

# TERM PAPER MODEL

University of California, Davis

# Lifespan

by

James R. Carey  
ID: 123456789

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## **SUMMARY**

This paper is a mini-review of the literature on theoretical, evolutionary, ecological and demographic aspects of lifespan with particular emphasis on lifespan in humans. The paper is divided into four main sections. The first section introduces and frames the life span concept including a discussion of conventional and abstract perspectives, death and extinction, and boundary (e.g. beginning and end points) issues. The next section is concerned with evolutionary aspects of life span including the evolution of senescence, life span as a life history adaptation, the ecology of life span, roles of the elderly and the concept of 'limits'. The third main section considers human life span in a variety of contexts including humans as primates, male-female mortality differentials, age classification and theory of life span extension. The final section looks at the future of human life span including scientific and biomedical determinants and demographic ontogeny at both individual and societal levels.

## 1. INTRODUCTION

Life span is an evolved life history characteristic of an organism that refers to the duration of its entire life course. Application of the concept is straightforward at both individual and cohort levels and specifies the period between birth and death for the former (individual) and to the average length of life or life expectancy at birth for the latter (including both real and synthetic cohorts). However, when life span is applied to a population or a species it requires a modifier to avoid ambiguity (Goldwasser 2004). Maximum observed life span is the highest verified age at death, possibly limited to a particular population, cohort or species in a specified time period. The overall highest verified age for a species is also called its record life span. The theoretical highest attainable age is known either as maximum potential life span, maximum theoretical life span or species-specific life span.

Maximum observed life spans (i.e. longevity records) are not synonymous with theoretical maximums for at least two reasons. First, maximum longevity is an inappropriate general concept because an animal dies before the age of infinity, not because it cannot pass some boundary age but because the probability of its riding out the ever present risk of death for that long is infinitesimally small (Gavrilov and Gavrilova 1991). In other words, there is no identifiable age for each species to which some select individuals can survive but none can live beyond. Second, the record age of a species is heavily influenced by the number of individuals observed. That is, the longevity records for species in which the life spans of large numbers of individuals have been observed will be significantly greater than the corresponding figure for a species with the same longevity but represented by a few dozen individuals. For the vast majority of longevity records by species, the number of individuals at risk is completely unknown.

## 2. EVOLUTION

### 2.1 Evolutionary Origins of Senescence

Bell (Bell 1988) established the deep connection between the two invariants of life—birth and death—by demonstrating that protozoan lineages senesce as the result of an accumulated load of mutations. The senescence can be arrested by recombination of micronuclear DNA with that of another protozoa through conjugation. Conjugation (sex) results in new DNA and in the apoptotic like destruction of old operational DNA in the macronucleus. Thus, rejuvenation in the replicative DNA and senescence of operational DNA is promoted by sexual reproduction.

When this is extended to multicellular organisms, sex and somatic senescence are inextricably linked (Clark 1996). In multicellular sexually reproducing organisms, the function of somatic cells (i.e. all cells constituting the individual besides the germ cells) is survival and the function of the replicative DNA—the germ cells—is reproduction. Prior to bacteria, the *somatic* DNA was the *germ line* DNA; prior to multicellular animals, the *somatic cell* and the *germ cell* were undifferentiated. Like the macronuclei in the paramecia, the somatic cells senesce and die as a function of their mitotic task of ensuring the survival and development of the germ cells. The advent of sex in reproduction allowed endogenous repair of replicative DNA (Clark 1996) while in multicellular organisms the replication errors of somatic growth and maintenance are segregated from the DNA passed on to daughter cells are discarded at the end of each generation. Thus senescence is built into the life history concept of all sexually reproducing organisms; sex is an adaptation to circumvent mutational errors in somatic growth during reproduction.

### 2.2 Life Span as an Evolutionary Adaptation

In evolutionary biology an “adaptation” is a characteristic of organisms whose properties are the result of selection in a particular functional context. Just as the different bird beaks are adaptations for exploiting different niches that must be balanced with the other traits such as body size and flight propensity, the longevity of an animal is also an adaptation that must be balanced with other traits, particularly with reproduction. The variations in the relationship between reproduction and longevity can only make sense when placed within the context of such factors as demographics, duration of the infantile

period, number of young, and the species' ecological niche—the organism's overall life history strategy. Inasmuch as life spans differ by 5,000-fold in insects (2-day mayflies to 30 year termite queens), by 60-fold in mammals (2-year mice to 122 years in humans), and by 15-fold in birds (4 year songbird to 60 year albatross), it is clear that life span is a life history adaptation that is part of the larger life history of each species.

### 2.3 Evolutionary Ecology of Life Span

The literature on aging and longevity contains descriptions of only a small number of broad life span correlates, including the well known relationship between longevity and both body mass and relative brain size and the observation that animals that possess armor (e.g. beetles; turtles) or capability of flight (e.g. birds; bats) are often long-lived. But major inconsistencies exist within even this small set of correlates (Carey and Judge 2000, 2001b). For example, there are several exceptions regarding the relationship of extended longevity and large body size (e.g. bats are generally small but most species are long-lived) and this positive relationship may be either absent or reversed within certain orders including a negative correlation within the Pinnipeds (seals and walruses) and no correlation within the Chiroptera (bats). Likewise, the observation that flight ability and extended longevity are correlated does not provide any insight into why within-group (e.g. birds) differences in life span exist, nor does it account for the variation in longevity in insects where adults of the majority of species can fly.

A classification system regarding the life span correlates of species with extended longevity that applies to a wide range of invertebrate and vertebrate species consists of two categories. The first is *environmentally-selected life spans*. This category includes animals whose life histories evolved under conditions in which food is scarce and where resource availability is uncertain or environmental conditions are predictably adverse part of the time. Some of the longest-lived small and medium-sized mammals (rodents; foxes; small equines and ungulates) live in deserts where rainfall and, thus reproduction, is episodic and unpredictable including gerbils, rock hyrax, and feral asses. The recent findings that the life span of bowhead whales, *Balaena mysticetus*, (a solitary species of baleen whales) may exceed 200 years (George et al. 1999) is another important example of how environmental factors shape life span through *direct natural selection*. Bowhead whales live in the harsh environment of the Arctic Ocean with low prey densities and thus require great investment in fat storage, body, mass, and thermoregulatory mechanisms. Cetacean biologists studying this species suggested that these stressors led to slow growth, delayed maturity, and subsequently extended longevity to ensure reproductive success (George et al. 1999).

The second category is *socially-selected life spans*. This category includes species that exhibit extensive parental investment, extensive parental care, and eusociality (social strategy arising from the study of ants, bees, wasps, termites that have overlapping generations, cooperative care of young, and a reproductive division of labor). The extended longevity of animals in this category results from natural, sexual, and kin selection and includes all of the social primates including humans.

This classification system places the relationship of life span and two conventional correlates, relative brain size and flight capability, in the context of life history. That is, brain size is related to the size of the social group and the degree of sociality which, in turn, is linked to extended life span. And intensive parental care is linked to flight capability in birds and bats which, in turn, is also linked to extended life span. For example, most bird species are monogamous with both sexes helping in the rearing (e.g. one can protect the nest while the other collects food). The reproductive strategy of the majority of bat species is to produce only a single altricial (naked and helpless), relatively large offspring at a time—flight preempts the possibility of the female foraging for food while gestating multiple young. Thus bat maternal investment in a single offspring is substantial.

### 3. HUMANS

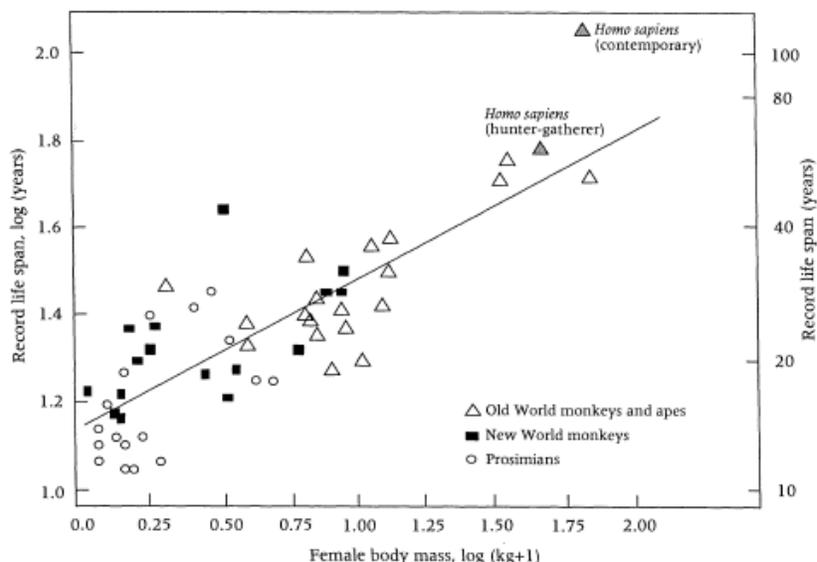
#### 3.1 Life Span Patterns: Humans as Primates

Estimates based on regressions of anthropoid primate subfamilies or limited to extant apes indicate a major increase in longevity between *Homo habilis* (52-56 years) to *H. erectus* (60-63 years) occurring roughly 1.7 to 2 million years ago (Judge and Carey 2000). Predicted life spans for small-bodied *H. sapiens* is 66-72 years. From a catarrhine (Old World monkeys and apes) comparison group, a life span of 91 years is predicted when contemporary human data are excluded from the predictive equation (see Table 1). For early hominids to live as long or longer than predicted was probably extremely rare; the important point is that the basic Old World primate design resulted in an organism with the potential to survive long beyond a contemporary mother's ability to give birth. This suggests that post-menopausal survival is not an artifact of modern life style but may have originated between 1 and 2 million years ago coincident with the radiation of hominids out of Africa

The general regression equation expresses the relationship of longevity to body and brain mass when 20 Old World anthropoid primate genera are the comparative group (Fig. 1). Ninety one years is the predicted longevity for a 50 kg primate with a brain mass of 1250 gm (conservative values for humans) when case deletion regressions methods are employed (each prediction is generated from the equation excluding the species in question) and 72 when humans are included within the predictive equation. When 6 genera of apes are used as the comparison group the regression equation is:

$$\log_{10} LS = 1.104 + 0.072(\log_{10} Mass) + 0.193(\log_{10} Brain)$$

yielding a predicted human longevity of 82.3 years. Thus, a typical old world primate with the body size and brain size of *Homo sapiens* can be expected to live between 72 and 91 years with good nutrition and protection from predation.



**Fig. 1.** Mean record captive life spans (years) by female body mass (kg+1) for 53 genera of primates (Source: Carey and Judge 2001a).

#### 3.2 Exceptional Ages in Humans

Jeune (Jeune and Vaupel 1995) suggested that most of the literature on centenarians is based on the hypothesis of a secret of longevity which is summarized in four assertions, each of which is debatable: maximum longevity is fixed, longevity is genetically determined, centenarians always existed, and centenarians are qualitatively different. The first assertion is inconsistent with mortality patterns in both humans and non-human species. The second assertion is inconsistent with estimates of heritability estimates of longevity which are between 0.2 and 0.3, the third assertion is improbable based on the

estimated mortality levels that persisted before 1800, and the last assertion is tautological and thus unverifiable since the criteria for being different (i.e. being a centenarian) cannot be tested any other way than actually living to at least 100 years. Vaupel and Jeune (Jeune and Vaupel 1995) claimed that supercentenarians did not exist prior to 1950 and centenarians not before 1800 in any population.

The oldest verified age to which a human being has ever lived is 122 years and 167 days by the Frenchwoman Jeanne Calment who was born on February 21<sup>st</sup>, 1875 and died on August 4, 1997 (Robine and Allard 1998). Other long-livers include Sarah Knauss, Mare Meiller, Chris Mortinson, and Charlotte Hughs who lived 118.1, 117.6, 115.8, and 115.6 years, respectively (Robine and Vaupel 2001, Maier et al. 2010). Madame Calment as well as these four long-livers all died between 1993 and 1999. Thus the five oldest persons whose ages of death have been verified died within the last decade.

**Table 1.** Estimates of longevity for fossil hominids, based on hominoid body size relationships range from 42-44 years for *Australopithecus* to 50 years for *Homo erectus*. Incorporation of brain mass increased estimates for *H. habilis* from 43 years to 52-56 years and for *H. erectus* from 50 years to 60-63 years (Source: Carey and Judge 2001a).

Hominid species	Life Span (yrs)	Change
<i>Australopithecus afarensis</i>	46.6	8.4
<i>Homo habilis</i>	55.0	7.0
<i>H. erectus</i>	62.0	10.9
<i>H. sapiens</i> (pre-historical)	72.9	49.1
<i>H. sapiens</i> (contemporary)	122.0	

### 3.3 Theory of Longevity Extension

Improved health and increased longevity in societies may set in motion a self-perpetuating system of longevity extension (Carey and Judge 2001a). This positive feedback relationship may be one reason why human life span has been continuing to increase and it is based on the demographic tenet that increased survival from birth to sexual maturity reduces the number of children desired by parents, *ceteris paribus*. Because of the reduced drain of childbearing and rearing, parents with fewer children remain healthier longer, raise healthier children with higher survival rates which, in turn, fosters yet further reductions in fertility. Greater longevity of parents also increases the likelihood that they can contribute as grandparents to the fitness of both their children and grandchildren. And the self-reinforcing cycle continues.

The decline in mortality rates during the early stages of industrialization in the U.S. was probably one of the forces behind the expansion of educational effort and growing mobility of people across space and between occupations. Whereas previous conditions of high mortality and crippling morbidity effectively reduced the prospective rewards to investment in education during the pre-industrial period, prolonged expectancy for working life span must have made people more ready to accept the risks and costs of seeking their fortunes in distant places and in new occupations. The positive feedback of gains in longevity on future gains involves a complex interaction among the various stages of the life cycle with long-term societal implications in terms of the investment in human capital, intergenerational relations, and the synergism between technological and physiological improvements. In other words, long-term investment in science and education provides the tools for extending longevity which, in turn, make more attractive the opportunity cost of long-term investments in individual education, and thus help humans gain progressively greater control over their environment, their health and overall quality of life.

Whereas the positive correlation between health and income per capita is very well known in international development, the health-income correlation is partly explained by a causal link running the other way—from health to income (Bloom and Canning 2000). In other words, productivity, education, investment in physical capital, and “demographic dividend” (positive changes in birth and death rates) are all self-reinforcing—these factors can contribute to health and better health (and greater longevity) contributes to their improvements.

#### 4. FUTURE

Predictions of changes in human longevity in both the near- and medium-term are typically made using analytical methods such as extrapolation, relational modeling (i.e. reference population), mortality model (e.g. Gompertz), cause-of-death elimination, and stochastic methods (Olshansky 1988, Tuljapurkar et al. 2000). The usual mortality component of population forecasts is provided by extrapolation of past trends in mortality and the issue regarding which model to choose is to decide how to perform the extrapolation (Keyfitz 1982). Tuljapurkar (Tuljapurkar et al. 2000) used stochastic modeling to predict life expectancies in 2050 ranging from 80 to 83 years for the United States and from 83 to 91 years in Japan. Two forecasting methods described in Oeppen and Vaupel (Oeppen and Vaupel 2002) included : i) use of a model that considers the gap between national performance and the best-practice level (i.e. highest world-wide life expectancy). This approach predicts that the life expectancy of U.S. females in 2070 would be between 92.5 and 101.5; and ii) use of a model that considers the rapidity of improvement in mortality over a long period. This approach used by Japan predicts that life expectancy of Japanese females in 2070 will be between 87.6 and 94.2. These forecasts are to be distinguished from forecasts based on expected medical discoveries or estimated danger of mass starvation. Thus as Keyfitz notes (Keyfitz 1982), the standard models cannot predict the ‘corners’ (i.e. major changes); this is not what they are designed to do.

The future of human life span should be also be considered in the context of *possibility*—the constructive, scenario-building aspects of science that is akin to the conceptual arts (Gill 1986). Whereas predictions of changes in life expectancy are usually considered to point to *precise* results, the recognition of life span possibilities are correlated with *vision* and includes the effects on longevity of scientific and medical breakthroughs. That is, prophecies that are not fixed and foreordained but rather based on the recognition of a present evolving toward a future of *multiple demographic alternatives*. These are not based on rates of change in life expectancy, per se, but rather on elements that will change the rate of change itself.

Integrating concepts related to different life span *possibilities* into research and policy planning is important for several reasons (Sierra et al. 2009). *First*, it will establish closer connections between the biological discoveries on the nature of aging and how these, at least in theory, might impact individuals and society. Currently there is very little exchange of ideas between biologists and demographers in this context. *Second*, considering possibilities may suggest different analytical models in which different types of scientific breakthroughs could be included in the predictions. For example, a breakthrough in therapeutic cloning would have sweeping implications for organ replacement (e.g. kidneys, livers, etc) and hence for saving the lives of people with diseases that infect organs that can be cloned. *Third*, a program to consider future life span possibilities would provide a framework for a wide range of other disciplines (e.g. sociology; human development; economics; business) to engage in creative discussion about the nature of future society. *Fourth*, considering future possibilities for human life span will provide a foundation for policy makers to consider medical, economic, and political contingencies in which life span increases are much greater than predicted by standard mortality modeling methods. Exploring a variety of possibilities based on potential scientific breakthroughs would ensure that policy makers have considered a wide variety of possible scenarios for the demographic future of both developed and the developing countries.

**WORD COUNT=3,135**

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