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SHORT COMMUNICATION

A database of vertebrate longevity records and their relation to other life-history traits

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Abstract

Longevity is a major characteristic of animals that has long fascinated scientists. In this work, we present a comprehensive database of animal longevity records and related life-history traits entitled AnAge, which we compiled and manually curated from an extensive literature. AnAge started as a collection of longevity records, but has since been expanded to include quantitative data for numerous other life-history traits, including body masses at different developmental stages, reproductive data such as age at sexual maturity and measurements of reproductive output, and physiological traits related to metabolism. AnAge features over 4000 vertebrate species and is a central resource for applying the comparative method to studies of longevity and life-history evolution across the tree of life. Moreover, by providing a reference value for longevity and other life-history traits, AnAge can prove valuable to a broad range of biologists working in evolutionary biology, ecology, zoology, physiology and conservation biology. AnAge is freely available online (http://genomics.senescence.info/species/).

Introduction

The longevity of animals has long fascinated scientists. Already Aristotle in his c. 350 BC treatise *On Longevity and Shortness of Life* reflected on the diversity of lifespans observed in nature. Although the causes for differences in longevity between species and populations remain a subject of debate (Finch, 1990; Charnov, 1993; Austad, 2001; de Magalhaes *et al.*, 2007), they appear to reflect a combination of ecological, evolutionary, and ultimately genetic and physiological factors (Harvey & Purvis, 1999). Longevity is also an important component of life history. Understanding the timing and evolution of life histories is a key theme in evolutionary biology as well as crucial to studies in ecology, zoology and conservation biology.

Comparative studies have an enormous potential to inform about the evolution of whole organisms, yet require adequate datasets that entail time and effort to collect. Herein, we present an extensive and comprehensive database of animal longevity records entitled AnAge. Started in 2003, AnAge was compiled from the literature as well as from other large-scale datasets and currently features 4122 entries. Because longevity has been reported to correlate with a number of other life-history traits, such as body size, age at sexual maturity and growth rates (Stearns, 1992; Charnov, 1993), and with certain widely-studied physiological traits like body temperature and basal metabolic rate (Harvey & Purvis, 1999; White & Seymour, 2004), we also incorporated extensive data on these traits. The aim of this work is to expand and update on a previous formal description of AnAge (de Magalhaes *et al.*, 2005) and discuss how a broad number of biologists – in particular evolutionary biologists, but also ecologists, zoologists, and field biologists – can employ this unique and powerful resource.

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Data collection and organization

Data on longevity were initially obtained from traditional sources (Nowak, 1999; Carey & Judge, 2000). Following an extensive review of the literature, however, records were dramatically updated and expanded (see below). Currently, AnAge incorporates data from over 800 sources, including books, journal articles, websites and databases, plus many personal communications. All extant vertebrate species for which we found information on longevity or ageing were added to our database.

Quantitative data, in particular longevity records from which maximum lifespan is derived, have to pass a set of predefined criteria in order to be added to AnAge, including having specific, factual information regarding the data and the species they refer to, and coming from reliable sources. Longevity records based on single or a few animals are normally excluded, as detailed elsewhere (de Magalhaes *et al.*, 2005, 2007). Crucially, longevity data are manually curated to assure their accuracy and we make an effort to consult the original reference. If obtained from authoritative sources, other life-history traits are sometimes incorporated using automated methods. Each AnAge entry includes not only quantitative data on longevity and life-history traits, but also comments and observations. Anecdotal claims are included in the observations section, though these normally do not form the basis for the quantitative values of each entry as we aim to provide a consistent dataset that can be used in comparative studies. Each entry cites all sources used to derive the data referring to that entry.

For maximum lifespan, AnAge features the highest reported value which in some taxa (e.g. nonflying terrestrial mammals) tends to come from animals in captivity. Although longevity in captivity is thought to be the product of selection driven by environmentally imposed mortality in the wild (Saether & Gordon, 1994; de Magalhaes *et al.*, 2007), if available we also include information on the lifespan of wild populations. Whether the maximum lifespan of a given species comes from a specimen in the wild or in captivity is indicated for the vast majority of species.

One caveat in using longevity records in comparative studies is the bias resulting from differences in sample sizes. To minimize these effects, one recent improvement to AnAge was the inclusion of an estimate of sample size. For longevity records obtained from species in captivity, estimates of sample size were obtained from the International Species Information System (http://www.isis.org/), a global database of the zoological community. Estimates of wild-derived records were typically obtained from the sources of the longevity data, such as banding studies in birds. Sample sizes reflect differences in orders of magnitude in the number of specimens for each species and are classified as 'tiny' (fewer than 10 specimens), 'small' (10–100), 'medium' (100–1000), 'large' (over 1000) and 'huge'. Human beings are the only species with a sample size classified as 'huge' and this classifier was included to mark the special status of the human species in this context.

Table 1 Summary of data in build 10 of AnAge ordered by taxa.

Taxa (scientific name)	No. entries	Longevity records	Life-history traits*	Metabolism
Mammals (Mammalia)	1331	1000	1298	422
Birds (Aves)	1098	1029	1061	172
Reptiles (Reptilia)	539	518	83	16
Amphibians (Amphibia)	169	157	113	18
Fishes (Actinopterygii, Cephalaspidomorphi, Chondrichthyes and Sarcopterygii)	962	948	583	
Nonchordates	28	13	6	

*Number of species with data for at least one trait.

For a subset of species, demographic parameters such as mortality rates and Gompertz parameters obtained from mortality data are also included. Software to analyse the demographic rate of ageing is also available in the form of an SPSS script (http://genomics.senescence.info/software/demographic.html).

Life-history traits included in AnAge are age at sexual maturity for males and females, gestation/incubation period, weaning, litter/brood size, litters/broods per year, inter-litter interval, weight at birth, weight at weaning, adult weight and postnatal growth rate (Table 1). Values are often averaged across sexes, geographical locations and literature sources, and thus represent typical species values. Major variations in life-history characteristics with environmental conditions or between subspecies are referred to in the observations. Similarly, although age at sexual maturity is usually used, we include in the observations section information on age at first reproduction if the two values differ substantially. Field data took priority over captive data if both were available, though gross discrepancies (e.g. for pets or livestock) are mentioned in the observations. Data were derived from several standard sources (Hayssen *et al.*, 1993; Nowak, 1999; Ernest, 2003; Poole, 2005; Weigl, 2005; Froese & Pauly, 2008). For some taxa such as birds and mammals, also included are body temperature and basal metabolic rate from established sources (McKechnie & Wolf, 2004; Savage *et al.*, 2004). We previously obtained a detailed view of the relationship between longevity and the various other traits in AnAge, which may serve as a reference for further studies using AnAge (de Magalhaes *et al.*, 2007).

Although the focus of AnAge is on vertebrates, several other exceptional longevity records – even in invertebrates, plants and fungi – are included. These isolated records are not intended to be used in comparative studies but are featured to showcase the biodiversity of ageing phenotypes. There is, in fact, a bias in AnAge for species taxonomically closer to humans. In other words, more detailed information is included in primate entries than in entries for species of other mammalian orders, mammals tend to be better annotated than species of other classes and so on. AnAge follows the taxonomy of the Integrated Taxonomic Information System (http://www.itis.gov/).

Although our database is extensive, and at least for some taxa comprehensive, we encourage researchers to provide us with feedback and alert us to missing references and new discoveries.

Validation and data quality assessment

For AnAge to be useful for researchers, its data must be reliable. Therefore, in addition to our quality control efforts described above during data collection, we employ a number of methods to assess the quality and integrity of data in AnAge prior to releasing a new build version. Succinctly, we have automated methods to detect outliers, in particular life-history traits of species that diverge from the expected values from allometric relationships and/or taxonomy. Outliers, which might for example be two species of the same genus with very different lifespans, are then manually verified. Particular attention is given to longevity data and we frequently consult experts when faced with suspicious or poorly-documented longevity claims.

To assess the quality and depth of AnAge, we compared the longevity data in AnAge with the longevity records compiled by Carey & Judge (2000). Of the 1756 species in common between the two datasets, more than half (993) had a higher longevity in AnAge, including 396 species for which the longevity record was over 50% higher. This highlights the pace with which longevity data – no doubt driven by the current information age – have been improved and the importance of using up-to-date, manually-curated datasets for comparative studies. In addition to the common 1756 species, there were several hundred species in Carey & Judge (2000) whose taxonomy had been updated in AnAge.

We found 89 species with a higher longevity in Carey & Judge (2000) than in AnAge. All of these were manually verified and we found they represent errors of various types in Carey & Judge (2000) or in the original sources, including confusion between species, records referring to subspecies now classified as a different species, and undocumented records found by AnAge curators and expert consultants to be dubious. The most glaring example of the latter is the 6 year record longevity in both the wild and in captivity listed in Carey & Judge (2000) for the house mouse (*Mus musculus*). Because *M. musculus* is a major model of ageing, there is an extensive literature on this species and animals living up to 6 years have not been documented. The longest-lived mouse is widely acknowledged to have lived nearly 5 years in Andrzej Bartke's laboratory (Pilcher, 2003). Interestingly, because this was a mutant animal, we did not find it adequate for species comparisons and hence the maximum lifespan of *M. musculus* in AnAge is presently 4 years as it represents the longevity record of wild-derived mice in captivity (Miller *et al.*, 2002) [Correction added on 24 June 2009, after first online publication: text ''because this was a mutant animal'' replaces text ''because this was a mutant and calorie-restricted animal''].

We also compared AnAge with the life-history characteristics of placental nonflying mammals compiled by Ernest (2003). Again reflecting the up-to-date nature of AnAge, for the 907 species in common between the two datasets, 643 of them had a higher longevity in AnAge and the few (51) with a lower longevity were deemed to represent errors or unverified longevity records. We found relatively few discrepancies in the other life-history traits: only 48 differed more than two-fold between the two datasets. A closer inspection revealed that most of these referred to adult body mass, which is possibly due to the fact that Ernest (2003) employs adult body mass of females in cases of strong sexual dimorphism while averaged values are featured in AnAge. Therefore, we conclude that the data in AnAge are highly accurate and in accordance with those reported by other authors with the few discrepancies stemming from methodological differences in data acquisition and processing.

To allow researchers to infer the quality of the data in AnAge, another recent development in AnAge was the inclusion of a qualifier of our confidence in the longevity data. This qualifier is based on the reliability of the original reference from which maximum lifespan was obtained, sample size, whether a given species has been studied and breeds in captivity, and whether there are any conflicting reports. Confidence in the longevity data is hence classified as: 'low' (only used for species without an established maximum lifespan in AnAge), 'questionable', 'acceptable' and 'high'. This new development will allow researchers to better design studies based on the AnAge dataset.

Usage and applications

AnAge is freely available online (http://genomics.senescence.info/species/) and features a user-friendly interface and search engine. Entries can be searched at any taxonomic level or using common names. A browser is also available that allows users to browse through the taxonomy of entries in AnAge. Though the system has an intuitive design, additional help pages are present on the website to guide visitors. The entire AnAge dataset can also be downloaded as an XML or tab-delimited file.

The main goal of the AnAge database is to catalogue and synthesize data and information on longevity and ageing in animals, even if mostly in vertebrates, and serve as a resource for comparative biology studies, in particular of longevity and life history. Among vertebrates, longevity varies between the 211 years of the bowhead whale (*Balaena mysticetus*) and the 0.16 years or 59 days of the pygmy goby (*Eviota sigillata*). Understanding this huge variation in lifespans, also observed in lower taxa, is a major scientific endeavour. As such, AnAge has been widely used for comparative studies of ageing (Lehmann *et al.*, 2008; Min & Hickey, 2008), including experimental studies (Seluanov *et al.*, 2008), and is arguably the benchmark dataset for studying longevity across the tree of life. Other studies have employed the life-history traits in AnAge to focus on broader features of molecular evolution (Han *et al.*, 2008; Nabholz *et al.*, 2008), ecology (Lynch & Fagan, 2008) and in conservation biology (Jorge, 2008). As most studies of whole organisms benefit from knowing the longevity and life history of the organism under study, AnAge can be useful to a broad range of biologists, as further detailed below.

AnAge is a valuable resource for life-history studies, in particular for understanding the evolution of life-history strategies which is a major area of research (Stearns, 1992; Ernest, 2003). Clearly, having quantitative measurements for a number of life-history traits is crucial for employing the comparative method. Therefore, the large AnAge database can save researchers the time and effort necessary to compile species-specific data from the literature. While incorporating phylogenies is in our future plans for AnAge, researchers presently wishing to apply the comparative method using AnAge are advised to employ the phylogenies of other resources, like the Tree of Life Project (http://tolweb.org/) and TimeTree (http://www.timetree.org/), as well as those of primary publications (e.g. Bininda-Emonds *et al.*, 2007).

By providing a reference value for longevity and other life-history traits, AnAge can be useful in many types of ecological studies, including the context of evolutionary ecology. Succinctly, the life history of an organism depends on numerous ecological factors, including diet, biogeography and predation, and having general life-history values can help researchers study how ecological factors are related to lifespan and life history, a key component of ecological research (Harvey & Purvis, 1999), and how environmental factors shape the evolution of lifespan. AnAge can also be useful for conservation efforts and for preserving biodiversity, for instance, by providing typical lifespan and reproductive data for studies of animals in ecosystems under anthropogenic stress and by helping researchers predict extinction risks (Garcia *et al.*, 2008; Morris *et al.*, 2008).

Longevity records are also an important reference for zoos and pet owners to optimize husbandry conditions and veterinary care. Lastly, and given the public interest in how long animals live, AnAge has an educational mission and the roughly 7000 visitors per month our website has received in the past 12 months reflect this.

AnAge is regularly updated, which is a key attribute for modern research. As demonstrated above, it greatly updates and extends the work by previous researchers such as Carey & Judge (2000) and Ernest (2003), it allows electronic access to datasets only previously available in print (Hayssen *et al.*, 1993; Weigl, 2005) and it provides large-scale, organized data and information obtained from many texts and resources such as Finch (1990) and Nowak (1999), which facilitates data access, search and retrieval by scientists.

The latest build of AnAge (build 11, released on 7 May 2009) features 4122 entries of which 4098 refer to species and 24 represent higher taxa (Table 1). The latter only include relevant comments and observations, not quantitative data.

Concluding remarks

With the growing importance of modern high-throughput technologies to understand life histories (Roff, 2007), and thanks to progress in bioinformatics and computer science, online databases are becoming increasingly more important for research. By providing a vast collection of longevity and other life-history data, we hope AnAge will assist researchers performing comparative studies and also serve as a tool for researchers working on a broad range of biological disciplines including evolutionary biology, ecology, conservation biology, genetics and zoology.

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