

Maternal investment and post-natal growth in bats

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Synopsis

We analysed post-natal growth data for body mass from 33 species of free-ranging and captive bats, using the logistic growth equation. When these data were examined by means of linear regression and covariance analysis, we found that growth rates decreased linearly with increasing asymptotic body mass. When we removed the effect of body mass, growth rates showed no significant differences with respect to diet (insect or fruit), taxonomic affiliation (Megachiroptera or Microchiroptera), growth condition (captive or free-ranging), or basal metabolic rate. Climate (tropical or temperate) was the only variable that had a significant effect on post-natal growth rates, with temperate bats growing faster than tropical species. This climatic effect was also evident when insectivorous bats were examined separately. While post-natal growth rates may provide a valuable index of maternal investment, milk energy output of females during lactation should provide the most direct link between the environment and growth of pups. Milk composition and milk-energy output as indices of maternal investment have been investigated in only a few species of bats. From the limited data available it appears that the milk of insectivorous species contains a higher percentage of dry matter, fat and protein than does that of frugivorous species.

Introduction

Although post-natal growth is an important life-history trait in vertebrates (Case 1978; Ricklefs 1979) and an important index of maternal investment (Oftedal 1984; Kirkwood 1985; Costa, Le Boeuf, Huntley & Ortiz 1986; Gittleman & Oftedal 1987; Oftedal & Gittleman 1988; McLaren 1993), little attention has been given to the proximate and evolutionary forces influencing post-natal growth rates in mammals. Moreover, few life-history analyses of mammals have included representatives of the Chiroptera, the second largest order of mammals in number of species. Previous analyses of life-history variation in this group have either grossly under-represented bats (e.g. Wootton 1987; Harvey & Read 1987; Read & Harvey 1989;

Promislow & Harvey 1990) or excluded them entirely (e.g. Millar 1981; Western & Ssemakula 1982; Martin 1984; Martin & MacLarnon 1985). Proximate factors known to influence growth rates include food supply, climate, habitat, maternal factors and social environment. In the following account, we examine interspecific patterns of post-natal growth in bats, and consider factors that may be important selective forces in moulding these patterns of growth.

Previous reviews of post-natal growth in bats (Orr 1970; Tuttle & Stevenson 1982) have been largely qualitative. Case's (1978) allometric analysis of post-natal growth in vertebrates included 17 species of bats, but his conclusions are limited because he analysed only the early linear period of growth and did not remove the effects of body size. Moreover, the growth data on bats that were available at the time of Case's analysis were strongly biased towards small insectivorous species (<30 g as adults), most of which were members of a single family (Vespertilionidae). From the various mammal species that Case (1978) analysed, he considered bats to have intermediate growth rates, although he gave no explanation for this pattern.

The objectives of the present review are to compare patterns of post-natal growth in the Chiroptera using data representing a wide range of asymptotic body masses (3.6 g to 557 g), phylogeny (Megachiroptera and Microchiroptera), diet (insects or fruit), climate (temperate or tropical), and study conditions (free-ranging or captive). We also review the available data on milk composition in bats. While our analyses of post-natal growth and milk composition are still limited to relatively few species, they offer some insight into factors that may affect maternal investment patterns in the Chiroptera.

Bats are unique among mammals in that females provide their young with milk until they achieve at least 90% of adult wing dimensions and at least 70% of adult (postpartum) body mass (Fig. 1). Generally, bat pups are not capable of sustained flight and foraging until they achieve adult wing dimensions, and thus remain nutritionally dependent on their mothers for longer periods of time than do the young of most terrestrial mammals (Barclay this volume pp. 245–258). Perhaps because of this constraint, bats have smaller litter sizes than terrestrial mammals, although litter masses at birth are comparable for the two groups (Kurta & Kunz 1987). Thus, the energy and nutrients that female bats invest in their pups should play a crucial role in the pattern of post-natal growth before pups achieve flight (Barclay 1994). Although individuals of some species begin to fly and feed on solid food well before they are fully weaned, patterns of post-natal growth should be strongly influenced by the quality and quantity of milk allocated to, and assimilated by, pups during the pre-weaning period.

Methods

Data on post-natal growth were analysed for 33 species of bats (Table 1), representing four of 17 families and both suborders (Megachiroptera and Microchiroptera). Because our analysis is based on less than 4% of the total number of species currently recognized (Koopman 1993), our conclusions must be considered preliminary. We evaluated published and unpublished data on post-natal growth (body mass, g) and used the logistic growth model for our analysis, because previous studies (Kunz & Robson in press) indicated that this model, when compared with von Bertalanffy and Gompertz models (Zullinger, Ricklefs, Redford & Mace 1984) best fits the empirical data for bats (also see Hughes, Rayner & Jones in press). Although forearm length is an important variable in growth studies (Kunz 1987), we chose body mass because it appears to be more sensitive to environmental variation (K. M. Hoying & T.H. Kunz unpubl). We used the Marquardt-Levenberg algorithm (Marquardt 1963) to derive growth parameters from the logistic equation:

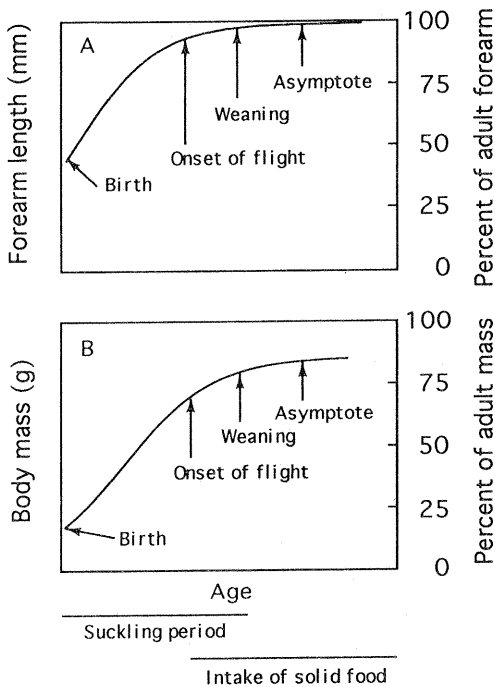


Fig. 1. Generalized model for post-natal growth in bats, showing the relationships between growth of (A) forearm length and (B) body mass, and the timing of birth, suckling, onset of flight, weaning and intake of solid food.

Table 1. Logistic growth constants of bats and their physiological and ecological correlates.

Taxonomic affiliation	Logistic growth parameters			Physiological and ecological correlates				Source
	Growth constant (K)	Asymptotic mass (A)	Adult mass (g)	BMR ^a	Diet ^b	Climate ^c	Condition ^d	
Megachiroptera								
Pteropodidae								
<i>Hypsignathus monstrosus</i>	0.0072	463.0	—	—	fr	tr	ca	Bradbury (1977)
<i>Pteropus hypomelanus</i>	0.0124	469.7	470.1	211.6	fr	tr	ca	T. H. Kunz (unpubl.); B. K. McNab (pers. comm.)
<i>Pteropus poliocephalus</i>	0.0238	557.0	598.0	316.9	fr	te	ca	T. H. Kunz (unpubl.); Bartholomew, Letner & Nelson (1964)
<i>Pteropus pumilus</i>	0.0217	132.7	194.2	127.2	fr	tr	ca	T. H. Kunz (unpubl.); B. K. McNab (pers. comm.)
<i>Pteropus scapulatus</i>	0.0170	379.1	362.0	242.5	fr	tr	ca	G. O'Brien (pers. comm.)
Microchiroptera								
Emballonuridae								
<i>Taphozous georgianus</i>	0.0506	25.33	—	—	in	tr	fl	Jolly (1990)
<i>Taphozous longimanus</i>	0.0686	20.54	—	—	in	tr	fl	Krishna & Dominic (1983)
Molossidae								
<i>Molossus molossus</i>	0.1010	11.47	15.6	17.2	in	tr	ca	Häusser, Möller & Schmidt (1981); McNab (1969)
<i>Tadarida brasiliensis</i>	0.1680	10.63	10.4	20.8	in	te	fl	Kunz & Robson (in press); Herreid & Schmidt-Nielsen (1966)
Noctilionidae								
<i>Noctilio albigentris</i>	0.0573	25.37	27.0	23.8	in	tr	ca	Brown, Brown & Grinnell McNab (1989)
Phyllostomidae								
<i>Artibeus jamaicensis</i>	0.0340	52.89	45.0	56.3	fr	tr	ca	Taft & Handley (1991); McNab (1989)
<i>Carollia perspicillata</i>	0.0629	17.30	14.9	31.4	fr	tr	ca	Kleiman & Davis (1979); McNab (1989)
<i>Desmodus rotundus</i>	0.0109	26.90	29.0	26.4	bl	tr	ca	Schmidt & Manske (1973) McNab (1989)

(Cont.)

Physiological and ecological correlates

Logistic growth parameters

Taxonomic affiliation	Logistic growth parameters			Physiological and ecological correlates				
	Growth constant (K)	Asymptotic mass (A)	Adult mass (g)	BMR ^a	Diet ^b	Climate ^c	Condition ^d	Source
<i>Phyllostomus discolor</i>	0.0530	42.41	34.0	35.02	fr	tr	ca	Rother & Schmidt (1985) McNab (1989)
<i>Phyllostomus hastatus</i>	0.0620	77.72	84.0	70.56	fr,in	tr	fl	A. Stern & T. H. Kunz (unpubl.); McNab (1989)
Rhinolophidae								
<i>Rhinolophus ferrumequinum</i>	0.1250	15.64	—	—	in	te	ca	R. Ransome <i>et al.</i> (unpubl.)
Vespertilionidae								
<i>Antrozous pallidus</i>	0.0955	22.27	00.0	00.00	in	te	ca	Brown (1976)
<i>Eptesicus fuscus</i>	0.1470	12.80	16.9	20.28	in	te	fl	Burnett & Kunz (1982); Herreid & Schmidt-Nielsen (1966)
<i>Eptesicus serotinus</i>	0.0404	28.84	—	—	in	te	ca	Kleiman (1969)
<i>Miniopterus schreibersii</i>	0.0744	15.47	—	—	in	te	fl	Dwyer (1963)
<i>Myotis daubentonii</i>	0.0690	9.75	—	—	in	te	fl	Krátký (1981)
<i>Myotis lucifugus</i>	0.2242	6.70	6.5	9.3	in	te	fl	Kunz & Anthony (1982); Hock (1951)
<i>Myotis myotis</i>	0.1500	20.91	—	—	in	te	fl	Krátký (1970)
<i>Myotis velifer</i>	0.1670	8.94	11.9	7.7	in	te	fl	T. H. Kunz & S. K. Robs (unpubl.); Riedesel & Williams (1976)
<i>Nyctalus lasiopterus</i>	0.1220	29.66	—	—	in	te	ca	Maeda (1972)
<i>Nyctalus noctula</i>	0.1310	19.77	—	—	in	te	ca	Kleiman (1969)
<i>Pipistrellus mimus</i>	0.1103	3.36	—	—	in	tr	fl	S. Isaac & G. Marimuthu (comm.)
<i>Pipistrellus pipistrellus</i>	0.1198	3.95	—	—	in	te	fl	Rakhmatulina (1971)
<i>Pipistrellus savii</i>	0.1870	5.48	—	—	in	te	fl	Tiuonov (1992)
<i>Pipistrellus subflavus</i>	0.1340	4.98	—	—	in	te	fl	K. M. Hoying & T. H. K. (unpubl.)
<i>Plecotus auritus</i>	0.2500	5.87	—	—	in	te	ca	De Faniis & Jones (1995)
<i>Scotophilus beatrix</i>	0.1033	28.57	—	—	in	tr	fl	Krishna & Dominic (1988)
<i>Vespertilio superans</i>	0.1680	11.66	—	—	in	te	fl	Tiuonov (1989)

^aBasal metabolic rate. ^bfr = fruit; in = insects; bl = blood. ^ctr = tropical; te = temperate. ^dfl = field; ca = captivity

$$M(t) = A \{e^{-K(t-I)} + 1\}^{-1}$$

where M = mass (g), A = asymptotic size, K = growth constant (days^{-1}), and I = inflection point.

In theory asymptotic body mass is achieved by bats when the post-natal growth rate becomes zero, usually in the season of birth. Asymptotic mass of young bats is usually less than adult mass, because it does not include accretionary growth after the first year, nor does it include the deposition of fat in autumn which is characteristic of most temperate species in the post-weaning period. When possible, growth parameters were derived directly from the analysis of original growth data. However, because few published studies on post-natal growth included original data, either graphically or in tabular form, we derived growth curves (and growth parameters) from published graphs or from plotted data points using the program DigiMatic (Version 2.0.1 for Macintosh). This software made it possible to represent data points and line graphs digitally from published and unpublished growth curves that otherwise would not be available for comparison. Graphs were plotted using SigmaPlot (Version 4.11 for Macintosh).

Our allometric analysis is based on data for post-natal growth rates for both free-ranging and captive bats. In the case of captive bats, only the growth data from young suckled by their mothers were used for analysis—data on hand-fed bats were excluded. We did not include data for some species because the original data or curves did not allow us to compute each of the parameters for the logistic growth equation. Thus, we could not use data on post-natal growth that only included the early linear phase of post-natal growth (e.g. O'Farrell & Studier 1973; Tuttle 1975; McWilliam 1987). Moreover, we did not include data on growth curves derived from cross-sectional (grab) samples of wild populations (e.g. Short 1961; Medway 1972; Pagels & Jones 1974; Yokoyama, Ohtsu & Uchida 1979; Thomas & Marshall 1984), or when we judged the asymptotic body masses to deviate markedly from those of free-ranging populations (e.g. Jones 1967; Noll 1979). When growth data were available for both sexes in sexually dimorphic species, we only used data for females. When growth rates did not differ between sexes, growth parameters were based on combined data. Ideally, we would have preferred to use growth data only for free-ranging bats, but obtaining post-natal growth data on some free-ranging species is impractical, especially for the large pteropodids and small solitary species.

For allometric analyses, we used \log_{10} transformations on continuous variables, including the logistic growth constant, asymptotic body mass and basal metabolic rate, to improve the symmetry of data for analysis (Hoaglin, Mosteller & Tukey 1983). We chose least-squares regression analysis instead of reduced major axis analysis to maintain a constant dimensionality of slopes across different data sets. We used regression analysis to test for significant allometric relationships, and analysis of covariance (ANCOVA) to test for

data set for homogeneity of variance. If the slopes of regressions were the same, we then tested for differences in intercepts.

The \log_{10} of the logistic growth constant (K) for pup mass was used as the dependent variable; independent variables included \log_{10} asymptotic mass and BMR (continuous variables). Categorical variables included taxonomic affiliation (Megachiroptera and Microchiroptera), diet (insects and fruit), climate (temperate and tropical) and growth condition (captive and free-ranging). We chose the species as the primary unit for allometric analysis, although there are criticisms of this approach (see Harvey & Mace 1982). Suborder designations were used to test for taxonomic affiliation because sample sizes for most taxonomic groups (e.g., genus or family) were too small for meaningful analysis. Climate designations (temperate and tropical) probably are not independent of diet, because frugivorous species are known almost exclusively from tropical climates (except *Pteropus poliocephalus*); however, because obligate insectivory is found in both temperate and tropical regions (six tropical and 17 temperate species in the present study), we used these data to test for climatic effects.

Results and discussion

Interspecific patterns of post-natal growth

Among the 33 species analysed, we found a significant negative correlation between post-natal growth rate and asymptotic body mass ($r^2 = 67.0\%$, $F = 65.87$, $P < 0.0005$) (Fig. 2). To examine the effects of diet, we omitted the one omnivore (*Phyllostomus hastatus*) and sanguivore (*Desmodus rotundus*) from the data set. With these two species removed the correlation of the allometric relationship increased by 10.8% ($r^2 = 77.8\%$, $F = 106.05$, $P < 0.0005$). When the effects of body mass were removed, the additional increase (+ 1.9%) due to diet (insects and fruit) was not significant ($F = 3.68$, $P = 0.065$). However, the coefficient of determination for frugivorous species ($r^2 = 70.6\%$, $n = 8$) was greater than that for insectivorous species ($r^2 = 26.5\%$, $n = 23$). This suggests that fruit-eating bats may have greater nutritional constraints and feed on a narrower range of food quality. We found no significant phylogenetic effect (Megachiroptera vs. Microchiroptera) on post-natal growth ($F = 0.2601$, $P = 0.614$) after removing the effect of body mass (Fig. 3a). However, the absence of a significant phylogenetic effect is not surprising, given the small sample of megachiropterans ($n = 5$) available for analysis. Moreover, we found no significant effect of growth condition (captive vs. field) on post-natal growth ($F = 1.493$, $P = 0.231$) after removing the effect of body mass (Fig. 3b). However, because the variance in captive versus field data for log growth rates differs significantly ($P < 0.05$, captive, $r^2 = 62.0\%$, and free-ranging, $r^2 = 25.5\%$), the statistical validity of this comparison remains questionable.

After the effect of body mass was removed, climate (temperate vs. tropical)

was the only climatic variable that significantly affected post-natal growth rates ($F = 9.63$, $P = 0.004$), indicating that temperate species have higher growth rates than their tropical counterparts (Fig. 3c). Because frugivorous species are known primarily from tropical regions (except *Pteropus poliocephalus*) and insectivorous species are known from both climatic regions, we examined the effects of climate by comparing growth rates between temperate and tropical insectivorous species. From this analysis, the negative allometric relationship ($r^2 = 26.6\%$) for all insectivorous bats was significant ($F = 8.93$, $P = 0.007$) and post-natal growth rates of temperate insectivorous species were significantly greater ($F = 4.72$, $P = 0.042$) than those of insectivorous bats from tropical regions (Fig. 3d). The effects of climate increased (+ 11%) the overall allometric relationship among insectivorous species to 37.6% but the separate coefficients of determination for tropical (21.0%, $n = 6$) and temperate insectivores (21.7%, $n = 17$) were lower. Asymptotic body mass had no significant effect on post-natal growth for tropical insectivorous species

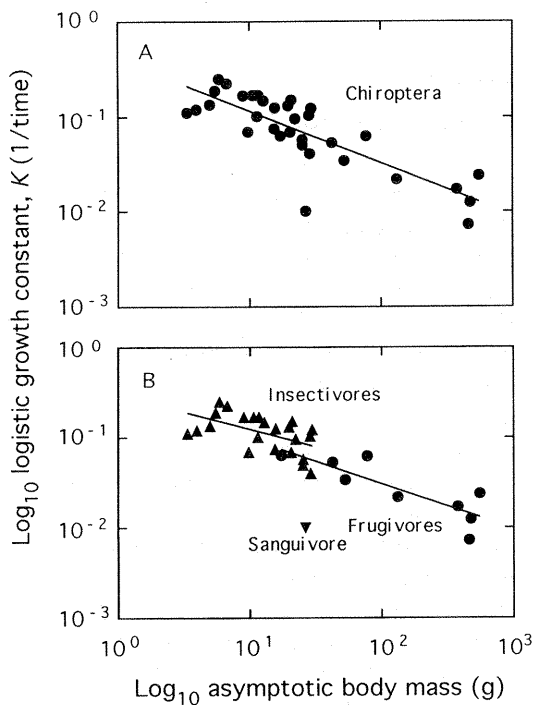


Fig. 2. (A) Allometric relationship between post-natal growth rates and asymptotic body mass in the Chiroptera. (B) After removing the effect of asymptotic body mass, there was no significant effect of diet (insectivory or frugivory) on post-natal growth. The single sanguivore was not included in this analysis, but it appears to have a relatively slow growth rate for its body mass.

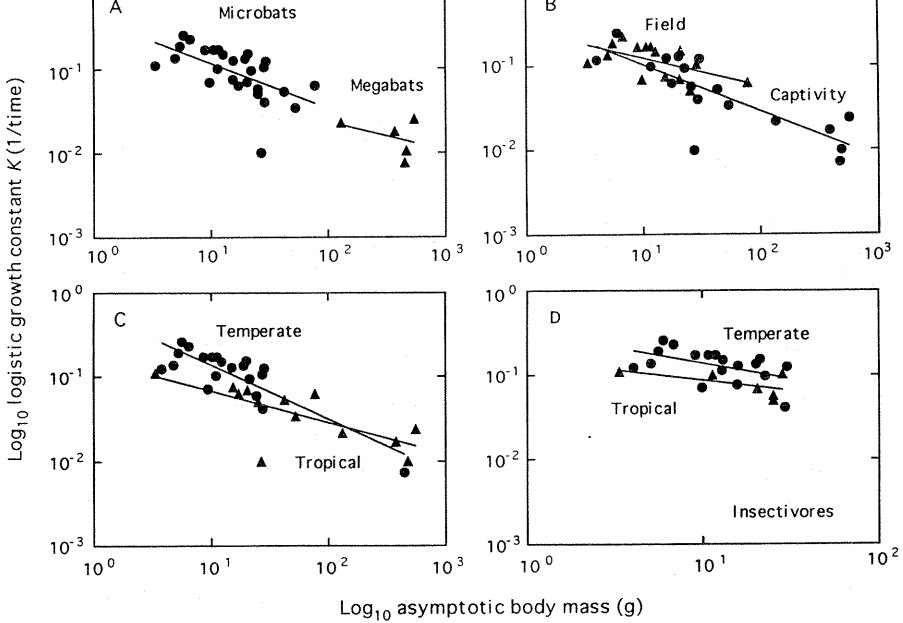


Fig. 3. (A) Allometric relationship between post-natal growth rate, asymptotic body mass and phylogeny (megabats or microbats). When the effect of body mass was removed there was no significant effect of phylogeny on post-natal growth rate. (B) Allometric relationship between post-natal growth rates, asymptotic body mass and growth condition (captive or free-ranging). When the effect of body mass was removed, there was no significant effect of growth condition on post-natal growth rate. (C) Allometric relationship between post-natal growth rate, asymptotic body mass and climate (temperate or tropical). When the effect of body mass was removed there was a significant effect of climate. (D) Allometric relationship between post-natal growth rates and asymptotic body mass for temperate and tropical insectivorous bats. When the effect of body mass was removed there was a significant difference in growth rates between these two groups.

($P = 0.201$), perhaps because of small sample size. Thus, tropical species appear to have growth rates that are independent of asymptotic body mass, whereas temperate species are negatively correlated. When we examined the effects of study condition on post-natal growth rates of insectivorous species, we found no significant differences ($F = 1.29$, $P = 0.89$), although the coefficient of determination for laboratory-reared bats ($r^2 = 52.0\%$, $n = 7$) was 3.6 times greater than that for free-ranging bats ($r^2 = 14.2\%$, $n = 16$).

The higher coefficient of determination for bats reared in captivity as opposed to free-ranging bats suggests that extrinsic factors may have a more important influence on post-natal growth rates in captive than in free-ranging bats. This observation suggests that the nutritional conditions in captivity may push post-natal growth rates to their maximum, whereas growth conditions experienced by free-ranging bats appear to be more variable. When

we also found a significant negative correlation of post-natal growth rates with asymptotic body mass ($r^2 = 82.6\%$, $F = 67.54$, $P < 0.005$, $n = 15$), but the overall effect of diet was not significant ($F = 1.23$, $P = 0.289$). Notwithstanding, post-natal growth rates in frugivores were more strongly correlated with asymptotic mass ($r^2 = 70.6\%$, $F = 17.85$, $P = 0.006$) than were those in insectivores ($r^2 = 52\%$, $F = 7.50$, $P = 0.041$). This result further supports the hypothesis that the growth rates of frugivores may be constrained by a relatively uniform diet, whereas insectivorous bats are more likely to experience variation in food quality and quantity and, thus, exhibit more variation in growth rates.

Because post-natal growth rates are negatively correlated with basal metabolic rate (BMR) and diet in birds and terrestrial mammals (McNab 1988, 1989, 1992), we expected to find a similar correlation for bats. Although growth rate was significantly correlated with asymptotic body mass ($r^2 = 62.7$, $F = 26.21$, $P < 0.005$, $n = 16$), we found no additional effects due either to whole animal BMR ($r^2 = 59.8\%$), $F = 0.005$, $P = 0.94$) or mass-specific BMR ($r^2 = 59.8\%$, $F = 0.002$, $P < 0.96$).

Our allometric analysis revealed that bats from temperate regions have higher post-natal growth rates than do tropical species, and growth rates of tropical frugivores are among the lowest among the Chiroptera. A conspicuous exception to this generalization is the sanguivorous vampire bat, *Desmodus rotundus*, which has the slowest growth rate ($K = 0.01$) among all the species that we examined (Fig. 2, Table 1). Unfortunately, data on post-natal growth rates for free-ranging frugivorous bats do not exist, partly because many fruit-eating species are solitary (or occupy inaccessible foliage roosts) and they are less amenable to study than are gregarious species which live in caves or buildings. If frugivorous bats in captivity are being pushed to their maximum growth limits owing to high planes of nutrition, we would expect free-ranging species overall to have lower rates than those observed in captivity. We suggest that frugivorous species that roost in caves and other enclosed roosts should be the focus of future studies, to help clarify these effects of diet and growth conditions on post-natal growth rates in bats.

The majority of species included in our analysis were from temperate regions and feed primarily on insects and other arthropods. No data on temperate frugivorous or omnivorous species exist, so the only valid comparison we could make was between temperate and tropical insectivorous taxa. Our analysis shows that temperate and tropical insectivorous species differ in growth rates, suggesting a strong selection pressure for faster growth rates in cooler climates. One hypothesis to account for higher growth rates at more northern latitudes is that bats may be selected in response to a shorter growing season. This would allow individuals to achieve maximum somatic growth and to deposit important fat reserves in preparation for winter hibernation or migration. Our interpretation is consistent with Boyce's (1979) hypothesis that

environments.

Methodological considerations

Observed post-natal growth rates in bats may be affected by the methods used to collect the empirical data as well as by the methods used in their analysis. Acceptable methods for collecting empirical growth data for bats were reviewed by Kunz (1987). These include marking and measuring individual pups at birth and monitoring changes in their linear size and their body mass on subsequent days. This method is equally appropriate for free-ranging and captive situations. In field situations, however, successful recaptures of pups will vary, depending upon the size of the colony, the fidelity that mothers and their pups show to the roost and the access that investigators have to the pups. Growth rates derived from measurements of pups captured on different dates (so-called cross-sectional samples) are less desirable and are usually biased towards measurements of smaller and younger pups, because they are usually easier to capture than older, more elusive individuals. Thus, growth rates based on cross-sectional samples are usually lower than those determined from capture–recapture data (Kunz 1987). In studies where cross-sectional samples have been used in growth analysis, corrections based on known-age individuals were necessary to compensate for this potential bias (see Tuttle 1975).

Milk composition

Reports of milk composition for a wide range of terrestrial and marine mammals show considerable interspecific variation in both quality and quantity produced (Oftedal 1984, 1985; Ortiz, Le Boeuf & Costa 1984). Much of this variation can be attributed to differences in maternal diet. For example, carnivorous and insectivorous species typically produce milk higher in protein and fat than do those which feed on mixed diets of plants and animals or exclusively on plant parts. Even among animal-eating mammals, marked differences in milk composition reflect the general composition of their diets (Gittleman & Oftedal 1987). Thus, we would predict that bats which feed on fruit and nectar should have slower post-natal growth rates than those which feed on insects and vertebrates. Why sanguivorous bats should have such slow growth rates remains puzzling, especially given the high protein content of blood available to lactating females.

Although milk composition has been investigated for several species of bats (Huibregtse 1966; Jenness & Studier 1976; Kunz, Stack & Jenness 1983; Quicke, Sowler, Berry & Geddes 1984), few data are available for meaningful interspecific comparisons, either because the stage of lactation was not reported or because sample sizes were too small to be representative. Moreover, few reliable data are available for making comparisons across dietary categories. From our analyses of milk samples of four species of

Tadarida brasiliensis (Kunz, Stack *et al.* 1983; Kunz, Oftedal, Robson, Kretzmann & Kirk in press), one omnivorous species (*Phyllostomus hastatus*), and three frugivorous species (*Pteropus hypomelanus*, *P. rodricensis*, and *P. vampyrus*) (T. H. Kunz, A. A. Stern & O. T. Oftedal unpubl.), significant interspecific differences are evident. Milks of insectivorous bats generally have higher dry matter, fat and protein content than do those of omnivorous or frugivorous species. The relatively low fat, protein and dry matter content of milk from frugivores is consistent with the relatively low fat and protein content of fruit eaten by most plant-visiting bats (Morrison 1980; Fleming 1988; Kunz & Diaz in press). Although we found no significant effect of adult diet on post-natal growth in bats based on our allometric analysis ($P = 0.065$), we expect that milk composition and milk-energy output will prove to be important factors influencing post-natal growth rates in bats.

Conclusions

Previous comparative studies on post-natal growth of bats have been mostly qualitative. Results of our comparative analysis, showing an inverse relationship between post-natal growth rates and asymptotic body mass, are consistent with findings reported for other mammalian taxa. The significant negative correlation between post-natal growth rates in bats and climate (temperate or tropical) is consistent with life-history models that predict higher post-natal growth rates in highly seasonal environments. Although basal metabolic rate (BMR) was highly correlated with body mass and growth rates in other mammalian taxa, we found no significant effect of BMR on growth rates in bats that could not be explained by asymptotic body mass. Although post-natal growth rates in bats and other mammals can provide valuable indices of maternal investment, milk-energy output of females during lactation should offer the most direct link between environmental effects and pup growth. We suggest that future studies on post-natal growth in bats include estimates of food availability, maternal diet, milk composition and milk-energy output of mothers, time of first solid food, duration of lactation, and the maternal pup environment, to help clarify factors that influence post-natal growth rates.

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