



## Review

## Bats and birds: Exceptional longevity despite high metabolic rates

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## ABSTRACT

Bats and birds live substantially longer on average than non-flying mammals of similar body size. The combination of small body size, high metabolic rates, and long lifespan in bats and birds would not seem to support oxidative theories of ageing that view senescence as the gradual accumulation of damage from metabolic byproducts. However, large-scale comparative analyses and laboratory studies on a few emerging model species have identified multiple mechanisms for resisting oxidative damage to mitochondrial DNA and cellular structures in both bats and birds. Here we review these recent findings, and suggest areas in which additional progress on ageing mechanisms can be made using bats and birds as novel systems. New techniques for determining the age of free-living, wild individuals, and robustly supported molecular phylogenies, are under development and will improve the efforts of comparative biologists to identify ecological and evolutionary factors promoting long lifespan. In the laboratory, greater development of emerging laboratory models and comparative functional genomic approaches will be needed to identify the molecular pathways of longevity extension in birds and bats.

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## 1. Introduction

Bats and birds live substantially longer than non-flying homeotherms of similar body size (Austad and Fischer, 1991; de Magalhaes et al., 2007; Prinzinger, 1993). Within mammals, the largest differences in longevity tend to occur between orders, whereas among birds the largest differences occur between genera (Fig. 1). On average, maximum bat lifespans are 3.5 times longer than non-flying eutherian mammals after correcting for body size (Fig. 1, Wilkinson and South, 2002). Records now exist of tiny bat “Methuselahs”, such as the 7 g Brandt’s bat (*Myotis brandti*), surviving in the wild for over four decades (41 years, Gaisler et al., 2003; Podlutzky et al., 2005). Similarly, many birds live three times longer than mammals of the same body size (Fig. 1, Holmes and Austad, 1995a; Holmes and Austad, 1995b). Although reports of centenarian parrots are apocryphal, cockatoos and Amazon parrots do exhibit extreme lifespans after accounting for body mass (Munshi-South and Wilkinson, 2006). A salmon-crested cockatoo (*Cacatua moluccensis*) named “King Tut” lived at the San Diego Zoo for at least 65 years (Brouwer et al., 2000); much larger birds, such as the Andean condor (*Vultur gryphus*), may live up to 75 years (Finch, 1990).

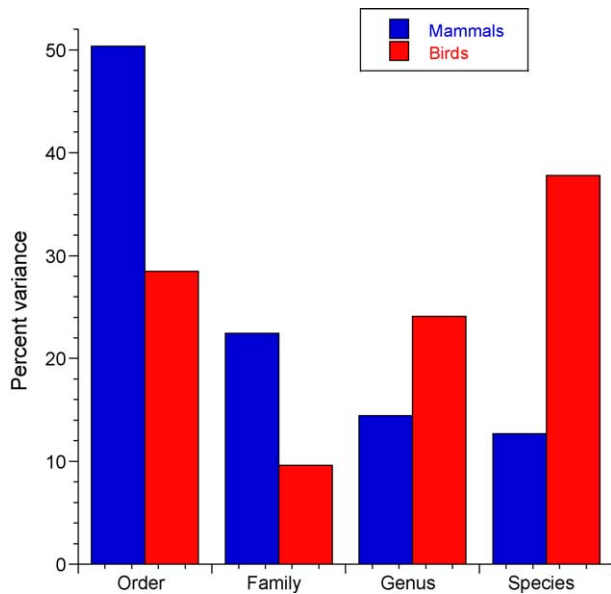
Evolutionary theories of longevity provide explanations for why bats and birds have evolved long lifespans. These theories predict

that average lifespan should increase as the probability of death caused by extrinsic factors (e.g. accidents, infectious disease, and predation) decreases (Austad and Fischer, 1991). Deleterious mutations that act late in life will be exposed to relatively strong selection in populations that do not experience high extrinsic mortality at young ages (Austad, 1997), and thus will not accumulate over time. Antagonistic pleiotropy caused by late-acting deleterious mutations that have positive benefits early in life will also have a weaker impact on populations with low extrinsic mortality risk (Partridge, 2001). Experimental data supporting evolutionary theories are scarce, but natural “experiments” comparing insular vs. mainland populations of both marsupials (Austad, 1993) and mice (Harper, 2008; Miller et al., 2000) indicate that insular populations experiencing lower predation risk have evolved greater longevity. Ageing rates are directly related to mortality risk in birds and mammals (Ricklefs, 1998; Ricklefs and Scheuerlein, 2001), and flight is believed to be the primary characteristic that helps birds and bats avoid extrinsic mortality early in life (Holmes and Austad, 1994). Bats and birds represent two independent evolutionary origins of flight, and thus comparative research may reveal common evolutionary pathways to long lifespan.

Life history tradeoffs may also explain why long lifespans have evolved in bat and bird species, because lifespan evolves as a consequence of joint selection for current reproduction along with survival and future reproduction. The “disposable soma” theory of ageing predicts that species experiencing low extrinsic mortality can make substantial investments in growth and somatic

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**Fig. 1.** Percent variance explained in log maximum longevity for 993 species of birds and 977 species of mammals. These values were obtained from a mixed model with log body weight as a covariate and taxonomic level as nested random effects using JMP 5.0.1.2. Body weight and longevity data were taken from the AnAge database (de Magalhaes et al., 2005). The “Species” category refers to the longevity for each species corrected for body weight (i.e. the residuals from the mixed model).

maintenance rather than early reproduction because they will have many opportunities to reproduce over a long lifespan (Kirkwood, 2002). However, investments in brain size (Isler and Van Schaik, 2009), developmental times (Barclay et al., 2004), and most commonly, reproductive rates (Bennett and Owens, 2002; Lack, 1968; Speakman, 2008), are believed to induce tradeoffs with longevity in birds and bats. The tradeoffs operating in these two taxa are not always the same, but the evidence discussed below suggests that these tradeoffs exert significant selective pressure on longevity.

The question of *how* bats and birds live a long time has attracted considerable attention, because of the combination of small body size, long lifespan and high metabolic rate in these groups. These characteristics seemingly contradict “rate of living” theories of ageing that propose a positive correlation between body size and longevity due to lower metabolic rates in larger species (Pearl, 1928). Bats have higher metabolic rates and ultimately use twice as much energy over their lifetimes compared to other mammals (Austad and Fischer, 1991). Hibernation slows down the rate of energy use, and hibernating bats do live 6 years longer on average than non-hibernating bats (Wilkinson and South, 2002). However, non-hibernating bats still live longer than other mammals of the same body size (Brunet-Rossinni and Austad, 2004). Similarly, birds have higher metabolic rates than mammals (Holmes and Austad, 1995b), and long-lived bird species use more energy over their lifetimes (Furness and Speakman, 2008) and have higher field metabolic rates than shorter lived bird species (Moller, 2008).

The patterns above, combined with the failure of recent studies to find evidence of a clear relationship between basal metabolic rate and longevity (de Magalhaes et al., 2007), have prompted researchers to investigate mechanistic explanations for how the flying vertebrates avoid negative physiological effects of their high metabolism. Oxidative theories of ageing predict that reactive oxygen species (ROS) generated by mitochondrial metabolism result in cumulative, irreversible damage leading to senescent decline (Sanz et al., 2006). Bats and birds would seemingly provide little support for this hypothesis given that their high metabolic rates should result in substantial oxidative stress and ageing

(Buffenstein et al., 2008). However, below we review recent studies that provide evidence of specific physiological mechanisms through which bats and birds either prevent or repair ROS damage.

Bats and birds are potentially excellent non-model systems to examine the evolution of longevity, especially in a comparative framework. Large longevity and life history datasets collected from wild populations now exist for both groups, primarily due to long-term banding studies (Ricklefs, 2008; Wilkinson and South, 2002) and increasingly sophisticated ageing methods (Brunet-Rossinni and Wilkinson, 2009; Chaney et al., 2003; Vleck et al., 2003). Some long-lived birds, such as the parrots, have been kept in captivity for a long enough time to amass corroborated maximum lifespans for many species (Brouwer et al., 2000). Most of these records are freely available to researchers in a well-curated online database (AnAge, de Magalhaes et al., 2005). Comparative analyses have also benefited from the development of methods, such as independent contrasts analysis, that control for phylogenetic effects (Garland et al., 1992). Species data cannot be treated as statistically independent because species are related by descent from common ancestors (Felsenstein, 1985), but shared phylogenetic history has not always been accounted for in comparative ageing studies (Speakman, 2005). The availability of well-supported phylogenies was previously an impediment to these types of analyses, but the increasing acceptance of consensus “supertrees” (all extant mammals, Bininda-Emonds et al., 2007, bats, Jones et al., 2002, oscine passerine birds, Jonsson and Fjeldsa, 2006) and the production of robust molecular phylogenies (parrots, Wright et al., 2008) have largely removed these impediments.

Mechanistic research on longevity in bats and birds has lagged because few species have been kept in laboratory colonies (Holmes and Ottinger, 2003). However, the number and diversity of bird species in labs is slowly increasing, with long-lived budgerigars (*Melopsittacus undulatus*) showing particular promise as a model system (Ogburn et al., 2001; Pamplona et al., 2005). Captive bat colonies have been maintained for behavioral and physiological studies in the past (Brunet-Rossinni and Austad, 2004), and now a few extremely long-lived *Myotis* species are emerging as ageing research models (Brunet-Rossinni, 2004). These advances suggest that bats and birds are leading candidates for the “non-model” outgroup system sought by ageing researchers (Holmes and Kristan, 2008).

## 2. Longevity research in bats

### 2.1. Evolution of long lifespan and the risk of extrinsic mortality in bats

Hypothetical selective pressures responsible for the evolution of long lifespan in bats generally fall into two categories: (1) adaptations that lower the risk of extrinsic mortality (evolutionary theories of ageing), and (2) life history tradeoffs that favor long lifespan (disposable soma theory of ageing). Escape from extrinsic mortality due to the evolution of flight in bats is consistent with evolutionary theories for long lifespan, but convincing evidence for a general association between flight and longevity in mammals is scarce. Flying and gliding mammals exhibit longer lifespans (Austad and Fischer, 1991; Holmes and Austad, 1994), but flight or gliding behavior have evolved so few times in mammals that rigorous, phylogenetically controlled studies are not possible.

Roosting in caves should lower the risk of extrinsic mortality for bats, as caves provide protection from extreme weather events. Caves may also be inaccessible to predators, and communal roosting may provide increased vigilance against predators that do reach the cave. Among chiropterans, bats that occasionally roost in caves live longer than bats that never or always use caves, independently of reproductive rate, body mass, hibernation, or

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