Evolutionary Ecology Research, 2001, **3**: 465–476

Bat life histories: Testing models of mammalian life-history evolution

Kate E. Jones* and Ann MacLarnon

School of Life Sciences, University of Surrey Roehampton, West Hill, London SW15 3SN, UK

ABSTRACT

Over the last decade, important advances in mammalian life-history evolution have been made with the emergence of two theoretical life-history models by Charnov and by Kozlowski and Weiner. Here we test predictions from Charnov's model using both phylogenetic comparative techniques and cross-species analyses in bats (Mammalia: Chiroptera). We find some support for Charnov's life-history model in terms of the predicted values for the interrelationships of the length of the juvenile period and adult mortality, and his predicted invariants are also well supported. However, annual fecundity is not significantly correlated with body size as predicted. Overall, the evidence presented here does not offer convincing support for the applicability of Charnov's model to bats. We propose that an explanation for these results is that bats decouple the age at which sexual maturity is reached from the age at which adult size is reached, because of the constraints of flight. This violates one of the assumptions not only of Charnov's model, but also of the more general model of Kozlowski and Weiner.

Keywords: bats, comparative analyses, evolution, independent contrasts, life-history models.

INTRODUCTION

Within mammals, although there is an enormous diversity of life histories, life-history traits do tend to covary in predictable ways (Stearns, 1983, 1992; Harvey *et al.*, 1989; Read and Harvey, 1989; Promislow and Harvey, 1990). Life-history patterns show a continuous distribution across mammalian species, and species can be placed along a 'fast–slow' continuum (Read and Harvey, 1989). The 'slow' end corresponds to large, slow-maturing, long-lived species producing small numbers of large offspring, and the 'fast' end corresponds to small, short-lived species producing large numbers of small, rapidly maturing offspring. Several attempts have been made to explain this variation in life histories, often citing one particular factor in a causal role (reviewed in Harvey and Purvis, 1999). Body size has been the main focus used to explain the diversity in life histories (Western, 1979; Calder 1996). However, patterns of covariation persist even after the statistical removal of body size (Stearns, 1983; Read and Harvey, 1989). More recent studies have illustrated the

---

* Address all correspondence to Kate Jones, Department of Biology, University of Virginia, Charlottesville, VA 22904-4328, USA. e-mail: kate.jones@virginia.edu

importance of mortality rates to explanations of the pattern of covariation in life-history traits (Harvey and Zammuto, 1985; Promislow and Harvey, 1990, 1991). Over the last decade, important advances in life-history theory have been made with the emergence of two optimality life-history models that build on the importance of mortality patterns in explaining the diversity of mammalian life histories (Charnov, 1991; Kozlowski and Weiner, 1997). Both models offer an explanation as to why there is the observed covariation in age at maturity, fecundity and mortality, independent of body mass.

According to Charnov's (1991) model, selection acts to maximize an individual's lifetime reproductive success given the mortality rates imposed by the environment. Altering the age at which sexual maturity is reached enables the optimization of reproductive success. Individuals that are older and, therefore, larger at sexual maturity have more energy available to them to invest in offspring production per unit time after reaching maturity. However, it takes time to grow large and this leads to a trade-off between the age and size at which maturity is reached and the likelihood of survival to maturity. It is further suggested that the covariation of mortality rates with both birth rate and age at sexual maturity, which is found in mammals independent of variation in size, can be explained by species having different growth rates for their body size (Charnov, 1991). Growth in Charnov's model is described by the 'growth law', where $\mathrm{d}W/\mathrm{d}T = AW^{0.75}$, where A is the growth coefficient, W is body mass and T is time (eqn 5.2 in Charnov, 1993). Recently, Kozlowski and Weiner (1997) produced a more general life-history model that does not assume either that this 'growth law' determines growth or that within-species allometries are representative of between-species allometries (as Charnov's model does). Their model gives a central role to ecological differences that optimize age and size at maturity through an interaction between the rates of energy assimilation, respiration and mortality with body size. Kozlowski and Weiner's (1997) model makes very similar predictions to Charnov's (1991) model; indeed, they view his model as a special case of their own.

Both models have had some empirical support (Purvis and Harvey, 1995, 1997), although only Charnov's (1991) model permits rigorous testing. Tests of both models have largely been confined to analyses across broad taxonomic groups. It has been suggested that patterns found at the micro-evolutionary level among species within smaller clades may be substantially different to those found across broad taxonomic levels (Stearns, 1992; Bauwens and Diaz-Uriarte, 1997), but few studies have addressed this question. Bats are a large group of nocturnal volant small-bodied mammals (mean mass approximately 18 g; Jones, 1998), forming a closely related clade of approximately 916 species (Koopman, 1993). It has been shown that bat species, relative to body size, are at the very 'slow' end of the 'fast–slow' continuum within mammals – that is, they are long-lived organisms producing small numbers of large offspring (Tuttle and Stevenson, 1982; Kurta and Kunz, 1987; Read and Harvey, 1989; Austad and Fischer, 1991; Hayssen, 1993; Barclay, 1994, 1995; Hayssen and Kunz, 1996). Apart from preliminary analyses presented in Jones and Purvis (1997), major questions about life-history variation in this group have not previously been investigated. In fact, bats (the second largest order of mammals) have been under-represented or ignored in most life-history studies to date (see Barclay, 1994). This paper tests the predictions of Charnov's optimality model with empirical data from bat species, to investigate its validity in explaining patterns of life-history evolution within this little studied mammalian order. Comment is also made on the implications of the results for Kozlowski and Weiner's (1997) model.

METHODS

Life-history data were compiled from primary and secondary literature sources for 308 bat species. The life-history variables used were as follows (definitions of variables are given in Jones, 1998): adult female body mass, W (g; $n = 308$ species); annual fecundity, b ($n = 179$); weaning age (days, $n = 123$); weaning mass (g, $n = 59$); ratio of weaning to adult female mass, δ ($n = 59$); length of the juvenile period, α (months, $n = 53$); adult female mortality rate, M ($n = 26$); product of α and b ($\alpha \cdot b$, $n = 49$); and product of α and M ($\alpha \cdot M$, $n = 11$).

Related species share associations among many characteristics by descent from common ancestors and species data cannot therefore be treated as independent points for statistical analyses (Felsenstein, 1985). We used the CAIC computer package (Purvis and Rambaut, 1995) to transform the species data set into phylogenetically independent contrasts (using algorithms in Felsenstein, 1985; Pagel, 1992) in an attempt to overcome potential problems of phylogenetic inertia. However, we present the results obtained from analysis of both species data and from phylogenetically independent contrasts, as recommended by Garland *et al.* (1999). CAIC requires an estimate of the phylogeny for the species under investigation. As no one reconstruction for all the required 308 taxa was available, a composite phylogeny or a 'phylogenetic supertree' (*sensu* Sanderson *et al.*, 1998) was calculated by combining information from 53 different systematic studies. Where there were overlapping estimates of the phylogenetic relationships of a species, these were combined using MRP (Matrix Representation with Parsimony) (Baum, 1992; Ragan, 1992). Methods for tree combination followed those of previous MRP estimations for primates (Purvis, 1995) and carnivores (Bininda-Emonds *et al.*, 1999). However, a modification to the MRP algorithm used in Purvis (1995) was not applied, following criticism by Ronquist (1996), and all source trees received equal weighting in the analysis (following Bininda-Emonds *et al.*, 1999). The following clades were assumed to be monophyletic: Chiroptera, all families (*sensu* Koopman, 1993), tribes Cynopterini (except for *Myonycteris*; Springer *et al.*, 1995) and Pleconti, subfamilies Carollinae, Desmodontinae, Kerivoulinae, Miniopterinae, Murininae, Nyctophilinae, Phyllonycterinae and Stenodermatinae and all genera (*sensu* Koopman, 1993) [except for the following: *Artibeus* (Owen, 1991), *Emballonura* (Griffiths *et al.*, 1991), *Pipistrellus* (Volleth and Heller, 1994), *Rousettus* (Kirsch *et al.*, 1995), *Saccopteryx* (Griffiths and Smith, 1991) and *Tadarida* (Freeman, 1981)]. The phylogenetic sources are given in the Appendix. A copy of the supertree is available from the authors on request. In the absence of knowledge about the branch lengths throughout the whole tree, branch lengths were all set to the same arbitrary length in the CAIC program (Purvis and Rambaut, 1995). Violation of this assumption will lead to some heteroscedasticity in the contrasts (Garland *et al.*, 1992); any contrast point with a Studentized residual greater than 3 was therefore omitted from subsequent analyses (Jones and Purvis, 1997).

All variables were $\log_{10}$-transformed prior to analysis. Least-squares regression was used to estimate the allometric scaling of the slopes of the life-history variables to body size (forced through the origin for contrasts; Garland *et al.*, 1992). Testing for a relationship between two variables, while controlling for the effects of a third variable, was carried out using multiple least-squares regression (Sokal and Rohlf, 1995). The statistical tests, which were two-tailed, were performed using SPSS/PC release 6.0 (Norušis, 1993). Where appropriate, a sequential Bonferroni correction (Rice, 1989) was applied when interpreting the results of analyses of associations between life-history variables.

RESULTS

The predictions of Charnov's (1991) model for the relationships between life-history variables and body size are given some support within bats (Table 1). The significance and the value of the various relationships tested between adult mortality rate (M), annual fecundity (b), length of the juvenile period (α) and body mass (W) depend to some extent on the method of analysis used. Analysis with species values gives support to Charnov's prediction of the scaling of length of juvenile period to body mass, and analysis using independent contrasts gives support for the scaling of adult mortality to body mass (see Table 1). Annual fecundity shows no significant association with body mass either using species data or independent contrasts.

There is support from analyses with independent contrasts for two of the three predictions of the interrelationships between life-history variables α, b and M when adult body mass is held constant in a multiple regression, but for only one of the three predicted relationships using species data (see Table 1). Charnov's prediction that the ratio of weaning mass to adult mass (δ) is invariant with adult mass is supported in the analyses with independent contrasts. However, a significant negative relationship is found with species values (i.e. smaller species wean offspring at a higher mass in relation to adult body mass than larger species). As predicted, the products of α and b and of α and M are both found to be uncorrelated with body mass using both species values and contrasts.

Estimating the value of Charnov's (1991) growth coefficient, A, relies on the value of the intercept from life-history allometries. Figure 1 compares the relationship, using species values, between the length of the juvenile period (measured between weaning and sexual maturation) and body size in bats, primates and other mammalian species. The growth coefficient, A, for the different groups is calculated using the intercept of the regression line with the y axis where $A = -\ln(\text{intercept})$. Using these data, the growth coefficient for bats is 0.91, compared with 0.65 and 1.25 for primates and other mammals, respectively (Purvis and Harvey, 1995; Ross and Jones, 1999).

DISCUSSION

Life-history relationships with body size

There was little support for Charnov's predicted relationships between life-history variables and body mass in bats. These results are supported by a previous preliminary study (Jones and Purvis, 1997), which found that a large amount of bat life-history variation is independent of size. This size independence is unusual for mammals in general (Read and Harvey, 1989; Purvis and Harvey, 1995), but is consistent with studies that have investigated life-history variation within small mammals (Purvis and Harvey, 1996). The degree of support for Charnov's (1991) predicted allometries found in the present study did depend on the types of analyses used. The differences between the analytical methods may illustrate the importance of explicitly taking phylogenetic relatedness into account in comparative analyses of this nature: a phylogenetic bias in these data is likely, as there is a general bias in the bat literature towards studies of species that are mainly from only two Chiropteran families (Rhinolophidae and Vespertilionidae). However, there are circumstances where results from independent contrasts analyses are problematic, for example when characters

Table 1. Comparison between Charnov's (1991, 1993) model predictions of the regression relationships between log life-history variables and those seen within bat species for both species values (first line) and independent contrasts (second line) (regression calculated through the origin for contrasts) prior to Bonferroni correction

Log life-history variables	Charnov's prediction	Regression exponent	d.f.	P-value	r^2	k
Adult mortality rate (M) *vs* adult female body mass (W)	–0.25	–0.02 (–0.39 to 0.34)	24	0.89	0.00	–0.18
		–0.45 (–0.85 to –0.05)	18	< 0.05	0.25	
Length of juvenile period (a) *vs* W	0.25	0.21 (0.00 to 0.41)	51	< 0.05	0.07	0.50
		0.20 (–0.01 to 0.40)	35	0.07	0.09	
Annual fecundity (b) *vs* W	–0.25	–0.03 (–0.08 to 0.02)	177	0.30	0.01	–0.11
		–0.01 (–0.08 to 0.06)	111	0.81	0.00	
Adult mortality rate (M) *vs* length of juvenile period (a) (holding W constant)	Negative	0.07 (–1.38 to 0.53)	8	0.72	0.03	–0.16
		–0.48 (–0.92 to –0.03)	7	< 0.05	0.68	
Annual fecundity (b) *vs* adult mortality rate (M) (holding W constant)	Positive	0.14 (–0.12 to 0.40)	18	0.27	0.07	–0.13
		0.34 (–0.02 to 0.69)	14	0.07	0.24	
Annual fecundity (b) *vs* length of juvenile period (a) (holding W constant)	Negative	–0.25 (–0.38 to –0.13)	46	< 0.001	0.28	0.06
		–0.22 (–0.40 to –0.03)	33	< 0.05	0.23	
Ratio of weaning to adult weight (δ) *vs* W	Invariant	–0.09 (–0.16 to –0.02)	57	< 0.05	0.11	–0.10
		–0.07 (–0.19 to 0.05)	36	0.27	0.03	
Product of a and b ($a \cdot b$) *vs* W	Invariant	0.11 (–0.07 to 0.30)	47	0.21	0.03	0.49
		0.04 (–0.18 to 0.25)	34	0.74	0.00	
Product of a and M ($a \cdot M$) *vs* W	Invariant	–0.13 (–1.39 to 1.13)	9	0.82	0.01	0.68
		0.02 (–0.40 to 0.44)	8	0.92	0.00	

Note: CI = the 95% confidence intervals of the regression exponent; d.f. = degrees of freedom; P-value = probability of the regression line being significantly different from zero; r^2 = percentage of variance explained; k = intercept.

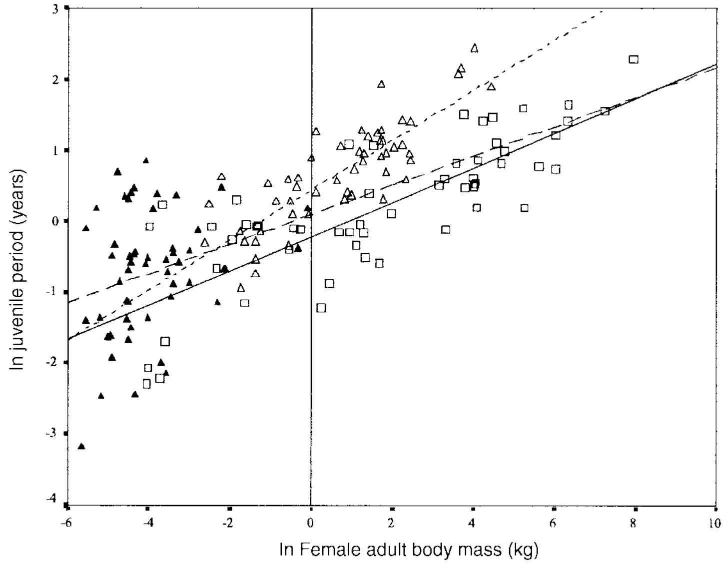

Fig. 1. Comparison in mammals of the allometry of length of the juvenile period. ▲ = bat species, △ = primates, □ = species from other mammalian orders. – – – represents the regression line found in bats ($y = 0.21x + 0.1$, $P < 0.05$, $r^2 = 0.07$, d.f. = 52), - - - - represents the regression line found in primates ($y = 0.35x + 0.4$, $P < 0.001$, $r^2 = 0.69$, d.f. = 52; data from Ross and Jones, 1999) and —— represents the regression line found in other mammals ($y = 0.24x + -0.2$, $P < 0.001$, $r^2 = 0.64$, d.f. = 54; data from Purvis and Harvey, 1995).

have evolved under Price's (1997) 'niche space' model (Harvey and Rambaut, 2000), or when the data are of poor quality (Purvis and Webster, 1999).

Neither analyses by independent contrasts nor analyses using species values offer convincing support or refutation of Charnov's predictions. An important exception is for the relationship between annual fecundity and body mass: here neither method offers support for the model (predicted coefficient: –0.25; observed: –0.03 species values, –0.02 contrasts). However, this does not necessarily invalidate the model as a whole (Charnov, 2000). If growth scales with an exponent different from the assumed value of 0.75, the scaling exponent of annual fecundity and body mass, which equals 1 minus the growth exponent in Charnov's model (eqn 4 in Charnov, 2000), will differ from –0.25. If the growth exponent were 1, for example, then the scaling exponent of annual fecundity to body mass would be predicted to be zero. This is congruent with the results of the analyses for bats as the growth exponent is insignificantly different from a value of 1 (1.23, 95% confidence limits 0.90–1.55, $P < 0.001$, $r^2 = 0.72$, $n = 26$) for species values, and the scaling exponent for annual fecundity to body mass is insignificantly different from zero.

Life-history covariation

The correlations between bat life-history variables (controlling for body size) also give mixed support for Charnov's (1991) predictions, although here the pattern is more consistent for the two analytical methods. The correlation found between annual fecundity and length of juvenile period (independent of size) fits the model's predictions – that is, bats that delay maturity produce fewer offspring. Also, there is some evidence that bats that delay maturity have lower mortality rates. These results are also supported from case studies in the literature. For example, although no formal analysis was done, Rachmatulina (1992) observed that mortality rates are on average lower in those bat species producing only one young per pregnancy and with later sexual maturation, compared with those species producing twins and earlier maturities. Interspecifically, Ransome (1995) also showed that later breeding female horseshoe bats (*Rhinolophus ferrumequinum*) have higher survival rates than those females breeding earlier in life.

These results suggest that within bat species there does seem to be a 'fast–slow' continuum of life-history traits that is independent of body size. This agrees with findings in other mammals and analyses across mammalian orders (e.g. Stearns, 1983; Read and Harvey, 1989; Promislow and Harvey, 1990). Bat species at the 'slow' end (such as the leaf-nosed bat *Hipposideros fulvus* and the false vampire bat *Megaderma lyra*) reach reproductive maturity later, have smaller litters and have fewer offspring per year than 'faster' species (such as the pygmy pipistrelle *Pipistrellus mimus* and the mouse-eared bat *Myotis myotis*), which mature more quickly, have larger litters and a greater annual fecundity.

Life-history invariants

The strongest support for Charnov's model from analyses of bat data was the predicted 'invariants' (i.e. for the prediction that there are relationships between some life-history variables, independent of body mass variation). These results are mostly independent of the analytical method used. Charnov's (1991) model predicts that low birth rates, late sexual maturity and low mortality rates in bats will be correlated with slow growth rates (of both themselves and their offspring) relative to body size. The results suggest that bat species *are* characterized by slow growth rates for their body size (low values of A; see Fig. 1) compared with typical mammals, and other studies have shown that primates have even slower growth rates for their size (Charnov and Berrigan, 1993; Ross and Jones, 1999). This suggests that bats (as well as primates) differ from typical mammals in having lower production rates. Relatively late ages at sexual maturation, low fecundities and long lifespans, have all been demonstrated empirically in bats compared with other non-primate mammals (Tuttle and Stevenson, 1982; Read and Harvey, 1989; Austad and Fischer, 1991).

Although there is some support for Charnov's optimality model from these analyses, the evidence does not demonstrate that it is completely applicable to bats. The model has received general support within mammals (Purvis and Harvey, 1995) and within primates (Ross and Jones, 1999), although there are some discrepancies (see Purvis and Harvey, 1995, 1997). We suggest that one of the reasons that bats may not fit Charnov's model is because flight constrains bats to reach adult size before reaching reproductive maturity (near adult dimensions are necessary for flight to occur; Barclay, 1994). This unique factor of bat biology, among mammals, may impose a unique constraint on life-history features. The need to reach adult size for independent feeding may be the cause of the difference between the age at which sexual maturity is reached and the age when adult size is reached in bats, which is a unique difference among mammals. Examining data from 15 different bat species, the difference between the age at which adult size is reached (i.e. using age at first flight) and age at sexual maturity (using age at first pregnancy) is significantly different (paired sample *t*-test: $t_{14} = 7.97$, $P < 0.001$ using species values). This apparent delay in attaining sexual maturity after reaching optimal size is not explained by Charnov's model and, although it is not possible to test Kozlowski and Weiner's (1997) model explicitly with the available data, their model would have the same problem, as it assumes that animals stop growing at the same age as they reach sexual maturity.

Understanding why bats delay reproduction after reaching optimal size is crucial to understanding the life-history evolution in bats. A recent paper investigating altricial birds (which also grow to adult size much in advance of the age of first reproduction) suggests that competition for breeding sites determines their age at maturity (Charnov, 2000). It suggests that the ratio of non-breeders to breeders is a demographic invariant for altricial birds, and that birds only change from non-breeder to breeder status when the ratio goes above its critical value. However, it is unlikely that the same explanation holds for bats, as there is little evidence for competition for roosting sites between breeders and non-breeders; non-parous females typically return together with parous females to a common roosting site to breed (Racey, 1982).

Another possibility is that seasonality may play an important role in determining the age at maturity in bats. Bat species may delay breeding to coincide with food resource availability. For example, most, if not all, temperate bat species undergo a prolonged period of hibernation during the winter when food availability is at its lowest, and do not start reproducing until the following spring (Racey, 1982). To facilitate this, several different reproductive delays have evolved within the order (e.g. sperm storage: Racey, 1979; delayed implantation: Mutere, 1969; delayed embryonic development: Fleming, 1971). Further analyses are required to test the seasonality hypothesis but it is clear that current life-history models do not explain the apparent decoupling of selection on age of attainment of adult size and age at sexual maturity in bats.

ACKNOWLEDGEMENTS

We thank Virginia Hayssen who kindly gave K.E.J. access to her mammal reprint collection, and Mark Brigham, Ric Charnov, Andy Purvis, Caroline Ross and Andrea Webster for discussion. Financial support was provided by the University of Surrey Roehampton (graduate bursary for K.E.J.) with additional support from the NERC (GR8/04371).

REFERENCES

Austad, S.N. and Fischer, K.E. 1991. Mammalian ageing, metabolism and ecology: Evidence from the Bats and Marsupials. *J. Gerontol.*, **46**: 47–53.

Barclay, R.M.R. 1994. Constraints on reproduction by flying vertebrates: Energy and calcium. *Am. Nat.*, **144**: 1021–1031.

Barclay, R.M.R. 1995. Does energy or calcium availability constrain reproduction by bats? *Symp. Zool. Soc. Lond.*, **67**: 245–258.

Baum, B.R. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and the desirabilty of combining gene trees. *Taxon*, **41**: 3–10.

Bauwens, D. and Diaz-Uriarte, R. 1997. Covariation of life-history traits in lacertid lizards: A comparative study. *Am. Nat.*, **149**: 91–111.

Bininda-Emonds, O.R.P., Gittleman, J.L. and Purvis, A. 1999. A complete phylogeny of the Carnivora (Mammalia): A synthesis of recent investigations. *Biol. Rev.*, **74**: 143–175.

Calder, W.A. 1996. *Size*, *Function and Life-history*, 2nd edn. Cambridge, MA: Harvard University Press.

Charnov, E.L. 1991. Evolution of life-history variation among female mammals. *Proc. Nat. Acad. Sci. USA*, **88**: 1134–1137.

Charnov, E.L. 1993. *Life-history Invariants*: *Some Explorations of Symmetry in Evolutionary Ecology.* Oxford: Oxford University Press.

Charnov, E.L. 2000. Evolution of life-history variation among species of altricial birds. *Evol. Ecol. Res.*, **2**: 365–373.

Charnov, E.L. and Berrigan, D. 1993. Why do female primates have such long lifespans and so few babies? *or* Life in the slow lane. *Evol. Anthropol.*, **1**: 191–194.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.*, **125**: 1–15.

Fleming, T.H. 1971. *Artibeus jamaicensis*: Delayed embryonic development in a neotropical bat. *Science*, **171**: 402–404.

Freeman, P.W. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): Morphology, ecology, evolution. *Fieldiana Zool.*, **7**: 1–173.

Garland, T., Harvey, P.H. and Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.*, **41**: 18–32.

Garland, T., Midford, P.E. and Ives, A.R. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am. Zool.*, **39**: 374–388.

Griffiths, T.A. and Smith, A.L. 1991. Systematics of emballonuroid bats (Chiroptera: Emballonuridae and Rhinopomatidae), based on hyoid morpholgy. *Bull. Am. Mus. Nat. Hist.*, **206**: 62–83.

Griffiths, T.A., Koopman, K.F. and Starrett, A. 1991. The systematic relationship of *Emballonura nigrescen*s to other species of *Emballonura* and to *Coleura* (Chiroptera: Emballonuridae). *Am. Mus. Novitates*, **2996**: 1–16.

Harvey, P.H. and Purvis, A. 1999. Understanding the ecological and evolutionary reasons for life-history variation: Mammals as a case study. In *Theoretical Ecology*: *Advances in Principles and Applications* (J. McGlade, ed.), pp. 232–248. Oxford: Blackwell Scientific.

Harvey, P.H. and Rambaut, A. 2000. Comparative analyses for adaptive radiations. *Phil Trans. R. Soc. Lond. B*, **355**: 1–7.

Harvey, P.H. and Zammuto, R.M. 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature*, **315**: 319–320.

Harvey, P.H., Promislow, D.E.L. and Read, A.F. 1989. Life-history variation in placental mammals: Unifying the data with the theory. In *Oxford Surveys in Evolutionary Biology* (P.H. Harvey and L. Partridge, eds), pp. 13–31. Oxford: Oxford University Press.

Hayssen, V. 1993. Empirical and theoretical constraints on the evolution of lactation. *J. Dairy Sci.*, **76**: 3213–3233.

Hayssen, V. and Kunz, T.H. 1996. Allometry in litter mass in bats: Maternal size, wing morphology, and phylogeny. *J. Mammalogy*, **77**: 476–490.

Jones, K.E. 1998. Evolution of bat life-histories. PhD dissertation, University of Surrey, Roehampton.

Jones, K.E. and Purvis, A. 1997. An optimum body size for mammals? Comparative evidence from bats. *Funct. Ecol.*, **11**: 751–756.

Kirsch, J.A.W., Flannery, T.F., Springer, M.S. and Lapointe, F.J. 1995. Phylogeny of the Pteropodidae (Mammalia: Chiroptera) based on DNA hybridisation, with evidence for bat monophyly. *Aust. J. Zool.*, **43**: 395–428.

Koopman, K.F. 1993. Bats. In *Mammal Species of the World*: *Taxonomic and Geographic Reference* (D.E. Wilson and D.M. Reeder, eds), pp. 137–241. Washington, DC: Smithsonian Institution Press.

Kozlowski, J. and Weiner, J. 1997. Interspecifc allometries are by-products of body size optimization. *Am. Nat.*, **149**: 352–380.

Kurta, A. and Kunz, T.H. 1987. Size of bats at birth and maternal investment during pregnancy. *Symp. Zool. Soc. Lond.*, **57**: 79–106.

Mutere, F.A. 1969. The breeding biology of equatorial vertebrates: Reproduction in the fruit bat *Eidolon helvum* at latitude 0°20′N. *J. Zool. Lond.*, **155**: 153–161.

Norušis, M.J. 1993. *SPSS Version 6.0*. Cary, NC: SPSS Inc.

Owen, R.D. 1991. The systematic status of *Dermanura concolor* (Peters, 1865) (Chiroptera: Phyllostomidae), with description of a new genus. *Bull. Am. Mus. Nat. Hist.*, **206**: 18–25.

Pagel, M.D. 1992. A method for the analysis of comparative data. *J. Theor. Biol.*, **156**: 431–442.

Price, T. 1997. Correlated evolution and independent contrasts. *Phil. Trans. R. Soc. Lond. B*, **352**: 519–529.

Promislow, D.E.L. and Harvey, P.H. 1990. Living fast and dying young: A comparative analysis of life-history variation among mammals. *J. Zool. Lond.*, **220**: 417–437.

Promislow, D.E.L. and Harvey, P.H. 1991. Mortality rates and the evolution of mammal life histories. *Acta Oecologica*, **12**: 119–137.

Purvis, A. 1995. A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond. B*, **348**: 405–421.

Purvis, A. and Harvey, P.H. 1995. Mammal life-history evolution: A comparative test of Charnov's model. *J. Zool. Lond.*, **237**: 259–283.

Purvis, A. and Harvey, P.H. 1996. Miniature mammals: Life-history strategies and macroevolution. *Symp. Zool. Soc. Lond.*, **69**: 159–174.

Purvis, A. and Harvey, P.H. 1997. The right size for a mammal. *Nature*, **386**: 332–333.

Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Comp. Applic. Biosci.*, **11**: 247–251.

Purvis, A. and Webster, A.J. 1999. Phylogenetically independent contrasts and primate phylogeny. In *Comparative Primate Socioecology* (P.C. Lee, ed.), pp. 44–72. Cambridge: Cambridge University Press.

Racey, P.A. 1979. The prolonged storage and survival of spermatozoa in Chiroptera. *J. Reprod. Fertility*, **56**: 391–402.

Racey, P.A. 1982. Ecology of bat reproduction. In *Ecology of Bats* (T.H. Kunz, ed.), pp. 57–104. New York: Plenum Press.

Rachmatulina, I.K. 1992. Major demographic characteristics of populations of certain bats from Azerbaijan. In *Prague Studies in Mammalogy* (J. Horacek and V. Vohralik, eds), pp. 127–141. Prague: Charles University Press.

Ragan, M.A. 1992. Phylogenetic inference based on matrix representation of trees. *Molec. Phylogen. Evol.*, **1**: 53–58.

Ransome, R. 1995. Earlier breeding shortens life in female greater horseshoe bats. *Phil. Trans. R. Soc. Lond. B*, **350**: 153–161.

Read, A.F. and Harvey, P.H. 1989. Life-history differences among the eutherian radiations. *J. Zool. Lond.*, **219**: 329–353.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.

Ronquist, F. 1996. Matrix representation of trees, redundancy, and weighting. *Syst. Biol.*, **45**: 247–253.

Ross, C. and Jones, K.E. 1999. Socioecology and the evolution of primate reproductive rates. In *Comparative Primate Socioecology* (P.C. Lee, ed.), pp. 73–136. Cambridge: Cambridge University Press.

Sanderson, M.J., Purvis, A. and Henze, C. 1998. Phylogenetic supertrees: Assembling the trees of life. *Trends Ecol. Evol.*, **13**: 105–109.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*, 3rd edn. New York: Freeman.

Springer, M.S., Hollar, L.J. and Kirsch, J.A.W. 1995. Phylogeny, molecules versus morphology, and rates of character evolution among fruitbats (Chiroptera: Megachiroptera). *Aust. J. Zool.*, **43**: 557–582.

Stearns, S.C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, **41**: 173–187.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

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

Volleth, M. and Heller, K.G. 1994. Phylogenetic relationships of vespertilionid genera (Mammalia: Chiroptera) as revealed by Karyological analysis. *Zeitschrift für Zoologische Systematik und Evolutionforschung*, **32**: 11–34.

Western, D. 1979. Size, life-history and ecology in mammals. *Afr. J. Ecol.*, **17**: 184–204.

APPENDIX: SOURCES FOR THE BAT PHYLOGENETIC SUPERTREE

Clade	Sources
Inter-familial relationship	Arnold *et al.* (1982) *Occas. Papers Mus. Texas Tech. Univ.*, **77**: 1–15
	Baker *et al.* (1991) *Bull. Am. Mus. Nat. Hist.*, **206**: 42–53
	Griffiths and Smith (1991) *Bull. Am. Mus. Nat. Hist.*, **206**: 62–83
	Luckett (1980) In *Proceedings of the Fifth International Bat Research Conference* (D.E. Wilson and A.L. Gardner, eds), pp. 245–265. Lubbock, TX: Texas Tech Press
	Novacek (1980) In *Proceedings of the Fifth International Bat Research Conference* (D.E. Wilson and A.L. Gardner, eds), pp. 317–330. Lubbock, TX: Texas Tech Press
	Pierson *et al.* (1986) *Nature*, **323**: 60–63
	Pierson (1986) As cited by Simmons (1993) *Am. Mus. Novitates*, **3077**: 1–35
	Robbins and Sarich (1988) *J. Mammalogy*, **69**: 1–13
	Smith (1976) *Spec. Pub. Mus. Texas Tech. Univ.*, **10**: 49–69
	Sudman *et al.* (1994) *J. Mammalogy*, **75**: 365–377
	Van Valen (1979) *Evol. Theory*, **4**: 103–121
Pteropodidae	Andersen (1912) *Catalogue of the Chiroptera in the Collection of the British Museum*, 2nd edn. London: British Museum (Natural History)
	Baker *et al.* (1991) *Bull. Am. Mus. Nat. Hist.*, **206**: 42–53
	Colgan and Flannery (1995) *Syst. Biol.*, **44**: 209–220
	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
	Hill (1992) In *IUCN Old World Fruit Bats: An Action Plan for Their Conservation* (S.P. Mickleburgh, A.M. Huston and P.A. Racey, eds), p. 160. Switzerland: Gland
	Hood (1989) *J. Morphology*, **199**: 207–221
	Kirsch *et al.* (1995) *Aust. J. Zool.*, **43**: 395–428
	Springer *et al.* (1995) *Aust. J. Zool.*, **43**: 557–582
Rhinopomatidae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn, pp. 40–91. Oxford: Oxford University Press
Emballonuridae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
	Griffiths and Smith (1991) *Bull. Am. Mus. Nat. Hist.*, **206**: 62–83
	Griffiths *et al.* (1991) *Am. Mus. Novitates*, **2996**: 1–16
	Robbins and Sarich (1988) *J. Mammalogy*, **69**: 1–13
Nycteridae	Griffiths (1994) *Am. Mus. Novitates*, **3090**: 1–17
	Griffiths (1997) *J. Mammalogy*, **78**: 106–116
Megadermatidae	Griffiths *et al.* (1992) *Am. Mus. Novitates*, **3041**: 1–21
	Hand (1985) *Aust. Mammalogy*, **8**: 5–43
Rhinolophidae	Bogdanowicz and Owen (1992) *Zeitschrift für Zoologische Systematik und Evolutionforschung*, **30**: 142–160

Appendix—*continued*

Clade	Sources
Hipposideridae	Koopman (1994) *Handbook of Zoology. Mammalia, Vol. 8. Chiroptera: Systematics.* Berlin: de Gruyter
Noctilionidae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
Mormoopidae	Arnold *et al.* (1982) *Occas. Papers Mus. Texas Tech. Univ.*, **77**: 1–15 Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
Phyllostomidae	Baker *et al.* (1989) *Syst. Zool.*, **38**: 228–238 Baker *et al.* (1994) *J. Mammalogy*, **75**: 321–327 Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press Honeycutt and Sarich (1987) *J. Mammalogy*, **68**: 508–517 Koop and Baker (1983) *Occas. Papers Mus. Texas Tech. Univ.*, **83**: 1–12 Lim (1993) *Cladistics*, **9**: 147–165 Lim and Engstrom (1995) In *Proceedings of the Tenth International Bat Research Conference*, Boston, MA. *Bat Research News*, **36**: 2 Owen (1987) *Spec. Pub. Mus. Texas Tech. Univ.*, **26**: 1–65 Pacheco and Patterson (1991) *Bull. Am. Mus. Nat. Hist.*, **206**: 101–120 Patton and Baker (1978) *Syst. Zool.*, **27**: 449–462 Pumo *et al.* (1996) *J. Mammalogy*, **77**: 491–503 Simmons (1996) *Am. Mus. Novitates*, **3158**: 1–34 Smith (1976) *Spec. Pub. Mus. Texas Tech. Univ.*, **10**: 49–69 Van den Bussche and Baker (1993) *J. Mammalogy*, **74**: 793–802
Natalidae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
Furipteridae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press
Vespertilionidae	Bogdanowicz *et al.* (1995) *Bat Research News*, **36**: 50–51 Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press Frost and Timm (1992) *Am. Mus. Novitates*, **3034**: 1–16 Handley (1959) *Proc. US Nat. Mus.*, **100**: 95–246 Hill and Harrison (1987) *Bull. Br. Mus. Nat. Hist.* (*Zool.*), **52**: 225–305 Horacek (1991) *Myotis*, **29**: 17–29 Kitchener and Caputi (1985) *Records W. Aust. Mus.*, **12**: 85–146 Morales and Bickham (1995) *J. Mammalogy*, **76**: 730–749 Qumsiyeh and Bickham (1993) *J. Mammalogy*, **74**: 376–382 Sudman *et al.* (1994) *J. Mammalogy*, **75**: 365–377 Tumlison and Douglas (1992) *J. Mammalogy*, **73**: 276–285 Volleth and Heller (1994) *Zeitschrift für Zoologische Systematik und Evolutionforschung*, **32**: 11–34 Williams *et al.* (1970) *J. Mammalogy*, **51**: 602–606
Molossidae	Corbet and Hill (1991) *A World List of Mammalian Species*, 3rd edn. Oxford: Oxford University Press Freeman (1981) *Fieldiana Zool.*, **7**: 1–173