

Candidate Bird Species for Use in Aging Research

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Abstract

Birds live about 3 times as long as an average mammal of similar size. They exhibit this remarkable resistance to the degenerative processes of aging despite traits such as elevated body temperature, a rapid metabolic rate, and high blood glucose that might lead one to expect them to be especially short-lived. Although birds appear to age slowly, the patterns of age-related deterioration and development of disease parallel in many ways those of mammals such as humans. Therefore, birds may reveal novel mechanisms of resistance to senescence. A previous impediment to the use of birds in modern biomedical research was the inability to perform targeted genetic manipulations, which has revolutionized the use of other model species. But with the publication of the whole genome sequence of two bird species and the development of gene knockdown technology and tissue-specific transgenesis, this impediment seems to be disappearing. At least five bird species deserve special attention for development as models of successful aging. Three of these species—budgerigars, canaries, and zebra finches—are common cage birds and are already used extensively in the study of vocal learning and sustained neurogenesis in adulthood. In addition, two wild species—the European starling and the house sparrow—may also make excellent models for aging research.

Key Words: bird; budgerigar (*Melopsittacus undulatus*); canary (*Serinus canaria*); domestication; house sparrow (*Passer domesticus*); longevity; senescence; starling (*Sturnus vulgaris*); zebra finch (*Taeniopygia guttata*)

Introduction: Why Birds Are of Exceptional Biogerontological Interest

Francis Bacon (1638) first noted the exceptional longevity of birds compared with mammals nearly 400 years ago, and observers have since documented that birds

live approximately 3 times as long as same-size mammals when both are maintained in salubrious captive conditions (Holmes and Austad 1995). Much more is known about bird longevity in the wild (thanks to decades of large-scale bird banding projects) than in captivity, whereas most scientific information about mammalian longevity comes from captive populations—yet the data clearly show that, even living in the wild, birds survive nearly twice as long as mammals cosseted in captivity (Holmes and Austad 1995)!

Although there is considerable anecdotal exaggeration of avian longevity (as there is of human longevity), confirmed records are striking. Some captive cockatoos, for instance, live into their 60s (Brouwer et al. 2000), a number of wild seabird species their 40s or even 50s (Staav and Fransson 2008) (Table 1), and some gull species survive into their 30s (AnAge, the Animal Aging and Longevity Database; <http://genomics.senescence.info/species>¹). These longevities seem particularly remarkable considering that most of these species weigh less than a kilogram, yet live much longer than, say, pet dogs living under the best conditions (Waters 2011). Thus birds appear to be much better designed for survival than most mammals.

The above comparisons require some context, though. The range of longevities among mammals is considerably greater than among birds: a large number of mammal species (e.g., house mice, shrews, and many small marsupials) survive only 1 to 3 years even in the laboratory, whereas some mammals such as humans and bowhead whales are longer-lived than any bird species (Austad 2010b). Similarly, the range of body sizes among birds is much smaller than among mammals—there are no birds the size of cows, horses, or whales. Nevertheless, over the range of body sizes common to both groups, birds live much longer.

So long-lived are some bird species in nature that earlier researchers assumed they did not age at all (Botkin and Miller 1974). In fact, some authors have claimed that animals generally do not age in nature, assuming that environmentally imposed, nonsenescent mortality is so high in the wild that animals die long before aging can become apparent. Although this is a reasonable hypothesis, it turns out to be false for both birds and mammals (Brunet-Rossinni and Austad 2006): senescence in the wild is common in both groups, although, as mentioned, birds live consistently longer and begin to show signs of senescence at much later ages.

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¹This and other websites cited in this article were accessed on December 22, 2010.

Table 1 Body mass and longevity records for selected bird species

Species	Longevity record (years)	Body mass (g)	Source
Budgerigar (<i>Melopsittacus undulatus</i>)	21(c)	40(c)	Brouwer et al. (2000)
Canary (<i>Serinus canaria</i>)	24(c)	21(c)	Carey and Judge (2000)
Zebra finch (<i>Taeniopygia guttata</i>)	14.5(c) ^a 8.0(c)	12	AnAge ^b ; Moe et al. (2009)
Northern fulmar (<i>Fulmaris glacialis</i>)	51	540	Paul M. Thompson, personal communication ^c
Manx shearwater (<i>Puffinus puffinus</i>)	51	450	BTO
Arctic tern (<i>Sterna paradisaea</i>)	34	110	North American BBL
European starling (<i>Sturnus vulgaris</i>)	23	82	Staaav and Fransson (2008)
House sparrow (<i>Passer domesticus</i>)	20	28	Staaav and Fransson (2008)

BTO, British Trust for Ornithology (www.bto.org; this and other websites cited here accessed on December 22, 2010) banding records for Britain and Ireland; North American BBL, North American Bird Banding Program Longevity Records (www.pwrc.usgs.gov/BBL/homepage/longvrec.htm); (c), longevity record for birds in captivity

^aThis record is more anecdotal than most; 8 years is the maximum published report that I can find from a research colony (Moe et al. 2009).

^bAnimal Aging and Longevity Database (<http://genomics.senescence.info/species>)

^cPersonal communication with Paul M. Thompson, University of Aberdeen, April 2007.

Naturally, bird species vary in their longevity depending on a variety of factors. A recent comprehensive analysis of more than 900 species found that body size, diet (herbivores live longer than carnivores or omnivores), sociality (more highly social species live longer), and breeding insularity (island vs. mainland species) were all related to species longevity (Wasser and Sherman 2010). These observations are consistent with an evolutionary perspective according to which species less subject to extrinsic mortality evolve longer lives (Williams 1957).

When birds do show signs of senescence, they exhibit many of the same age-related diseases and disabilities as mammals. For instance, as they age birds contract a broad variety of cancers and are subject to diabetes, arthritis, cataracts, and congestive heart failure, and some species are even prone to atherosclerosis (Harrison and Harrison 1986). Like humans and other mammals, older birds are also more susceptible to a host of infectious diseases (Hausmann et al. 2005).

Surprisingly, birds display a comparative survival advantage over mammals despite several traits that, according to several popular theories of aging, suggest that they should be short-lived. For example, birds maintain about a 3°C higher body temperature than mammals (Harrison and Harrison 1986), which could predispose them to higher rates of damaging protein glycoxidation (Cerami 1985), a process by which glucose molecules attach to proteins and thus interfere with their function. Protein glycoxidation can be a particular problem for birds as their blood glucose concentrations

are several times higher than those of mammals (Holmes and Austad 1995).

In addition, birds have generally higher metabolic rates than mammals (Furness and Speakman 2008), which could subject them to higher levels of cellular damage from reactive oxygen species (ROS). But despite their higher metabolic rates, there is no consensus on whether birds as a group have higher or lower levels of oxidative damage to tissues than mammals. Studies of isolated mitochondria indicate that birds produce fewer ROS per amount of oxygen consumption than mammals (Lambert et al. 2007; Pamplona et al. 1999), possibly due to a lower concentration of ROS-producing electron transport chain Complex I (Lambert et al. 2010). However, whether this extends to less oxidative damage to tissues is not clear. Several papers have noted that lipid peroxidation is lower in at least some organs of birds than in mammals (e.g., Pamplona et al. 1999), possibly because lipids in bird cellular membranes are typically more peroxidation-resistant than mammal membrane lipids (Hulbert et al. 2007). On the other hand, oxidative DNA lesions appear to be greater in birds than mammals (Hamilton et al. 2001).

The conclusions described above should be considered provisional, as the use of state-of-the-art techniques to measure oxidative damage is as yet limited to relatively few tissues in relatively few bird species. Older techniques frequently suffered from problems of insensitivity, nonspecificity, and a danger of artifactual results due to oxidative damage during tissue storage or biochemical isolation procedures (Chaudhuri et al. 2006; Hamilton et al. 2001; Montuschi et al. 2007).

Advantages and Challenges of Using Birds in Research

Given that birds live so long despite their biological features, they clearly should be of interest to biogerontologists as examples of successful resistance to senescence-inducing processes. What then might be the advantages and possible obstacles to developing avian species as laboratory models?

Advantages

There are roughly twice as many bird species (~10,000) as mammal species (~5,000) worldwide (Clements 2007; Nowak 1999). A considerable advantage of developing birds as models of successful aging is that dozens of species have already been domesticated either for commercial purposes or as pets, so captive husbandry, including commercially available food, caging, and a wide range of supplies, is well developed for numerous species. Also, many species are small (<30 g) and gregarious and can therefore be maintained at relatively high densities in research colonies (in keeping with available information about avian and species-specific husbandry; for reviews, Bateson and Feenders 2010; Kalmar et al. 2010). In addition, bird behavior and neurophysiology are quite well known, so multiple assessments are possible to determine bird healthspan as distinct from lifespan, which is particularly timely in light of a recent shift in the aging research community to a focus on healthspan (Kirkland and Peterson 2009).

What experimental paradigms might be possible with long-lived birds? The most obvious are cell-based; for instance, the molecular basis of long-lived birds' superior resistance to oxidative stress could be investigated by knocking out or overexpressing various candidate genes presumed to be responsible for this resistance. Similarly, it may be possible to transfect short-lived bird cells with candidate genes from longer-lived, more stress-resistant species. Transfection of mammalian cells with genes from long-lived birds might also be informative. Other experimental paradigms may also develop with innovations such as the development of avian-induced pluripotent stem cells.

Challenges

There are some limitations to the use of birds in research. The first has to do with the paucity of bird species that are truly short-lived. Clearly, the most logical approach to investigating mechanisms that enable birds to age successfully would be to compare the cellular, molecular, and physiological processes of interest in long-lived, slowly aging species with those of short-lived, rapidly aging species. Ideally, these species would be closely related and similar in both body size and as many other traits as possible except longevity. But short-lived species (those with a maximum longevity under benign conditions of, say, less than 7 years) are rare and largely confined to the weakly

flying order Galliformes (chickens, pheasants, quail) (Holmes et al. 2001).

Published data from band recoveries in natural populations suggest that some passerine species live no longer than 7 years in nature, but this estimate likely represents a lack of information about their longevity rather than a truly short life. In fact, an analysis of published longevity records in nature of 475 North American species indicates that the total number of band recoveries for a species explains a greater fraction (49%) of the variation in maximum field longevity than does body size (32%) (Austad 2010a).

The shortest-lived bird species with a wealth of information from both wild and captive populations is the common quail (*Coturnix coturnix*), which lives less than a year in the wild; captive males rarely live beyond 4 to 5 years and females live about 1 year less. The Japanese quail (*Coturnix japonica*), a domesticated variant of the common quail, reaches full adulthood in 2 to 3 months, and reproductive males have a lifespan of 3 to 5 years, females 2½ to 3 years. Reproductive senescence occurs earlier, as fertility decreases 30-50% by 70 weeks of age (Ottinger 2001). Such a rapid life history is rare to nonexistent in other groups of birds.

A second limitation (which may be disappearing) is the difficulty of genetic manipulation in birds. Molecular manipulation of gene activity is a defining feature—and one of the most powerful tools—of modern biology. Yet the technology for gene knockdown and germline transgenesis in birds has been slow to develop (Sang 2004). Recently, however, reliable tissue-specific transgenesis has been reported in several bird species, including quail and zebra finches (Agate et al. 2009; Scott et al. 2010). In addition, robust techniques for gene knockdown by RNA interference are now available (Das et al. 2006) and researchers have identified factors regulating avian embryonic stem cells (Laval et al. 2007). These advances, combined with the fact that there are now high-quality whole genome sequences for both chickens (Cogburn et al. 2007) and zebra finches (Warren et al. 2010), suggest that avian molecular genetics is poised for rapid development.

Bird Species of Exceptional Promise as Models for Aging Research

Model organisms used in biomedical research often derive from domesticated stocks or strains—and, if not, they quickly become domesticated as laboratory husbandry inevitably genetically selects for certain traits, some of which are obvious and some of which remain elusive. For instance, laboratory domestication typically selects for accelerated developmental rate, larger body size, increased fecundity, and reduced longevity (Gems and Riddle 2000; Linnen et al. 2001; Miller et al. 2002), but in mice, at least, there also appears to have been inadvertent selection for traits such as longer telomeres (Hemann and Greider 2000) and pineal gland dysfunction (Goto et al. 1989). So domestication can affect species in unexpected ways. Of course, these caveats do not disqualify

domesticated stocks and strains from being highly useful in biomedical research, as the wild success of the laboratory mouse attests, but they do warrant attention.

In the case of birds, domestication can complicate the development of new models for aging research because species longevity information may come from wild-derived genotypes or stocks or strains that differ in significant ways from those developed for research. It is therefore necessary to verify the longevity of any genotypes adopted for research. Although such verification can take years with relatively long-lived birds, it is vital to validating the model.

Both domesticated and nondomesticated species of birds are candidates for development in aging research, with one notable exception: the chicken (*Gallus gallus*). Because of its commercial importance it is by far the most thoroughly studied avian species in virtually every aspect of its biology, but there are several reasons chickens fail as an avian model for aging research. First, they are too large (ranging in size from less than 1 kg to several kg) and require considerable space per individual to be maintained in healthful conditions. Second, they have been extensively modified by genetic selection for growth rate or rate of egg laying or particular plumage characteristics; because of this selection, there are more than 60 recognized chicken breeds that differ greatly in their biology. Finally, but perhaps most importantly, chicken longevity is undefined: incredibly, there are no available survival curves for chickens and lifespan estimates run from 7 years (Damerow 2010) to a reported (but unverified) maximum of 30 years from a 100-year-old publication (Mitchell 1911). Undoubtedly, there are large differences in longevity among breeds and between all domesticated varieties and their wild ancestor, the red jungle fowl. Yet, given their size chickens—even at the most extreme longevity estimates—are relatively short-lived for a bird.

Because so little is known about longevity in chickens compared with numerous other bird species, I describe a few more promising candidate species below.

Domesticated Species

Birds have been popular pets for centuries and some species have adapted well to captivity. The following are among the most popular pet birds and thus have a wide array of specialized diets, cages, and supplies developed specifically for them.

Budgerigars

Commonly (but improperly) called parakeets, budgerigars (*Melopsittacus undulatus*) are mouse-size (40-50 g), highly gregarious, seed-eating desert and grassland parrots native to Australia. Introduced into Europe in the mid-19th century, they quickly became a darling of bird fanciers and are now one of the most popular pet bird species in the world (Kavanaugh 1987). Domesticated budgerigars have been bred for a variety of plumage and body type characteristics

such that more than 20 color mutants and around 100 “varieties” are widely available. Wild budgerigars are considerably smaller (~30 g) than domesticated varieties and have primarily green plumage with yellow heads and throats and black feather markings.

Budgerigars breed easily in captivity year-round. They are physiologically capable of breeding by 5 to 6 months of age, but are more successful and remain healthier if they do not begin breeding until they are 10 to 12 months old (Davids 2006). Females lay clutches of three to five eggs, from which chicks hatch after about 18 days and leave the nest about 1½ months later.

Budgerigars live about 7 years on average, with a maximum reported longevity of 21 years (Brouwer et al. 2000). However, like the chicken, individual “varieties” likely have a broad range of longevities and the genotype of the 21-year longevity record is not known.

The budgerigar is not a stranger to the laboratory either. It is commonly used in behavioral and sensory neurophysiological studies. Aging studies on these birds have focused on properties of their cultured cells and have shown that, compared with mouse cells, budgerigar kidney epithelium-derived cells survived better when exposed to a variety of oxidative stressors (H₂O₂, paraquat, γ -irradiation, and 95% oxygen) (Ogburn et al. 1998). Similarly, budgerigar embryonic fibroblasts were more resistant to oxidative stressors than cells from the shorter-lived Japanese quail, a phenomenon that depended on active gene expression during the stress (Ogburn et al. 2001).

Budgerigars are probably second to the chicken among bird species in terms of knowledge about their basic physiology and pathophysiology (Ritchie et al. 1994), so establishing solid longevity information about commonly used varieties is a project worth pursuing.

Canaries

Wild canaries (*Serinus canaria*) are small, drab, greenish-gray, striped fringillid finches native to the Canary Islands (whence their name), Madeira, and the Azores (Moustaki 2008). First bred in captivity in 17th century Europe because of the striking beauty of their song, domesticated canaries have since been genetically selected by fanciers for plumage color and form, body shape, and song characteristics. Along the way, canaries were hybridized with an assortment of other species in the same avian family such as house finches, bullfinches, linnets, and serins. While most of these matings produced sterile offspring, a few did not, so it is possible that the modern domesticated canary carries genes from several other species (Birkhead 2004).

Like other popular cage birds, domesticated canaries can breed year-round if their light cycle is manipulated appropriately (12-14 hours of daylight). They begin breeding at about 10 to 12 months of age and produce a clutch of about five eggs over 5 days. These are incubated for about 2 weeks, and the chicks fledged roughly 18 days after the end of incubation;

thus about 40 days pass from egg laying to fledging (Moustaki 2008). As with many other domesticated birds, there are no formal survival studies, but the conventional wisdom among canary fanciers is that longevities of 10+ years are common; the reported captive longevity record is 24 years (Carey and Judge 2000). Furthermore, as in the budgerigar, cultured cells from canaries exhibit enhanced resistance to oxidative stress (Ogburn et al. 1998).

The canary has also been used extensively for years in research and, in modern times, neurological studies.² As is characteristic of songbirds, the canary communicates using learned vocalizations, an ability thought to be otherwise confined to humans and very few other species (Warren et al. 2010); the neurophysiological and endocrine basis of this learning has therefore been the subject of study for several decades (for recent reviews, Ball and Balthazart 2010; Fee and Scharff 2010; Margoliash 2010). An unexpected consequence of the study of “song control nuclei” and how they change developmentally and seasonally was the discovery of adult neurogenesis in the canary brain (Goldman and Nottebohm 1983), a finding that has since been extended to other songbirds (Nottebohm 2005) as well as to mammals (Bondolfi et al. 2004). This finding overthrew an entrenched dogma that adult neurogenesis did not exist in birds or mammals.

The large corpus of background information on many aspects of canary biology, combined with their exceptionally long lives (3-5 times as long as the similar-size mouse), makes them an attractive candidate for mechanistic aging studies.

Zebra Finches

Like the budgerigar, the wild zebra finch (*Taeniopygia guttata*) is widespread throughout the interior of Australia. Because of its small size (Table 1), ease of breeding, and relatively short time to sexual maturity (4 months), the zebra finch has become by far the most thoroughly studied songbird species (Clayton et al. 2005).

The reproductive pattern of zebra finches is virtually identical to that of canaries, including clutch size, incubation period, and time until fledging (O'Connor 2008). The neuroanatomy and physiology of song learning, song production, and adult neurogenesis have also been well studied in zebra finches (Clayton 2000; Mello et al. 1992), as have the neuroendocrinology and development of sex differentiation (Holloway and Clayton 2001), flight energetics (Hambly et al. 2002), impact of early life events on adult phenotype (Fisher et al. 2006; Spencer et al. 2009), and a host of behavioral and ecological traits (Zann 1996). By at least one metric, telencephalization, the zebra finch brain is significantly

more humanlike than that of the rat or mouse (Johnson and Whitney 2005).

The tools of genetic manipulation are also much more thoroughly developed in zebra finches than in any other songbird. For instance, there is now a high-quality whole genome sequence available for the zebra finch (Warren et al. 2010), and techniques are available for tissue-specific transgenesis in this species using lentiviral vectors (Scott et al. 2010).

Without question, zebra finches have manifold advantages as avian models of many biological processes. Are they also suitable as a model of delayed or successful aging? The answer to that question hinges on how long they live under laboratory conditions, but for a species so thoroughly described there is surprisingly little solid information on their longevity. In the wild, there have been reports that they can live as long as 5 years (Zann 1996). In research colonies there are reports of their living as long as 8 years (Moe et al. 2009) and 4.1 years on average (1500 days; 54% of the birds still alive; Bolund 2009), but in this second colony survival beyond this was not reported. Clearly zebra finches live considerably longer than laboratory mice, although exactly how much longer cannot be quantified. Given what is known from research colonies, an anecdotal report from a pet owner of a zebra finch that lived 14½ years seems faintly possible, but not particularly likely.

Nondomesticated Species

The three common pet and research species described above would seem to be the most promising immediate candidates for development as models of successful aging. But there is no reason to limit this discussion to domesticated species.

Some birds adapt well to the laboratory even when captured directly from the wild. These species have not been genetically altered by domestication and thus are free of some of the disadvantages of domestication such as inadvertent selection for unwanted traits. However, development of a species as a research model requires a steady supply of known-age individuals, so if these species become seriously interesting to laboratory researchers they will inevitably become domesticated. During the domestication process, it might be worth devoting some effort to attempt to minimize the selective pressure inherent in the standard development of production colonies.

Note that for nondomesticated species, longevity records typically derive from natural populations; the lifespan of birds in captivity, where many sources of extrinsic mortality such as predation, food shortage, or the vicissitudes of climate are absent, might be substantially longer. Additionally, field records suggest that animals that have survived under the challenging conditions of the natural world have managed to remain healthy for nearly as long. Lifespan in nature, in other words, is more likely to approximate healthspan than would be true of animals in the laboratory.

²Most famously, of course, humans used the canary as an early warning system for the presence of dangerous gases in coal mines (Moustaki 2008).

In the next two sections I present two nondomesticated species that warrant special attention as possible candidates for aging research.

European Starling

Probably the most common wild-caught species used in a wide array of biological studies (PubMed lists more than 500 publications) is the European starling (*Sturnus vulgaris*). This 80 g insectivorous songbird, native to Eurasia, has been introduced in North America, Australia, and a host of islands. It thrives in urban areas and at times congregates in enormous flocks of tens of thousands of individuals. Both male and female starlings sing and produce a great variety of sounds, including those mimicking human voices (Van Hout et al. 2009). Because starlings adapt well to captivity they are popular both as pets and in research, so many details of their basic biology and husbandry are known.

Wild starlings first breed at 2 years of age; clutch size and timing of the breeding cycle are similar to those of canaries and zebra finches—clutches consist of about five eggs, which are incubated for about 2 weeks, and nestlings fledge about 3 weeks after hatching. Starlings breed seasonally (spring and summer) in the wild, but studies of the responsiveness of their reproductive system to photoperiod suggest that they could reproduce year-round in the laboratory (Asher and Bateson 2008; Stevenson et al. 2009).

Starlings have been used for experiments in cognitive neuroscience, toxicology, neuroendocrinology, stress physiology, reproductive biology, auditory physiology, and numerous other fields (Engel et al. 2006; Swaddle and Johnson 2007; Van Hout et al. 2009). Genetic resources for starlings are not available, although with modern sequencing technology, careful attention to breeding structure in captive populations, and appropriate effort, such resources could be established fairly quickly.

Long-term data indicate the potential suitability of starlings for aging research. Enormous numbers of wild starlings have been banded and later recovered—a 1983 study reported that, in the United States alone, more than 750,000 individuals had been banded and more than 24,000 recovered (Clapp et al. 1983). The longest-lived bird recaptured in the United States was just over 15 years and in the United Kingdom 17½ years (Clapp et al. 1983); the European Union for Bird Ringing (EURING; www.euring.org) databank lists an individual that lived almost 23 years (Staaav and Fransson 2008). Thus it is clear that starlings can live a very long time in the wild. But surprisingly, given how often wild starlings are adopted as pets, there is very little information on their longevity in captivity. Clearly though, assuming that captive husbandry is adequate, starlings might routinely live at least into their teens in the laboratory.

House Sparrow

Like the European starling, the house sparrow (*Passer domesticus*) is native to Eurasia but has been widely introduced

to other parts of the world—North and South America, Southern and Western Africa, Australia, New Zealand, and a host of smaller islands—where it has flourished. It is the most widely distributed wild bird species in the world (Anderson 2006). Substantially smaller than the starling, this 25-30 g, seed-eating, highly gregarious songbird is strongly associated with human populations, nesting colonially on or near buildings, and even breeding inside large buildings, warehouses, and mines.

The reproductive pattern of house sparrows is fairly typical of songbirds, and studies of their reproductive biology (Anderson 2006; Hegner and Wingfield 1986) suggest that they could probably be induced to reproduce year-round in captivity under a regulated photoperiod. In lower latitudes where favorable conditions for reproduction occur throughout most of the year, house sparrows may mate and even lay eggs when they are only a few months old, while still retaining their juvenile plumage. But first-time breeders regardless of age are typically unsuccessful, at least in nature (Anderson 2006).

House sparrows have been the subject of extensive field studies but rather fewer laboratory studies. Although some research on their neuroanatomy and physiology is available (Cassone et al. 2008; Chang and Karasov 2004; McGuire and Bentley 2010), most studies have focused on questions relevant to their lives in nature; there are thus extensive records on house sparrow survival and longevity in nature, but virtually no information from captive birds. About half of adult house sparrows have been reported to die annually in nature, a mortality rate that, if it remains constant, indicates that only about one bird in a thousand would live as long as a decade (Summers-Smith 1990); yet house sparrows have been recorded in Europe to live nearly 20 years (Staaav and Fransson 2008) and in the United States more than 15 years (Klimkiewicz and Futcher 1987), so the annual mortality rate is likely much lower. Very little aging research has been done on house sparrows, although one paper reports the surprising finding that mitochondria from house sparrow liver produces considerably more oxygen-free radicals than similar tissue from mice (Brown et al. 2009).

Because house sparrows live so comfortably in proximity to humans, they might adapt to laboratory life quite easily, and if so make an excellent research model of successful aging.

Conclusions

Because birds are so long-lived compared with mammals—despite features such as high blood glucose and metabolic rate as well as elevated body temperature, any of which might a priori indicate that they should be shorter-lived—they could reveal novel mechanisms of resistance to damaging aging processes.

Until recently, the use of birds in modern biomedical research was limited by the inability to perform targeted gene manipulations, but that limitation seems to be disappearing as techniques are now available for both tissue-specific

transgenesis and gene knockdowns in birds. Moreover, with the sequencing of two complete avian genomes, a host of new molecular tools should soon be available for use in selected bird species.

Like the house mouse, which before its adoption as a biomedical research model was domesticated as a pet, several pet bird species—budgerigars, canaries, and zebra finches—are increasingly used in neurological research and thus might be easily adaptable for aging research. It is also possible that nondomesticated species such as starlings or house sparrows, with their well-authenticated histories of living exceptionally long lives under the challenging conditions of the natural world, may be rewarding additions to the bestiary of aging research.

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