form at the end of these long bones (cartilage cells are replaced by bone cell), two epiphyseal gaps (growth plates) can be observed (Fig. 14.8) as the distal gap of the fourth metacarpal and the proximal gap of the first phalanx of the fourth finger. Before the bony epiphyses begin to form on the phalanges and metacarpals (i.e., before cartilage is replaced by bone cells), the two growth plates macroscopically appear as a single (or total) gap. At this stage, separate growth plates are histologically conspicuous in x-rays (Kunz and Anthony, 1982).Once the bony epiphyses begin to form, two epiphyseal gaps (proximal and distal gaps, PG and DG, respectively) can be measured. Until bone cells replace the epiphyseal cartilages, and the diaphyses of the metacarpal or phalanges fuse with their respective epiphyses, both the proximal and distal gaps can be measured. We recommend taking gap measurements at the fourth metacarpal-phalangeal joint because our previous observations indicate that this joint is the last one in which the epiphyses fuse with the diaphyses.

The total gap of the fourth metacarpal-phalangeal joint is measured from the distal end of the metacarpal diaphysis to the proximal end of the phalangeal diaphysis. Once the epiphyses form, the proximal gap of the metacarpal-phalangeal joint is measured from the distal end of the metacarpal diaphysis to the proximal end of the metacarpal epiphysis. The distal gap is measured from the proximal end of the phalangeal diaphysis to the distal end of the phalangeal epiphysis (Fig. 14.8).

Changes in body mass, length of forearm, and length of total epiphyseal gaps during the postnatal period in *Perimyotis subulatus* (from Hoying and Kunz, 1998) are shown in Fig. 14.9. During the early linear period of postnatal growth, measurements of length of forearm (Fig. 14.9B) are less variable than those of body mass (Fig. 14.9A) or length of the total epiphyseal gap (Fig. 14.9C); thus, length of forearm is used for quantifying growth rates and developing age-estimation equations during this period. Subsequently, the total gap is formed by the epiphyseal cartilages of metacarpal and phalanx and can be measured until such time that either the metacarpal and phalangeal growth plates close visibly (i.e., when the bony diaphysis fuse with the bony epiphysis). From studies on several bat species, we have found that the distal gap is the first to close. The total gap generally increases in length during the early period of growth, but once growth plates begin to form, the total gap, proximal, and distal gaps become shorter (i.e., the cartilaginous growth plates are replaced by bone cells). Once the bony epiphyses form, typically at about 12 to 24 days of age, the total, proximal, and distal gaps begin to decrease linearly depending upon the species (Fig. 14.8B).

Estimating Age of Pups

When young bats are marked and measured on the day of birth and subsequently recaptured and remeasured for length of forearm and epiphyseal gaps, these data not only can be used to quantify growth rates, but they also can be used for estimating the age of pups. The first step toward developing age estimation equations is to run separate linear regressions on length of forearm and epiphyseal gap lengths versus age (days) based on initially marked and recaptured pups. A series of regression and correlation analyses should be run on these two datasets to establish the most appropriate segment for developing age-predictive equations. Growth of the forearm is generally

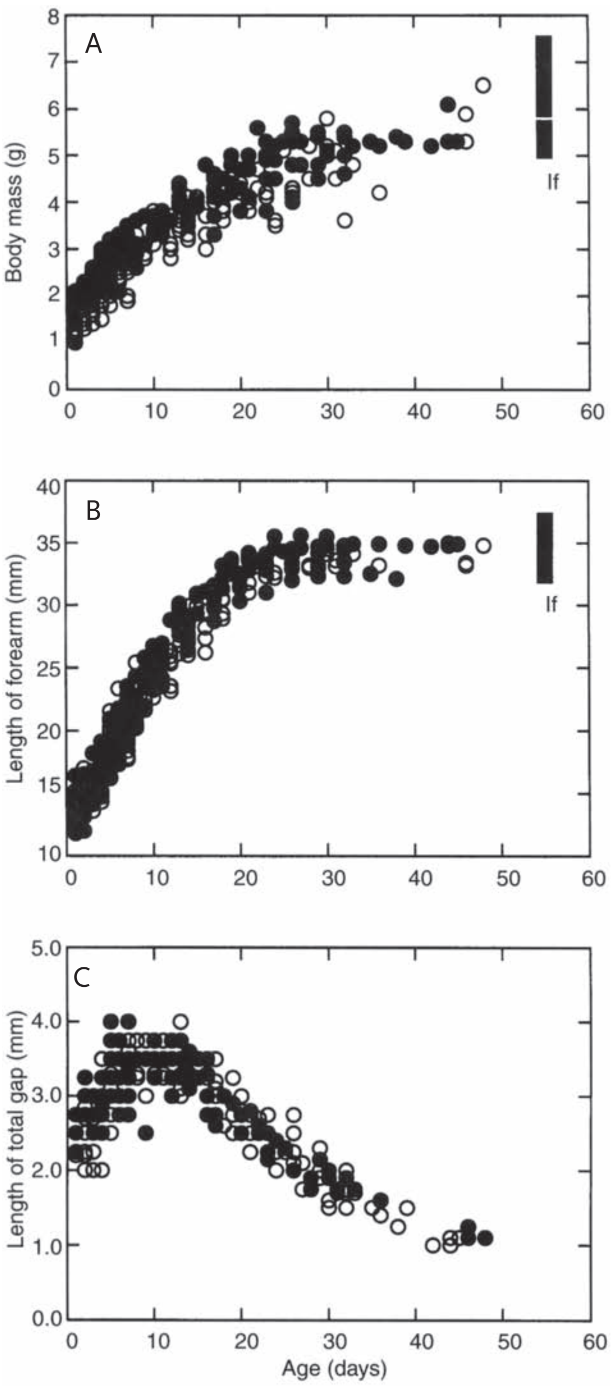

Figure 14.9. Postnatal changes in body mass (A), length of forearm (B), and total epiphyseal gfap length (C) in *Perimyotis subflavus* during the postnatal period. *From Hoying and Kunz, 1998*.

linear for the first two to three weeks (depending upon species), but then it undergoes a nonlinear phase as the length of forearm approaches asymptotic size.

For quantifying the linear growth phase of the length of the forearm, we recommend that the growth data be first inspected visually during the linear growth period, followed by an iterative procedure to delete or add days at the upper end of the curve for selecting a dataset that has the highest *r*-squared values. The regression equation that yields the highest correlation coefficient should be used for estimating linear growth rates of the length of forearm and for developing the most reliable age-estimation equation for this character.

When deriving age estimation equations for the length of epiphyseal gaps, we have found that measurements taken during the early linear phase of growth are highly variable and thus have a higher r-squared value than can be obtained from measurements of length of forearm. Changes in length of the forearm will provide the best trait for estimating age during the early period of postnatal growth (before asymptotic size is reached), and changes in the epiphyseal gap lengths beginning at the age when the changes in the length of the forearm are no longer reliable for estimating age (i.e., when the length of forearm of young bats fall within the range of adult dimensions, Fig. 14.9B) provide the best dataset for estimating age after the asymptotic size of the forearm length has been achieved.

Age-related changes in total, proximal, and distal gaps are generally linear, thus linear regressions, correlations, and confidence intervals can be run on these variables. However, because measurements of total gap are less variable than those recorded for the proximal and distal gaps, the r-squared values are larger (and confidence intervals smaller) for this variable. For this reason, measurements of total gap provide the most reliable estimates of age. Notwithstanding, we recommend taking measurements of proximal and distal gaps, because equations derived from these variables potentially can be used to quantify growth rates beyond what is possible after the total gap measurement can no longer be measured.

Age-estimation Equations

Once the appropriate linear-growth segments of the forearm and epiphyseal gaps have been identified and plotted, age-estimation equations with confidence intervals can be derived by reversing the axes, with the linear measurements on the *x*-axis and age on the *y*- axis (Fig. 14.10). This procedure is the same as using a model II regression (Sokal and Rohlf, 1995), where both variables (age and linear size) are measured with error. The age-estimation equations derived for length of forearm and epiphyseal gaps can then be used to estimate ages of young bats captured for other studies on postnatal development. For example, a female's stage of lactation can be determined by capturing previously unmarked mother-pup pairs, measuring the length of forearm and epiphyseal gaps, and using derived age-estimation equations to estimate the age of the attached pup and hence stage of lactation of the mother.

The value of quantifying linear changes (decrease in the length) in epiphyseal gap measurements during the postnatal period is that age estimation equations derived from these data often double or even triple the age at

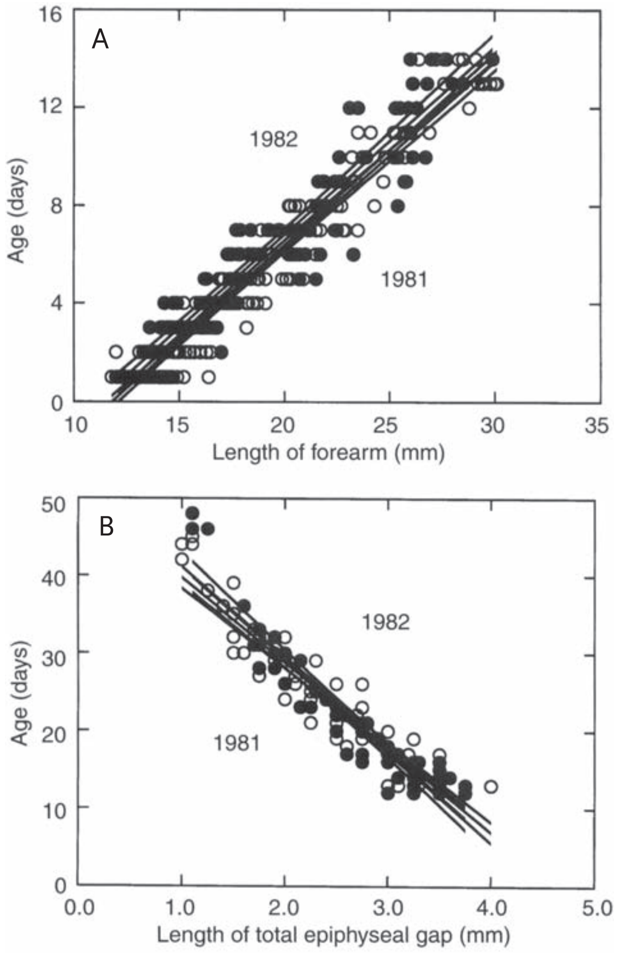

Figure 14.10. Scatter plots of linear growth measurements used to derive age-predictive equations for *Perimyotis subflavus*. A, length of forearm (x-axis) versus age (y-axis); B, length of total epiphyseal gap (x-axis) versus age. *From Hoying and Kunz, 1998.*

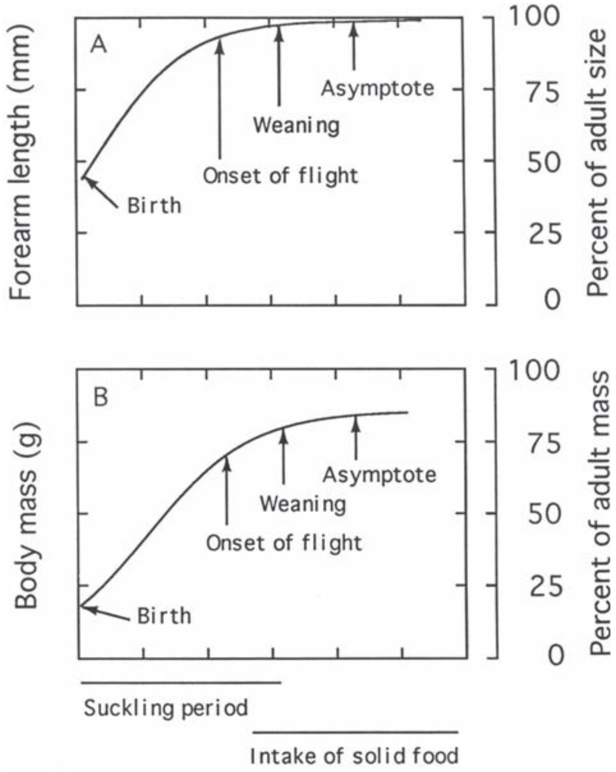

Figure 14.11. A generalized model of postnatal growth in bats, showing the growth rates at birth, onset of flight, and weaning and the asymptotic size for length of forearm (A) and body mass (B) *From Kunz and Hood, 2000.*

which one can confidently estimate the age of pups during the postnatal period. Reliable estimates of age have proven valuable for quantifying other aspects of postnatal development, including changes in body composition (Studier and Kunz, 1995; Reynolds and Kunz, 2000), milk composition (Kunz et al., 1995), muscle development (Powers et al., 1991), wing development (Isaac and Marimuthu, 1996; Stern et al., 1997; Papidimitrou et al., 1996; Priya, 2005), ontogeny of flight (Powers et al., 1991; Priya, 2005), and ontogeny of echolocation (Moss et al., 1997). Using data from length of forearm and total epiphyseal gap length, Krochmal and Sparks (2007) derived nonlinear equations suitable for estimating ages of *Myotis septentrionalis* and *M. lucifugus* during the postnatal period, yielding results with a high degree of confidence, and thus could be used in a similar manner to using linear equations.

Many other investigators have quantified postnatal development of bats' wings in captivity (Jones, 1967; De Fanis and Jones, 1996) and in the field (Kunz, 1973, 1974; O'Farrell and Studier, 1973; Buchler, 1980). Bats captured in the field and subsequently evaluated in the laboratory also can be aged based on changes in the lengths of epiphyseal gaps. Bat researchers benefit from knowing the age of young bats when assessing ontogenetic changes in morphological and behavioral traits. For example, studies on postnatal development of the brain, echolocation, skull dentition, and behavior (reviewed in Adams and Pederson, 2000), could have benefited from using age-estimation equations derived for free-ranging bats. Notwithstanding, one should exercise caution when applying age-estimation equations derived from a single colony for a given species and to others of the same species, or from one year to another, because growth rates are known to vary among years (Hoying and Kunz, 1998; Reynolds, 1999). That stated, the benefits derived even from approximate estimates of age could help advance knowledge about age-related development.

Growth Models and Analytical Considerations

When data on linear measurements of body mass are available for the entire growth period, data can be evaluated using classical growth models (e.g., logistic, von Bertalanffy, and Gompertz). To determine which growth model is the most appropriate to describe growth rates and asymptotic size (Fig. 14.11), results should be evaluated using all available models. Although Kunz (1974) found that the von Bertalanffy model was an appropriate growth model to describe postnatal growth in *Eptesicus fuscus*, subsequent analyses have shown that the logistic model, when compared to either the von Bertalanffy or Gompertz models, was usually the best fit to describe postnatal growth of bats (Kunz and Stern, 1995; Kunz and Robson, 1995; Stern and Kunz, 1998; but see Hughes et al., 1995). To evaluate the effects of extrinsic factors on postnatal growth and development, Kunz and Stern (1995) analyzed growth data only for body mass because this variable is more sensitive to environmental variation than length of forearm (also see Hoying and Kunz, 1998).

Studies on postnatal growth of free-ranging and captive bats ideally should be based on the recapture and measurements of known-age, marked individuals (longitudinal sampling). In field situations, however, successful recaptures of pups may vary depending on the size of the colony, fidelity of mothers and their pups to the roost site, and relative access that investigators have to mothers and pups (Kunz, 1987). For this reason, other methods have been used to quantify postnatal growth and development in free-ranging bats. Limitations of these approaches are briefly described below.

Postnatal growth rates derived from measurements of pups captured on different dates (cross-sectional or cohort samples) usually yield highly biased results compared to longitudinal sampling. Cross-sectional sampling involves collecting young bats on different dates and deriving average increases in linear measurements over the course of the parturition and growth periods. Growth rates derived from this method are significantly lower than those derived from longitudinal sampling (Fig. 14.12). As the growth period progresses, it is often easier to capture smaller and younger pups, and as a result, the empirical growth curves derived from this method produce lower slopes than those based on the recapture of marked individuals. Baptista et al. (2000) demonstrated these differences by analyzing growth data on free-ranging little brown bats (*Myotis lucifugus*) using both longitudinal and cross-sectional sampling methods. They found that cross-sectional samples significantly underestimated growth rates for length of forearm, body mass, and length of total epiphyseal gaps. In fact, growth rates derived from cross-sectional samples underestimated length of forearm and body mass by 40% and 30%, respectively. In a study where cross-sectional sampling was used, corrections based on growth rates of known-age individuals were needed to compensate for potential biases (see Tuttle, 1975). Because no independent comparisons are available to validate this and other growth curves where cross-sectional samples have been used (Short, 1961; Dwyer, 1963; Pagels and Jones, 1974; Thomas and Marshall, 1984), results of these studies are not comparable to studies in which longitudinal sampling has been used (see Baptista et al., 1998), and thus are questionable with respect to characterizing postnatal growth and development of the species being investigated.

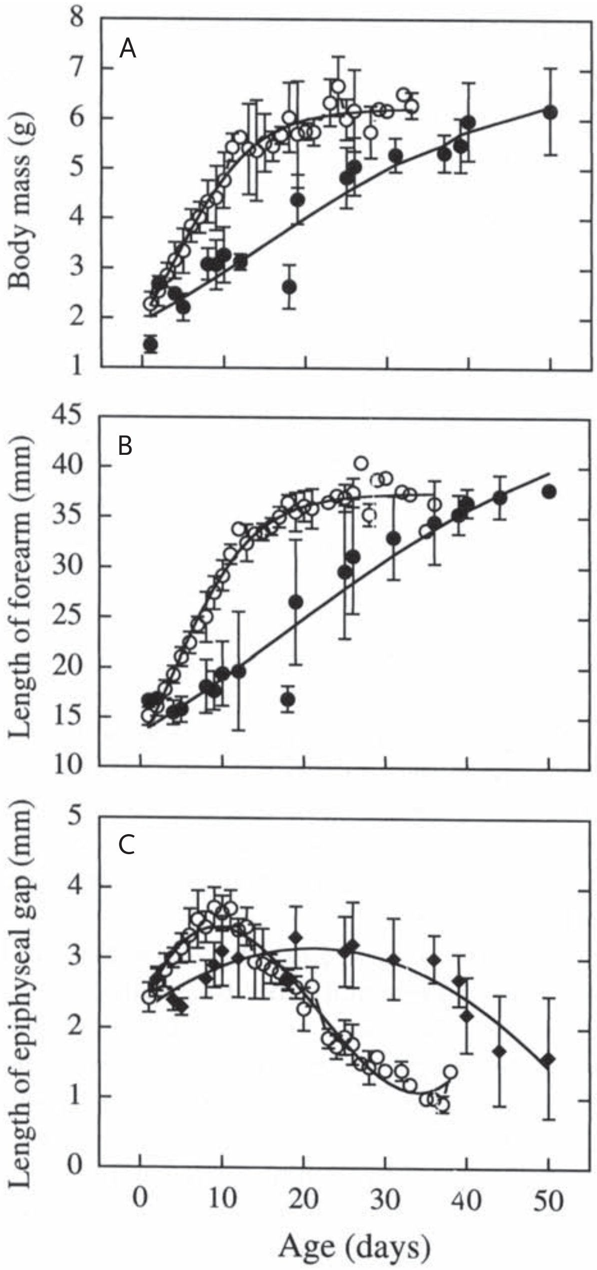

Figure 14.12. Comparison of postnatal growth trajectories of length of forearm and total epiphyseal gap length in the little brown myotis (*Myotis lucifugus*) based on longitudinal (capture-mark-recaptures) and cohort (grab) sampling protocols). Note that the perceived growth rates derived from cohort sampling are significantly lower than those derived from longitudinal sampling. *From Baptista et al. (1998).*

Several investigators have characterized postnatal growth and development of bats by conducting various types of allometric analyses, for example, by comparing one linear variable with that of another or comparing linear variables with body mass (e.g., Dymond, 1936; Sigmund, 1964; Hayward, 1970; Krátky, 1970, 1981; Yokoyama et al., l975, 1979). These analyses provide information on rates of change of one variable relative to another, but they provide little or no information for assessing age-related changes in postnatal growth of these variables.

If studies on growth and development of bats are conducted in captivity, care must be taken to ensure that feeding schedules provide adequate nutrition, appropriate roosting environments, and adequate space to allow bats to exercise (McLean, 1995; Priya, 2005). Thus, postnatal growth rates of some species reared in captivity may differ from those derived from free-ranging populations (Kunz, 1987; Kunz and Sterns, 1995). For example, captive *Antrozous pallidus* and *Pipistrellus pipistrellus* grew faster than individuals of the same species from free-ranging populations (Kunz, 1987), and similar differences were reported for *Epomophorus wahlbergi* (Sowler, 1983). Although differences in roost environment and social conditions invariably exist between captive and free-ranging colonies, contrasting planes of nutrition may account for most of the observed differences. Free-ranging bats also may experience depressed growth rates owing to fluctuating and sometimes unpredictable environmental conditions that reduce the availability of food to mothers or depress metabolic rates of pups and mothers (Hoying and Kunz, 1998).

EVALUATING ONTOGENY OF FLIGHT

Assessing the ontogeny of flight by growing bats requires knowledge of changes in wing size and shape as well as the biomechanics and behavior of flight at different ages. Use of flight tests of known-aged young, combined with changes in their ability to echolocate can provide important insight into how this and other functions during development are linked to form.

Flight Tests

Several studies have quantified changes in wing dimensions during postnatal development in captive bats (e.g., Struhsaker, 1961; Jones, 1967; Davis, 1969; Kleiman, 1969; Joller, 1977; Buchanan, 1987; Hughes et al., 1989), or quantified changes based on estimated ages of young bats captured in the field (Kunz, 1973; O'Farrell and Studier, 1973; Buchler, 1980; Kunz and Anthony, 1982; Jones and Kokurewicz, 1994; Hoying and Kunz, 1998;). Kleiman and Davis (1979) dropped bats from above the ground (height not designated) to assess flight ability in captive *Carollia perspicillata*. They generally found that young bats before the age of 14 days dropped to the ground with wings extended, but made little or no effort to flap their wings. By age of 15–16 days, pups began to flap their wings when released but could not maintain altitude or make turns. By day 18, young *Carollia* could maintain altitude and avoid obstacles and by day 24 had perfected flight. The flight of young bats could be distinguished from adults for several weeks more because they flew more slowly and erratically than adults.

In a study on free-ranging *Myotis lucifugus*, Powers et al. (1991) used a drop-box (Fig. 14.13) to quantify flight ability beginning with first volancy. They found that individuals were capable of drop-evoked flapping behavior at about 10 days of age, of short horizontal flight by about 17 days, and could sustain adult-like flight at about 24 days of age. Buchler (1980) captured free-ranging juvenile *M. lucifugus* flying at about 19–20 days of age. By trapping bats with harp traps as they emerged at dusk from roost sites, Kunz (1973) and Kunz and Anthony (1996) demonstrated that the young bats departed later during the emergence period than older individuals, and that within a period of about 2 weeks, the emergence pattern of young converged on flight patterns that were typical of adults, but generally flew more slowly. The minimum age of young *M. lucifugus* was 15 days when they were first captured in harp traps as they departed from a barn, but the average age was 18 days (Kunz and Anthony, 1996). Kunz (1973) and Kunz and Anthony (1996) suggested that the later departure of bats when young bats first began to fly might provide an opportunity for them to perfect their flight and echolocation skills in the absence of adult bats. Young *Phyllostomus hastatus* began to fly in their seventh week, which correlated with growth and development of wings and reached 84% of adult wing area, 95% of adult aspect ratio, and 89% of adult wingspan (Stern et al., 1997).

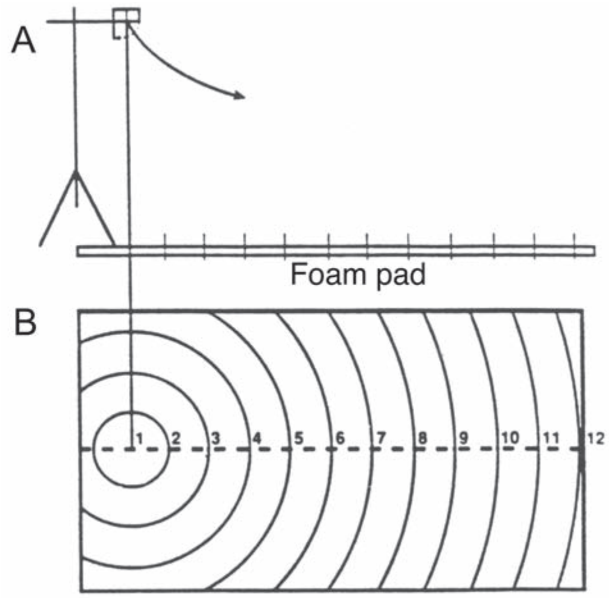

Figure 14.13. Schematic diagram of a launching apparatus used for conducting flight tests to quantify the ontogeny of flight echolocation in the little brown myotis (*Myotis lucifugus*). A, cross-sectional view of apparatus and foam landing pad. B, upper surface of the landing pad, marked off in successive distances from the drop point. *From Powers et al., 1990.*

Assessing Morphological Development of Wings

Wing tracings have been routinely used to evaluate growth and development of the wings of bats and for assessing the ontogeny of flight (e.g., Powers et al., 1991; Hughes et al., 1995; Stern and Kunz 1995; Isaac, and Marimuthu. 1997; Fig. 14.14). Although tracing of wing profiles is in itself a relatively simple task, acquiring standardized images among individuals can be challenging. Standardization and accuracy are especially important for analyses of wing shape, and thus the conditions under which the wing profiles are obtained are critical for obtaining reliable results.

To evaluate morphological wing development, ideally, one should measure each region of the bats' flight membrane. Wing flight membranes can be easily divided into three functional regions (Fig. 14.15):

- The *propatagium* lies posterior to the forearm and extends from the shoulder to the wrist. This membrane forms the leading edge or power portion of the patagium, and fine control of lift can be achieved relative to the angle of attack.
- The *plagiopatagium* lies between the forearm, body, rear leg, and the fifth digit. This membrane reaches its anterior border along the posterior edge of the humerus and ulna. It controls maneuverability, amount of lift, and fine control of flight.
- The *dactylopatagium* stretches between the fifth and first digits. This is the power portion of membrane that generates the majority of force for gross movement.

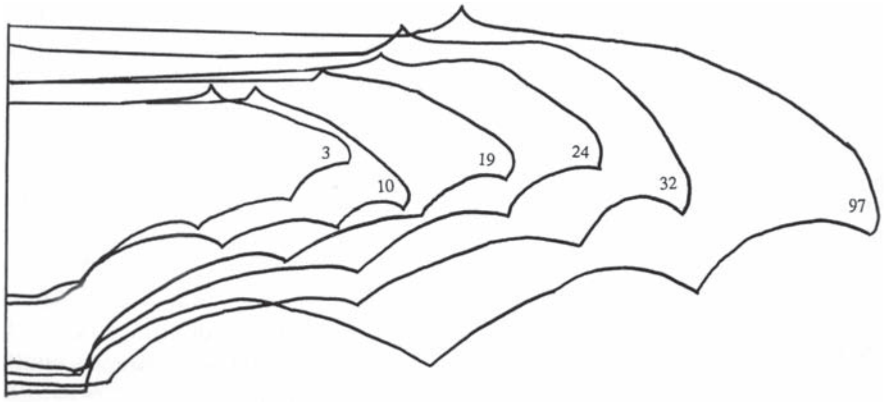

Figure 14.14. Series of wing tracings of the greater spear-nosed bat (*Phyllostomas hastatus*) recorded during the postnatal growth period (numbers indicate age in days). *From Stern et al., 1997.*

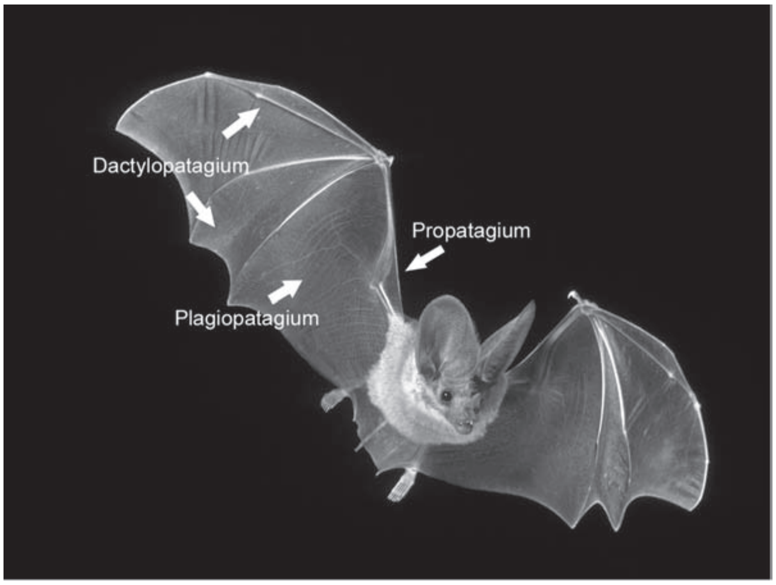

Figure 14.15. Three functional regions of a bat's wing (e.g., *Macrotus californicus*): the propatagium, plagiopatagium, and dactylopatagium. Many species also have a tail membrane, or uropatagium, as is the case for *Macrotus californicus*, shown here. *Photo courtesy of J. S. Altenbach.*

Figure 14.16. Wings of an anesthetized bat pinned to a flat surface for recording wing area and wing elements. *Photo by R. A. Adams.*

Additionally, most bat species also possess a tail membrane, or uropatagium, which extends between the medial borders of the rear legs and in many species encloses the tail vertebrae. The uropatagium is used by bats during flight to increase maneuverability and also by insectivorous species to facilitate the capture of aerial insects.

Tracing the outlines of wings of live individuals in the field or laboratory can pose challenges with respect to standardization and accuracy, making it the least appealing method for gathering such data, especially for analysis of wing shape. When tracing wing areas of live bats, the most effective method is accomplished by restraining the bat and pushing down lightly on the elbow joint, causing the finger bones to extend. Photographing the wing with a digital camera decreases the amount of time that a bat has to be restrained and ultimately provides a more accurate profile for analysis (e.g., such as SigmaScan software, Inc, used to measure and calculate the area of the wing.). Stern et al. (1997) used a procedure developed by Norberg and Rayner (1987) to trace the wings of newly born *Phyllostomas hastatus* that were banded and subsequently retraced at 5-day intervals. Area of the wing was measured from individuals placed venter-down on a sheet of white paper. The right wing was extended perpendicular to the body axis and the trailing edge of the uropatagium was aligned with the body's midline. A mark was made to indicate nosetip and a tracing was made from shoulder to the tip of the calcar. A straight line was drawn from nosetip to calcar to indicate the axis of the body. Each measurement was taken in triplicate using a Keuffel and Esser polar planimeter, averaged, and multiplied by two to give total wing area.

Free-ranging bats also can be anesthetized (see Barnard, this volume; Lollar and Schmidt-French, 1998) so that the wing can be extended, pinned out, and accurately consistently traced or photographed (Fig. 14.16). This method has several disadvantages, as each individual requires about 20 minutes to prepare and trace. The administration of anesthesia under field conditions also can be challenging because of uncertain doses and the fact that bats may revive before tracing can be completed.

Adams (1996a, 1997) captured pregnant female bats and maintained them in the laboratory, and after females gave birth, juveniles were euthanized at various stages of development. Wings were pinned out in a highly precise and uniform manner using a cardboard grid; a protractor was used to measure angles of wing elements. This procedure minimized error and allowed profiles to be drawn from the standardized wing layouts. Although this method represents a best-case scenario for controlling error when collecting wing profiles, in many cases, euthanizing individuals is not an option and one must revert to gathering data from live individuals.

Assessing Changes in Wing Shape and Wing Loading

Variables for assessing growth and development of shape and wing loading are summarized in Box 14.1. Wing loading—the ratio of body mass to wing (surface) area—sets an upper limit on the mass that a bat can effectively carry in flight, whether the additional mass is imposed by a stomach full of food, a transported food item, or a developing fetus. Bats with lower intrinsic wing loadings should be better able to carry extra mass than those with higher wing loadings (Norberg and Fenton, 1988; Norberg and Rayner, 1987). For example, a full-term fetus can increase wing loading in adults by up to 44% over nongravid conditions (Funakoshi and Uchida, 1981; Hoying and Kunz, 1998) and is thus expected to increase the power required to sustain flight (Hayssen and Kunz, 1996).

Wing loading among the Microchiroptera is highly variable, which may reflect their diverse dietary habits and foraging strategies (Hayssen and Kunz, 1996). The highest wing-loading values are found among the molossids and phyllostomids. Members of these families have wing loadings that are similar to those predicted by dimensional analysis and thus may function near the physical limits of dimensional scaling (Hayssen and Kunz, 1996). Vespertilionids and rhinolophids have the lowest wing-loading values relative to body mass, allowing species represented by these families to carry the same proportions of their body mass as molossids and phyllostomids at a lower energetic cost (Hayssen and Kunz, 1996). Therefore, low intrinsic wing loadings among the vespertilionids may be a key factor promoting the evolution of litter sizes greater than one.

For a majority of species, there is a general lack of shape analyses of bat wing development. Analysis of ratios of linear measurements integrates shape and size and has been the norm for analysis of wing shape in adult bats (Farney and Fleharty, 1969; Fenton, 1972; Norberg and Rayner, 1987). Other studies of wing "shape" in bats (Burnett, 1983; Myers, 1978; Williams and Findley, 1979) did not adjust data for independence of size.

Birch (1997) compared wing shapes between adult *Eptesicus fuscus*, *Pipistrellus hesperus*, and *Tadarida brasiliensis* using principle component analysis (PCA) and relative-warp analysis (see also Bogdanowicz, this volume). Al-

BOX 14.1. Parameters for assessing growth and development of the bat wing

Wing span (*S*): Linear distance between tips of the outstretched wings. *Units*: mm or cm. *Methods to calculate*: Has been reported in the literature in several ways: Stern et al. (1997) used two times the distance from the body axis to the wingtip.

Aspect ratio (AR): The ratio of wingspan to wing area. Although sometimes referred to as wing shape (Norberg, 1990), aspect ratio does not measure wing shape directly (Adams, 1998). *Methods to calculate*: Wingspan squared divided by wing area (Aldridge, 1986; Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Stern et al., 1997). *Units*: none.
Hartman (1963) and Smith and Starrett (1979) use *Overall Aspect Ratio* [2 × (length of forearm × 2)^2]/area; *Aspect Ratio of Plagiopatagium*: (length of forearm × 2)^2/(area of plagiopatagium); and *Aspect Ratio of Wingtip*: (length of digit 3 × 2)^2.

Tip index: Vaughan (1970) considered the wing tip of a bat's wing to be the propulsive portion. Findley et al. (1972) measured tip index as ratio of length of digit 3 to length of forearm. A high tip index (2.00) indicates a proportionately long third digit, whereas a low index (1.00) indicates a relatively short wing tip (Smith and Starrett, 1979).

Wing loading (*L*): Body mass of the animal divided by the wing area. *Units*: Newtons per square millimeter or meter (N/mm^2 or N/m^2; Smith and Starrett, 1979). *Methods to calculate*: Body mass divided by wing area (Adams, 1996a). Stern et al. (1997) used body mass times $9.8\,m/s^2$ divided by wing area, where $9.8\,m/s^2$ represents acceleration due to gravity. Hayssen and Kunz (1996) calculated *L* using body mass calculated as length squared divided by area calculated as length squared.

Body mass (BM): Measured in grams (g).

Wing shape: Size-free shape of the wing (no units).

though this study did not focus on ontogeny of wings, this type of analysis can be used effectively to evaluate changes in wing shape in juvenile bats of different age. After determining interlandmark distances and running PCA on these linear dimensions, Birch (1997) calculated decomposition of the thin-plate spline by its relative warps (Bookstein, 1989, 1990, 1991; Birch, 1997). He calculated a mean wing shape from four wing profile photographs of each specimen by decomposing landmarks into triangles scaled to the same baseline. Differences in shape were then retained in the position of the third vertex of comparative triangles. He calculated landmark centroids as the sum of squared distance between the centroid of the form and mean centroid size and mean landmark configuration from the four photographs of each specimen. The Turkey-Kramer multiple comparison test was used to test for differences in centroid size. Plots of landmark centroids (Fig. 14.17) indicate displacement of vectors giving magnitude and direction of landmark movement necessary when comparing wing form among various species.

Adams (1998) integrated linear measurements of skeletal growth with that of landmark portrayals of the truss network in *Myotis lucifugus* (Fig. 14.18; Bookstein, 1990) of the patagium analyzed with PCA. Euthanized bats, each representing a different stage of flight development, were pinned to graph paper in a manner similar to that used in wing tracing. He then established seven standardized landmarks that were easily distinguishable based upon parts of the wing that undergo significant changes during ontogeny (Jones, 1967; Powers et al., 1991; Adams, 1992; Birch, 1997). The seven landmarks were then connected using 13 truss elements representing linear distances between all landmarks, as shown in Figure 14.18. Each landmark was connected to five other landmarks, creating redundancy in the analysis important for accuracy (Bookstein, 1991). A digitizing pad was used to measure distances between all connected landmarks represented by the 13 trusses. Principal component analysis (PCA) on truss element distances was used to analyze the dimensions of size and shape. Truss elements were standardized using "size-out," a procedure that used PC-1 scores to standardize morphometric data. One-way ANOVA was used to test for significant differences in wing shapes between juveniles and subadults. In addition, compensation scores of bone length for each wing element, minus the humerus, were calculated using summed residual scores from bivariate plots. Results indicated compensatory growth (Tumilson, 1990) of wing elements and stasis of patagium shape during growth and development in *Myotis lucifugus* (Adams, 1998).

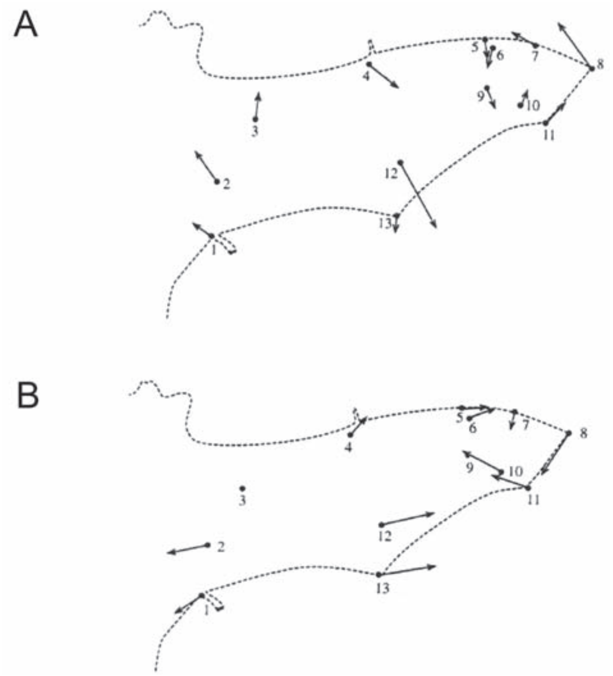

Figure 14.17. Landmark centroids are used in relative warp analysis to depict displacement of vectors that show both the magnitude and direction of movement when wing forms of different species are compared.

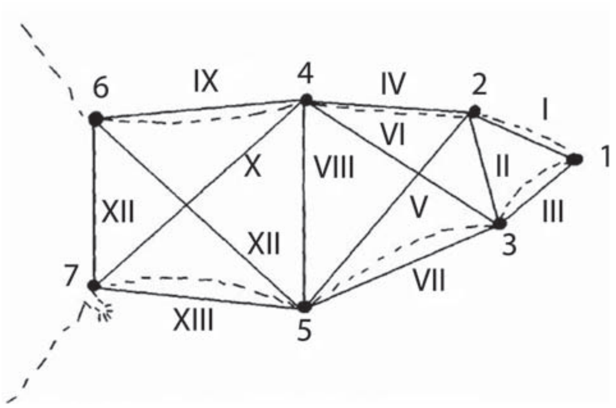

Figure 14.18. Principal components analysis of linear measurements of skeletal growth in the little brown myotis, *Myotis lucifugus*, compared to a truss network of landmarks of the patagium.

Assessing Muscle Development

Gross anatomy of adult flight muscles has been described for several bat species (Vaughan, 1959; Hermanson and Altenbach, 1981; Schutt et al., 1994; Hermanson, 1998). The pectoralis muscle and other flight muscles of bats, unlike most mammals, have a singular function, that being fast-twitch, highly oxidative, contractile properties poorly suited for anaerobic specialization (Brigham et al., 1990), and thus are homogenous in fiber type (Powers et al., 1991; Hermanson et al., 1998). Powers et al. (1991) found that the wet mass of pectoralis and acromiodeltoideus muscles in young *Myotis lucifugus* increased linearly,

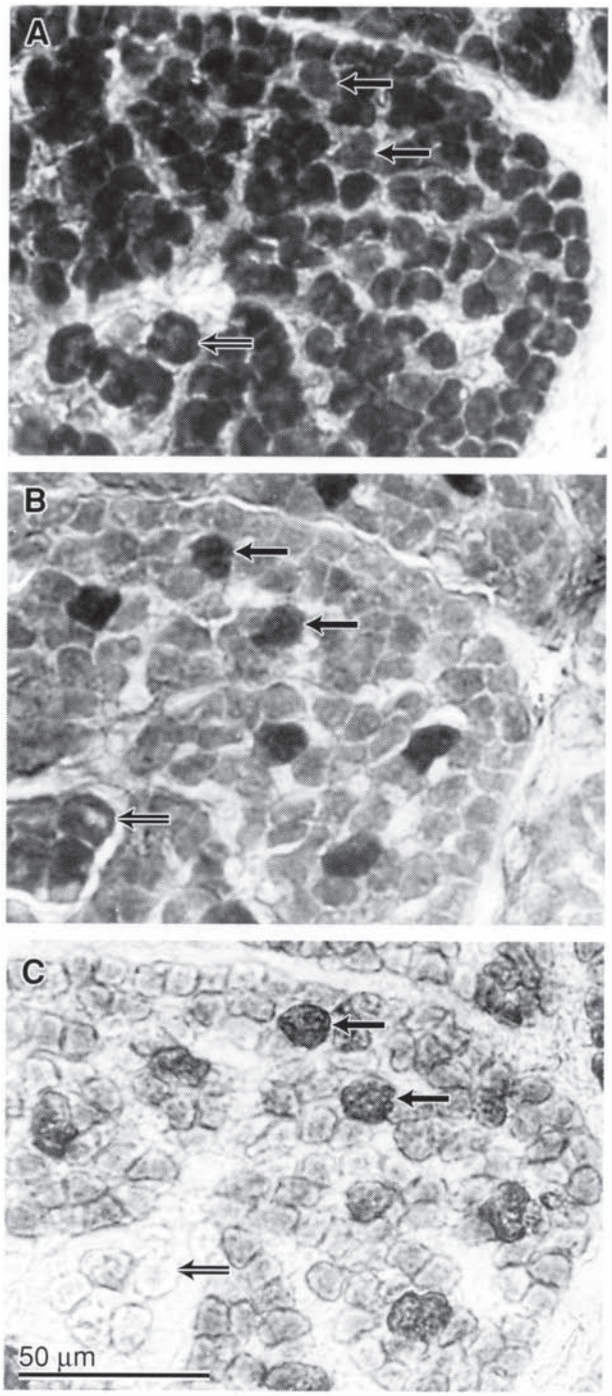

Figure 14.19. Transverse sections of the pectoralis muscle from a 12-hour old little brown myotis, *Myotis* lucifugus, stained for myocin ATPase. A, following alkaline preincubation (pH 10.3); B, following acid preincubation at pH 4.4; C, after reaction with anti-slow (S58) myocin antibody. Type II, presumed fast-twitch fibers, stain darkly, and type I fibers shown not stain following alkaline preincubation. However, at this age, transitional isoforms appear to cause all fibers to react positively in this myosin ATPase reaction. In the acid preincubation myosin ATPase study, all presumed slow-twitch (type I) fibers stained darkly and correlate with serial sections reacted against anti-slow antibodies, including many type I myosin positive fibers. Two type I fibers are indicated with arrows. Note that significant connective tissue continues to infiltrate the space between fibers and muscle fascicles. Some central nuclei are still present (double arrows). *From Hermanson, 2000.*

attaining adult mean values at ages 23 and 26 days, respectively, at about the same age they achieved adult-like flight and echolocation behavior (also see Kunz and Anthony, 1996; Moss et al., 1997). In addition, muscle fibers of the acromiodeltoideus were larger in cross-section than the pectoralis muscle during the postnatal period.

Hermanson (2000) compared the muscle ontogeny of bats to that of other mammals. Late gestational samples of transverse sections of long bone muscles stained for myosine ATPase following acid preincubation at pH 4.3. Transverse sections of pectoralis muscle from a 12-hour old *M. lucifugus* (Fig. 14.19) were also stained for ATPase using several treatments. Samples were stained following alkaline incubation at pH 10.3; following acid preincubation at pH 4.4; and after reaction with anti-slow ($S_5$8) myosin antibody.

Hermanson (2000) demonstrated that in the early prenatal and early postnatal period, type I fibers in *M. lucifugus* that are less than 4 days of age are distributed sporadically in the pectoralis. No type I fibers are found in adults or even in juveniles capable of spontaneous flapping behavior. In hindlimb muscles, however, type I myosin was present in about 10% of the sample. Whether type I fibers in bats are lost during embryological development, as in chick embryos, or are transformed into fast twitch type II fibers remains unknown (McLearn et al., 1995). Schutt et al. (1994) used SDS polycrylamide gel electrophoresis to document the presence of multiple transitional myosin heavy chain isoforms in prenatal and neonatal *Myotis lucifugus*.

FUTURE DIRECTIONS IN RESEARCH ON POSTNATAL GROWTH

Future studies on postnatal growth rates and development in bats should be designed to integrate data on local climate, food availability, maternal diet, milk composition, milk energy yield, nonenergetic parental effort, wing development, flight, and echolocation. Studies should be designed to compare parental effort and postnatal growth and development in species from different geographic areas, different colony sizes, and seasons. We would expect populations that occur in highly seasonal, temperate environments to exhibit higher growth rates than those from subtropical and tropical environments, except that growth rates in extreme latitudes and elevations may be reduced. In temperate climates, we would expect female young to grow faster than males, because the benefits that might confer higher fitness benefits for those born early because females would have more time to reach sexual maturity in their first year. Males typically do not reach sexual maturity until their second year, thus selection would favor higher maternal investment in females than males in temperate, hibernating species. In tropical environments, where food resources are often highly variable in time, space, and quality (including flowers, fruits, and insects), we would expect to find seasonal and intraspecific differences in growth rates in those species that produce two or more litters per year.

Relationships between pup growth, colony size, the thermal environment of roosts, and the development of thermoregulatory capacity of young should be thoroughly investigated. We would expect higher growth rates in individuals that roost in the warmest environments and that maintain elevated body temperatures during the postnatal period. Parental effort and postnatal growth rates in bats should be sensitive to environmental conditions, especially in degraded habitats (which may lead to increased foraging time and reduced energy transfer to pups), and changes in the abundance and availability of food resources (seasonal and interyear variation in insect, fruit, and nectar production). Studies on parental care in bats should be extended to investigate how parental effort is adjusted to variation in benefits to offspring and costs to the parents as reflected in the fitness of individuals. Finally, future studies on postnatal growth and development in bats should focus attention on frugivorous, nectarivorous, sanguivorous, and carnivorous species, and should include mechanisms of mother-pup recognition by acoustic communication, spatial memory, olfactory, and visual cues as well as ontogeny of skeletal traits, flight muscles, echolocation, and foraging behavior.

APPENDIX 14.1

Studies Reporting Postnatal Changes in Body Mass, Length of Forearm, or Epiphyseal Gaps in Captive and Free-ranging Bats

Explanation of symbols. Growth conditions: C=captive; W=wild caught. Diet: F=frugivorous; C=carnivorous; I=insectivorous. Climate: TR=tropical; TE=temperate. Measurements recorded: BM=body mass; FA=length of forearm; EP=epiphyseal gap length. Type: L0=longitudinal; CO=cohort.

Taxa	Growth Condition	Diet	Climate	BM	FA	EP	Type	Reference
Megachiroptera								
Pteropodidae								
Cynopterus brachyotis	C	F	TR	X	X		LO	Kunz and Hood (2000)
Cynopterus sphinx	W	F	TR	X			LO	Krishna and Dominic (1983)
	C	C	TR	X	X	X	LO	Priya (2005)
Epomophorus gambianus	W	F	TR		X		CO	Thomas and Marshall (1984)
Epomophorus wahlbergi	C/W	F	TR		X		LO	Sowler (1983)
Epomops buettikoferi	W	F	TR		X		CO	Thomas and Marshall (1984)
Hypsignathus monstrosus	C	F	TR	X	X		LO	Bradbury (1977b)
Micropteropus pusillus	W	F	TR		X		CO	Thomas and Marshall (1984)
Pteropus hypomelanus	C	F	TR	X	X		LO	Kunz and Hood (2000)
Pteropus poliocephalus	C	F	TR	X	X		LO	Kunz and Hood (2000)
Pteropus pumilus	C	F	TR	X	X		LO	Kunz and Hood (2000)
Pteropus rodricensis	C	F	TR	X	X		LO	Kunz and Hood (2000)
Pteropus scapulatus	C	F	TR	X	X		LO	G.M. O'Brien, pers. comm.
Pteropus vampyrus	C	F	TR	X	X		LO	Kunz and Hood (2000)
Rousettus leschenaulti	C	F	TR	X	X	X	LO	Elangovan et al. (2002)
	C	F	TR	X	X	X	LO	Priya (2005)
Rousettus sp.	C	F	TR		X		LO	Kulzer (1961)
Microchiroptera								
Emballonuridae								
Peropteryx kappleri	W	I	TR	X	X		CO	Giral et al. (1991)
Taphozous longimanus	W	I	TR	X	X		CO	Krishna and Dominic (1983)
Hipposideridae								
Hipposideros terasensis	W	I	T	X	X	X	LO	Cheng and Lee (2002)
Megadermatidae								
Megaderma lyra	C	C	T	X	X	X	LO	Rajan and Marimuthu (1999)
Molossidae								
Molossus molossus	C	I	TR	X	X		LO	Häussler et al. (1981)
Tadarida condolura	C	I	TR		X		LO	Kulzer (1962)
Tadarida brasiliensis cynocephala	W	I			X		CO	Pagels and Jones (1974)
Tadarida brasiliensis mexicana	W	I	TE		X		CO	Short (1961)
Tadarida brasiliensis mexicana	W	I	TE	X	X	X	LO	Kunz and Robson (1995)
Noctilionidae								
Noctilio albiventiris	C	I	TR	X	X		LO	Brown et al. (1983)
Phyllostomidae								
Artibeus jamaicensis	C	F	TR	X	X		LO	Taft and Handley (1991)
Artibeus watsoni	W	F	TR	X	X		LO	Chaverri and Kunz (2006)
Carollia perspicillata	C	F	TR	X	X		LO	Kleiman and Davis (1979)
	W	F	TR	X	X	X	LO	Cosson et al. (1993)
Desmodus rotundus	C	B	TR		X		LO	Schmidt and Manske (1985)
Phyllostomus discolor	C	F	TR	X	X		LO	Rother and Schmidt (1985)
Phyllostomus hastatus	W	F/I	TR	X	X	X	LO	Stern and Kunz (1998)
Rhinolophidae								
Rhinolophus cornutus	W	I	TE		X		LO	Yokoyama and Uchida (1979)
Rhinolophus ferrumequinum	C	I	TE	X	X		LO	Hughes et al. (1995)
	W	I	TE		X		LO	McOuat and Andrews (1995)
	W	I			X		CO	Dietz et al. (2007)
Rhinolophus hipposideros	W	I	TE		X		CO	Gaisler (1960)
	C	I	TE		X		LO	Rybár(1971)
	W	I	TE	X	X		LO/CO	Reiter (2004)
Rhinolophus mehelyi	W	I	TE	X	X	X	LO	Sharifi (2004a)
Vespertilionidae								
Antrozous pallidus	C	I	TE		X		LO	Orr (1954)
	W	I	TE	X	X		LO	Davis (1969)

(continued)

APPENDIX 14.1 (*continued*)

Taxa	Growth Condition	Diet	Climate	BM	FA	EP	Type	Reference
	C	I	TE	X	X		LO	Brown (1976)
	W	I	TE	X	X	X	LO	R. Sidner (pers. comm.)
Eptesicus fuscus	W	I	TE	X	X		LO	Davis (1968)
	W	I	TE	X	X		LO	Kunz (1974)
	W	I	TE	X	X	X	LO	Burnett and Kunz (1982)
	W	I	TE	X	X	X	LO/CO	Baptista et al. (1998)
				X	X	X	LO	Hood et al. (2002)
Eptesicus serotinus	C	I	TE	X	X		LO	Kleiman (1969)
Lasiurus borealis	W	I	TE		X		CO	Stangl et al. (1996)
Lasiurus cinereus	W	I	TE	X	X	X	LO	Kolhler and Barclay (2000)
Miniopterus schreibersii	W	I	TE	X	X		CO	Dwyer (1963)
Miniopterus schreibersii natalensis	W	I	TR	X	X		CO	van de Merwe (1978)
Miniopterus schreibersii	W	I	TE		X		LO	Serra-Cobo (1989)
Myotis adversus	W	I	TE		X		CO	Dwyer (1963)
Myotis blythii	C	I	TE	X	X	X	LO	Sharifi (2004a)
Myotis daubentonii	W	I	TE	X	X		LO	Krátky (1981)
Myotis grisescens	W	I	TE	X	X		LO/CO	Tuttle (1975)
	W	I	TE	X	X		LO/CO	Tuttle (1976)
Myotis macrodactylus	W	I	TE		X		LO	Maeda (1976)
Myotis nattereri	C	I	TE	X	X		LO	Swift (2001)
Myotis lucifugus	W	I	TE	X	X	X	LO	Kunz and Anthony (1982)
	W	I	TE	X	X	X	LO/CO	Baptista et al. (2000)
	W	I	TE	X	X		LO	Reynolds (1999)
	W	I	TE	X	X	X	LO	Krochmal and Sparks (2007)
Myotis myotis	W	I	T	X	X		LO	Krátky (1970)
	W	I	T		X		LO	Joller (1977)
	W	I	TE	X	X	X	LO	de Paz (1986)
Myotis septentrionalis	W	I	TE	X	X	X	LO	Krochmal and Sparks (2007)
Myotis thysanodes	W	I	TE	X	X		LO	O'Farrell and Studier (1973)
Myotis velifer	W	I	TE	X	X		LO	Kunz (1973)
	W	I	TE	X	X	X	LO	Kunz and Robson, unpubl. data)
Nyctalus lasiopterus	C	I	TE	X	X		LO	Maeda (1972)
Nyctalus noctula	C	I	TE		X		LO	Kleiman (1969)
Nycticeius humeralis	C	I	TE	X	X		LO	Jones (1967)
Perimyotis subflavus	W	I	TE	X	X	X	LO	Hoying and Kunz (1998)
Plecotus auritus	C	I	TE	X	X		LO	DeFanis and Jones (1995a)
	C	I	TE	X	X	X	LO	McLean (1995)
Coynorhinus townsendii	W	I	TE		X		LO	Pearson (et al. (1952)
Pipistrellus mimus	W	I	TR	X	X	X	LO	Isaac and Marimuthu (1996)
Pipistrellus pipistrellus	W	I	TE	X	X		LO	Rakhmatulina (1972)
	C	1	TE	X	X			Kleiman (1969)
	W	I	TE	X	X		LO	Boyd and Myhill (1987)
	C	I	TE	X	X		LO	Hughes et al. (1995)
Pipistrellus (Hypsugo) savii	W	I	TE	X	X		LO	Tiunov (1992)
Plecotus auritus	C	I	TE		X		LO	De Fanis and Jones (1995)
Scotophilus heathi	W	I	TR	X	X		LO	Krishna and Dominic (1983)
Vespertilio murinus	C	I	TE		X		LO	Kozhurina (1998)
Vespertilio superans	W	I	TE	X	X		LO	Funakoshi and Uchida (1981)
	W	I	TE	X	X		LO	Tiunov (1989)

ACKNOWLEDGMENTS

We are grateful to the many individuals who produced the original data from which this review was developed. We thank the following students and colleagues who directly contributed their knowledge to make this chapter possible: Edythe Anthony, Chris Burnett, Gloriana Chaverri, Jiri Gaisler, Karen Hoying, Scott Pederson, Simon Robson, Scott Reynolds, April Stern, and Katherine Thibault. Preparation of this paper was made possible by grants from the National Science Foundation and the Lubee Bat Conservancy to THK.

LITERATURE CITED

Adams, R. A. 1992. Stages of development and sequence of bone formation in the little brown bat, *Myotis lucifugus*. Journal of Mammalogy 73: 160–167.

———. 1996a. Onset of flight and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. Journal of Mammalogy 78: 239–246.

———. 1996b. Size-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): is there an ontogenetic niche? Canadian Journal of Zoology 74: 1204–1210.

———. 1997. Onset of volancy and foraging patterns of juvenile little brown bats. Journal of Mammalogy 78: 239–246.

———. 1998. Evolutionary implications of developmental and functional integration in bat wings. Journal of Zoology (London) 246: 165–174.

———. 2000. Wing ontogeny, shifting niche dimensions, and adaptive landscapes. Pp. 275–316, In: Ontogeny, Functional Ecology and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Adams, R. A., and S. C. Pederson. 2000. Ontogeny, Functional Ecology and Evolution of Bats. Cambridge University Press, Cambridge, United Kingdom.

Adams, R. A., and M. Thibault. 2000. A comparative perspective on the ontogeny of flight muscles in bats. Pp. 333–361, In: Ontogeny, Functional Ecology and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Aldridge, H. D. J. N. 1986. Kinematics and aerodynamics of the greater horseshoe bat, *Rhinolophus ferrumequinutn*, in horizontal flight at various flight speeds. Journal of Experimental Biology 126: 479–497.

Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56: 763–778.

Altringham, J. D., and M. B. Fenton. 2003. Sensory ecology and communication in the Chiroptera. Pp. 90–127, In: Bat Ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago.

Anthony, E. L. P., and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58: 775–786.

Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. Oecologia 51: 151–156.

Ansell, W. F. H. 1986. Records of bats in Zambia carrying non-volant young in flight. Arnoldia Zimbabwe 9: 315–318.

Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). Journal of Mammalogy 71: 420–427.

Audet, D., and M. B. Fenton. 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Physiological Zoology 61: 197–204.

Austad, S. N. and K. E. Fischer. 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. Journal of Gerontology 46: B47–53.

Baagoe, H. J. 1977. Age determination in bats (Chiroptera). Videnskabelige Meddelelser fra Danske Naturhhistorisk Forehing 140: 53–93.

Balasingh, J., J. Koliraj, and T. H. Kunz. 1995. Tent construction by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae) in southern India. Ethology 100: 210–229.

Balcombe, J. P. 1990. Vocal recognition of pup by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. Animal Behaviour 39: 960–966.

Balcombe, J. P., and G. F. McCracken. 1992. Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? Animal Behaviour 43, 79–87.

Baptista, T., C. S. Richardson, and T. H. Kunz. 2000. Growth rates and age estimation in free-ranging bats: methodological and analytical considerations. Journal of Mammalogy 81: 709–718.

Barclay, R. M. R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. American Naturalist 144: 1021–1031.

———. 1995. Does energy or calcium availability constrain reproduction by bats? Symposia of the Zoological Society of London 67: 245–258.

Barclay, R. M. R., and R. M. Brigham (eds.). 1996. Bats and Forests Symposium, October 19–21, 1995. Victoria, British Colombia, Canada Research Branch, British Columbia Ministry of Forests, Victoria, British Columbia Working Paper No. 23.

Barclay, R. M. R., and L. D. Harder. 2003. Life histories of bats; life in the slow lane. Pp. 209–256, In: Bat Ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago.

Barclay, R. M. R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–60, In: Bats in Forests: Conservation and Management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore.

Bartholomew, G. A, P. Leitner, and J. E. Nelson. 1964. Body temperature, oxygen consumption and heart rate in three species of Australian flying foxes. Physiological Zoology 37: 179–188.

Bassett, J. E. 1984. Litter size and postnatal growth rate in the pallid bat, *Antrozous pallidus*. Journal of Mammalogy 65: 317–319.

Beecher, M. D. 1982. Signature systems and kin recognition. American Zoologist 22: 477–490.

Begum, K. M., and K. M. Alexander. 1993. Specialized skin glands of behavioral relevance in the microchiropteran bat, *Megaderma lyra*. Bat Research News 34: 11–12.

Bhat, H. R., and T. H. Kunz. 1995. Fruit and flower clusters used as roosts by the short-nosed fruit bat, *Cynopterus sphinx*, near Pune, India. Journal of Zoology (London) 235: 597–604.

Bhatnagar, K. P. 1980. The chiropteran vomernasal organ: its relevance to the phylogeny of bats. Pp. 289–316, In: Proceedings 5th International Bat Research Conference (D. E. Wilson and A. L. Gardner, eds.). Texas Tech Press, Lubbock, Texas.

Bielby, J., G. M. Mace, O. R. P. Bininda-Emonds, M. Cardillo, J. L. Gittleman, K. E. Jones, C. D. L. Orme, and A. Purvis. 2007. The fast-slow continuum in mammalian life history: an empirical reevaluation. American Naturalist 169: 748–757.

Birch, J. M. 1997. Comparing wing shape of bats: the merits of principal-components analysis and relative-warp analysis. Journal of Mammalogy 78: 1187–1198.

Bishop, C. M., G. Jones, C. M. Lazarus, and P. A. Racey. 1992. Discriminate suckling in pipistrelle bats is supported by DNA fingerprinting. Molecular Ecology 1: 255–258.

Bloss, J., R. E. Acree, J. M. Bloss, W. R. Hood, and T. H. Kunz. 2002. Colony recognition in big brown bats, *Eptesicus fuscus*, using olfactory cues: behavioral and chemical analyses. Journal of Chemical Ecology 28: 799–814.

Bonaccorso, F. B. 1998. Bats of Papua New Guinea. Conservation International, Washington, DC.

Bookstein, F. L. 1989. Principal warps: thin-plate spline and the decomposition of deformations. IEEE Transaction on Pattern Analysis and Machine Intelligence 11: 567–585.

———. 1990. Introduction to methods for landmark data. Pp. 215–225, In: Proceedings of the Michigan Morphometrics Workshop (F. J. Rohlf and F. L. Bookstein, eds.). Special Publication No. 2. University of Michigan Museum of Zoology, Ann Arbor, Michigan.

———. 1991. Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge University Press, Cambridge, United Kingdom.

Boyce, M. S. 1979. Seasonality and patterns of natural selection for life histories. American Naturalist 114: 569–583.

Boyd, I. I., and D. G. Myhill. 1987. Variations in the post-natal growth of pipistrelle bats (*Pipistrellus pipistrellus*). Journal of Zoology (London) 213: 750–755.

Boughman, J. W. 1998. Vocal learning by greater spear-nosed bats. Proceedings of the Royal Society of London, Series B 265: 227–233.

Bradbury, J. W. 1977a. Social organization and communication. Pp. 1–72, In: Biology of Bats, Volume 3 (W. A. Wimsatt, ed.). Academic Press, New York.

———. 1977b. Lek mating behaviour in the hammer-headed bat. Zietschrift für Tierpsychologie 45: 225–255.

Bradbury, J. W., and L. H. Emmons. 1974. Social organization in some Trinidad bats. I. Emballonuridae. Zietschrift für Psychologie 36: 137–183.

Bradshaw, G. V. R. 1962. Reproductive cycle of the California leaf-nosed bat, *Macrotus californicus*. Science 136: 644–646.

Brigham, R. M., and A. C. Brigham. 1989. Evidence for association between a mother and its young during and after foraging. American Midland Naturalist 121: 205–207.

Brigham, R. M., J. E. Cebek, J. E. and M. B. C. Hickey. 1989. Intraspecific variation in the echolocation calls of two species of insectivorous bats. Journal of Mammalogy 70: 426–428.

Brigham, R. M., C. D. Ianuzzo, and M. B. Fenton. 1990. Histochemical and biochemical plasticity of muscle fibers in the little brown bat (*Myotis lucifugus*). Journal of Comparative Physiology B 160: 183–186.

Brosset, A. 1962a. The bats of central and western India. Pt. 1. Journal Bombay Natural History Society 59: 1–57.

———. 1962b. The bats of central and western India. Pt. 3. Journal Bombay Natural History Society 59: 707–746.

———. 1969. Researches sur la biologie des Chiropteres troglophiles dans la Nord-est du Gabon. Biologica Gabonica 5: 93–116.

Brown, P. L. 1976. Vocal communication in the pallid bat, *Antrozous pallidus*. Zietschrift für Psychologie 41: 34–54.

Brown, P. L., A. D. Grinnell, and J. E. Harrison. 1978. The development of hearing in the pallid bat, *Antrozous pallidus*. Journal of Comparative Physiology 126: 169–182.

Brown, P. L., T. W. Brown, and A. D. Grinnell. 1983. Echolocation, development and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. Behavioral Ecology and Sociobiology 13: 287–298.

Buchanan, G. D. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56: 763–778.

Buchler, E. R. 1980. Development of flight, foraging and echolocation in the little brown bat (*Myotis lucifugus*). Behavioral Ecology and Sociobiology 6: 211–218.

Burnett, C. D. 1983. Geographic and secondary sexual variation in the morphology of *Eptesicus fuscus*. Annals of the Carnegie Museum of Natural History 52: 139–162.

Burnett, C. D., and P. V. August. 1981. Time and energy budgets for day-roosting in a maternity colony of *Myotis lucifugus*. Journal of Mammalogy 62: 758–766:

Burnett, C. D., and T. H. Kunz. 1982. Growth rates and age estimation in *Eptesicus fuscus* and comparison with *Myotis lucifugus*. Journal of Mammalogy 63: 33–41.

Campbell, P., N. M. Reid, A. Zubaid, A. M. Adnan, and T. H. Kunz. 2006. Comparative roosting ecology of *Cynopterus* (Chiroptera: Pteropodidae) fruit bats in peninsula Malaysia. Biotropica 38: 725–734.

Carter, T. C., and J. M. Menzel. 2007. Behavior and day-roosting ecology of North American foliage-roosting bats. Pp 61–81, In: Conservation and Management of Bats in Forests (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore.

Case, T. J. 1978. On the evolution and adaptive significance of post-natal growth rates in terrestrial vertebrates. Quarterly Review of Biology 53: 243–282.

Charnov, E. L. 2001. Evolution of mammal life histories. Evolutionary Ecology Research 3: 531–535.

Charnov, E. L., and S. K. Morgan. 2006. The offspring-size/clutch-size trade-off in mammals. American Naturalist 167: 578–582.

Chaverri, G., and T. H. Kunz. 2006. Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). Journal of Zoology (London) 270: 650–656.

Cheng, H.-C., and L.-L. Lee. 2002. Postnatal growth, age estimation, and sexual maturity in the Formosan leaf-nosed bat (*Hipposideros terasensis*). Journal of Mammalogy 83: 785–793.

Cosson, J.-F., F. Rodolphe, and M. Pascal. 1993. Détermination de l'âge individuel, croissance post-natale et ontogenèse précoce de *Carollia perspicillata* (L. 1758) (Chiroptera, Phyllostomidae). Mammalia 57: 565–578.

Costa, D. P., B. J. Le Boeuf, A. C. Huntley, and C. L. Ortiz. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. Journal of Zoology (London) 209: 21–33.

Crichton, E. G., and P. H. Krutzsch (eds.). 2000. Reproductive Biology of Bats. Academic Press, San Francisco.

Daly, M. 1979. Why don't males lactate? Journal of Theoretical Biology 78: 325–345.

Davis, R. 1969. Growth and development of young pallid bats *Antrozous pallidus*. Journal of Mammalogy 50: 729–736.

———. 1970. Carrying young by flying female North American bats. American Midland Naturalist 83: 186–196.

Davis, R. B., C. F. Herreid II, and H. L. Short. 1962. Mexican free-tailed bats in Texas. Ecological Monographs 32: 311–346.

Davis, W. H., R. W. Barbour, and M. D. Hassell. 1968. Colonial behavior of *Eptesicus fuscus*. Journal Mammalogy 49: 44–50.

Dechmann, D. K. N., E. K. V. Kalko, B. König, and G. Kerth. 2005. Mating system of a Neotropical roost-making bat: the white-throated, round-eared bat, *Lophostoma silvicolum* (Chiroptera: Phyllostomidae). Behavioral Ecology and Sociobiology 58: 316–325.

DeFanis, E., and G. Jones. 1995a. Post-natal growth, mother-infant interactions, and development of vocalizations in the vespertilionid bat, *Plecotus auritus*. Journal of Zoology (London) 235: 85–97.

———. 1995b. The role of odour in the discrimination of conspecifics by pipistrelle bats. Animal Behaviour 49: 835–839.

———. 1996. Allomaternal care and recognition between mothers and young pipistrelle bats (*Pipistrellus pipistrellus*). Journal of Zoology (London) 240: 781–787.

De Paz, O. 1986. Age estimates and postnatal growth in the mouse bat *Myotis myotis* (Borkhausen 1797) in Guadalajara, Spain. Mammalia 50: 243–251.

Dietz, C, I. Dietz, and B. M. Siemers. 2007. Growth of horseshoe bats (Chiroptera: Rhinolophidae) in temperate continental conditions and the influence of climate. Mammalian Biology 72: 129–144.

Dwyer, P. D. 1963. The breeding biology of *Miniopterus schreibersii blepotis* (Temminck) (Chiroptera) in north-eastern New South Wales. Australian Journal of Zoology 11: 219–240.

———. 1964. Seasonal changes in activity and weight of *Miniopterus schreibersii blepotis* (Chiroptera) in northeastern New South Wales. Australian Journal of Zoology 12: 52–59.

———. 1970. Social organization in the bat, *Myotis adversus*. Science 168: 1006–1008.

Dwyer, P. D., and E. Hamilton-Smith. 1965. Breeding cave and maternity colonies of the bent-winged bat in south-eastern Australia. Helictite 4: 3–21.

Dymond, J. R. 1936. Life history notes and growth studies on little brown bats, *Myotis lucifugus lucifugus*. Canadian Field-Naturalist 50: 114–116.

Eales, L. A., D. J. Bullock, and P. J. B. Slater. 1988. Shared nursing in captive pipistrelle bats (*Pipistrellus pipistrellus*)? Journal of Zoology (London) 216: 584–587.

Elangovan, V., H. Raghurum, E. Y. S. Priya, and G. Marimuthu. 2002. Postnatal growth, age estimation and development of foraging behavior in the fulvus fruit bat *Rousettus leschenaulti*. Journal of Biosciences 27: 695–702.

Ernest, S. K. M. 2003. Life history characteristics of non-volant placental mammals. Ecology 84: 3401 (Ecological Archives E084–093).

Esser, K.-H. 1994. Audio-vocal learning in a non-human mammal: the lesser spear-nosed bat *Phyllolstomus discolor*. NeuroReport 5: 1718–1720.

Esser, K.-H., and U. Schmidt. 1989. Mother-infant communication in the lesser spear-nosed bat, *Phyllostomus discolor* (Chiroptera, Phyllostomidae): evidence for acoustic learning. Ethology 82: 156–168.

Farney, J. P., and E. D. Fleharty. 1969. Aspect ratio, loading, wing span, and membrane areas of bats. Journal of Mammalogy 50: 362–367.

Fenton, M. B. 1972. The structure of aerial-feeding bat faunas as indicated by ears and wing elements. Canadian Journal of Zoology 50: 287–296.

———. 1985. Communication in the Chiroptera. Indiana University Press, Bloomington.

———. 1994. Assessing signal variability and reliability: "to thine own self be true." Animal Behaviour 47: 757–764.

Fenton, M. B., J. J. Belwood, J. H. Fullard, and T. H. Kunz. 1976. Responses of *Myotis lucifugus* (Chiroptera: Vespertilionidae) to distress calls of conspecifics and to other sounds. Canadian Journal of Zoology 54:1443–1448.

Francis, C. M., E. L. P. Anthony, J. A. Brunton, and T. H. Kunz 1994. Lactation in male fruit bats. Nature 367: 691–692.

Fujita, M. 1986. A latitudinal comparison of growth and development in the little brown bat, *Myotis lucifugus*, with implications for geographic variation in adult morphology. Ph.D. diss., Boston University, Boston, Massachusetts.

Funakoshi, K., and T. A. Uchida. 1981. Feeding activity during the breeding season and post-natal growth in the Namie's frosted footed bat, *Vespertilio superans superans*. Japanese Journal of Ecology 31: 67–77.

Gaisler, J. 1960. Postnatal Entwicklung der Kleinen Hugeisennase (*Rhinolophus hipposideros*) unter naturlichen Bedingungen. Symposia Theriologica 1960: 429–444.

Gelfand, D. L., and G. F. McCracken. 1986. Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). Animal Behaviour 34: 1078–1096.

Giral, G. E., M. S. Alberico, and L. M. Alvaré. 1991. Reproduction and social organization in *Peropteryx kappleri* (Chiroptera, Emballonuridae) in Colombia. Bonner Zoologische Beitraege 42: 225–236.

Gittleman, J. L., and O. T. Oftedal. 1987. Comparative growth and lactation energetics in carnivores. Symposia of the Zoological Society of London 57: 41–77.

Gopukuman, N., P. T. Nathan, P. S. Doss, A. Prakash, K. Emmanuel, J. Balasingh, G. Marimuthu, and T. H. Kunz. 2003. Early ontogeny of foraging behavior in the short-nosed fruit bat *Cynopterus sphinx* (Megachiroptera): preliminary results. Mammalia 67: 139–145.

Gould, E. 1971. Studies of maternal-infant communication and development of vocalization in the bats *Myotis* and *Eptesicus*. Communications in Behavioral Biology 5: 263–313.

———. 1975. Experimental studies on the ontogeny of ultrasonic vocalizations in bats. Developmental Psychology 8: 333–346.

———. 1977. Echolocation and communication. Pp. 247–279, In: Biology of Bats of the New World Family Phyllostomatidae, Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Texas Tech University Press, Lubbock, Texas.

Grinevitch, L., S. L. Holroyd, and R. M. R. Barclay. 1995. Sex difference in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. Journal of Zoology (London) 235: 301–309.

Gubernick, D. J., and P. H. Klopfer (eds.). 1981. Parental Care in Mammals. Plenum Press, New York.

Gustin, M. K., and G. F. McCracken. 1987. Scent recognition between females and pups in the bat *Tadarida brasiliensis mexicana*. Animal Behaviour 35: 13–19.

Habersetzer, J., and G. Marimuthu. 1986. Ontogeny of sounds in the echolocating bat *Hipposideros speoris*. Journal of Comparative Physiology A 158: 247–257.

Hamilton, I. M., and R. M. R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). Canadian Journal of Zoology 72: 744–749.

———. 1998. Ontogenetic influences on foraging and mass accumulation by big brown bats (*Eptesicus fuscus*). Journal of Animal Ecology 67: 930—940.

Hanwell, A., and M. Peaker. 1977. Physiological effects of lactation on the mother. Symposia of the Zoological Society of London 41: 297–311.

Hartman, F. A. 1963. Some flight mechanisms of bats. Ohio Journal of Science. 63:59–65.

Harvey, P. H., and A. F. Read. 1988. How and why do mammalian life histories vary? Pp. 213–232, In: Evolution of Life Histories of Mammals (M. S. Boyce, ed.). Yale University, New Haven, Connecticut.

Häussler, V. U., E. Möller, and U. Schmidt. 1981. Zur haltung and jugendentwicklung von *Molossus molossus* (Chiroptera). Zeitschrift für Säugetierkunde 46: 337–351.

Hayssen, V., and T. H. Kunz. 1996. Allometry of litter mass in bats: comparisons with respect to maternal size, wing morphology, and phylogeny. Journal of Mammalogy 77: 476–490.

Hayssen, V., A. van Tienhoven, and A. van Tienhoven. 1993. Asdell's Patterns of Mammalian Reproduction. Cornell University Press, Ithaca, New York.

Hayward, B. J. 1970. The natural history of the cave bat, *Myotis velifer*. Western New Mexico Research in Science 1: 1–74.

Hermanson, J. W. 1998. Chiropteran muscle biology: a perspective from molecules to function. Pp. 127–139, In: Bat Biology and Conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution, Washington, DC.

———. 2000. A comparative perspective on the ontogeny of flight in bats. Pp. 362–392, In: Ontogeny, Functional Ecology and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Hermanson, J. W., and J. S. Altenbach. 1981. Functional anatomy of the primary downstroke muscles in the pallid bat, *Antrozous pallidus*. Journal of Mammalogy 62: 795–800.

Hermanson, J. W., and K. T. Wilkins. 1996. Pre-weaning mortality in a Florida nursery roost of *Myotis austroriparius* and *Tadarida brasiliensis*. Journal of Mammalogy 67: 751–754.

Hermanson, J. W., J. M. Ryan, M. A. Cobb, J. Bentley, and W. A. Schutt, Jr. 1998. Histochemical and electrophoretic analysis of the primary flight muscle of several phylostomid bats. Canadian of Zoology 76: 1983–1999.

Herreid, C. F., II. 1967. Temperature regulation, temperature preferences, tolerance, and metabolism of young and adult free-tailed bats. Physiological Zoology 40: 1–22.

Hewison, A. J. M., J.-M. Gaillard, P. Kjellander, C. Toïgo, O. Liberg, and D. Delorme. 2005. Big mothers invest more in daughters: reversed sex allocation in a weakly polygynous mammal. Ecology Letters 8: 430–437.

Hodgkison, R., S. T. Balding, A. Zubaid, and T. H. Kunz. 2003. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata*, Thomas (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. Journal of Tropical Ecology 19: 667–676.

Hofer, M. A. 1981. Parental contribution to the development of their offspring. Pp. 77–116, In: Parental Care in Mammals (D. J. Gubernick and P. H. Klopfer, eds.). Plenum Press, New York.

Holroyd, S. L. 1993. Influences of some extrinsic and intrinsic factors on reproduction by big brown bats (*Eptesicus fuscus*) in southeastern Alberta. M.Sc. thesis, University of Calgary, Alberta, Canada.

Hood, W. H., J. Bloss, and T. H. Kunz. 2002. Intrinsic and extrinsic sources of variation in size at birth and rates of postnatal growth in the big brown bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Journal of Zoology (London) 258: 355–363.

Hoying, K. M., and T. H. Kunz. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus*. Journal of Zoology (London) 45: 15–27.

Hughes, P., and J. M. V. Rayner. 1993. The flight of pipistrelle bats *Pipistrellus pipistrellus* during pregnancy and lactation. Journal of Zoology (London) 230: 541–555.

Hughes, P., J. M. V. Rayner, and G. Jones. 1995. Ontogeny of "true" flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. Journal of Zoology (London) 236: 291–318

Hughes, P. M., J. R. Speakman, G. Jones, and P. A. Racey. 1989. Suckling behavior in the pipistrelle bat (*Pipistrellus pipistrellus*). Journal of Zoology (London) 219: 665–670.

Huibregtse, W. H. 1966. Some chemical and physical properties of bat milk. Journal of Mammalogy 47: 551–554.

Isaac, S., and G. Marimuthu. 1996. Postnatal growth and age estimation in the Indian pygmy bat *Pipistrellus mimus*. Journal of Mammalogy 77: 199–204.

———. 1997. Development of the wing in the Indian pygmy bat, *Pipistrellus mimus*. Journal of Bioscience 22: 193–2002.

Jayaprakash, M., and K. M. Alexander. 1993. Chemosignal eliciting specialized skin glands of behavioural relevance of the megachiropteran bat, *Pteropus giganteus*. Bat Research News 34: 23 (Abstract).

Joller, V. H. 1977. Zur Ontogenese von *Myotis myotis*. Borkhausen (Verglichen mit Jener von *Acomys cahirinus dimidiatus*). Naturforschende Gesellschaft (Basel), 86: 87–151.

Jones, C. 1967. Growth, development, and wing loading in the evening bat, *Nycticeius humeralis* (Rafinesque). Journal of Mammalogy 48: 1–19.

———. 2000. The ontogeny of behavior in bats: a functional perspective. Pp. 362–392, In: Ontogeny, Functional Ecology and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Jones, G., and R. D. Ransome. 1993. Echolocation calls of bats are influenced by maternal effects and change over a lifetime. Proceedings of the Royal Society of London, Series B 252: 125–128.

Jones, G., and T. Kokurewicz. 1994. Sex and age variation in echolocation calls and flight morphology of Daubenton's bats *Myotis daubentonii*. Mammalia 58: 51–50.

Jones, G., P. M. Hughes, and J. M. V. Rayner. 1991. The development of vocalizations in *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during post-natal growth and the maintenance of individual vocal signatures. Journal of Zoology (London) 225: 71–84.

Jones, G., T. Gordon, and T. Nightingale. 1992. Sex and age differences in the echolocation calls of the lesser horseshoe bat, *Rhinolophus hipposideros*. Mammalia 56: 189–193.

Jones, G., M. Morton, P. M. Hughes, and R. M. Budden. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. Journal of Zoology (London) 230: 385–400.

Jones, G., P. Laurent Duverge, and R. D. Ransome. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symposia of the Zoological Society of London 67: 309–324.

Kalko, E. K. V., K. Ueberschaer, D. Dechmann. 2006. Roost structure, modification, and availability in the white-throated round-eared bat, *Lophostoma silvicolum* (Phyllostomidae) living in active termite nests. Biotropica 38: 398–404.

Keeler, J. O., and E. H. Studier. 1992. Nutrition in pregnant big brown bats (*Eptesicus fuscus*) feeding on June beetles. Journal of Mammalogy 73: 426–430.

Kirkwood, J. K. 1985. Patterns of growth in primates. Journal of Zoology (London) 205: 1123–1136.

Kleiman, D. G. 1969. Maternal care, growth rate, and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. Journal of Zoology (London) 157: 187–211.

Kleiman, D. G., and T. M. Davis. 1979. Ontogeny and maternal care. Pp. 377–402, In: Biology of Bats of the New World Family Phyllostomatidae, Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University, Lubbock, Texas.

Koehler, C. E., and R. M. R. Barclay. 1988. The potential for vocal signatures in the calls of young hoary bats (*Lasiurus cinereus*). Canadian Journal of Zoology 66: 1982–1985.

———. 2000. Postnatal growth and breeding biology of the hoary bat (*Lasiurus cinereus*). Journal of Mammalogy 81: 234–244.

Kozhurina, E. I. 1998. Early postnatal ontogeny and main periods of the development in parti-colored bats *Vespertilio murinus* (Chiroptera: Vespertilionidae). Folia Zoologica 48: 33–48.

Krátky, J. 1970. Postnatale Entwicklung der des Grossmausohrs, *Myotis myotis* (Borkhausen 1797). Vestnik Ceskoslovenské Spolecnosti Zoologichké 34: 202–218.

———. 1981. Postnatale Entwicklung der Wasserfledermaus, *Myotis daubentoni* Kuhl 1819 und bisherige Kenntnis dieser Problematik im Rahmen der Unterordnung Microchiroptera (Mammalia: Chiroptera). Folia Musei Rerum Naturalium Bohemiae Occidentalis 16: 3–34.

Krebs, J. R., and N. B. Davies. 1991. An Introduction to Behavioural Ecology. Blackwell, Scientific Publications, Oxford, United Kingdom.

Krishna, A., and C. J. Dominic. 1983. Growth of young and sexual maturity in three species of Indian bats. Journal of Animal Morphology and Physiology 30: 162–168.

Krochmal, A. R., and D. W. Sparks. 2007. Timing of birth and estimate of age of juvenile *Myotis septentrionalis* and *Myotis lucifugus*. Journal of Mammalogy 88: 649–656

Kulzer, E. 1958. Untersuchungen über die Biologie von Flughunden der Gattung *Rousettus* Gray. Zeitschrift für Morphologie und Oekologie der Tiere 47: 374–402.

———. 1961. Über die biologie der Nil-Flughunde (*Rousettus aegyptiacus*). Natur und Volk 91: 219–228.

———. 1962. Über die Jugendentwicklung der Angola-Bulldogfledermaus *1962)* (A. Smith 1933) (Molossidae). Säugtierkundliche Mitteilungen 10: 116–124.

Kunz, T. H. 1973. Population studies of the cave bat (*Myotis velifer*) reproduction, growth, and development. Occasional Papers, Museum of Natural History, University of Kansas 15: 1–43.

———. 1974. Reproduction, growth and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. Journal of Mammalogy 55, 1–12.

———. 1982. Roosting ecology of bats. Pp. 1–50, In: Ecology of Bats (T. H. Kunz, ed.). Plenum Press, New York.

———. 1987. Post-natal growth and energetics of suckling bats. Pp. 395–420, In: Recent Advances in the Study of Bats (M. B. Fenton, P. Racey, and R. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

———. 1988. Methods of assessing the availability of prey to insectivorous bats. Pp. 191–210, In: Ecological and Behavioral Methods for the Study of Bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, DC.

Kunz, T. H., and E. L. P. Anthony. 1982. Age estimation and postnatal growth in the little brown bat, *Myotis lucifugus*. Journal of Mammalogy 63: 23–32.

Kunz, T. H., and E. D. Pierson. 1994. Bats of the World: An introduction. Pp. 1–46, In: Walker's Bats of the World (by R. W. Nowak). Johns Hopkins University Press, Baltimore.

Kunz, T. H., and S. K. Robson. 1995. Postnatal growth and development of the Mexican free-tailed bat, *Tadarida brasiliensis*: birth size, growth rates and age estimation. Journal of Mammalogy 76: 769–783.

Kunz, T. H., and A. A. Stern. 1995. Maternal investment and post-natal growth in bats. Symposia of the Zoological Society of London 67: 63–77.

Kunz, T. H., and E. L. P. Anthony. 1996. Variation in the timing of nightly emergence behavior in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Pp. 225–236, In: A Volume in the Memory of J. Knox Jones, Jr. (H. H. Genoways and R. J. Baker, eds.). Contributions in Mammalogy, Texas Tech University, Lubbock, Texas.

Kunz, T. H., and G. F. McCracken. 1996. Tents and harems: apparent defense of foliage roosts by tent-making bats. Journal of Tropical Ecology 12, 103–116.

Kunz, T. H., and W. H. Hood. 2000. Parental care and postnatal growth in the Chiroptera. Pp. 415–468, In: Reproductive Biology of Bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, New York.

Kunz, T. H., and D. J. Hosken. 2009. Male lactation: why, why not, and is it paternal care? Trends in Ecology and Evolution.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89, In: Bat Ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago.

Kunz, T. H., M. H. Stack, and R. Jenness. 1983. A comparison of milk composition in *Myotis lucifugus* and *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Biology of Reproduction 28: 229–234.

Kunz, T. H., S. K. Robson, and K. A. Nagy. 1998a. Economy of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. Journal of Mammalogy 79: 631–642.

Kunz, T. H., J. A. Wrazen, and C. D. Burnett. 1998b. Changes body mass and body composition in pre-hibernating little brown bats (*Myotis lucifugus*). Ecoscience 5: 8–17.

Kunz, T. H., A. L. Allgaier, J. Seyjagat, and R. Caligiuri. 1994a. Allomaternal care: helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera: Pteropodidae). Journal of Zoology (London) 232: 691–700.

Kunz, T. H., M. S. Fujita, A. P. Brooke, and G. F. McCracken. 1994b. Convergence in tent architecture and tent-making behavior among neotropical and paleotropical bats. Journal of Mammalian Evolution 2: 57–78.

Kunz, T. H., O. T. Oftedal, S. K. Robson, M. B. Kretzmann, and C. Kirk. 1995. Changes in milk composition during lactation in three species of insectivorous bats. Journal of Comparative Physiology B 164: 543–551.

Kurta, A., and T. H. Kunz. 1987. Size of bats at birth and maternal investment during pregnancy. Symposia of the Zoological Society of London 57: 79–106.

Kurta, A., K. A. Johnson, and T. H. Kunz. 1987. Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. Physiological Zoology 60: 386–397.

Kurta, A., G. P. Bell, K. A. Nagy, and T. H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). Physiological Zoology 62: 804–818.

Kurta, A., T. H. Kunz, and K. A. Nagy. 1990. Energy and water flux in free-ranging big brown bats (*Eptesicus fuscus*). Journal of Mammalogy 71:59–65.

Kwiecinski, G. G., L. Krook, and W. A. Wimsatt. 1987. Annual skeletal changes in the little brown bat, *Myotis lucifugus lucifugus*, with particular reference to pregnancy and lactation. American Journal of Anatomy 178: 410–420.

Lewis, S. E. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76: 481–496.

Licht, P., and P. Leitner. 1967. Behavioral responses to high temperatures in three species of California bats. Journal of Mammalogy 48: 52–61.

Lollar, A. and B. Schmidt-French. 1998. Captive Care and Medical Reference for the Rehabilitation of Insectivorous Bats. David Chapman, Austin, Texas.

Loughry, W. J., and G. F. McCracken. 1991. Factors influencing female-pup scent recognition in Mexican free-tailed bats. Journal of Mammalogy 72: 624–626.

Maeda, K. 1972. Growth and development of large noctule, *Nyctalus lasiopterus* Schreber. Mammalia 36: 269–278.

———. 1976. Growth and development of the Japanese large-footed bat, *Myotis macrodactylus*, I. External characters and breeding habits. Journal of Growth 15: 29–40.

Mann, G. 1960. Neurobiologia de *Desmodus rotundus*. Investigaceones Zoologica Chilenas 6: 79–99.

Marimuthu, G. 1988. Mother-young relations in an insectivorous bat, *Hipposideros speoris*. Current Science 57: 983–987.

Martin, R. D. 1984. Scaling effects and adaptive strategies in mammalian lactation. Symposia of the Zoological Society of London 51: 87–117.

Martin, R. D., and A. M. McLarnon. 1985. Gestation period, neonatal size and maternal investment in placental mammals. Nature 313: 220–223.

Masters, W. M., S. C. Jacobs, and J. A. Simmons. 1991. The structure of echolocation sounds used by the big brown bat, *Eptesicus fuscus*: some consequences for echo processing. Journal of the Acoustical Society of America 89: 1402–1413.

Masters, W. M., K. A. S. Raver, and K. A. Kazial. 1995. Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. Animal Behaviour 50: 1243–1260.

Matsumura, S. 1979. Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): development of vocalization. Journal of Mammalogy 60: 76–84.

———. 1981. Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): vocal communication in three-week old infants. Journal of Mammalogy 62: 20–28.

Matsumura, S., and T. A. Uchida. 1975. Language of bats. Gengo 4: 624–632.

Matthews, L. H. 1969. The Life of Mammals, Vol. 1. Universe Books, New Jersey.

Maynard Smith, J. 1977. Parental investment: a perspective analysis. Animal Behaviour 25: 1–9.

McCracken, G. F. 1984. Communal nursing in Mexican free-tailed bat maternity colonies. Science 223: 1090–1091.

———. 1993. Locational memory and female-pup reunions in Mexican free-tailed bat maternity colonies. Animal Behaviour 45: 811–813.

McCracken, G. F., and J. W. Bradbury. 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. Behavioral Ecology and Sociobiology 8: 11–34.

McCracken, G. F., and M. K. Gustin. 1991. Nursing behavior in Mexican free-tailed bats maternity colonies. Ethology 89: 305–321.

McCracken, G. F., M. K. McCracken, and A. T. Vawter. 1994. Genetic structure in migratory populations of the bat *Tadarida brasiliensis mexicana*. Journal of Mammalogy 75: 500–514.

McLean, J. A. 1995. Maternal Investment in the Brown Long-eared Bat (*Plecotus auritus*). Ph.D. diss., University of Aberdeen, Scotland.

McLean, J. A., and J. R. Speakman. 1997. Non-nutritional maternal care in the brown long-eared bat. Animal Behaviour 54: 1193–1204.

McLearn, D., R. Medville, and D. M. Noden. 1995. Muscle cell death during development of head and neck muscles in the chick embryo. Developmental Dynamics 202: 365–377.

McOuat, T. P., and P. T. Andrews. 1995. The influence of climate on the growth rate of *Rhinolophus ferrumequinum* in West Wales. Myotis 32: 69–79.

McWilliam, A. N. 1987. The reproductive and social biology of bats in a seasonal environment. Pp. 324–350, In: Recent Advances in the Study of Bats (M. B. Fenton, P. Racey, and R. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

Metcalfe, N. B., P. Monahan 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution 16: 254–260.

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31: 370–386.

———. 1981. Pre-partum reproductive characteristics of eutherian mammals. Evolution 35: 1149–1163.

Morrison, D. W., and S. H. Morrison. 1981. Economics of harem maintenance by a neotropical bat. Ecology 62: 864–866.

Moss, C. F., D. Redish, G. Grounden, and T. H. Kunz. 1997. Ontogeny of vocal signals in the little brown bat, *Myotis lucifugus*. Animal Behaviour 54: 131–141.

Mueller, H. C., and N. S. Mueller. 1979. Sensory basis for spatial memory in bats. Journal of Mammalogy 60: 198–201.

Müller, H. E., M. Pinus, and U. Schmidt. 1980. *Aeromonas hydrophilia* as a normal intestinal bacterium of the vampire bat (*Desmodus rotundus*). Zentralblatt für Veterinaermedizin B 27: 419.

Mumford, R. E., and D. A. Zimmerman. 1964. Notes on *Choeronycteris mexicana*. Journal of Mammalogy 43: 101–102.

Myers, P. 1978. Sexual selection in size of vespertilionid bats. American Naturalist 112: 701–712.

Nelson, J. E. 1964. Vocal communication in Australian flying foxes (Pteropodidae: Megachiroptera). Zeitschrift für Tierpsychologie 21: 857–870.

———. 1965. Behaviour of Australian Pteropodidae (Megachiroptera). Animal Behaviour 13: 544–556.

Norberg, U. M. 1990. Vertebrate Flight. Springer-Verlag, Berlin.

Norberg, U. M., and J. M. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London, Series B 316: 335–427.

Norberg, U. M., and M. B. Fenton. 1988. Carnivorous bats? Biological Journal of the Linnean Society 33: 383–394.

Obrist, M. 1995. Flexible bat echolocation: the influence of individual, habitat, and conspecifics on sonar signal design. Behavioral Ecology and Sociobiology 36: 207–219.

O'Farrell, M. J., and E. H. Studier. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). Ecology 54: 18–30.

Oftedal, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Symposia of the Zoological Society of London 51: 33–85.

———. 1985. Pregnancy and lactation. Pp. 215–238, In: The Bioenergetics of Wild Herbivores (R. J. Hudson and R. G. White, eds.). CRC Press, Boca Raton, Florida.

Oftedal, O. T., and J. L. Gittleman. 1988. Patterns of energy output during reproduction in carnivores. Pp. 355–378, In: Carnivore Behavior, Ecology, and Evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.

Orr, R. T. 1954. Natural history of the pallid bat, *Antrozous pallidus* (LeConte). Proceedings of the California Academy of Sciences 28: 165–246.

———. 1970. Development: prenatal and postnatal. Pp. 217–231, In: Biology of Bats, Vol. 1 (W. A. Wimsatt, ed.). Academic Press, New York.

O'Shea, T. J., and T. A. Vaughan. 1977. Nocturnal and seasonal activities of the pallid bat, *Antrozous pallidus*. Journal of Mammalogy 58: 269–284.

Pagels, J. F., and C. Jones. 1974. Growth and development of the free-tailed bat, *Tadarida brasiliensis cynocephala* (Le Conte). Southwestern Naturalist 19: 267–276.

Papadimitriou, H. M., S. M. Swartz, and T. H. Kunz. 1996. Ontogenetic and anatomical variation in mineralization of the wing skeleton of the Mexican free-tailed bat, *Tadarida brasiliensis*. Journal of Zoology (London) 240: 411–426.

Pearl, D. L., and M. B. Fenton. 1996. Can echolocation calls provide information about group identity in the little brown bat (*Myotis lucifugus*)? Canadian Journal of Zoology 74: 2184–2192.

Pearson, O. P., M. R. Koford, and A. K. Pearson. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33: 273–320.

Pederson, S. C. 2000. Skull growth and the acoustical axis of the head in bats. Pp. 174–213, In: Ontogeny, Functional Ecology, and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Pine, R. H. 1972. The bats of the genus *Carollia*. Technical Monographs, Texas Agricultural Experiment Station, Texas A&M University 8: 1–125.

Pond, C. P. 1977. The significance of lactation in the evolution of mammals. Evolution 31: 177–199.

Porter, F. L. 1979. Social behavior in the leaf-nosed bat, *Carollia perspicillata*. I. Social organization. Zeitschrift für Tierpsychologie 49: 406–417.

Powers, L. V., S. C. Kandarian, and T. H. Kunz. 1991. Ontogeny of flight in the little brown bat, *Myotis lucifugus*: behavior, morphology, and muscle histochemistry. Journal of Comparative Physiology A 168: 675–685.

Priya, Y. S. 2005. Postnatal growth, wing morphology, and flight development in pteropoidid bats. Ph.D. diss., Madurai Kamaraj University, Madurai, India.

Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. Journal of Zoology (London) 220: 417–437.

Racey, P. A., and S. M. Swift. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. Journal of Animal Ecology 54: 205–215.

Radhamani, T. R., G. Marimuthu, and M. K. Chandrashekaran. 1990. Relationships between infant size and carrying of infants by hipposidereid mother bats. Current Science 59: 602–603.

Rajan, K. M., and G. Marimuthu. 1999. Postnatal growth and age estimation in the Indian false vampire bat (*Megaderma lyra*). Journal of Zoology (London) 248: 529–534.

Rakhmatulina, I. K. 1972. The breeding, growth and development of pipistrelles in Azerbaidzhan. Soviet Journal of Ecology 2: 131–136 (English translation).

Ralls, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51: 245–276.

———. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 111: 917–937.

Ransome, R. D. 1978. Daily activity patterns of the greater horseshoe bat, *Rhinolophus ferrumequinum*, from April to September. Pp. 71–82, In: Proceedings of the Fourth International Bat Research Conference (R. J. Olembo, J. B. Castelino, and F. A. Mutre, eds.). Kenya National Academy for Advancement of Arts and Science, Kenya Literature Bureau, Nairobi.

Rasmuson, T. H., and M. R. R. Barclay. 1992. Individual variation in the isolation calls of newborn big brown bats (*Eptesicus fuscus*): is variation genetic? Canadian Journal of Zoology 70: 698–702.

Read, A. F., and P. H. Harvey. 1989. Life history differences among the eutherian radiations. Journal of Zoology (London) 219: 329–353.

Reiter, G. 2004. Postnatal growth and reproductive biology of *Rhinolophus hipposideros* (Chiroptera: Rhinolophidae). Journal of Zoology (London) 262: 231–241.

Reynolds, R. S. 1999. Variation in life-history traits in the little brown bat, *Myotis lucifugus*.(Chiroptera: Vespertilionidae). Ph.D. diss., Boston University, Boston, Massachusetts.

Reynolds, R. S., and T. H. Kunz. 2000. Changes in body composition during reproduction and postnatal growth in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Ecoscience 7: 10–17.

Richards, G. C. 1989. Nocturnal activity of insectivorous bats relative to temperature and prey availability in tropical Queensland. Australian Wildlife Research 16: 151–158.

Ricklefs, R. W. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biological Reviews 54: 269–290.

Rolf, D. A. 2003. Life History Evolution. Sinauer, Sunderland, Massachusetts.

Rolseth, S. L., C. E. Koehler, and R. M. R. Barclay. 1994. Differences in diets of juvenile and adult hoary bats, *Lasiurus cinereus*. Journal of Mammalogy 75: 394–398.

Rother, V. G., and U. Schmidt. 1985. Die ontongenetische entwicklung der vokalisation bei *Phyllostomus discolor* (Chiroptera). Zeitschrift für Säugetierkunde 50: 17–26.

Rybár, P. 1969a. Ossification of bones as age criterion in bats (Chiroptera). Práce a Studie Prírodní, Pardubice 1: 115–136. [In Czech with English summary.]

———. 1969b. A contribution to the study of bones in the bat *Myotis myotis* Borkausen 1797 in regard to the age determination. Práce Krajského Musea v Hradci Králové A 10: 89–101. [In Czech with English summary.]

———. 1971. On the problems of practical use of ossification of bones as age criterion in the bats (Microchiroptera). Práce a Studie-Prírodní, Pardubice 3: 97–121. [In Czech with English summary.]

Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. Oecologia 80: 562–565.

Serra-Cobo, J. 1989. Primary results of the study of *Miniopterus schreibersi* growth. Pp. 163–173, In: European Bat Research (V. Hanak, I. Horacek, and J. Gaisler, eds.). Charles University Press, Prague.

Sharifi, M. 2004a. Postnatal growth and age estimation in the Mehely's horseshoe bat (*Rhinolophus mehelyi*). Acta Chiropterologica 6: 155–161.

———. 2004b. Postnatal growth in *Myotis blythii* (Chiroptera, Vespertilionidae). Mammalia 68: 283–289.

Scherrer, J. A., and G. S. Wilkinson. 1993. Evening bat isolation calls provide evidence for heritable signatures. Animal Behaviour 46: 847–860.

Schmidt, U. 1972. Social calls of juvenile vampire bats (*Desmodus rotundus*) and their mothers. Bonner Zoologiske Beitraege 4: 310–316.

———. 1973. Olfactory threshold and odour discrimination of the vampire bat (*Desmodus rotundus*). Periodicum Biolgorum 75: 89–92.

Schmidt, U., and U. Manske. 1973. Die Jugentwicklung der Vampirfledermause (*Desmodus rotundus*). Zeitschrift für Säugetierkunde 38: 14–33.

Schnitzler, H.-U., E. Kalko, L. Miller, and A. Surlykke. 1987. The echolocation and hunting behavior of the bat, *Pipistrellus kuhlii*. Journal of Comparative Physiology A 161: 267–274.

Schutt, W. A., Jr., M. A. Cobb, J. L. Petrie, and J. W. Hermanson. 1994. Ontogeny of the pectoral muscle in the little brown bat, *Myotis lucifugus*. Journal of Morphology 220: 295–305.

Scott, J. P. 1968. Observation. Pp. 17–30, In: Animal Communication (T. A. Sebok, ed.). Indiana University Press, Bloomington.

Short, H. L. 1961. Growth and development of Mexican free-tailed bats. Southwestern Naturalist 6: 156–163.

Sigmund, L. 1964. Relatives Wachstum und intraspezifische allometrie der Grossmausohr (*Myotis myotis* Borkh.). Acta Universitatis Carolinae, Biologica 234–303.

Simmons, N. B. 2005. Order Chiroptera, Pp. 312–529, In: Mammal Species of the World: A Taxonomic and Geographic Reference (D. E. Wilson and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore.

Smith J. D., and A. Starrett. 1979. Morphometric analysis of chiropteran wings. Pp. 229–316, In: Biology of Bats of the New World Mamily Phyllostomatidae, Part III (R. J. Baker, J. K. Jones, Jr., and D. C. Carter). Museum of Texas Tech University, Lubbock, Texas.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. 3rd ed. W. H. Freeman and Company, New York.

Sowler, S. 1983. Growth and reproduction in the fruit bat, *Epomphorus wahlbergi*. Ph.D. diss., University of Natal, Republic of South Africa.

Stangl, F. B., Jr. W. W. Dalquest, and J. V. Grimes. 1996. Observations on the early life history, growth, and development of the red bat, *Lasiurus borealis* (Chiroptera Vespertilionidae), in North Texas. Pp. 139–148, In: Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. (H. H. Genoways and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock, Texas.

Steele, S. R. E. 1991. The Energetics of Reproduction in the Evening Bat, *Nycticeius humeralis*. M.S. thesis, University of Maryland, College Park.

Stephan, H., and P. Pirlot. 1970. Volumetric comparison of the brain structures in bats (an attempt at a phylogenetic interpretation). Bijdragen tot de Dierkunde 40: 95–98.

Stern, A. A. 1995. Growth and reproductive energetics of the greater spear-nosed bat, *Phyllostomus hastatus*. Ph.D. diss., Boston University, Boston.

Stern, A. A., and T. H. Kunz. 1998. Intraspecific variation in postnatal growth in the greater spear-nosed bat. Journal of Mammalogy 79: 755–763.

Stern, A. A., T. H. Kunz, and S. Bhatt. 1997a. Seasonal wing loading and the ontogeny of flight in the greater spear-nosed bat, *Phyllostomus hastatus*. Journal of Mammalogy 78: 1199–1209.

Stern, A. A., T. H., Kunz, E. H. Studier, and O. T. Oftedal. 1997b. Milk composition and lactational output in the greater spear-nosed bat, *Phyllostomus hastatus*. Journal of Comparative Physiology A 167: 389–398.

Sterns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.

Storz, J. F., H. R. Bhat, and T. H. Kunz. 2000. Social structure of a polygynous tent-making bat, *Cynopterus sphinx* (Megachiroptera). Journal of Zoology (London) 250: 151–165.

Struhsaker, T. T. 1961. Morphological factors regulating flight in bats. Journal of Mammalogy 42: 152–159.

Studier, E. H., and T. H. Kunz. 1995. Accretion of nitrogen and minerals in suckling bats, *Myotis velifer* and *Tadarida brasiliensis*. Journal of Mammalogy 76: 32–42.

Studier, E. H., and M. J. O'Farrell. 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae)—I. Thermoregulation. Comparative Biochemistry and Physiology A 41: 567–595.

Studier, E. H., V. L. Lysengen, and M. J. O'Farrell. 1973. Biology of *Myotis thysangodes* and *M. lucifugus* (Chiroptera: Vespertilionidae)—II. Bioenergetics of pregnancy and lactation. Comparative Biochemistry and Physiology A 44: 467–471.

Studier, E. H., D. P. Viele, and S. H. Sevick. 1991. Nutritional implications for nitrogen and mineral budgets from analysis of guano of the big brown bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Comparative Biochemistry Physiology A 100: 1035–1039.

Suthers, R. A. 1970. Vision, olfaction, taste. Pp. 265–309, In: Biology of Bats (W. A. Wimsatt, ed.). Academic Press, New York.

Swartz, S. M., M. B. Bennett, and D. R. Carrier. 1994. Wing bone stress in free flying bats and the evolution of skeletal design for flight. Nature 359: 726–729.

Swift, S. M. 2001. Growth rate and development in infant Natterer's bats (*Myotis nattereri*) reared in a flight room. Acta Chiropterologica 3: 217–223.

Taft, L. K., and C. O. Handley, Jr. 1991. Reproduction in a captive colony. Pp. 19–41, In: Demography and Natural History of the Common Fruit Bat, *Artibeus jamaicensis*, Barro Colorado, Panama (C. O. Handley. Jr., D. E. Wilson, and A. L. Gardner, eds.). Smithsonian Contributions in Zoology, No. 51, Smithsonian Institution Press, Washington, DC.

Tamsitt, J. R., and D. Valdivieso. 1963. Records and observations of Colombian bats. Journal of Mammalogy 44: 168–180.

Tan, K. H., A. Zubaid, and T. H. Kunz. 1998. Tent construction and social organization in *Cynopterus brachyotis* (Chiroptera: Pteropodidae) in peninsular Malaysia. Journal of Natural History 31: 1605–1621.

Thomas, D. W., and A. G. Marshall. 1984. Reproduction and growth in three species of West African fruit bats. Journal of Zoology (London) 202: 265–281.

Thomas, D. W., G. P. Bell, and M. B. Fenton. 1987. Variation in echolocation call frequencies of North American vespertilionid bats: a cautionary note. Journal of Mammalogy 68: 842–847.

Thomson, C. E., M. B. Fenton, and R. M. R. Barclay. 1985. The role of infant isolation calls in mother-infant reunions in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 190: 285–295.

Timm, R. M. 1987. Tent construction by bats of the genera *Artibeus* and *Uroderma*. Pp. 187–212, In: Studies in Neotropical Mammalogy: Essays in Honor of Phillip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana (Zoology), New Series 9, Field Museum of Natural History, Chicago.

Tiunov, M. P. 1989. The postnatal growth and development of *Vespertilio superans* (Chiroptera) Zoologicheskii Zhurnal 68: 156–160. [In Russian.]

———. 1992. Parturition, postnatal growth and development of youngs in *Hypsugo savii* (Chiroptera). Zoologicheskii Zhurnal 71: 91–95. [In Russian.]

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179: 90–92.

Trune, D. R., and C. N. Slobodchikoff. 1976. Social effects of roosting on the metabolism of the pallid bat (*Antrozous pallidus*). Journal of Mammalogy 57: 656–663.

Tumilson, R. 1990. Studies of taxonomy and geographic variation in plecotine bats of North America. Ph.D. diss., Oklahoma State University, Stillwater.

Turner, D., A. Shaughnesy, and E. Gould. 1972. Individual recognition between mother and infant bats (*Myotis*). Pp. 365–371, In: Animal Orientation and Navigation (S. R. Galler et al., eds.). National Aeronautics Space Administration, NASA SP-262, Washington, DC.

Tuttle, M. D. 1975. Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. Occasional Papers, Museum of Natural History, University of Kansas 36: 1–24.

———. 1976. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. Ecology 57: 587–595

Tuttle, M. D., and D. Stevenson. 1982. Growth and survival of bats. Pp. 105–150, In: Ecology of Bats (T. H. Kunz, eds.). Plenum Press, New York.

Twente, J. W. 1955. Some aspects of habitat selection and other behavior of cave dwelling bats. Ecology 36: 706–732.

Van der Merve, M. 1978. Postnatal development and mother-infant relationships in the natal clinging bat *Miniopterus schreibersi natalensis* (A. Smith 1834). Pp. 309–322, In: Proceedings of the fourth International Bat Research Conference (R. I. Olembo, J. B. Castelino, and F. A. Mutere, eds.). Kenya National Academy for Advancement of Arts and Sciences, Nairobi, Kenya.

Vater, M. 2000. Evolutionary plasticity and ontogeny of the bat cochlea. Pp. 137–173, In: Ontogeny, Functional Ecology, and Evolution of Bats (R. A. Adams and S. C. Pederson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Vaughan, T. A. 1959. Functional morphology of three bats: *Eumops, Myotis, Macrotus*. University of Kansas Publications, Museum of Natural History 12: 1–153.

———. 1970. Flight patterns and aerodynamics. Pp. 195–215, In: Biology of Bats, Vol. 1 (W. A. Wimsatt, ed.). Academic Press, New York.

———. 1976. Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). Journal of Mammalogy 57: 227–248.

———. 1977. Behavioral thermoregulation in the African yellow-winged bat. Journal of Mammalogy 68: 376–377.

Vaughan, T. A., and T. J. O'Shea. 1976. Roosting ecology of the pallid bat, *Antrozous pallidus*. Journal of Mammalogy 57: 19–42.

Vaughan, T. A., and R. P. Vaughan. 1987. Parental behavior of the African yellow-winged bat (*Lavia frons*). Journal of Mammalogy 68: 217–223.

Vehrencamp, S. L., F. G. Stiles, J. W. Bradbury. 1977. Observations on the foraging behavior and avian prey of the neotropical carnivorous bat, *Vampyrum spectrum*. Journal of Mammalogy 58: 469–478.

Voigt, C. C., D. K. N. Dechmann, J. Bender, J. B. Rinehart, R. H. Michener, and T. H. Kunz. 2007. Mineral licks attract neotropical seed-dispersing bats. Ecology Research Letters, doi:10.1155/2007/34212.

Wang, L. C., and M. W. Wolowyk. 1988. Torpor in mammals and birds. Canadian Journal of Zoology 66: 133–137.

Watkins, L. C., and K. A. Shump. 1981. Behavior of the evening bat, *Nycticeus humeralis*, at a nursery roost. American Midland Naturalist 105: 258–268

Western, D., and J. Ssemakula. 1982. Life history patterns in birds and mammals and their evolutionary significance. Oecologia 54: 281–290.

Wilde, C. J., C. H. Knight, and P. A, Racey. 1999. Influence of torpor on milk protein composition and secretion in lactation bats. Journal of Experimental Zoology 284: 35–41.

Wilkinson, G. S. 1984. Reciprocal food sharing in vampire bats. Nature 309: 181–184.

———. 1985. The social organization of the common vampire bat. I. Pattern and cause of associations. Behavioral Ecology and Sociobiology 17: 111–121.

———. 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. Animal Behaviour 34: 1880–1889.

———. 1987. Altruism and co-operation in bats. Pp. 299–323, In: Recent Advances in the Study of Bats (M. B. Fenton, P. Racey, and R. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

———. 1988. Social organization and behavior. Pp. 85–97, In: Natural History of Vampire Bats (A. M. Greenhall and U. Schmidt, eds.). CRC Press, Boca Raton, Florida.

———. 1992a. Communal nursing in the evening bat, *Nycticeius humeralis*. Behavioral Ecology and Sociobiology 31: 225–235.

———. 1992b. Information transfer at evening bat colonies. Animal Behaviour 44: 501–518.

Williams, D. F., and J. S. Findley. 1979. Sexual size dimorphism in vespertilionid bat. American Midland Naturalist 102: 113–126.

Wilson, D. E. 1971. Ecology of *Myotis nigricans* on Barro Colorado Island, Panama Canal Zone. Journal of Zoology (London) 163: 1–13.

Winchell, J. M., and T. H. Kunz. 1996. Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 74: 432–441.

Wootton, J. T. 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. Evolution 41: 732–749.

Yokoyama, K., T. A. Uchida. 1979. Functional morphology of wings from the standpoint of adaptation for flight in Chiroptera. II. Growth and changes in mode of life during the young period in *Rhinolophus cornutus cornutus*. Journal of the Faculty of Agriculture, Kyuishu University 23: 185–198.