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Parental Care and Postnatal Growth in the Chiroptera

Thomas H. Kunz and Wendy R. Hood

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10.1 INTRODUCTION

How parents influence the fitness of offspring has generated a large body of empirical and theoretical literature. The importance of parental care in determining reproductive success in bats has received less attention compared with other aspects of reproduction. Efforts to integrate research on mother–infant recognition, lactation, non-nutritional care and postnatal growth have largely been descriptive. In this chapter we review the available literature on parental care and postnatal growth in bats and invite others to further investigate how these traits vary among species and how parental effort can be adjusted to the variation in costs and benefits to both parents and offspring. We follow Clutton-Brock (1991) in defining parental care as ‘any form of parental behavior that appears likely to increase the fitness of parents and offspring.’

Interspecific and intraspecific variation in parental care in mammals can largely be linked to differences in the amount of energy and nutrients allocated to offspring in the form of milk, but non-nutritional care also may influence this variation. These differences may be associated with several factors, including phylogeny, diet, offspring gender, litter size, climate, habitat and risk of predation. Depending on the relative availability of food, environmental changes may increase or reduce efforts of parental expenditure in offspring (Clutton-Brock, 1991). In this review we examine patterns of parental effort in bats and summarize factors that appear to influence patterns of postnatal growth in the Chiroptera in an effort to determine how parents contribute to the development of their young.

10.2 PARENTAL CARE

In bats, as in most other mammals, mothers provide a continuum of protection to their offspring from gestation to weaning. In the foetal period, the mother's womb protects the foetus from many environmental stimuli and strongly affects the biochemical and thermal environment in which the offspring develops. After birth, the mother's direct biochemical influences are limited to the milk that she supplies. In addition, non-nutritional care may be provided and can include sensory stimulation, thermal influence, and pup retrieval and transport.

Maternal interactions with a developing infant can be divided into two major phases. The first phase of interactions occurs during pregnancy when hormones and antibodies regulate placental nutrients, oxygen and waste exchange with the foetus. The second phase occurs when the mother influences the newborn through major sensory systems (tactile, olfactory, thermal, auditory and visual) and the biochemical 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. Notable exceptions include studies by Nelson (1965), Bradbury and Vehrencamp (1977a,b), Thomson *et al.* (1985), McCracken and Gustin (1991), and Wilkinson (1985, 1992a). In this chapter we review various parent-infant interactions including nutritional and non-nutritional forms of care. We discuss nutritional investment that mothers make in young bats, largely in the context of milk production and yield. In addition, we describe mammary form and function in bats, suckling behavior, regurgitation (a special case of maternal care in *Desmodus*), and the incidence of spontaneous secretion of milk by males. Acoustic communication and its role in mother-pup recognition and reunions has received moderate attention, but few studies have investigated the role of spatial, olfactory, visual and tactile cues in these contexts.

Most newborn bats are functionally altricial at birth; they are naked and have a limited ability to regulate their body temperature. 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 are important for promoting mother-infant recognition, tactile interactions are important for the development of appropriate social and locomotor

functions, and suckling behavior is obviously essential for the transfer of milk. Alloparental behavior, when it occurs, may facilitate the development of parenting skills, cohesion of groups, and socialization (McKenna, 1981; Kunz *et al.*, 1994a). Retrieval of a pup that has fallen from its roost is a relatively common occurrence in bats, and because this behavior also involves transporting young in flight, maternal effort may be high in some species because most young bats are unable to fly until they reach 90 per cent of adult wing dimensions (Kunz, 1987; Barclay, 1995). 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.

In most species of mammals, including bats, the primary care-givers are females. However, in some species, males assume a more active role. For example, paternal care may involve the construction and/or defense of roosts or the defense of female groups (see McCracken and Wilkinson, this volume). Recent evidence suggests that males of at least one species (*Dyacopterus spadecius*) maintains active mammary tissue at certain times of year (Francis *et al.*, 1994). This finding suggests that nutritional care by males may be possible, but there is no current evidence that pups are suckled by these males.

10.2.1 Sensory Interactions and Mother-Infant Recognition

Bats that roost in large aggregations appear to rely on a combination of spatial memory, acoustic, olfactory, tactile and/or visual cues to identify young or to communicate with conspecifics. Early observations on bats suggest that females which form large aggregations suckled young indiscriminately (*Tadarida brasiliensis*, Davis *et al.*, 1962; *Miniopterus australis* and *M. schreibersii*, Brosset, 1962b). However, more recent studies on these and other species have shown that nearly all female bats selectively suckle 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 rafinesquei*, 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.

Although most animals rely on one form of communication over others (Scott, 1968), female bats may 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 (De Fanis and Jones, 1995b).

Mother-offspring interactions may occur well past the onset of weaning in some species (Bradbury, 1977a). Although we are unaware of any experimental evidence to support this claim, recognition of weaned young appears to occur in *Desmodus rotundus* (Wilkinson, 1988), *Myotis adversus* (Dwyer, 1970), *Pteropus vampyrus*, and *P. hypomelanus* (W.R. Hood, personal observation). For species of bats that are relatively long-lived (Austed and Fischer, 1991) and highly philopatric (Lewis, 1995), we would expect roost mates to develop some form of individual

young at least in captivity. *Phyllotis brasiliensis* pups were collected from the same populations in experimental trials, and were individually distinctive and genetically separated (e.g., *Phyllotis* spp. in Gelfand and McCracken 1995). *Nycticeius humeralis*, *Sturnella* spp. (Gelfand and Jones, 1995a).

Directive calls (i.e., mothers as they search distances up to one meter and McCracken, 1992). discernible among individuals considered to be highly

Vocal communication is also important to the volant. A young *Saccop* roosts during the day, and emits a variety of vocalizations, stimulating its parents (Barnard 1974). As the pup approaches the roost, the pup emitted audible vocalizations (Barnard and Vaughan (1977) report that this behavior presumably promotes communication with the roost.

Vocal communication early in the postnatal mothers emit continuous 'lead signals' (i.e., direct Uchida, 1975; and search alternating signaling in pattern of infant vocal precisely overlaps the call infant also appear to e *Pteropus* (Nelson, 1965) (Schmidt, 1972), *Antrozous ferrumequinum* (Matsun

Acoustic recognition was verified experimentally in (1972) placed *Myotis* pups with its mother and another pup 75% of the tests. Despite calls of different infants, a large maternity colony olfaction, as in *Rousettus* (Gustin and McCracken) lactating female *T. brasiliensis* pup and an unrelated pup

The segmented nature of isolation calls appears to help mothers locate their

young at least in captive situations (Davis, 1970). 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., attractive calls, Matsumura, 1981) are often emitted by mothers as they search for their young. They can be distinguished by 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 (Balcombe and McCracken, 1992), a characteristic considered to be highly suitable for effective communication.

Vocal communication is also likely 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 the mother emitted several vocalizations, stimulating her pup to return to the roost (Bradbury and Emmons, 1974). As the pup approached its mother and climbed upon 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 promotes contact between mother and pups upon return of the mother to the roost.

Vocal communication between mothers and pups appears to be most complex early in the postnatal period. Infant bats which become separated from their mothers emit continuous broad-band 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 *Tadarida brasiliensis* (Gustin and McCracken, 1987). Balcombe (1990) evaluated call recognition by lactating female *T. brasiliensis*, and when they were presented with calls of their pup and an unrelated pup, the mothers showed a significant preference for calls

from their own young. Similar observations were reported for *P. pipistrellus* (De Fanis and Jones, 1996).

In some species, isolation calls appear to 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 mothers and pups exchange isolation and directive calls. In a series of experiments, Esser (1994) demonstrated that when pups of *P. discolor* were isolated from conspecifics at birth and hand reared, 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 *Nycticeius 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 coordinate foraging movements of other members in the same social group (Boughman, 1998).

Echolocation calls may be used by some species for individual recognition, but these are probably less important in mother-pup interactions. Individual variation in FM 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). Echolocation calls produced by adult *E. fuscus* were highly repeatable (>70%), compared to young (12 to 80%) but self-consistency increased with age (Masters *et al.*, 1995). In *Pipistrellus pipistrellus*, echolocation calls of pups were correctly discriminated in 82% of the trials by six-day old infants and by 91% in 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*, suggesting a genetic basis to vocal signatures (Masters *et al.*, 1995).

The characteristics of echolocation calls of young bats also appear to change with age, where the frequencies of young bats are typically lower than 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 (RF) emitted by young *R. ferrumequinum* are highly correlated with the RF calls of their mothers – older females raise young with lower RFs than do younger females. Thus, age-related changes in echolocation calls of bats 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 apparently are unable to recognize individuals. Because calls of pups are dynamic, females apparently are unable to rely on a single acoustic cue for pup recognition. Alternatively, 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 stimuli

Several investigators have suggested that female bats recognize their own young using olfaction, although few studies have been conducted to test this hypothesis. The presence of odoriferous glands in females and their young, observations of maternal or mutual sniffing and apparent scent marking have been reported for several species. Females of *Nycticeius humeralis* possess a submandibular gland that increases in size by nearly 25% within three days of parturition. Immediately before departing to forage, females apparently used this gland to mark the face of young bats less than or equal to two 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 which may be important for sharing odors and for establishing mother-infant bonds (Jayaprakash and Alexander, 1993). Specialized skin glands become hypertrophied during lactation in *Megaderma lyra* (Begum and Alexander, 1993), and females of *Tadarida brasiliensis* actively produce odoriferous secretions from their muzzle and touch their chins to their own pup several times when selecting them and while nursing (Gustin and McCracken, 1987). Odor profiles of subaxial secretions from individual *Noctilio leporinus* are unique (Brooke, 1994), but the role of these secretions in mother-pup recognition has not been determined.

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 by sniffing 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 (De Fanis and Jones, 1995a). When females of *Pipistrellus pipistrellus* return to their roost, they move through the cluster of young bats, moving their heads, apparently sniffing for their young (Rakhmatulina, 1972). De Fanis and Jones (1995b) demonstrated that adult females of *P. pipistrellus* were able to discriminate between the odors of females from their own and different colonies. 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 their 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 (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. Females showed a preference for the odor of their pup over that of a randomly chosen pup, and showed a significant preference for their 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 system 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 the 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 which 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 stimuli

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. Considering the relatively well-developed visual system of bats (Suthers, 1970), we would expect mothers and pups to communicate visually whenever possible. 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, response of the recipient 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 likely that mothers and pups should also rely on visual stimuli for recognition.

Tactile stimuli and grooming

Some types of tactile stimulation provided by the mother may be important for stimulating urination and defecation in bat pups, as reported for other mammals

(see Hofer, 1981). 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 such tactile stimulation is directed toward specific roost mates, including infants, or is simply a consequence of contact clustering remains to be clarified. In maternity colonies of *Myotis lucifugus* and *Pipistrellus 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 lowers parasite loads invites further study. Contact clustering does reduce metabolic rates in some young and adult bats (*M. thysanodes*, O'Farrell and Studier, 1973; *Tadarida brasiliensis*, Herreid, 1967; *Antrozous pallidus*, Trune and Slobotchkoff, 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.

10.2.2 Lactation, Milk and Related Nutritional Effort

Mammals are unique in their ability to produce milk from specialized mammary glands. Production of milk is generally considered the most costly aspect of mammalian reproduction (Millar, 1977; Oftedal, 1985; Gittleman and Oftedal, 1987), and likely has the most important influence on reproductive success (Maynard Smith, 1977; Pond, 1977; Daly, 1979). Milk composition and output are generally more closely correlated with suckling behavior and diet than with phylogeny (Ben Shaul, 1962). Energetic requirements of lactation scale negatively with increasing body size, and thus lactation is most costly in small mammals (Hanwell and Peaker, 1977; Oftedal, 1985). Since bats are a diverse group, with a wide range of life histories, dietary specializations, and body sizes (Kunz, 1982; Hill and Smith, 1984; Kunz and Pierson, 1994), interspecific comparisons among the Chiroptera should provide additional insight into how these variables influence parental effort.

Mammary glands, nipples and false nipples

Mammary glands of lactating females can usually be recognized by the whitish tissue that lies directly beneath the skin (Racey, 1988; Kunz *et al.*, 1996). These glands are typically flattened, disk-shaped structures that extend from the mid-thoracic to the axillary region. Over the course of a female's annual life cycle, mammary glands progress from being undeveloped during the non-breeding season to well developed at peak lactation (Heideman, 1988). Mass of mammary glands can be substantial, as the emptied mammary glands of lactating *Tadarida brasiliensis* average 8% of a female's post-absorptive body mass (Davis *et al.*, 1962). Mammary glands may account for an even greater percentage of a female's body mass in some pteropodids such as *Cynopterus brachyotis* (Dobson, 1878).

All female bats possess at least one pair of thoracic nipples, generally located in the anteriolateral pectoral position (Figure 10.1). Only two vespertilionid genera.



Figure 10.1 Lactating female Dayak fruit bat, *Dyacopterus spadecius* (Pteropodidae), showing an attached pup (left) and a well-developed nipple (right). Note the axillary position of the exposed nipple, which is characteristic of most bats. Photo by Charles M. Francis.

Lasiurus and *Otonycteris*, have two pairs of functional nipples. This extra pair of nipples is found in species where litter sizes are greater than two (Nowak, 1994). As in other mammals, the condition of nipples is an important criterion for parity, as relative nipple size can be used to distinguish parous and multiparous females from non-parous females (Racey, 1988).

Nipple morphology has been used to assess reproductive status of both microchiropterans (Ryberg, 1947; Sluiter, 1954; Sluiter and Bowman, 1951; Pearson *et al.*, 1952; Racey, 1974; Baage, 1977) and megachiropterans (Ryberg, 1947; Heideman, 1988; Francis *et al.*, 1994), but interpretations of reproductive status based on nipple size alone can be ambiguous (Racey, 1988). Distinguishing between primiparous and nulliparous females outside the breeding season is often difficult. In microchiropterans, nipples of nulliparous females, and sometimes primiparous females, are rudimentary and often give rise to tufts of hair, whereas nipples of older parous females are typically cornified and blackish or yellowish in color, with few or no hairs (Pearson *et al.*, 1952; Sluiter, 1954; Racey, 1974, 1988; Baage, 1977). Based on a combination of criteria, including relative nipple size, presence or absence of tufts of hairs on the nipple, and degree of nipple cornification, the assignment of females to relative stages of lactation and post-lactation may be possible (Heideman, 1988; Kunz *et al.*, 1996).

With the exception of a few species in which males reportedly lactate or have hypertrophied mammary tissue (Dobson, 1878; Ryberg, 1947; Francis *et al.*, 1994), males typically have rudimentary nipples and the mammary glands are absent or inconspicuous. The histomorphology of mammary tissue in lactating males of *Dyacopterus spadiceus* is indistinguishable from that of lactating females. Although the nipples of lactating females and males are darkened and cornified, the nipples of lactating males are considerably smaller than those of females (Francis *et al.*, 1994).

Some bats possess a pair of 'holdfast' nipples in the ventral, posterior-medial region, near the genitalia (Simmons, 1993). These 'false nipples' are present in all species of the families Craseonycteridae, Megadermatidae, Rhinopomatidae and Rhinolophidae, where they are present ubiquitously in females but occur inconsistently in males. A lactiferous function of false nipples has been confirmed in some species of Rhinolophidae and Rhinopomidae based on the expression of milk and/or the characteristic texture, color, and ductal branching of mammary tissue (Simmons, 1993). Pubic nipples appear to act primarily as holdfasts for infants (Simmons, 1993). Young bats in the Rhinolophidae and Rhinopomidae adopt unusual postures when attached to pubic nipples in which the pup's head is positioned posteriorly on the female's ventral surface and their legs are wrapped around the neck of their mother (Gaur and Shahrohk, 1989; Duangkhae, 1990; Vaughan and Vaughan, 1987; Simmons, 1993).

Nursing behavior

Early studies described nursing behavior in *Tadarida brasiliensis* and include such statements as 'mothers apparently act as one large dairy herd delivering milk passively to the first aggressive customer' (Davis *et al.*, 1962) and in *Miniopterus schreibersii* that 'suckling of young is not an individual but a communal business' (Brosset, 1962b). However, more recent studies suggest that non-offspring nursing does not occur in bats (e.g., *Antrozous pallidus*, Davis, 1969; Brown, 1976; *Eptesicus fuscus*, Davis *et al.*, 1968; *Myotis lucifugus*, *M. thysanodes*, *M. velifer*, *Corynorhinus rafinesquei*, Pearson *et al.*, 1952; Twente, 1955; *Pipistrellus pipistrellus*, Hughes *et al.*, 1989; Bishop *et al.*, 1992, and *Rousettus aegyptiacus*, Kulzer, 1962) except in cases of mistaken identity (*Tadarida brasiliensis*, McCracken, 1984), when the opportunity for reciprocity is high (*Nycticeius humeralis*, Wilkinson, 1992a), or when maternal mortality is high among captive individuals (*Pipistrellus pipistrellus*, Eales *et al.*, 1988).

Young bats may attempt to suckle indiscriminately, as in *Pipistrellus pipistrellus*, *Myotis velifer*, and *Tadarida brasiliensis* (Hughes *et al.*, 1989; Twente, 1955; McCracken and Gustin, 1991). This behavior can lead to non-offspring suckling if the identity of young is mistaken (McCracken, 1984) or when opportunity for reciprocation is high (Trivers, 1971). Non-offspring nursing was observed in 18% of all suckling bouts in *Nycticeius humeralis* when young were greater than two weeks of age (Watkins and Shump, 1981; Wilkinson, 1992a), but this percentage is greater than expected if non-offspring nursing occurred randomly (Wilkinson, 1992a). Watkins and Shump (1981) suggested that after two weeks of age, selective nursing may be too energetically expensive for mothers. Wilkinson (1992a) found

that females of *N. humeralis* did not nurse matrilineal kin preferentially, but selectively nursed young females, and 73% of observed incidents of non-offspring nursing involved females whose pups had already begun to forage.

Wilkinson (1992b) postulated that female-biased communal nursing in *N. humeralis* gives both an immediate and delayed benefit to lactating females which experience variable hunting success, assuming that roostmates exchange information about feeding and roosting sites. He also suggested that communal nursing may increase with matrilineal colony size and thus give the immediate energetic benefit of mass reduction to those females with milk in their ducts and by giving them an opportunity to offload the milk prior to their next feeding bout. In *Tadarida brasiliensis*, non-offspring nursing occurs in approximately 17% of the females (McCracken, 1984), but because of large colony size and lack of group stability (Villa and Cockrum, 1962; Constantine, 1967; Cockrum, 1969), the evolution of communal nursing through kin selection or an opportunity for reciprocity is unlikely (McCracken and Gustin, 1991).

No cases of nursing have been observed where mutual auditory and olfactory exchanges were absent, making 'milk dumping' by *N. humeralis*, as suggested by Watkins and Shump (1981), unlikely. Instead, non-offspring nursing may be attributed largely to parental mistakes and milk stealing by young (McCracken and Gustin, 1991). Milk theft or 'adoptive' nursing may increase when animals are disturbed by human observers (Fogden, 1971).

Communal nursing appears to be more common in captive situations (*Macrotus californicus*, Gould, 1977; *Desmodus rotundus*, Schmidt, 1978, Mills, 1980; *Pipistrellus pipistrellus*, Eales *et al.*, 1988). In these instances, communal nursing situations may be more frequent because opportunities for reciprocation are higher. Although communal nursing has been documented for *D. rotundus* in captivity, this behavior has not been observed in the wild (Schmidt, 1972; Wilkinson, 1988). Individuals of *D. rotundus* regurgitate blood to starved roostmates (Wilkinson, 1984), but regurgitation is less energetically expensive than milk production. In a captive colony of *P. pipistrellus* (Eales *et al.*, 1988), five of eleven pups suckled from two females. These authors suggested that this behavior may have been associated with high infant mortality and the need for the mothers who lost their young to offload excess milk.

In many species of bats, newborn pups are attached almost continuously to their mothers, and appear to suckle on demand during both day- and night-roosting periods. In a few species, pups during their first few weeks of life may remain attached to their mothers while they are on nightly foraging bouts, as in *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), and *Desmodus rotundus* (Schmidt and Manske, 1973). In other species, suckling is not constant, but instead milk is provisioned to pups on a regular schedule. In *Myotis thysanodes* (O'Farrell and Studier, 1973), *Miniopterus schreibersii* (Brosset, 1962b), *Miniopterus australis* and *M. pusillus* (= *macrocneme*; Hill, 1983; Sanborn and Nicholson, 1950), *Macrotus waterhousii* (Goodwin, 1970), and *Tadarida brasiliensis* (Davis *et al.*, 1962; Pagels and Jones, 1974; McCracken and Gustin, 1991; Kunz *et al.*, 1995b), females leave their offspring in a cluster with other pups

and roost apart with other females during the day. Typically, females find and suckle their young soon after they return from foraging and again in the late afternoon.

In some species of bats, energy density of milk may be closely linked to suckling frequency. Kunz *et al.* (1995b) found that energy density of milk in *Tadarida brasiliensis*, a bat that nurses its young on a schedule following each of two nightly foraging periods, is higher than that of *Myotis velifer* and *M. lucifugus*, both of which allow their young to remain attached to their nipple throughout the day. Notwithstanding, the amount of time a pup remains attached to its mother's nipple throughout the day does not imply that milk is produced in constant quantities. Further studies are needed to verify whether a bat's suckling schedule is correlated with its mother's milk composition. In most mammals the suckling schedule of females is not a reliable index of milk energy (Oftedal, 1984).

Mother-offspring conflict during the latter stages of lactation appears to be rare in bats, and mothers and their young of several species are known to forage together near or shortly after the onset of nutritional independence. Only one study has described overt mother-offspring conflict at the time of weaning. In the monogamous species, the young of *Lavia frons* were not weaned until nearly three weeks after they began to forage. During this period, females were occasionally observed 'grappling' and fending off young that were trying to suckle (Vaughan and Vaughan, 1986). Hughes *et al.* (1989) described females of *Pipistrellus pipistrellus* as being indifferent to the approach of their young as they reached weaning age, although active rejection was not observed.

Overt conflict between mother and young may not be common among bats. Mothers and their young have been observed or captured while flying together at the onset of weaning in some species: *Antrozous pallidus* (Bateman and Vaughan, 1974), *Cardioderma cor* (Vaughan, 1976), *Eptesicus fuscus* (Brigham and Brigham, 1989), *Lavia frons* (Vaughan and Vaughan, 1987), *Noctilio albiventris* (Brown *et al.*, 1983), and *Saccopteryx leptura* (Bradbury, 1977a). During their first year, juvenile *Desmodus rotundus* often feed from the same wound as their mothers (Wilkinson, 1985).

Milk composition and intake by young

Milk composition and milk energy intake by young bats, as indices of maternal effort, have been investigated in relatively few species. Both terrestrial and marine mammals exhibit considerable interspecific variation in both quality and quantity of milk produced (Oftedal, 1984, 1985; Oftedal and Iverson, 1995). Studies that have examined the nutritional requirements of female mammals and their young during lactation have largely focused on females and the proximate composition of milk. Few studies have explored the possibility that nutritional factors (e.g., minerals) other than energy and nutrients derived from fat, protein, and carbohydrates may influence postnatal growth of young bats (Barclay, 1994, 1995).

(a) *Macronutrient composition.* For species of bats in which the proximate composition of milk has been reported (Kunz *et al.*, 1983, 1995b; Oftedal and Iverson, 1995; Messer and Parry-Jones, 1997; Stern *et al.*, 1997; Korine and Arad,

Table 10.1 Composition of bat milks (all nutrient values are expressed as a per cent composition)

Taxa and Stage of Lactation (if given)	Wild or Captive ^a	Diet ^b	Dry Matter (%)	Fat (%)	Protein (%) ^c	Carbohydrate (%)	Citrate (%)	Ash (%)	Energy (kJ/g)	Sample Size ^d	Ref. ^e
Megachiroptera											
Pteropodidae											
<i>Epomophorus wahlbergi</i>	W,C	F	12.0	3.5	4.2	4.0	—	—	3.0 ^s	1 (13)	10
<i>Pteropus hypomelanus</i>	C	F	16.5 18.8	7.6 9.4	2.5 2.9	6.0 5.6	—	—	3.8 4.6	8–11 14–18	1
<i>Pteropus poliocephalus</i>	C	F	11.2 10.8 11.1 12.7	2.0 1.7 1.9 2.2	2.5 2.4 2.8 3.6	6.2 6.3 5.9 6.4	—	0.5 0.4 0.5 0.6	2.4 ^s 2.3 2.4 2.8	15 31 21 1–14	8
<i>Pteropus pumilus</i>	W	F	12.7	2.2	3.6	6.4	—	—	2.8	1–14	8
<i>Pteropus pumilus</i>	C	F	17.2 21.9	8.1 9.7	2.7 2.9	5.7 6.2	—	—	4.2 5.0	13 6–9	1
<i>Pteropus rodricensis</i>	C	F	18.9 22.3	8.9 8.3	3.1 3.5	6.2 6.8	—	—	4.6 5.9	4–7 5–10	1
<i>Pteropus vampyrus</i>	C	F	16.2 17.4	6.3 7.9	3.1 2.6	5.8 5.5	—	—	3.3 4.6	16–17 7	1
<i>Rousettus aegyptiacus</i>	W	F	— — —	2.7 7.1 9.0	2.2 2.3 2.9	5.7 6.1 5.5	—	—	2.5 4.3 5.1	1 (14) 2 (23) 2.6	3
Microchiroptera											
Molossidae											
<i>Tadarida brasiliensis</i>	W W	I I	34.4 25.3 ^f	18.9 16.3	11.1 C: 3.0 W: 3.2	3.7 2.8	— 0.2	0.7 —	10.5 ^s 8.2 ^s	NG 2 (10)	2 7
early peak	W	I	29.1 36.5	17.3 25.8	8.3 7.7	3.6 3.4	—	—	9.0 12.1	11 (64) 21 (71)	5
Phyllostomatidae											
<i>Artibeus cinereus</i>	W	F	30.8 ^f	23.0	C: 0.6 W: 3.4	3.8	0.1	—	10.4 ^s	1 (4)	7

<i>Artibeus jamaicensis</i>	W	F	30.6'	18.6	C: 1.1 W: 3.6	7.3	0.1	—	9.4 ^a	2	7
peak	C	F	17.8	9.0	3.6	6.1	—	—	5.3 ^a	21	9
<i>Carollia perspicillata</i>	W	F	—	—	C: ~7	4.1	0.2	—	—	1 (2)	7
<i>Glossophaga soricina</i>	W	N	11.0'	5.2	C: 1.1 W: 0.8	3.9	0.1	—	3.1 ^a	2 (12)	7
<i>Leptonycteris sanborni</i>	W	N	12.1 27.6'	1.7 18.5	4.4 C: 2.5 W: 1.8	5.4 4.8	0.2	0.6	2.6 ^a 8.9 ^a	NG 2 (13)	2 7
<i>Phyllostomus hastatus</i>	W	F, I	19.7 25.7 31.7 36.2'	9.1 13.0 16.9 29.0	7.8 9.1 9.7 C: 0.8 W: 2.3	4.0 4.0 4.0 4.1	—	—	5.9 7.7 9.5 12.5 ^a	31–32	11 7
<i>Vampyrus caraccioli</i>	W	F	—	—	—	—	0.1	—	—	2	7
<i>Vespertilionidae</i>	W	I	25.1'	16.4	6.2	2.5	—	—	8.4	4 (12)	4
<i>Eptesicus fuscus</i>	W	I	16.4'	6.0	C: 3.8 W: 3.5	3.1	0.2	—	4.6 ^a	2 (9)	7
<i>Myotis lucifugus</i>	W	I	25.2'	13.1	8.9	3.2	—	—	7.7	4 (7)	4
early	W	I	23.3'	14.3	5.8	3.2	—	—	6.9	6 (15)	4
mid	W	I	24.6'	12.4	8.7	3.5	—	—	7.5	3 (10)	5
late	W	I	26.5	12.4	9.5	3.9	—	—	7.4	4 (60)	5
early	W	I	27.1	15.8	8.5	4.0	—	—	8.6	3 (42)	5
<i>Myotis velifer</i>	W	I	25.4	11.6	9.2	4.0	—	—	7.1	3 (28)	5
early	W	I	32.4	19.9	10.7	4.4	—	—	10.6	3 (11)	5
<i>Myotis thysanodes</i>	W	I	40.5	17.9	12.1	3.4	—	1.6	10.4 ^a	1	6

^aIndicates whether bats were wild caught (W) or in captivity (C) prior to milking.

^bIndicates typical diet of species. Diets include insects (I), fruit (F), nectar (N), and blood (B). Note: Captive bats often receive nutrient supplements, however, published reports generally do not give a detailed description of the animal's diet.

^cWhen casein and whey proteins are presented rather than crude protein, each component is labeled C for casein and W for whey.

^dSamples from individual bats were pooled for analysis. Values in parentheses are number of bats milked, if different from sample size. All analyses were not performed for some samples. In this case, sample size is presented as a range. NG indicates sample size is not given.

^eReferences: 1. W.R. Hood and T.A. Kunz, unpublished data; 2. Huibregtse, 1966; 3. Korine and Arad, 1998; 4. Kunz et al., 1983; 5. Kunz et al., 1995b; 6. Jenness, 1974; 7. Jenness and Studier, 1976; 8. Messer and Parry-Jones, 1997; 9. Oftedal and Iverson, 1995; 10. Quicke et al., 1984; 11. Stern, 1995.

^fDry matter content is predicted from the sum of the fat, protein, and carbohydrate components.

^gEnergy content calculated from the energy equivalents of fat (38 kJ/g), protein (17 kJ/g), and carbohydrate (17 kJ/g). In some cases these values were presented by the authors in kcal/g. Values are converted to kJ/g (1 kcal = 4.184 kJ) to facilitate comparison with other studies.

1998; W.R. Hood and T.A. Kunz, unpublished; Table 10.1), the milk from insectivorous species generally has higher dry matter, fat, and protein content than from omnivorous or frugivorous species (Kunz and Stern, 1995; Table 10.1). Some of this variation may reflect species-specific differences in maternal diet. The relatively low fat, protein and dry matter content of milk of frugivorous species is consistent with this hypothesis given the relatively low fat and protein content of available fruit (Morrison, 1980; Fleming, 1988; Kunz and Diaz, 1995). Insectivorous bats produce milk with percentages of fat and protein which often exceed values reported for other small mammals, whereas carbohydrate content of milk is similar to that of other mammals (Jenness, 1974; Oftedal, 1984; Oftedal and Iverson, 1995). These findings also are consistent with Blaxter's (1961) hypothesis that small mammals produce milk of higher energy content than most large mammals.

For many species of bats, either the stage of lactation was not reported or sample sizes are too small to make meaningful interspecific comparisons. Jenness and Studier (1976) suggested that dry matter and fat content of the milk of some frugivorous phyllostomids (e.g., *Artibeus cinereus*, *Vampyroides caraccioli* and *Leptonycteris sanborni*) may be similar to that of insectivorous vespertilionids and molossids (but see Huibregtse, 1966). However, sample sizes in the two latter studies were inadequate to be considered representative of these species. This problem is further highlighted by comparing the results of Jenness and Studier (1976) for *Artibeus jamaicensis* ($n = 2$) with that of Oftedal and Iverson (1995; $n = 21$). The fat composition of milk at peak lactation reported by Oftedal and Taft (unpublished data, cited in Oftedal and Iverson, 1995) is half the value reported by Jenness and Studier (1976). Thus, based on a larger sample size, the values reported in Oftedal and Iverson are considered more representative, even though values derived from the latter study were from captive bats, and those from Jenness and Studier (1976), and Huibregtse (1966) from free-ranging populations. The nutritional plane of captive bats may differ from free-ranging bats (Studier and Wilson, 1979), although Messer and Parry-Jones (1997) found no significant differences between the milk composition of wild and captive *Pteropus poliocephalus*.

(b) *Fatty acid composition.* Fatty acids in bat milk have been identified for 13 species (Table 10.2) and, as in other mammals, the lipid fraction is composed almost entirely of triglycerides (Davies *et al.*, 1983; Jenness, 1985). Fatty acids which esterify to form triglycerides may originate from the diet or be synthesized *de novo* in the mammary gland (Iverson and Oftedal, 1995). The balance between *de novo* and dietary fatty acids found in milk can vary according to stage of lactation and diet (Iverson and Oftedal, 1995). Dietary and milk fatty acids for a given stage of lactation have not been reported for the milk of any bat species. Concentrations of linoleic (18:2) and linolenic (18:3) in insectivorous bats are higher than has been reported for other terrestrial mammals. The concentrations of these two fatty acids are also high in insectivorous marsupials and thus may reflect their insectivorous diet (Iverson and Oftedal, 1995). Fatty acid signatures of milk have been used to identify dietary items and dietary shifts in pinnipeds (Iverson, 1993; Iverson *et al.*, 1997), but whether such signatures ultimately prove useful for identifying dietary shifts in bats remains to be determined.

Table 10.2 Fatty acid composition of bat milks. All fatty acids expressed as a percentage of total fat composition. Fatty acids are expressed as length of fatty acid : number of double bonds

Taxa	Wild or Captive ^a	Diet ^b	10:0	12:0	14:0	14:1	16:0	16:1	16:2	18:0	18:1	18:2	18:3	Other ^c	Ref. ^d
Microchiroptera															
Molossidae															
<i>Tadarida brasiliensis</i>	W	I	trace	3.0	1.2	23.8	1.9	0.4	5.6	49.8	14.3	—	—	4	
Phyllostomidae															
<i>Artibeus cinereus</i>	W	F	—	7.5	—	38.0	6.5	—	5.2	41.0	0.4	—	2.0	2	
<i>Artibeus jamaicensis</i>	W	F	—	5.6	—	34.6	6.6	—	5.4	44.2	3.4	2.5	2.4	2	
<i>Carollia perspicillata</i>	W	F	—	9.4	—	32.6	7.6	—	2.5	24.9	3.5	—	0.4	2	
<i>Diphylla ecaudata</i>	W	B	—	4.0	—	37.2	6.6	—	4.9	43.1	4.2	—	—	2	
<i>Glossophaga soricina</i>	W	N	—	12.0	—	37.4	10.7	—	2.2	—	2.1	—	1.2	2	
<i>Leptonycteris sanborni</i>	W	N	trace	2.5	1.9	40.9	6.6	0.2	3.3	23.4	—	—	—	4	
<i>Vampyroides caraccioli</i>	W	F	—	2.0	—	31.2	11.4	—	2.1	24.9	0.6	1.8	2.3	2	
Vespertilionidae															
<i>Eptesicus fuscus</i>	W	I	—	3.9	1.5	21.5	8.3	—	7.4	37.9	15.7	2.1	1.9	3	
<i>Myotis lucifugus</i>	W	I	—	3.8	4.6	22.6	18.6	—	6.5	22.8	10.6	7.2	3.2	1	
	W	I	—	4.1	3.3	21.0	11.6	—	5.4	24.7	12.0	11.0	7.0	3	
<i>Myotis thysanodes</i>	W	I	—	0.3	0.9	18.7	7.5	—	4.0	36.0	22.2	9.3	0.5	1	

^aIndicates whether bats were wild caught (W) or in captivity (C) prior to milking.

^bIndicates typical diet of species. Diets include insects (I), fruit (F), nectar (N), and blood (B). Note: Captive bats often receive nutrient supplements, however, published reports generally do not give a detailed description of the animal's diet.

^cOther fatty acids include those fatty acids not measured directly. This column may include fatty acids described by other investigators.

^dReferences: 1. Glass and Jenness, 1971; 2. Jenness and Studier, 1976; 3. Kunz et al., 1983; 4. Stull et al., 1966.

Table 10.3 Mineral composition of bat milks. All mineral values expressed as ml/g dry mass (g)

Species	Wild or Captive ^a	Diet ^b	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Fe	P	Sample Size ^c	Ref. ^d
Megachiroptera										
Peropodidae										
<i>Cynopterus horsfieldi</i>	W	F	7.9	11.6	9.0	0.3	0.3	—	1	3
<i>Dyacopterus spadiceus</i>	W	F	3.0	16.8	14.3	0.4	0.3	—	1	3
<i>Megaerops ecaudatus</i>	W	F	5.7	25.7	20.5	0.7	0.5	—	1	3
<i>Pteropus hypomelanus</i>	C	F	—	6.2	8.3	0.6	—	6.4	19	2
<i>Pteropus vampyrus</i>	C	F	—	5.3	7.6	1.2	—	7.3	13	2
Microchiroptera										
Molossidae										
<i>Tadarida brasiliensis</i>	W	I	1.5	3.5	6.1	0.5	0.3	—	56	3, 4
Phyllostomidae										
<i>Carollia brevicauda</i>	W	F	2.5	33.1	3.8	0.6	—	—	1 (2)	3
<i>Carollia castanea</i>	W	F	1.6	26.1	2.5	0.4	—	—	9 (11)	3
<i>Carollia perspicillata</i>	W	F	1.9	28.4	2.3	0.3	—	—	4 (7)	3
<i>Phyllostomus hastatus</i>	W	F, I	10.2	5.5	8.5	0.6	—	—	1	3
Vespertilionidae										
<i>Eptesicus fuscus</i>	W	I	—	6.2	8.8	1.2	—	3.6	5 (49)	1

^aIndicates whether bats were wild caught (W) or in captivity (C) prior to milking.

^bIndicates typical diet of species. Diets include insects (I), fruit (F), nectar (N), and blood (B). Note: Captive bats often receive nutrient supplements, however, published reports generally do not give a detailed description of the animal's diet.

^cReferences: 1. W.R. Hood, unpublished data; 2. I.W.R. Hood et al., unpublished data; 3. Studier et al., 1995; 4. Studier and Kunz, 1995.

(c) *Mineral composition.* Mineral composition of bat milk has only been determined for two insectivorous (Studier and Kunz, 1995), eight frugivorous (Studier *et al.*, 1995; W.R. Hood and T.H. Kunz, unpublished), and one omnivorous species (Stern *et al.*, 1997) (Table 10.3). Moreover, stage of lactation and variation in mineral content of milk during the lactation period has only been reported for one insectivorous species, *Tadarida brasiliensis* (Studier and Kunz, 1995) and one omnivorous species, *Phyllostomus hastatus* (Stern *et al.*, 1997). Concentration of calcium, magnesium and sodium in the milk of *T. brasiliensis* declines over the course of lactation, whereas, potassium, nitrogen, and iron remain constant (Studier and Kunz, 1995). Similarly, both magnesium and calcium content decreased from birth until weaning in *P. hastatus*, but no change was observed in sodium (Stern *et al.*, 1997). Potassium, nitrogen and iron did not change over the course of lactation in *P. hastatus* (Stern *et al.*, 1997). Calcium, magnesium and potassium, however, did not vary over the course of lactation in captive *Pteropus hypomelanus* and *P. vampyrus* (W.R. Hood and T.H. Kunz, unpublished), although this may reflect a uniform diet. Sample sizes were small and stage of lactation was not reported for the frugivorous phyllostomids evaluated by Studier *et al.* (1995), thus a comparison among dietary habits could not be made. Notwithstanding, preliminary analyses suggest that the potassium content of milk in frugivorous species is generally higher than in omnivorous and insectivorous taxa (W.R. Hood and T.H. Kunz, unpublished).

Available evidence suggests that females of insectivorous bats may be severely calcium limited during lactation (Kwiecinski *et al.*, 1987; Studier *et al.*, 1991; Keeler and Studier, 1992). Young bats, as in other mammals, remain nutritionally dependent on their mothers until they are able to feed independently (Barclay, 1994; Kunz, 1987; Pond, 1977). While young of other mammals are weaned at nearly 40% of adult body mass, young bats are not weaned until they reach about 71% 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 reached adult dimensions (Kunz, 1987; Barclay, 1994, 1995), and mineralization of wing bones is almost complete (Swartz *et al.*, 1994; Papadimitriou *et al.*, 1996).

Bone is the primary reservoir of calcium within the body, and resorption of calcium from bone typically occurs when the diet does not meet current demands. Calcium demands are especially high during gestation and lactation, when females are faced with the additional burden of providing nutrients for foetal and neonatal development. Kwiecinski *et al.* (1987) found that bone density in females of *Myotis lucifugus* is lower during late gestation and lactation than at other times, suggesting that active bone resorption occurs at these times. In addition, based on foraging times and attack rates on insects, Aldridge and Brigham (1991) found that lactating females of *Eptesicus fuscus* foraged for a longer time than was expected to meet energetic demands, suggesting that dietary habits may be constrained by requirements other than energy. In contrast, calcium content of lactating females of *Miniopterus schreibersii* was not significantly different from those during the non-reproductive period (Bernard and Davison, 1995). Calcium absorption from bone can occur during lactation even in well nourished humans (Sowers *et al.*, 1993). Animals that experience bone loss during lactation may not remain in a state of

mineral stress. At least in humans, bone density recovers quickly following weaning, and even individuals that experience a subsequent pregnancy are not at risk for substantial bone loss (Sowers *et al.*, 1995).

(d) *Milk yield of mothers and intake by young.* An essential aspect of understanding nutritional and energetic requirements of lactation is a reliable estimate of milk yield. Milk yield has only been measured directly in four insectivorous and one omnivorous species (Table 10.4). 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 per 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 *Myotis lucifugus* and *Eptesicus fuscus* to be 19.3 and 29.7 kJ per day, respectively.

Predicted values for milk yield (Figure 10.4) are based on both the metabolic mass of females and their young, as described by Oftedal (1984). Females of *N. humeralis* which give birth to 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 the Oftedal (1984) equation is less than the predicted values (Kunz, 1987). Values of milk yield reported for captive *P. auritus* (McLean, 1995) are nearly two times higher than predicted from Oftedal's (1984) equation.

At least two species of bats that give birth to singletons produce more milk than predicted from both allometry and litter size. Stern (1995) found that free-ranging *Phyllostomus hastatus* produced a maximum of 15.7 ml per day of milk at peak lactation. This value is comparable to estimates of milk production, based on body size, for rodents that produce more than one young (Kenagy *et al.*, 1990; Rogowitz and McClure, 1995). At peak lactation, *Tadarida brasiliensis* has a milk energy yield three times predicted values (T.H. Kunz, unpublished).

Regurgitation: special case in Desmodus rotundus

In addition to provisioning 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 three months old, after which this behavior continues until the onset of weaning at approximately seven months (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, of which 75% occurred between mothers and their dependent young. The other 25% were between females and non-dependent young, relatives, and unrelated individuals. Thus, food sharing in *D. rotundus* appears to be associated with the degree of relatedness and the opportunity for reciprocation (Wilkinson, 1984). In this species, females belong to small, stable social groups of kin and non-kin, where opportunities for

Table 10.4 Milk yield in bats based on isotope dilution. Predicted values are based on Oftedal (1984)

Taxa	Wild or Captive ^a	Diet ^b	Litter Size	Mean Body Mass (g)	Milk Yield			Ref. ^c
					Measured (ml/day)	Measured (kJ/day)	Predicted (kJ/day)	
Phyllostomidae								
<i>Phyllostomus hastatus</i> ^d	W	F,I	1	87.6 ^e	15.7	112.6	109.3	4
Vespertilionidae								
<i>Eptesicus fuscus</i> ^e	W	I	2	20.2 ^e	—	45.7	62.7	1
<i>Myotis lucifugus</i> ^d	W	I	1	7.3 ^e	—	19.0	15.1	1
<i>Nycticeius humeralis</i> ^d	C	I	2.2	10.2 ^e	4.5	37.2	32.2	3
<i>Plecotus auritus</i>	C	I	1	7.1 ^e	2.6	22.3–23.2	13.4	2

^aIndicates whether bats were wild caught (W) or in captivity (C) prior to milking.

^bIndicates typical diet of species. Diets include insects (I), fruit (F), nectar (N), and blood (B). Note: Captive bats often receive nutrient supplements, however, published reports generally do not give a detailed description of the animal's diet.

^cReferences: 1. Kunz, 1987; 2. McLean, 1995; 3. Steele, 1991; 4. Stern, 1995.

^dValue for milk output at peak lactation.

^eVirginia Hayssen, personal communication.

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.

10.2.3 Non-nutritional Care

Thermal influences

The evolution of membranous wings allows bats to exploit an aerial niche for the acquisition of food, but the increased surface area gained with the evolution of flight also increases passive thermal conductance during flight and in roosting situations (Ochoa and Kunz, 1999). Increased thermal conductance lowers the ability of bats to maintain euthermy, and thus may increase the energetic demands of thermoregulation or alternatively lead to torpor and reduced energy expenditure. For bats, as in other altricial mammals, females often help maintain the euthermic body temperature of their young by sharing body heat through conduction and radiation. This thermal influence is directly proportional to the amount of time a mother spends in contact with its young.

Because newborn bats are 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 for heat. McLean and Speakman (1997) found that for *Plecotus auritus*, physical contact between mothers and pups declined as the pups increased in age. At ambient temperatures of 10 and 20°C, newborn *Myotis lucifugus* were unable to maintain their body temperature when they roosted alone (Fujita, 1986). However, when these pups were allowed to form clusters they maintained elevated body temperatures for longer periods at these same ambient temperatures.

A decrease in body temperature in lactating females can adversely affect milk protein synthesis and output by females (Wilde *et al.*, 1999), and indirectly the growth rates of pups (Hoying and Kunz, 1998). Because torpor reduces the general level of activity in mammals, this may adversely affect the maturation of the brain, internal organs, and muscles and lead to subsequent motor defects and reduced feeding efficiency (Gubernick and Klopfer, 1981).

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

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 modifies the

microclimate of the maternity roost by maintaining optimum roost temperatures (Licht and Leitner, 1967; Kunz, 1973).

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, respectively). Within these colonies, mother-pup pairs aggregate in dense clusters, and maintain their body temperatures greater than those which roost singly (Twente, 1955). Mean rates of oxygen consumption are lower in clusters than in individuals at ambient temperatures between 15–35°C, and percentage mass loss is also decreased giving cluster members a metabolic advantage (Herreid, 1967; Trune and Slobodchikoff, 1976).

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; Thomas, 1995; Hoying and Kunz, 1998). Because torpor slows physiological processes, including those required for milk production (Wilde *et al.*, 1999), this form of energy conservation can be disadvantageous during lactation. Some species, however, remain euthermic during lactation, and apparently do not enter torpor at this time; these include *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), *Macrotus californicus* (Bradshaw, 1962). Others, however, enter torpor when ambient temperatures are low and food resources are scarce – *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), *Pipistrellus subflavus* (Hoying and Kunz, 1998). Hamilton and Barclay (1994) examined differential use of torpor by males and females of *Eptesicus fuscus* during the reproductive season, and found that torpor is less frequent in females when foraging conditions are poor (Grinevitch *et al.*, 1995).

Pup retrieval and transport

Transport of young bats by mothers while foraging 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), but 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 among the insectivorous species include *Taphozous perforatus* and *Taphozous melanopogon* (Brosset, 1962a).

Transport of a pup during the lactation period is expected to increase a female's wing loading, decrease maneuverability and foraging efficiency (Norberg, 1987; Hayssen and Kunz, 1996), and increase energy expenditure (Hughes and Rayner,

1993). Since most insectivorous species seek moving prey, and many ingest up to 30% of their pre-feeding body mass during a single feeding bout (Kunz, 1974; Anthony and Kunz, 1977; Kunz *et al.*, 1995a), the additional load of transporting young bats in flight is expected to reduce the ability of a mother to feed efficiently. A small insectivorous bat, transporting one or two relatively large pups on prolonged foraging bouts, probably could not meet their daily energy demands while carrying pups.

Females of several species of bats have been observed or captured while carrying their non-volant young (Barbour and Davis, 1969; Fenton, 1969; Davis, 1970; Ansell, 1986; Baumgarten and Vieira, 1994), and some species actually carry volant young to foraging areas (Marimuthu, 1988; Radhamani *et al.*, 1990). Whether these females were transporting pups to alternative roosts in response to disturbance while on foraging bouts, is unknown in most situations. If predation is reduced by moving pups to alternative roosts, as in *Pteropus poliocephalus* (Nelson, 1965), *Saccopteryx bilineata* (Bradbury and Emmons, 1974), and *Uroderma bilobatum* (Lewis, 1992), the ability of predators to predict the location of potential prey should decrease.

Species that regularly move among several alternative tree roosts during the lactation period (Barclay and Brigham, 1996) should sustain mother-pup contact and reduce the risks 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, 1991, 1993), mothers are unlikely to transport their young on prolonged foraging flights unless they benefit by experiencing reduced risks of predation or young bats are able to learn important foraging skills (Radhamani *et al.*, 1990).

Alloparental care

Alloparental care (non-offspring care) has been observed in several species of mammals (Gubernick and Klopfer, 1981; Reidman, 1982), but reports of care-giving behavior by unrelated bats is rare. Observations of allogrooming in bats have been made mostly in captive situations. Under these conditions, females typically groom their young during and immediately following parturition (Kleiman, 1969; Kunz *et al.*, 1994a; McLean, 1995; W.R. Hood, personal observations). The most thorough documentation of allogrooming in bats was reported for *Plecotus auritus* (McLean and Speakman, 1997), where it was shown 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. Mothers may lick, nuzzle, scratch, rub, or hang in direct physical contact with their pups (Burnett and August, 1981; Winchell and Kunz, 1996). In *Desmodus rotundus*, allogrooming not only occurs between mother and offspring, but also this behavior is reciprocated among individuals of different age groups (Wilkinson, 1986). Allogrooming in *D. rotundus* appears to be independent of roost and ectoparasite levels, and thus may facilitate individual recognition in roosting situations and could facilitate food sharing (Wilkinson, 1986).

Alloparental care was observed at the time of parturition in captive *Pteropus rodricensis* (Kunz *et al.*, 1994a). A single female 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. Similar behaviors have been observed on other occasions in this species (W.R. Hood, personal observations). Reports of 'baby-sitting' have been made for *Myotis thysanodes* (O'Farrell and Studier, 1973) based on the presence of a few adult females in a maternity roost where large numbers of pups were present. An alternative explanation for this and similar observations is that females in late pregnancy may delay departure from a roost when parturition is imminent (Kunz, 1973), and thus give the appearance to an observer that adults were baby-sitting.

Most females selectively nurse their own offspring, although there have been reports of misdirected nursing in captive groups of *Pipistrellus pipistrellus* (Kleiman, 1969; Eales *et al.*, 1988; Hughes *et al.*, 1989; De Fanis and Jones, 1996). In free-ranging populations of *Tadarida brasiliensis* (McCracken and Gustin, 1991), pups may engage in milk stealing, and in *Nycticeius humeralis* mothers sometimes nurse unrelated offspring as the latter 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 non-related pups outweighed the costs, especially in colonies with high levels of relatedness. However, there is no evidence for reciprocity or kin-selection in either *T. brasiliensis* (McCracken *et al.*, 1994) or *N. humeralis* (Wilkinson, 1992a). Wilkinson (1992b) suggested that females of *N. humeralis* may gain an immediate benefit by dumping excess milk to unrelated offspring, if foraging costs are lower with a reduced body mass. Alternatively, females may gain a delayed 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).

10.2.4 Paternal Care

Pup and mate guarding

The roosting and social habits of most tropical species remain unknown (Kunz, 1982), and evidence for a male's contribution to roost establishment, maintenance, and mate and pup guarding are known for only a few species. In most temperate zone bats, maternity roosts are inhabited largely by females and their young, where males assume little or no responsibility for parenting. However, in tropical regions, males of some species defend roosts or harems and thus may invest considerable effort during the period when females are gravid and young are present. In *Carollia perspicillata*, *Phyllostomus hastatus* and *Artibeus jamaicensis*, males incur costs by defending females and their pups from other males at roost sites, although such defense may occur independently of the presence of pups (Porter, 1979; McCracken and Bradbury, 1981; Morrison and Morrison, 1981; Kunz *et al.*, 1998a). Harem males of some emballonurids (*Saccopteryx bilineata* and *S. leptura*) incur costs by

defending females on foraging grounds and at roost sites (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1977a), suggesting that such defense is not directly linked to paternal care of offspring. In some monogamous species, *Lavia frons* (Vaughan and Vaughan, 1987), *Cardioderma cor* (Vaughan, 1976), and *Vampyrum spectrum* (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 species make in the construction of tents, and defense of the same, could be included as paternal care, assuming that the investment that males make benefits their progeny. In one species where males have been observed in the act of tent making (*Cynopterus sphinx*, Balasingh *et al.*, 1995), harem males defend tents and their female occupants at least during the pregnancy and pup rearing periods. Twice each year, males of *C. sphinx* sever and modify stems, leaves, and vines of selected plant species, forming stem 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. Similar types of paternal effort can be expected for other tent-making species (Kunz *et al.*, 1994b; Kunz and McCracken, 1996; Timm, 1987; Tan *et al.*, 1998).

Male lactation

Direct parental care in most mammals is the exclusive domain of females (Clutton-Brock, 1991), although anecdotal evidence of mammary development and production of milk has been reported for males of some species, including bats. The first circumstantial evidence that male bats may lactate was suggested by Dobson (1878), who observed males of *Cynopterus brachyotis* and *C. sphinx* with nipples as large as those of lactating females. Although Dobson gave no evidence that milk was expressed from the mammary glands of males, he suggested that males may assist females by nursing young when twins were born (although twins are rare in the Pteropodidae). This suggestion has not been verified from behavioral or morphological evidence for these or other species (Ryberg, 1947). However, mammary hypertrophy and secretion of milk by males (male galactorrhoea) has been observed in two plant-visiting pteropodids, *Dyacopterus spadiceus* in Malaysia (Francis *et al.*, 1994) and *Pteropus capistratus* in Papua New Guinea (F. Bonaccorso, personal communication). Females and mature males of *D. spadiceus* captured in August at Kuala Lompat, Malaysia each had functional mammary glands. While 350 μ l of milk was expressed from the nipple of a single adult female, only 4–6 μ l of a similar fluid was expressed from males. The nipples of males were smaller and less keratinized than those of lactating females, suggesting little or no suckling had occurred (Francis *et al.*, 1994). Whether lactation in male bats is an aberrant condition or has functional significance remains to be clarified.

The environmental conditions and physiological status required to promote lactation are unknown in male bats. Lactation could be stimulated by alterations in hormone production (including elevated oestrogen and progesterone), liver malfunction (which may elevate circulating oestrogen due to the inability of the

liver to convert testosterone to dihydrotestosterone, an oestrogen precursor), and conversion of androgen into oestrogen locally within the mammary tissue as occurs during neonatal hypothalamic masculinization (Francis *et al.*, 1994). Consumption of plants which contain naturally occurring phytoestrogens, or consumption of plants contaminated with breakdown products of pesticides (many of which have oestrogenic properties) are likely alternative hypotheses to account for spontaneous lactation in males. It is also possible that male lactation in bats is an evolved condition. Because most mammals are polygynous, one would not expect lactation to have evolved in species with a polygynous mating system. However, monogamous relationships, where males and females share in the care of offspring, could provide the appropriate social conditions necessary for the evolution of lactation in males.

10.3 SIZE AND DEVELOPMENTAL STATE AT BIRTH

Bats exhibit several reproductive specializations which contrast with those of similarly-sized terrestrial mammals, including relatively long periods of gestation, small litters, and large neonatal body masses (Kurta and Kunz, 1987; Hayssen and Kunz, 1996). These specializations are generally considered adaptations to an aerial mode of locomotion which, among mammals, is exclusive to bats. Gestation in bats is relatively long, with the duration between copulation and parturition in many species extended by at least one of several forms of delay: delayed implantation, delayed development, and reduced foetal growth (Racey, 1973; Racey, 1982; Racey and Entwistle, this volume). Bats typically have singleton litters, but their litter mass is comparable to those of similar-size terrestrial mammals (Hayssen *et al.*, 1993; Hayssen and Kunz, 1996; Kurta and Kunz, 1987).

Litter mass among bats is highly correlated with maternal body mass, and this relationship is allometric, with smaller bats having relatively large offspring and larger bats having relatively small offspring (Hayssen and Kunz, 1996). Mean litter to maternal mass is 28.3% for microchiropterans and 17.7% for megachiropterans. Microchiropterans exhibit a greater range of litter masses relative to maternal mass, suggesting that litter size is not strictly constrained by maternal body size, as appears to be the case for megachiropterans where litter mass is more highly correlated with maternal body mass (Hayssen and Kunz, 1996).

Geometry of wing shape relative to body mass 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 and/or a developing foetus. Bats that have lower intrinsic wing loadings should be better able to carry greater mass relative to those with higher wing loadings (Norberg and Fenton, 1988; Norberg and Rayner, 1987). A full-term foetus can impose increases in wing loading up to 44% over non-gravid conditions (Funakoshi and Uchida, 1981; Hoying and Kunz, 1998), and thus would be 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 can be 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 these groups to carry the same proportions of their body mass as molossids and phyllostomids at lower energetic cost (Hayssen and Kunz, 1996). Thus, low intrinsic wing loadings among the vespertilionids may be a key factor in promoting the evolution of litter sizes greater than one.

Large size of bats at birth is generally associated with an advanced stage of development; yet this is true for only a handful of characteristics. Large size of neonates may support an advanced state of neuromuscular development at birth (Kurta and Kunz, 1987), as is evident by well-developed hind limbs, allowing pups to cling tenaciously to their mothers or the roost substrate. Despite their relatively large neonatal size, newborn bats are functionally altricial, based largely on the sparsity of their pelage, inability to thermoregulate (Fujita, 1986), and nutritional dependence on their mothers (Kurta and Kunz, 1987). Lactational requirements of females may be reduced if the gestational period is prolonged and young are born at an advanced size (Kurta and Kunz, 1987). This pattern appears to hold true only for members of the family Vespertilionidae, which have large young and a relatively short lactation period. By contrast, rhinolophids produce large neonates and nurse their young for extended periods (Hayssen and Kunz, 1996).

10.4 POSTNATAL GROWTH

Postnatal growth is an important life-history trait in mammals (Case, 1978; Ricklefs, 1979) because it reflects a major component of parental effort (Ofstedal, 1984; Kirkwood, 1985; Costa *et al.*, 1986; Gittleman and Ofstedal, 1987; Ofstedal and Gittleman, 1988; McLaren, 1993; Kunz and Stern, 1995). Published analyses of postnatal growth and life-history variation in mammals have grossly underrepresented bats (e.g., Wootton, 1987; Harvey and Read, 1988; Read and Harvey, 1989; Promislow and Harvey, 1990) or excluded them entirely (e.g., Millar, 1981; Western and Ssemakula, 1982; Martin, 1984; Martin and McLarnon, 1985). Despite the relatively recent allometric analyses of postnatal growth in bats (Kunz and Stern, 1995), little attention has been given to factors influencing individual variation, and few studies have considered proximate and evolutionary forces that may shape patterns of postnatal growth in the Chiroptera.

In Case's (1978) allometric analysis of postnatal growth in terrestrial vertebrates, he included only 17 species representing two families of bats. His analysis was limited because only the early period of linear growth was examined and the effects of body size were not removed from his analysis. Postnatal growth data on bats available at the time of Case's analysis (see Orr, 1970) were strongly biased toward small insectivorous species (<30 g as adults), and most of the taxa represented were members of a single family (Vespertilionidae). Case (1978) found from his analysis that bats had intermediate growth rates, although he offered no explanation for this conclusion. Tuttle and Stevenson (1982) summarized data on postnatal growth for 24 taxa, but included species on which both longitudinal and cross-sectional methods of data

collection were used (see below). The allometric analysis of Kunz and Stern (1995) included 33 taxa, representing seven families, and found that proximate factors known to influence postnatal growth rates include food supply, climate, habitat, maternal factors, and social environment. Here, we summarize interspecific and intraspecific patterns of postnatal growth in the Chiroptera by presenting empirical data, results derived from the logistic growth model, and an evaluation of both maternal and environmental factors judged to be important selective forces which may influence these patterns.

10.4.1 Growth Models and Analytical Considerations

Data on length of forearm, body mass at birth, age at weaning, and rates of postnatal growth derived from the logistic growth model are summarized in Table 10.5. Growth parameters for length of forearm and body mass were derived from the Marquardt-Levenberg algorithm (Marquardt, 1963). We used the logistic model because our previous findings (Kunz and Stern, 1995; Kunz and Robson, 1995; Stern and Kunz, 1998) showed that this model provides a better fit to empirical data than either the von Bertalanffy or Gompertz models (but see Hughes *et al.*, 1995). Kunz and Stern (1995) analysed growth data on body mass because this variable is more sensitive to environmental variation than length of forearm (see Hoying and Kunz, 1998).

Empirical methods for quantifying postnatal growth in bats are equally appropriate for free-ranging and captive populations (Kunz, 1987). Ideally, studies on postnatal growth should be based on the recapture and measurements of known-age, marked individuals. In field situations, successful recaptures of pups will vary depending on 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). In captive situations, 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).

Linear models, using least square regression for quantifying rates of change in length of forearm, body mass, and cartilaginous epiphyseal gaps can be used effectively to describe rates of change during different phases of the postnatal period (Kunz and Anthony, 1982; Burnett and Kunz, 1982; Cosson *et al.*, 1993; Kunz and Robson, 1995; Stern and Kunz, 1998). Equations derived from these analyses also can be valuable for assigning ages to bats during the postnatal period (Anthony, 1988) and stages of lactation to mothers when mother-pup pairs can be captured (Kunz *et al.*, 1995a).

Postnatal growth rates derived from measurements of pups captured on different dates (cross-sectional or grab samples) usually yield highly biased results as compared to mark-recapture data (longitudinal samples). As the growth period progresses, the capture of smaller and younger pups is often easier and, as a consequence, the empirical growth curves based on these data have lower slopes than those based on recaptured individuals. Baptista *et al.* (in press) quantified growth rates in free-ranging little brown bats (*Myotis lucifugus*) to compare longitudinal (mark-recapture) with cross-sectional samples. They found that cross-sectional samples significantly underestimated growth rates for length of forearm,

Table 10.5 Logistic growth in body mass and length of forearm for bats and their ecological and physiological correlates. Growth data and equations are derived as described by Kunz and Stern (1995). Only those studies where the exact age of pups is known are included. TR = tropical, TE = temperate.

Taxa	Wild or Captive ^a	Diet ^b	Climate	Litter Size	Weaning (d)	Mass at Birth (g)	Body mass ^c			Length of Forearm ^c			Reference			
							Mass at Birth (g)	Adult Mass (g)	Sample Size ^d	Asymptotic Mass (g)	Growth Constant K (1/time)	Forearm at Birth (mm)		Adult Forearm (mm)	Sample Size ^d	Asymptotic Forearm (mm)
Megachiroptera																
Pteropodidae																
<i>Cynopterus brachyotis</i>	C	F	TR	1.0	—	—	36.4	12 (81)	32.16	0.04	—	65.1 ^a	12 (81)	60.4	0.06	W.R. Hood & T.H. Kunz, unpublished
<i>Cynopterus sphinx</i>	C	F	TR	1.0	—	—	—	(8)	42.10	0.04	—	—	—	—	—	Krishna & Dominic, 1983
<i>Eptesiphorus wahlbergi</i>	C	F	TR	1.0	81.1	16.1	129.6	—	—	—	30.9	—	(13) ^m	82.4 ^m	0.03 ^m	Sowler, 1983
<i>Hypsignathus monstrosus</i>	C	F	TR	1.0	—	40.0	420.0 ^m	(8) ^m	435.0 ^m	0.01 ^m	—	134.0 ^m	(16) ^m	78.0 ^m	0.04 ^m	Bradbury, 1977b
<i>Pteropus hypomelanus</i>	C	F	TR	1.0	—	74.0	234.0 ^m	(17) ^m	191.9 ^m	0.52 ^m	—	120.0 ^m	(8) ^m	74.8 ^m	0.01 ^m	W.R. Hood & T.H. Kunz, unpublished
<i>Pteropus poliocephalus</i>	C	F	TR/TE	1.0	—	76.0	639.5	1(18)	583.9	0.02	—	149.1	1 (17)	153.2	0.03	W.R. Hood & T.H. Kunz, unpublished
<i>Pteropus pumilus</i>	C	F	TR	1.0	—	40.6	174.8	(95)	171.8	0.02	44.9	152.2	(102)	102.7	0.03	W.R. Hood & T.H. Kunz, unpublished
<i>Pteropus rodricensis</i>	C	F	TR	1.0	—	39.2	264.7	(166)	248.5	0.01	51.9	124.4	(180)	121.5	0.02	T.H. Kunz, unpublished
<i>Pteropus scapulatus</i>	C	F	TR	1.0	—	—	362.0	6 (81)	379.1	0.02	—	161.0	6 (69)	146.1	0.02	T.H. Kunz, unpublished
<i>Pteropus vampyrus</i>	C	F	TR	1.0	—	133.3	1132.6	(273)	755.5	0.02	79.5	224.7	(269)	190.4	0.03	G.M. O'Brien, pers. comm.
Microchiroptera																
Emballonuridae																
<i>Pteropteryx kappleri</i>	W	I	TR	1.0	—	1.5	12.8 ^a	2(18)	15.4	0.08	20.0	48.0 ^a	2 (18)	50.5	0.07	Giral et al., 1990
<i>Taphozous longimanus</i>	W	I	TR	1.0	17.5 ^a	—	29.0 ^a	(9)	20.6	0.07	—	61.6 ^a	—	—	—	Krishna & Dominic, 1983
Molossidae																
<i>Molossus molossus</i>	C	I	TR	1.0	65.0	3.6 ^a	15.1	14 (140)	12.3	0.08	17.0	38.1	15 (319)	40.7	0.05	Häussler et al., 1981
<i>Tadarida brasiliensis</i>	W	I	TE	1.0	—	3.2	12.0 ^a	49 (161)	10.6	0.17	18.5	43.0 ^a	49 (161)	44.6	0.09	T.H. Kunz & S.K. Robson, 1995
Noctilionidae																
<i>Natalio albigentris</i>	C	I	TR	1.0	80.5	—	37.7 ^a	20 (290)	25.4	0.06	—	65.0 ^a	20 (293)	57.9	0.07	Brown et al., 1983
Phyllostomidae																
<i>Artibeus jamaicensis</i>	C	F	TR	1.0	66.3	13.9	45.0 ^a	22 (97) ^m	52.8	0.04	33.5	60.5	22 (96)	60.5	0.08	Taft & Handley, 1991
<i>Carollia perspicillata</i>	C	F	TR	1.0	23.0	5.0	17.6	17 (21) ^a	17.2	0.10	24.2	43.6 ^a	17 (21) ^a	42.1	0.01	Kleiman & Davis, 1979
<i>Desmodus rotundus</i>	C	B	TR	1.0	285.0	7.0 ^a	29.0 ^a	4 (179)	29.9	0.01	—	59.0 ^a	—	—	—	Schmidt & Manske, 1973
<i>Phyllotomus discolor</i>	C	F	TR	1.0	—	7.0 ^a	39.7 ^a	6 (108)	42.5	0.05	—	62.4 ^a	6 (108)	65.5	0.01	Rother & Schmidt, 1985
<i>Phyllostomus hastatus</i>	W	F,I	TR	1.0	—	16.4	84.0 ^a	21 (197) ^m	77.9 ^m	0.06 ^m	34.4	81.9	20 (172) ^m	82.1 ^m	0.07 ^m	Stern & Kunz, 1998
								18 (168) ^f	68.3 ^f	0.06 ^f			18 (200) ^f	83.52 ^f	0.07 ^f	

Rhinolophidae														
<i>Rhinolophus ferrumequinum</i>	C	I	TE	1.0	60.0°	5.8°	22.9°	—	15.6	0.13	—	58.7°	—	Ransome et al., unpublished
Vespertilionidae														
<i>Antrozous pallidus</i>	C	I	TE	1.8	—	3.1°	18.8°	(377)	22.3	0.96	—	54.5°	(417)	Brown, 1976
<i>Eptesicus fuscus</i>	W	I	TE	2.0	36.0°	3.5°	20.2°	(256)	11.5	0.14	—	45.2°	(254)	W.R. Hood, unpublished data
<i>Eptesicus serotinus</i>	C	I	TE	1.5	24.0	5.8	23.5°	3 (28°)	28.9	0.04	—	53.0°	4 (22°)	Kleiman, 1969
<i>Myotis daubentonii</i>	W	I	TE	1.3	—	2.3	7.0	5-7 (10°)	7.5	0.10	14.9°	37.6	5-7 (10°)	Krátký, 1981
<i>Myotis macrodactylus</i>	W	I	TE	1.0	—	1.5°	7.1°	—	—	—	—	37.6°	—	Maeda, 1976
<i>Myotis lucifugus</i>	W	I	TE	1.0	25.0°	2.2	7.3°	(75)	6.8	0.22	15.8	36.4°	(65)	Kunz & Anthony, 1982
<i>Myotis myotis</i>	W	I	TE	1.0	31.5	6.2	24.9	53 (45)	26.6	0.09	23.7	63.7	53 (61°)	de Paz, 1986
<i>Myotis thysanodes</i>	W	I	TE	1.0	21.0	—	8.0°	—	—	—	—	47.6	—	O'Farrell & Studler, 1973
<i>Myotis velifer</i>	W	I	TE	1.0	43.0°	3.2°	8.9°	(280)	8.9	0.17	—	39.6°	(280)	T.H. Kunz & S.K. Robson, unpublished
<i>Nyctalus lasiopterus</i>	C	I	TE	1.7	—	5.3°	58.5°	(205)	26.2	0.12	22.1	62.0	5 (201)	Maeda, 1972
<i>Nyctalus noctula</i>	C	I	TE	1.2	60.0	5.7	20.4	10 (30)	27.6	0.12	—	51.0°	10 (27°)	Kleiman, 1969
<i>Nycticeius humeralis</i>	C	I	TE	2.1	30.0	2.0	10.2°	(63)	6.4	0.06	—	36.7°	28(162)	Jones, 1967
<i>Plecotus auritus</i>	C	I	TE	1.4	42.3	—	7.1°	—	5.9	0.25	—	38.0°	—	De Favis & Jones, 1995a
<i>Pipistrellus minimus</i>	W	I	TR	2.0	52.0	0.5°	2.0°	20 (92)	3.4	0.11	—	27.0°	20 (109)	Isaac & Marimuthu, 1996
<i>Pipistrellus pipistrellus</i>	W	I	TE	2.0	51.0	1.1	5.1	14-36 (13°)	3.7	0.04	—	31.4°	14-36 (13°)	Rakhamatulina, 1972
<i>Pipistrellus savii</i> (= <i>Hypsugo savii</i>)	W	I	TE	1.8	—	—	4.0°	(113)	5.5	0.19	—	—	(118)	Tiunov, 1992
<i>Pipistrellus subflavus</i>	W	I	TE	2.0	—	1.6	6.4	50 (383)	5.2	0.13	13.2	34.9	50 (401)	Hoying & Kunz, 1998
<i>Scotophilus heathi</i>	W	I	TR	1.9	21.0	5.0	33.5	(5°)	28.6	0.10	—	61.5°	—	Krishna & Dominic, 1983
<i>Vespertilio murinus</i>	C	I	TE	2.0	28-36	—	—	—	—	—	14.8	45.1	8	Kozhurina, 1998
<i>Vespertilio superans</i>	W	I	TE	2.0	35.0°	2.0°	18.4°	(64)	15.3	0.11	—	—	(71)	Tiunov, 1989

^aIndicates whether bats were wild caught (W) or in captivity (C) prior to milking.

^bIndicates typical diet of species. Diets include insects (I), fruit (F), nectar (N), and blood (B). Note: Captive bats may have also received nutrient supplements; however, this is generally not stated in published reports.

^cSex and forearm measurements differentiated as male (M) and female (F) for sexually dimorphic species.

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

^eVirginia Hayssen, personal communication.

body mass, and length of epiphyseal gaps. 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 were used (Dwyer, 1963; Pagels and Jones, 1974; Short, 1961; Thomas and Marshall, 1984), no further considerations are given to these studies in the present chapter.

Postnatal growth rates of some species reared in captivity may differ from those derived from free-ranging populations. For example, captive *Antrozous pallidus* and *Pipistrellus pipistrellus* grew faster than individuals of the same species in 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 reported differences in postnatal growth patterns. In several previous studies where bats have been reared in captivity, individuals were fed questionable diets and were seldom, if ever, given an opportunity to fly. 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 and/or depress metabolic rates of pups and mothers (Hoying and Kunz, 1998).

10.4.2 Interspecific Variation

Among the species of bats compared allometrically by Kunz and Stern (1995), a significant negative correlation was found between postnatal growth rates and body mass (Figure 10.2). No significant phylogenetic effect (Megachiroptera v. Microchiroptera) on postnatal growth was found after removing the effect of body mass. The absence of a significant phylogenetic effect was not surprising, given the small sample of megachiropterans ($n = 5$) available for analysis. After removing the effects of body mass, latitude (temperate v. tropical) was the only extrinsic variable that significantly affected postnatal growth rate, suggesting that temperate zone bats have higher growth rates than their tropical counterparts (Figure 10.3A). A significant negative allometric relationship was found separately for insectivorous bats, as species from temperate regions showed higher growth rates than those from tropical regions (Figure 10.3B). When tropical species were examined alone, no significant relationship between asymptotic body mass and postnatal growth was observed, perhaps because of small sample size.

Postnatal growth rates in frugivorous species were more associated with asymptotic mass than insectivorous species (Figure 10.4). This latter observation supports the hypothesis that postnatal growth rates in tropical frugivorous species may be influenced by a relatively constant diet, whereas insectivorous bats may more likely experience greater variation in food quality and quantity and, thus, exhibit more variation in growth rates. No effects of whole animal basal metabolic rate or mass-specific metabolic rate on postnatal growth rates of bats were found (Kunz and Stern, 1995).

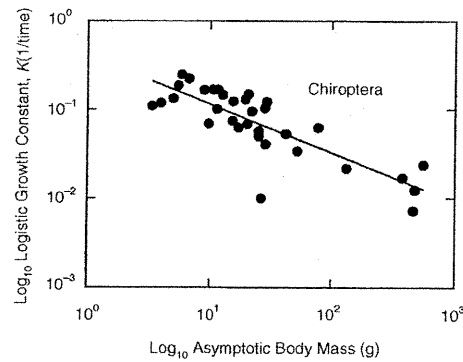


Figure 10.2 Allometric relationship between postnatal growth rates and asymptotic body mass in the Chiroptera (after Kunz and Stern, 1995).

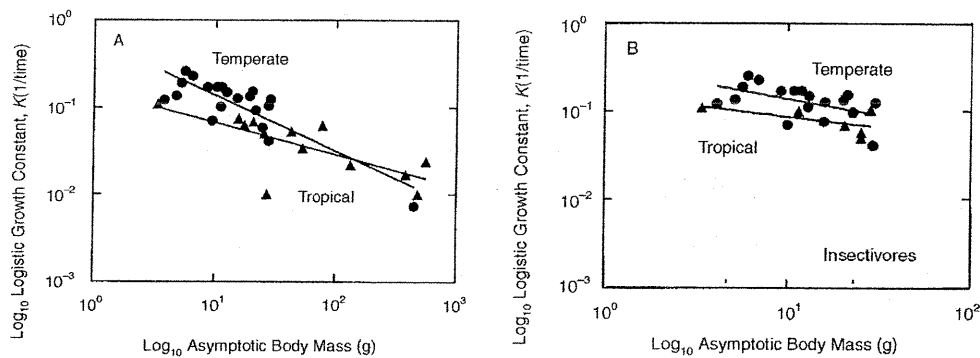


Figure 10.3 A. Allometric relationships between postnatal growth rates and asymptotic body mass in temperate (●) versus tropical zone (▲) bats ($F = 9.63$, $P = 0.004$). B. Allometric relationship between postnatal growth rates and asymptotic body mass for temperate (●) and tropical (▲) insectivorous bats ($F = 4.72$, $P = 0.042$) (after Kunz and Stern, 1995).

Postnatal growth rates of bats from tropical regions were among the lowest among the Chiroptera (Kunz and Stern, 1995), and the vampire bat, *Desmodus rotundus*, is a conspicuous further outlier. This species has the lowest growth rate among all bats that were examined by Kunz and Stern (1995). Whether this exceptionally slow growth rate reflects dietary constraints imposed by an exclusive blood meal, social conditions, or other factors invites further study.

The analysis by Kunz and Stern (1995) suggests a strong selection pressure for rapid growth rates in temperate climates. One hypothesis to account for these higher growth rates of bats in temperate, as opposed to tropical latitudes, may be explained by selection pressures in response to a shorter growing season. Faster growth rates in temperate latitudes would allow individuals to achieve maximum

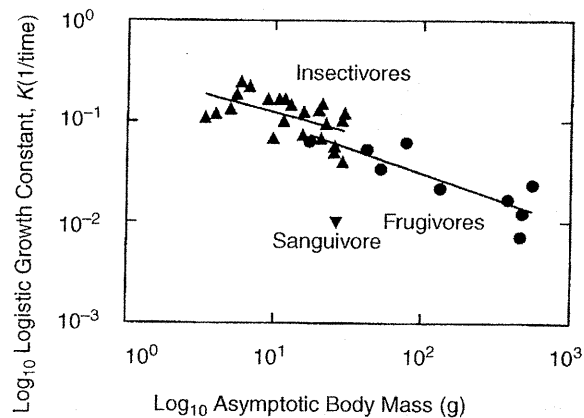


Figure 10.4 Allometric relationship between postnatal growth rates and asymptotic body mass in insectivorous (▲), frugivorous (●), sanguivorous (▼) bats. After removing the effect of asymptotic body mass, there was no significant effect of diet (insects v. fruit) on postnatal growth ($F = 1.23$, $P = 0.289$) (after Kunz and Stern, 1995).

somatic growth and to deposit important fat reserves before the onset of winter hibernation or migration (Kunz and Stern, 1995; Hoying and Kunz, 1998). This interpretation is consistent with Boyce's (1979) hypothesis that accelerated growth should be found among mammals living in highly seasonal environments, a characteristic of temperate regions. In this context, it would be interesting to compare postnatal growth rates of tropical species known to occur over a range of different altitudes.

10.4.3 Intraspecific Variation

When data on intraspecific variation in postnatal growth rates are examined, both quantitative and qualitative differences can be seen. Here we evaluate environmental and biotic factors known or suspected to affect intraspecific variation in postnatal growth rates in bats, including food supply and climate, latitude, diet, gender, litter size, colony size, season, and growth conditions (captive v. free-ranging). Because many of these factors are interdependent, we also consider possible interactions in an effort to interpret observed patterns of postnatal growth.

Local climate and food supply

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. 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.

In free-ranging bats, meteorological conditions directly affect both food abundance and quality as well as the behavioral and physiological condition of mothers and 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 food available to lactating females is an important factor explaining growth rates in bats. In their study of postnatal growth in *Pipistrellus subflavus* in eastern Massachusetts, Hoying and Kunz (1998) found significant inter-year variation in postnatal growth rates (Figure 10.5). They attributed this difference, in part, to the contrasting abundance of insects during the two years of study. Postnatal growth in body mass was slower in 1982 than in 1981. Births were delayed by nearly one week in 1982 and pups that were born during this inclement period experienced depressed growth. Not only were fewer flying insects available to lactating mothers, but unseasonably cool temperatures caused daily torpor 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).

Latitude and regional climate

Theoretically, populations of the same species 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 lower than those in New Hampshire (42°25'N). Although the general trend of higher growth rates in temperate v. tropical bats may hold in an

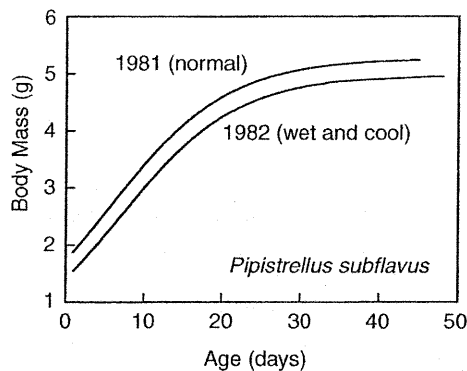


Figure 10.5 Effects of insect availability on postnatal growth rates in *Pipistrellus subflavus* in two different years (1981 and 1982). Bats increased in body mass at a significantly greater rate in 1981 than in 1982 ($F = 32.3, P < 0.001$). The year 1981 was characterized by normal seasonal temperature and precipitation, whereas 1982 experienced above normal precipitation and low ambient temperature (after Hoying and Kunz, 1998).

allometric analysis of different species (Kunz and Stern, 1995), Fujita's observation suggests that growth rate in the most northern part of a species' range may actually be lower, as influenced by energetic considerations (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 are higher for mothers and pups at colder, more northerly temperate latitudes, then less energy would be available for reproduction. For species with a geographic distribution that extends from intermediate into cool temperate latitudes, postnatal growth rates may indeed be lower at the highest latitudes. Thus, for species with geographic distributions that span from low to high latitudes (e.g., *Eptesicus fuscus*), we would predict a hyperbolic curve for 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 in the northern hemisphere (Kunz *et al.*, 1998b) may characterize a suite of life-history traits that limits its breeding distribution.

Season

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 which 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 polyoestrous species.

Gender

Gender-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 overall differences in postnatal growth rates appear to be correspondingly slight or nonexistent (Kunz, 1973; Kunz and Anthony, 1982; Burnett and Kunz, 1982; but see Kunz, 1974). Notwithstanding, some tropical frugivorous species (e.g., *Artibeus jamaicensis*, *Pteropus hypomelanus*, *Hypsignathus monstrosus*, and *Epomophorus wahlbergi*) and one omnivorous species (*Phyllostomus hastatus*) show significant sexual dimorphism in adults; this may be a consequence of gender-specific differences in 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

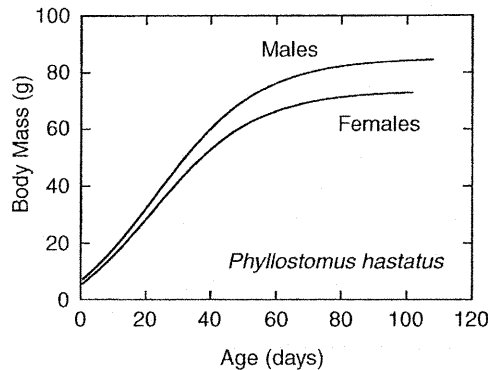


Figure 10.6 Effects of gender on postnatal growth in body mass in *Phyllostomus hastatus*. Males grew at a significantly greater rate ($t = 4.39$, $P < 0.001$) than did females from the same population in the same year (from Stern and Kunz, 1998).

resources to male pups often results in a high degree of sexual dimorphism in polygynous species (Figure 10.6 and Bradbury, 1977b), suggesting that postnatal growth rates are greater or growth continues longer in males than in females.

Litter size

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). Species in which twinning occurs can provide valuable data for comparing the effects of litter size on postnatal growth rates. Among North American bats which have litter sizes greater than one, postnatal growth rates have been quantified for *Antrozous pallidus*, *Pipistrellus subflavus*, and *Eptesicus fuscus*. Populations of *E. fuscus* in the western USA typically produce litter sizes of one, whereas those in the east typically produce twins (Burnett, 1983; Holroyd, 1993).

Comparisons of postnatal growth rates between populations from different geographic regions may be confounded by differences in climate, food availability, or both (see below). To avoid such geographic or other confounding effects on postnatal growth, ideally singletons and twins should be sampled from the same population. Bassett (1984) compared growth rates for length of forearm in singletons and twins of *A. pallidus* collected from the same population in California. In his captive study, 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 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 both length of forearm and body mass of twin pups grew significantly more slowly than the length of forearm and body mass of singleton pups.

Roost temperature and colony size

Conditions in the roosting environment of bats (Kunz, 1982) potentially have important direct and indirect effects on intraspecific variation in postnatal growth rates (Tuttle and Stevenson, 1982). Tuttle (1975) compared pre-weaning 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 allocated more energy to maintenance, and thus less energy was available for production (milk output by females and accretionary growth of pups). He also suggested that roost temperature was directly proportional to colony size, because large numbers of bats generated more heat and could more effectively increase the roost temperature of the cave (and thus reduce maintenance costs). Post-weaning growth in *M. grisescens* may also be influenced by colony size (Tuttle, 1976), as individuals from large colonies are expected to fly greater distances to feed than bats from small colonies. Tuttle argued that pups from large colonies allocated a greater amount of energy to nightly foraging flights, as pups from these colonies experienced slower post-weaning growth rates. These results suggest that interactions between roost location (relative to suitable foraging habitats, colony size and microclimate) should be considered when evaluating postnatal growth rates in bats.

10.4.4 Ontogeny of Flight, Echolocation and Feeding Behavior

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

The extent to which either or both parents assume roles in the development of communication and echolocation skills in bats has not been thoroughly 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. They include *Noctilio albiventris* (Brown *et al.*, 1983), *Eptesicus fuscus* (Brigham and Brigham, 1989), and *Desmodus rotundus* (Wilkinson, 1985, 1987). Other species, such as *Myotis myotis* (Audet, 1990), *M. lucifugus* (Buchler, 1980; Kunz and Anthony, 1996; Adams, 1996), *Pipistrellus pipistrellus* (Racey and Swift, 1985), and *Rhinolophus ferrumequinum* (Jones *et al.*, 1995) appear to develop foraging skills independent of their mothers. Thus, 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.

In monogamous species and in polygynous species that form harems, and in species where the putative father is present during the developmental period of pups, paternal influence on the development of vocalizations (including echolocation) and early flight and foraging can be expected. 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). Within a week of making their first foraging flights, pups practice wing flapping as they cling to their mothers. Pups may accompany either parent to a shared feeding territory, and may also use their parent's foraging perches. Similar observations have been reported for *Cardioderma cor*, where mother-pup contact is maintained by calls produced by the mothers at foraging sites (Vaughan, 1976).

10.5 CONCLUSIONS, PREDICTIONS AND FUTURE DIRECTIONS

Future studies on parental care and postnatal growth in bats should focus attention on frugivorous, nectarivorous, sanguivorous, and carnivorous species. Most published studies on mother-pup recognition have focused on temperate insectivorous species, thus research on tropical species with other dietary habits is warranted. Although the role of acoustic communication in mother-pup reunions has received considerable attention, the role of spatial memory, olfactory, and visual cues have largely been ignored. These modes of communication are likely to play an equally important role in the identification of kin. The role of tactile stimuli, especially associated with allogrooming in pup recognition, has not been investigated.

Analysis of milk composition has been reported for relatively few species of bats. Future studies should focus on milk composition of nectarivorous, frugivorous and carnivorous species, and include analysis at different stages of lactation along with estimates of milk yield. Comparisons of milk composition and milk energy output from different species and different life histories will ultimately make it possible to evaluate the relationship between milk yield and growth rates in bats. Among species represented by different feeding guilds, we would expect maternal effort and postnatal growth rates to be greatest in insectivorous and carnivorous species, intermediate for frugivorous species, and least for nectarivorous species. Why the postnatal growth rate of a sanguivorous species is so low relative to other species invites further study.

Future studies on postnatal growth rates should be designed to integrate data on local climate, food availability, maternal diet, milk composition, milk energy yield, and non-energetic parental effort. Studies should be designed to compare parental effort and postnatal growth in species from different geographic areas, different colony sizes, and seasons. We would expect postnatal growth rates in populations that occur in highly seasonal, temperate environments to exhibit higher growth rates than those from subtropical and tropical environments, except that growth in extreme latitudes may be reduced. In tropical environments, where food resources are often highly variable in time and space (including flowers, fruits, and insects), we would expect to find seasonal differences in growth rates in those species which produce two or more litters per year.

Relationships between pup growth, colony size and 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 maintain elevated body temperatures during the postnatal period. Parental effort and growth rates in bats should be sensitive to environmental conditions, especially if the habitat is degraded (which may increase foraging time and reduce energy transfer to pups), sizes of maternity colonies are reduced (with a decrease in thermal advantages that may accrue from warm roosts), and there are changes in the abundance and availability of food resources (seasonal and inter-year variation in insect, fruit, and nectar production). Finally, 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.

ACKNOWLEDGMENTS

We are grateful to numerous individuals who have assisted in the field and laboratory. These individuals include K. Atkinson, T. Baptista, D. Barber, F. Bonaccorso, S. Davidson, A. Field, D. Le Blanc, O.T. Oftedal, and J. Seyjagat, and R.M.R. Barclay, G. O'Brien, and E. Kozhurina made unpublished data available on postnatal growth. We also thank E. Studier, C. Voigt, and A. Stern for their critical reviews of an early version of this manuscript. Preparation of this paper was made possible by grants from the National Science Foundation (BSR 87-00585) and the Lube Foundation, Inc. to T.H.K. This chapter is publication no. 60 of the Lube Foundation.

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