

Life history, ecology and longevity in bats

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Summary

The evolutionary theory of aging predicts that life span should decrease in response to the amount of mortality caused by extrinsic sources. Using this prediction, we selected six life history and ecological factors to use in a comparative analysis of longevity among 64 bat species. On average, the maximum recorded life span of a bat is 3.5 times greater than a non-flying placental mammal of similar size. Records of individuals surviving more than 30 years in the wild now exist for five species. Univariate and multivariate analyses of species data, as well as of phylogenetically independent contrasts obtained using a supertree of Chiroptera, reveal that bat life span significantly increases with hibernation, body mass and occasional cave use, but decreases with reproductive rate and is not influenced by diet, colony size or the source of the record. These results are largely consistent with extrinsic mortality risk acting as a determinant of bat longevity. Nevertheless, the strong association between life span and both reproductive rate and hibernation also suggests that bat longevity is strongly influenced by seasonal allocation of non-renewable resources to reproduction. We speculate that hibernation may provide a natural example of caloric restriction, which is known to increase longevity in other mammals.

Key words: hibernation; life history; life span; reproductive effort; roost; senescence.

Introduction

For their body size, bats live longer than any other order of mammal (Bouliere, 1958; Austad & Fischer, 1991). Several explanations have been offered to account for this observation. The earliest hypothesis proposed that bats are long-lived because they reduce their metabolic rate during periods of torpor and hibernation (Bouliere, 1958). This claim was taken as evidence in support of the rate-of-living hypothesis (Pearl, 1928), one version of which predicts that life span should be inversely related to metabolic rate because toxic byproducts accumulate with age as a result of metabolism (Sohal, 1986). However,

previous studies indicated that the longevity of non-hibernating tropical bat species was no shorter than hibernating temperate bat species (Herreid, 1964) and all bats, including those that do not undergo hibernation, live longer than other mammals of comparable body size (Jurgens & Prothero, 1987; Austad & Fischer, 1991). Furthermore, marsupials, which have lower average metabolic rates than placental mammals, have much shorter life spans than bats and other placental mammals (Austad & Fischer, 1991). An alternative explanation for the relatively long life span of bats, as well as for birds and gliding mammals, is that the ability to fly reduces mortality risk (Austad & Fischer, 1991; Holmes & Austad, 1994). While this hypothesis has appeal for vertebrates, it is less clear if flying ability has reduced the risk of mortality among insects.

The risk of extrinsic mortality is believed to influence life span evolution because the force of natural selection declines with age. If extrinsic sources of mortality, such as predation, disease and accidents, are high, then mutations with late-acting deleterious effects will not be exposed to selection. Such deleterious mutations can either accumulate in a lineage until balanced by selection (Medawar, 1952; Hamilton, 1966) or exhibit antagonistic pleiotropy (Charlesworth, 1994; Williams, 1957; Partridge & Barton, 1993), in which case they must have a beneficial effect early in life, such as increased reproduction. In either case, a decline in age-specific survival and fertility, i.e. senescence, should evolve and decrease life span in proportion to the magnitude of the mortality risk (Austad, 1997). In support of this view, the rate of aging has been directly related to the risk of mortality for populations of birds and mammals (Ricklefs, 1998; Ricklefs & Scheuerlein, 2001). Furthermore, reproductive females of eusocial insects, which are protected in a colony, have much longer life spans than adults of solitary species (Keller & Genoud, 1997).

Rather than attempt to determine how bats differ from other mammals, in this study we aim to explain variation in the longevity of bats using differences in their ecology and life history. To this end we selected variables to include in our comparative analysis that seemed likely, *a priori*, to reflect species differences in risk of mortality from extrinsic sources. Thus, we assume that mortality risk by predation or accidents is influenced by body size, the presence of conspecifics, use of protected sites and the amount of time spent flying. Under these assumptions, we predict that the extrinsic risk of mortality should be lower for species of larger body size because they should have fewer predators than small bodied species. We also expect mortality risk to be lower for species that live in large colonies than for those living in small colonies because the per capita risk of predation should decrease with colony size as a consequence of predator dilution. Mortality risk should also be lower for species utilizing protected sites, such as caves, as day roosts or as hibernacula. Because hibernation duration in bats is influenced by temperature

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(Twente *et al.*, 1985), the magnitude of any hibernation effect on life span might also be expected to covary with the absolute value of the latitude at which each species lives. To the extent that collecting fruit and nectar requires less time than capturing animal prey, we would expect fruit- and nectar-feeding bats to experience lower extrinsic mortality risk than animal-feeding bats. Finally, we predict that the number of pups in a litter, as well as the number of births per year, will correlate positively with extrinsic mortality risk because time spent foraging increases with progeny production. For example, in the evening bat, *Nycticeius humeralis*, lactating females nursing two or three pups take more foraging trips each night than females without pups (Wilkinson, 1992).

Hibernation and reproductive rate may also influence life span, however, by altering how non-renewable resources are allocated between somatic maintenance and reproduction across seasons. Animals that hibernate, such as bats, or enter diapause, such as many insects, cease reproduction and often exhibit regression of reproductive tissues (Gustafson, 1979; Racey & Entwistle, 1999; Tatar & Yin, 2001). Because an organism must survive hibernation or diapause to reproduce later, such seasonal changes are consistent with the idea, often referred to as the disposable soma theory (Kirkwood & Rose, 1991; Kirkwood & Austad, 2000), that physiological support of reproduction detracts from survival. Thus, reproductive rate and hibernation may also be expected to covary with bat longevity even if these variables do not directly influence mortality risk from extrinsic factors.

Because closely related species are likely to share life history features as a consequence of recent common ancestry, a comparative analysis using species as separate data points may not accurately assess the degree to which evolution has resulted in correlated change between longevity and other variables. To evaluate this possibility, we also report comparisons among longevity and each ecological or life history factor using an analysis of phylogenetically independent contrasts (Felsenstein, 1985).

Results

The longevity of every species of bat in our data set exceeds that predicted for their body size from non-flying placental mammals (Fig. 1a). In a univariate analysis, body mass did not explain a significant amount of variation in bat longevity; however, evolutionary change in body mass positively covaried with evolutionary change in longevity (Table 1, Fig. 1). Average longevity also did not differ between animals kept in captivity and those observed in the wild ($F_{1,62} = 1.1$, $P = 0.30$). Six species have been recorded living over 30 years of age. Of these, five were observed in the wild – the 7-g long-eared (*Plecotus auritus*) and little brown bats (*Myotis lucifugus*), the 8-g Brandt's bat (*M. brandti*), the 23-g Blyth's bat (*M. blythii*) and the 24-g greater horseshoe bat (*Rhinolophus ferrumequinum*) – and one species was kept in captivity, the 1000-g giant flying fox (*Pteropus giganteus*).

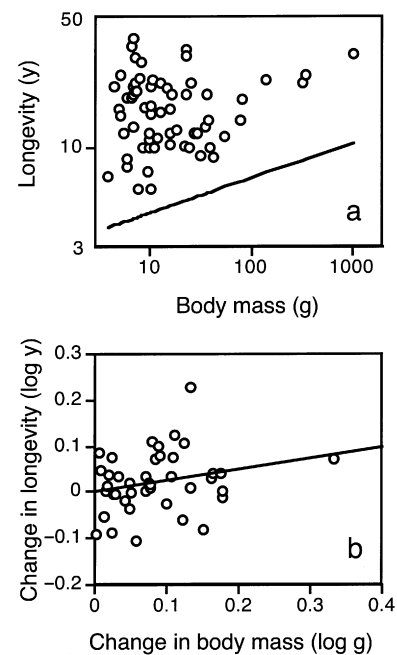


Fig. 1 (a) Maximum longevity recorded for 64 species of bats plotted against female body mass. The line indicates the least squares regression of longevity on body mass for 463 species of non-flying eutherian mammals (Austad & Fischer, 1991). (b) Independent contrasts of maximum longevity plotted against contrasts in body mass.

Table 1 Predictors of longevity in bats based on univariate regression or ANOVA analysis of species and phylogenetically independent contrasts

Factor	Species			Contrasts		
	d.f.	F	P	d.f.	F	P
Progeny per year	1,62	23.6	< 0.0001	1,40	19.4	< 0.0001
Hibernation	1,60	13.7	0.0005	1,5	10.3	0.024
Body mass (log)	1,62	1.5	0.23	1,40	7.3	0.010
Cave roosting	2,61	4.6	0.014	1,11	5.9	0.033
Latitude	1,62	14.6	0.0003	1,40	8.4	0.006
Colony size (log)	1,60	1.5	0.22	1,38	0.4	0.52
Diet	1,62	0.04	0.84	1,2	0.1	0.81

Reproductive rate, measured as the number of pups produced per year, explained the most variation in longevity in univariate analyses of both species and contrasts (Table 1). Female bats from species that either produce multiple pups per year or give birth multiple times per year had shorter longevity than species that produce a single pup per year (Fig. 2). The source of the longevity record had no effect on this relationship. The number of progeny produced per year was a significant predictor of longevity for both captive records ($F_{1,13} = 8.4$, $P = 0.012$) and field records ($F_{1,46} = 14.7$, $P = 0.0004$).

Hibernation and latitude were also significant predictors of longevity among species and contrasts. Hibernating species live, on average, 6 years longer than species that do not hibernate (Fig. 3). The only other variable to explain significant variation

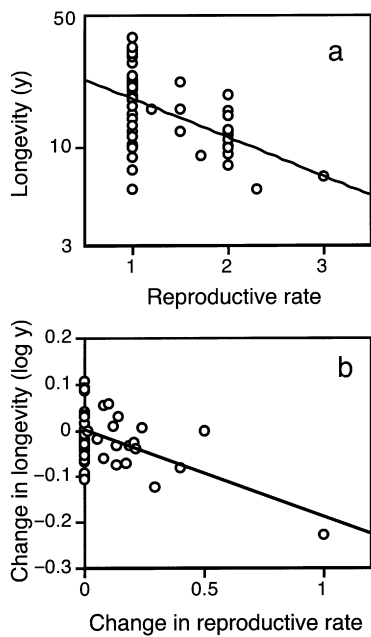


Fig. 2 (a) Least squares regression of maximum longevity plotted against reproductive rate. Reproductive rate is measured as average litter size multiplied by the number of litters produced per year. (b) Independent contrasts of maximum longevity plotted against contrasts in reproductive rate.

in longevity was cave roosting, which was also significant in both species and contrast analyses (Table 1). Bats that sometimes roost in caves live more than 5 years longer than bats that either never or always roost in caves (Fig. 4).

Stepwise analysis of covariance revealed that reproductive rate, body mass, hibernation and cave roosting exhibited significant and independent effects on longevity (Table 2). Together these four variables account for 58% of the variation in bat longevity. Body mass was significant in the multivariate, but not univariate, analyses, because the relationship between body mass and longevity is masked by an interaction involving hibernation, body mass and reproductive rate. ANCOVA of reproductive rate on hibernation and body mass revealed a significant effect of hibernation ($F_{1,58} = 15.2, P = 0.0002$) and a significant interaction between hibernation and body mass ($F_{1,58} = 9.2, P = 0.004$). Hibernating species have lower reproductive rates, on average (1.22 ± 0.06 progeny per year), than non-hibernating species (1.48 ± 0.13 progeny per year). But, reproductive rate decreases with body mass in non-hibernating species and increases with body mass in hibernating species. Regression analysis of contrasts after controlling for the most significant covariate confirmed that reproductive rate, female body size, hibernation and cave roosting exhibit correlated but independent evolutionary change with longevity (Table 2).

Discussion

Our comparative analysis of recorded life span in bats reveals that longevity is influenced by reproductive rate, tendency to hibernate, body mass and use of cave roosts but not by diet or

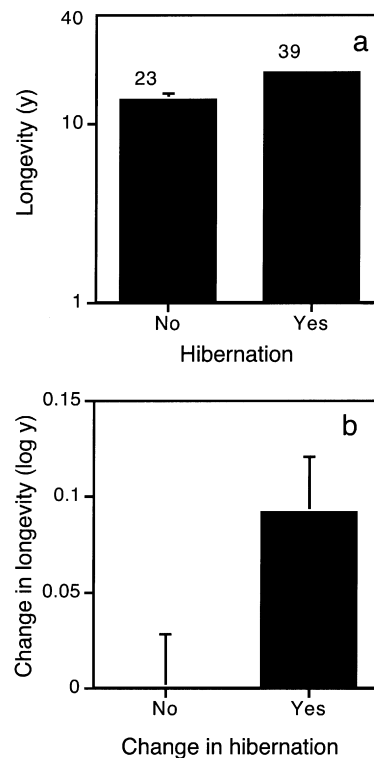


Fig. 3 (a) Average longevity \pm SE for bat species that do or do not hibernate. Numbers indicate sample size in each category. (b) Average change in longevity between phylogenetically independent comparisons in which hibernation was acquired.

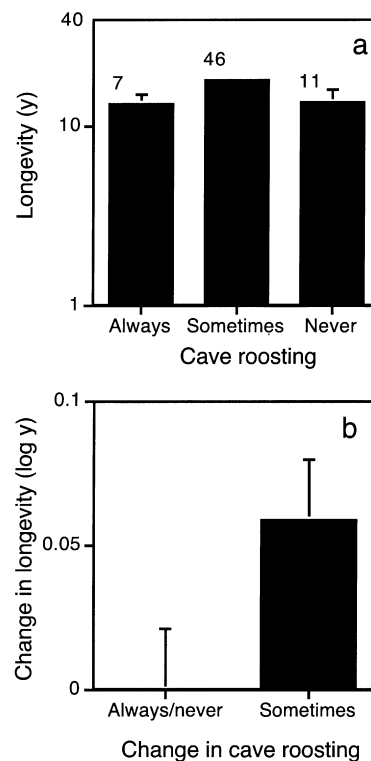


Fig. 4 (a) Average longevity \pm SE for bat species with different degrees of cave roost use. (b) Average change in longevity between phylogenetically independent comparisons in which occasional cave use was acquired.

Table 2 Predictors of longevity in bats based on ANCOVA for species and bivariate analysis of contrasts

Factor	Species			Contrasts			Variable controlled*
	d.f.	F	P	d.f.	F	P	
Progeny per year	1,56	16.4	0.0002	1,39	16.9	0.0002	Body mass (log)
Hibernation	1,56	17.4	0.0001	1,5	14.3	0.013	Progeny per year
Body mass (log)	1,56	14.2	0.0004	1,39	5.4	0.025	Progeny per year
Cave roosting	2,56	4.9	0.0107	1,11	5.2	0.043	Progeny per year

*The independent variable used to generate residual longevity for the contrast analyses.

colony size. Thus, the predicted influence of these ecological and life history factors on the risk of extrinsic mortality was generally supported for bats. On average, bats live 3.5 times as long as non-flying placental mammals of comparable body size. This difference is likely an underestimate because almost all of the life span records for non-flying eutherians come from captive populations (Austad & Fischer, 1991), whereas over half of the longevity records used in this study came from animals that were observed in the wild where extrinsic sources of mortality were not controlled. Furthermore, in contrast to most other studies, we were unable to detect any difference between longevity records recorded from captive and field sources, quite possibly because all records for hibernating species come from the field. Thus, we have no reason to think that the results reported here will change as additional records from captive individuals are included. Many of the longevity records may, though, increase as more animals are monitored. For example, even though we included all of the species that were used in previous reviews of bat longevity (Tuttle & Stevenson, 1982; Austad & Fischer, 1991; Carey & Judge, 2001), longevity records for a number of those species have subsequently increased.

Bat species that occasionally roost in caves exhibited greater longevity, independent of the effects of reproductive rate, body mass and hibernation, than those that either never or always roost in caves. Roost selection seems likely to be critical in avoiding predation. However, one might predict that exclusive cave use would provide greater protection from predation than occasional cave use. One way in which extrinsic sources of mortality would be predicted to be higher among exclusive than among occasional cave roosting species would be if ectoparasites or disease transmission were higher among exclusive cave roosting species. Ectoparasites are common among colonial species of bats, and several of these species are known to change roosts in a manner that would decrease their exposure to ectoparasites (Lewis, 1995; Wilkinson, 1985). More information on the incidence of transmittable diseases as a function of roosting habits in bats is needed.

The absence of any effect of diet on longevity appears to contradict our predictions. These predictions were, however, relatively weak as the connection between diet and mortality risk is unlikely to be simple. To facilitate analysis, we used a binary code for diet, i.e. species either fed predominantly on animal or plant material. An alternative approach using, for example, mode of prey capture, such as aerial hunting vs. gleaning, might

prove more informative. On the other hand, diet is a significant predictor of longevity in parrots (South and Wilkinson, unpublished data), even after removing effects of body size and phylogeny. In parrots, fruit and nectar feeding is associated with shorter life span than an omnivorous or granivorous diet. The difference in mortality risk between bats with fruit or nectar vs. animal diets may therefore be less than that between parrots with omnivorous and fruit diets.

Longevity was lower in species with high reproductive rate, as expected if bats exhibit a cost of reproduction (Partridge & Barton, 1993; Charlesworth, 1994). Because we observed comparable effects of reproductive rate on longevity using records from both captive and field sources, higher rates of reproduction cannot be increasing mortality rates solely by direct exposure to extrinsic factors. Rather, intrinsic sources of mortality must also have increased presumably as a consequence of selection for early reproduction, as expected if early reproduction exhibits antagonistic pleiotropy (Partridge, 2001).

In contrast to previous reports based on smaller data sets (Herreid, 1964; Austad & Fischer, 1991), we found that hibernation prolongs longevity independent of reproductive rate, body size and phylogeny. This result suggests that hibernation influences extrinsic sources of mortality risk, which could occur in more than one way. For example, hibernation may reduce the risk of mortality by predation. Bats typically hibernate in locations within caves that are inaccessible to predators and thermally stable (McNab, 1974). Alternatively, if hibernation is an adaptation to periods of unpredictable food availability, as many believe (Bartholomew, 1962; Twente & Twente, 1964), then hibernation may also reduce the risk of starvation. Evidence consistent with this interpretation includes accelerated onset of hibernation in calorie-restricted golden-mantled ground squirrels (Pulawa & Florant, 2000).

While we detected a positive effect of latitude in the univariate analysis of species longevity, latitude was not significant after controlling for phylogeny or hibernation. These results may indicate that while latitude is a good predictor of hibernation tendencies, it is inadequate to predict hibernation duration. Species differ in how they select hibernacula, with some migrating to more extreme latitudes to occupy cooler caves (McNab, 1974; Nagel & Nagel, 1991) and others differing in their hibernation duration even at the same temperature (Brack & Twente, 1985), presumably due to energetic constraints (Humphries *et al.*, 2002). Nevertheless, it is worth noting that the current

longevity record of 38 years is from a *Myotis brandti* male that was banded and resighted in Siberia (Khritankov & Ovodov, 2001). In addition, 23 other individuals of this species, all males, survived 25 or more years in this area. Thus, additional information on longevity from bats living at high latitudes may reveal that hibernation duration also acts to increase longevity, especially among males who do not allocate as many resources to reproduction as do females.

From a physiological perspective, hibernation may increase longevity because it reduces body temperature. Hibernating bats typically reduce their body temperature from about 40 °C to 6 °C, and then maintain that temperature for several weeks at a time. As a consequence, the metabolic rate of a hibernating bat is about 5% of its resting metabolic rate at room temperature and a fraction of a percent of its metabolic rate when endothermic at cold temperatures (Geiser, 1998). However, rather than increase the time available to expend a finite amount of energy as imagined by rate-of-living theory proponents, a more contemporaneous hypothesis would be that hibernation likely reduces the accumulation of intracellular oxidative damage (Austad, 1997).

Body mass is positively associated with longevity in most mammals (Harvey *et al.*, 1989; Austad & Fischer, 1991; Purvis & Harvey, 1995). The absence of an effect of body mass on longevity in bats has been a curious exception to this pattern without a clear explanation. The results of this study indicate that once the effects of reproductive rate and hibernation have been controlled, body mass does explain a significant amount of the remaining variation in longevity among species. The effect of body mass on longevity among species appears to be masked by an interaction between body mass, hibernation and reproductive rate. This interaction is not phylogenetically independent, as it does not mask the positive relationship between evolutionary change in body mass and longevity. The interaction between body mass, hibernation and reproductive rate, along with the significant effect of hibernation on reproductive rate that we observed, suggests that hibernation influences resource allocation between reproduction and somatic maintenance as a function of body size. In effect, hibernation appears to reduce the cost of reproduction relative to body size. These results strongly suggest that hibernation is a mechanism for conserving resources that can be used later for reproduction.

From an evolutionary perspective, life span can be viewed as the result of natural selection acting to maximize reproduction in the face of extrinsic sources of mortality. While our results are largely consistent with predictions of this theory, from a physiological perspective, the significant effects of reproductive rate, hibernation and body size that we detected on the longevity of bats are compatible with the disposable soma theory. This theory predicts that aging is a consequence of progressive deterioration of physiological function when resources are allocated to reproduction rather than survival (Kirkwood & Austad, 2000; Kirkwood & Rose, 1991). Until now, the only replicable method for increasing longevity in animals has been to restrict dietary intake of calories (Weindruch & Walford, 1988; Kirk,

2001; Lin *et al.*, 2002). Calorie restriction is consistent with the disposable soma idea because it causes most animals to shunt resources to somatic maintenance and away from reproduction (Shanley & Kirkwood, 2000). Calorie restriction also induces a wide variety of physiological and biochemical effects, with some, such as attenuation of oxidative damage, modulation of glycaemia and insulaemia, and improved ability to withstand exposure to low-intensity stress, favoured to have direct effects on longevity (Masoro, 2000). Because hibernation induces many of the same effects that have been reported to occur in calorie-restricted rodents, such as decreasing blood glucose, insulin and glycolytic enzyme activity while increasing protein synthesis, gamma globulin levels and antioxidant defences, the mechanisms by which longevity is affected by calorie restriction and hibernation may be similar (Walford & Spindler, 1997). Inducing hibernation experimentally has been shown to increase longevity (Lyman *et al.*, 1981). Thus, additional experiments are warranted to determine if hibernating animals, such as some bats, exhibit any of the same physiological (Sohal & Weindruch, 1996) or gene expression (Weindruch *et al.*, 2002) effects that have been noted for calorie-restricted rodents.

Experimental procedures

Data collection

Records of longevity and associated life history and ecological variables were obtained for 64 species of bats (see Supplementary materials <http://www.blackwell-science.co/products/journals/suppmat/ACE/ACE020/ACE020sm.htm>) either from the primary literature or from personal records of resighted or recaptured animals banded in the field. If more than one longevity record was available for a species, we used the larger value. Captive animals provide the most appropriate measure of longevity for this type of study because they are less susceptible to extrinsic sources of mortality. Consequently, we used longevity records from captive animals when they were available. However, many longevity records for bats come from recaptures or observations of banded animals in the field. To determine if there was any systematic difference between captive and field estimates, we compared longevity records between them.

When available, we used average body mass of the individuals for which longevity records were available. Otherwise, we used average body mass of females reported in the literature. Similarly, we either used the latitude where a longevity record was obtained or the latitude at the middle of a species' range as reported in the literature. Median colony size was taken from previous reviews (Hosken, 1997, 1998) or from species accounts in the literature. Reproductive rate was estimated as the product of average litter size and the average number of births per year. Bats utilize a variety of roosting sites, including foliage, caves, tree hollows, and man-made structures (Kunz, 1982) with some species using different types of roosts in different regions or times of the year. To reduce the potential complexity of this variable we scored roosting habit as either always in a cave, never

in a cave or sometimes use a cave. Similarly, we reduced the potential complexity associated with diet either to consuming animal matter or to consuming fruit or nectar. Species names follow Wilson & Reeder (1993).

Statistical analyses

To control for phylogenetic effects we estimated standardized independent contrasts for each variable using C.A.I.C. v.2.6.8 (Purvis & Rambaut, 1999). Because this analysis involves reconstruction of ancestral trait values, a phylogenetic hypothesis for all species must be used. Phylogenetic relationships among bats, especially the placement of families within the order, have long been controversial. To address this problem we used a 'supertree' (Sanderson *et al.*, 1998) for 916 extant species of bats that was created by combining 105 phylogenetic trees (Jones *et al.*, 2002). We assumed that all branch lengths were equal since C.A.I.C. performs reasonably well under this assumption when branch lengths are not known (Purvis *et al.*, 1994). To determine if correlated change had occurred between two continuous variables we used the CRUNCH algorithm to create contrasts and then tested if the slope of a least squares regression through the origin differed from zero. We used the BRUNCH algorithm for dichotomous variables and tested significance from a one-sample *t*-test on the contrasts of longevity.

To evaluate the possibility that independent factors are correlated, we conducted a stepwise analysis of covariance. We implemented this analysis by entering each variable into the model sequentially based on the magnitude of the *F*-statistic associated with that variable. Only variables that explained a significant additional portion of the variation in longevity were included in the model. We also conducted multivariate analyses on contrasts by controlling for the effects of one independent variable and then testing for the effects of another. When one of the variables was categorical and one was continuous, we first estimated the slope of the regression through the origin for the contrasts, and then obtained residuals from that line for each species. We then implemented the BRUNCH algorithm on the standardized contrasts of the residual longevity.

To meet assumptions of least squares regression, we used the base 10 logarithms of record longevity, colony size, and female body mass in all analyses. We did not transform reproductive rate or latitude because such transformations did not improve the distribution of residuals in either the species or contrast analyses. Because the BRUNCH algorithm can only be conducted on dichotomous variables, we recoded roosting type to either sometimes use a cave or not. Statistical analyses were conducted using Statview 5.0.1 and SuperANOVA.

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Supplementary material

The following material is available from <http://www.blackwell-science.com/products/journals/suppmat/ACE/ACE020/ACE020sm.htm>

Table S1 Longevity records and associated life history and ecological variables used in this study.

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