Improved Parameterization of Post-Fertile Survival: Post-reproductive lifespan is not a useful comparative measure

Abstract

Human females have the tendency to live well past their last birth; a trait that may or may not be unique. The measure generally used for studying this tendency, post-reproductive lifespan (PRLS) is not well-suited to comparative analysis, limiting our ability to understand the evolution of this trait and how unique humans are in this respect. In order to examine post-fertile survival (PFS) in a comparative context, we apply life table methods to data from human and non-human primate populations and generate new parameters to replace PRLS. We find that while the capacity for biologically significant PFS is widespread throughout the primates, humans are unique among primates in both the scale of their PFS and in experiencing significant PFS in a wide range of conditions, including hunter-gatherer conditions. PFS of human females far exceeds that of any non-humans in our dataset under any conditions, indicating that humans are extraordinary in this trait.

Introduction

Why do women generally become infertile in their fifth decade, but have the ability to live into their tenth (1)? Do other species experience significant post-fertile survival (2), and if so, are women really distinct in this regard? What role does environment play in determining post-fertile survival (3)?

To a significant extent how we answer these questions depends on how we measure the biological phenomenon they refer to. The fact of individuals living past reproductive cessation and the measurement used to quantify that fact are both generally referred to as post-reproductive lifespan (PRLS), and no distinction between phenomenon and measurement is generally made. However, other ways of measuring this phenomenon are possible, and potentially preferable. To differentiate the phenomenon (individuals surviving past reproductive cessation) from the measurement (age at death minus age at reproductive cessation) we refer to the phenomenon as post-fertile survival (PFS) and the measurement as PRLS.

PFS is the phenomenon of individuals or cohorts surviving past the age at which those individuals or cohorts cease to produce babies. Put another way, it is the demographic outcome of actuarial senescence being delayed as compared to reproductive senescence (4). Interest in PFS has been considerable, and many hypotheses have been proposed to explain it (2, 5, 6, 7), most famously the Grandmother Hypothesis (8, 9), which argues that PFS results from selective effects relating to grand-maternal care. Disagreements abound not only as to the evolutionary basis of human PFS, but also as to whether other species exhibit meaningful PFS and if so what this tells us about humans (2, 10, 11, 12).

PRLS in contrast, is the measurement of PFS in units of time. The exact means of measurement vary, as we discuss below. PRLS is necessarily a span of time, generally

given in years, measuring the distance between some measure of when reproduction ends and some later time at which survival ends. While the great majority of papers quantifying PFS have done so in terms of such a linear measure of time, (e.g. 2, 13, 14) this is not the sole possible parameterization. For example, one could measure the portion of adult females who are post-reproductive, or the percentage of total lifespan that is post-reproductive. Below we describe why alternative measures may be more useful for comparative purposes than PRLS has been, suggest specific parameterizations of these measures, and apply these parameters to answer comparative questions regarding PFS.

PRLS's limited value as a comparative measure

PRLS has been measured in a wide range of human populations (1), several primates (13), as well as many other mammals (2) and species as phylogenetically distant from us as yeast (15). Unfortunately, these data have only rarely been applied in a comparative framework (2, 13) to examining the proliferation of adaptive hypotheses proposed to explain human PFS. Given that the comparative method is one of biology's primary tools for understanding the evolution of traits (16), why haven't our data on PRLS been subjected to a more thorough comparative analysis?

The measure PRLS may itself be part of the problem. PRLS suffers from four main drawbacks as a comparative measure. First, it is calculated in a range of ways, often yielding measurements that cannot meaningfully be directly compared. Second, PRLS considers only those individuals who survive to reproductive cessation, and therefore can overstate the biological significance of the PFS. Third, PRLS is correlated with the overall longevity of the population, impeding comparisons between populations whose life-histories are not on identical time-scales. Finally, little progress has been made in identifying null expectations for PRLS. We address each of these limitations in turn. We then propose more useful parameterizations of PFS using data in the form of standard demographic life-tables and fertility-tables.

Inconsistent calculation of PRLS

Using individual level data, the measurement of PRLS would seem to be fairly straightforward. PRLS begins at the individual's last birth and ends when she dies (12). However, some practitioners subtract a measure of time during which the individual could have reproduced, but didn't (17), or don't consider an individual to be post-reproductive until she is some time past an advanced age (18), or other variations (2). Calculating PRLS when only population level data are available (as is often the case) becomes considerably more challenging. Using age-specific fertility and mortality data, one needs to decide how to measure when survival ends, as well as when reproduction ends. For example, the mean life-expectancy of a 45 year old woman in the United States in 1933 was 27.8 years (19), but many women in that cohort survived decades past 1961. For the purposes of measuring PRLS, when did that cohort die?

Many methods have been used to calculate PRLS, limiting its utility as a parameter in comparative contexts. Those who wish to compile measurements of PRLS published by different authors are figuratively left to compare the shelf-life of apples to the refrigerator hardiness of oranges. For example, Fedigan and Pavelka (13) present a table of PRLS for 20 primate species, all given in units of years, but calculated in six different ways. Fedigan and Pavelka advocate a standardization of the measurement of PRLS based on the individual based calculations of Caro et al. (12). This method, while appropriate for measuring the period of time in which an individual can be post-reproductive, can only be used where individual level data are available, limiting its usefulness for comparative purposes, because population summaries are far more often published than are complete individual level data.

PRLS as biased measure of PFS

In considering the importance of PFS to a population, we are likely to ask such questions as: What portion of the adult females in the population are post-reproductive? How likely is a juvenile to have a surviving post-reproductive grandmother (20)? For what portion of an adult's lifespan is she likely to be post-reproductive? PRLS is not a meaningful answer to any of these questions. It answers the narrower question: How much life remains to those individuals who have survived to the end of their fertility?

PRLS is measured based only on the experience of those living beyond reproductive cessation (2, 10-14, 20), and therefore loses all information on the large portion of the population who die before reproductive cessation. Figure 1 gives a hypothetical example of two populations with identical measures of PRLS but very different experiences of post-reproductive lifespan. PRLS gives little guidance as to how many post-fertile individuals to expect even in stable populations, because it does not take into account how many individuals live to be post-reproductive. Many authors (2, 13) address this problem by giving both PRLS and an estimate of what portion of individuals reach reproductive cessation. However, in order to be able to compare between species it is desirable to incorporate this information into our measurement of PFS, rather than give it as an additional piece of context.

PRLS correlated with overall longevity

Earth's organisms experience lifespans ranging from a few hours to many centuries (21). Even within the primates, maximum longevity varies from a few years to several decades (22). Comparing PRLS between populations whose life-histories are on very different scales is not informative. Minois and colleagues (15) document maximum PRLS of up to 75 hours for a population of yeast whose maximum budding lifespan is 125 hours. While 75 hours is long on the scale at which yeast live, a vertebrate population that lived no more than 75 hours after last childbirth would be considered to have no PRLS at all. The same principle applies when comparing more closely related species. For example, PRLS calculated as life expectancy at reproductive cessation is quite similar for captive *Pongo pygmaeus* (11.61 years) and *Lagotricha lagotricha* (10.75 years), but the overall

longevity of the one is roughly four times that of the other (present study), indicating a very different experience of PFS for species with very similar PRLS. Figure 2 plots PRLS against life expectancy at birth for 63 captive primate populations, revealing that most of the information in interspecies comparisons of PRLS is attributable to the overall scale on which organisms live. Any useful comparative measure of PFS must therefore control for the timescale on which the organisms live. Again, it is common practice when estimating PRLS to give overall longevity as an accompanying measure. We argue it must be incorporated into the parameter used for comparison.

No null expectation for PRLS

Few papers have attempted to establish any sort of null expectation for PRLS. Rather than discussing the null expectations for each of the many hypotheses proposed to explain PRLS, we focus on the broadest case. What is the expectation for PRLS if there is no selection for or against PRLS? That is, if reproductive senescence exactly parallels actuarial senescence, but there is no mechanism causing mortality shortly after reproduction, what will PRLS be? It cannot be zero unless every individual just happens to die instantly after having her last offspring. Indeed, even pacific salmon, the standard example of lack of PRLS, exhibit short but non-zero PRLS (23). Nor can PRLS be negative, as members of most species do not reproduce after death. Every population in which reproduction does not require instantaneous death has PRLS > 0. Determining whether PFS is extensive enough to carry biological significance requires a measure other than PRLS.

Primatologists have approached this problem by testing whether PRLS for individuals exceeds the mean plus two standard deviations of interbirth interval (12, 13). While this approach can roughly tell us that an individual underwent reproductive senescence before dying, it does not greatly aid in comparisons between populations.

Replacing PRLS

To replace PRLS, we calculate three measures of PFS from age-specific mortality and fertility rates, using customary life-table methodologies. Of these parameters, the first, G, is particularly useful in comparisons between populations. The second, S can also be used for comparative purposes, but is designed to be used in tests of significant difference from a biologically relevant null hypothesis. The third, the sexual dimorphism of S ($_{d}S$) is useful for asking whether PFS is a trait particular to females.

Life Table Data

A large segment of the science of demography relies on the life-table (24), and methods relating to this type of data have been developed extensively. Others have written urging biologists interested in life-histories to adopt these methods (25), and explaining the life-table's uses for biologists (26). In short, a life table presents age specific death rates, and numbers of deaths, and survivorship rates, and numbers of survivors and a set of standard age-specific parameters calculated from these rates. Many life tables, including those considered in the present paper, are accompanied by age-specific fertility rates, the mean

number of offspring born per year lived at each age.

Age-specific data are population averages. While life-tables lose much information contained in the individual life histories used to construct the tables, they are extremely useful in the calculation of population rates, and are foundational to the science of demography. An extremely useful characteristic of life-tables is the degree to which demographers have standardized their calculation, notation and usage. Because of this standardization data from diverse populations become directly comparable when each is presented in a well-constructed life-table.

The columns of the standard life-table mentioned in the following definition of parameters are as follows:
x represents age
L_x is the number of individual*years lived between ages x and x+1
m_x is age specific fertility, the total number of offspring born to all individuals between the ages of x and x+1 divided by L_x
l_x is the number of individuals surviving to x (Life-tables are generally presented with an arbitrary initial cohort size, or radix. Where radix=1 as is the case with the life-tables considered here, l_x represents the probability of the mean newborn surviving to x).
e_x is the remaining life expectancy at x
T_x is the total years lived after x, and can be calculated as $T_x=e_x*l_x$

Ages
While our life-tables include age specific data for each age, the definition of our parameters requires focusing on four particular ages. These are:

Age 0, starting at birth or hatching, the beginning of lifespan.

Age B, the beginning of fertile lifespan. We calculate B as the minimum age for which

$$\sum_{x=0}^{B} m_x \geq 0.05 \sum_{x=0}^{\infty} m_x$$

Age M, the end of fertile lifespan. We calculate M as the minimum age for which

$$\sum_{x=0}^{M} m_x \geq 0.95 \sum_{x=0}^{\infty} m_x$$

For the purposes of this paper, M is the age at which an individual becomes post-fertile. Our calculations of M for human natural-fertility populations are similar to published estimates of mean maternal age at last birth for such populations.

Age Z, the end of lifespan. We calculate Z as the minimum age for which

$$\sum_{x=0}^{z} l_x \geq 0.95 \sum_{x=0}^{\infty} l_x$$

In each case except age 0, these parameters exclude 5% of the area under one tail of the

relevant curve. For that reason, and because they are cumulative measures, these parameters are resistant to demographic outliers (e.g. human females who have babies in their late fifties or later). They are useful in determining near-endpoints, not extremes.

The simplest population measure of survival beyond age M is e_M, remaining life expectancy of those individuals who have survived to age M. This parameter is a measure of PRLS in that it is given as a length of time following reproductive cessation. As such it is of limited comparative value, as discussed above.

By multiplying $e_M * l_M = T_M$ we can account for both how many individuals become post-reproductive, and for how long they survive post-reproductively. T_M represents the mean expectation of a new-born individual for life beyond age M. While more informative than e_M, T_M is still of limited utility in comparing populations with different scales of longevity or different infant mortality rates.

These drawbacks can be overcome by comparing T_M to T_B. T_B gives the number of years an average newborn can expect to live as an adult, while T_M gives the number of years an average newborn can expect to live as a post-reproductive adult. For comparative analyses of PFS we therefore propose the parameter **G**

$$G = T_M / T_B$$

G has many desirable qualities. In addition to being independent of infant mortality rates and overall longevity, and dependent upon both how many individuals live to post-reproductive age and how long they live thereafter, it provides a highly intuitive measure of PFS. G is that proportion of life-expectancy at the beginning of reproductive life which is attributable to survival after the end of reproductive life. In a stationary population (one in which sizes and rates are unchanging), G tells us what portion of the adults are post-reproductive. For example, if G for the females in a stationary human population is .36, 36% of women in that population are post-reproductive. This dimensionless parameter is not greatly affected by infant mortality rates, and can be calculated from published mortality and fertility tables without need for the individual level data that went into these tables. G makes possible comparisons of PFS between populations, sexes, species, time periods, cohorts or any combination of these. G is not correlated with longevity or sample-size (but see below).

The main drawback to G is that there are no obvious predictions as to what G should be under various biological scenarios, and therefore no obvious null-hypotheses or statistical tests allowing G to be used to examine these scenarios. G is useful in comparing between populations and groups of populations, but less so in determining, for example, whether significant PFS is a "general mammalian trait", as Cohen (2) argues.

For these purposes we must employ a measure for which we have a means of examining significance. This becomes possible if we use Z, rather than $M+e_M$ as our measure of population age at death.

We can then define:

$$S = \frac{Z - M}{Z}$$

S is a robust measure of PRLS as a portion of fertile lifespan. While S does not take into account what portion of adults become post-reproductive, Z results from an integration of the age specific mortality curve, and therefore S is less obdurate to changes in mortality rate of reproductive individuals than are traditional measures of PRLS. S also has the desirable property of allowing a clear prediction under the null hypothesis that a population has no meaningful PFS. While it is not possible for an individual to invest in reproduction after she dies, it is possible for a population to reach a state of actuarial decline before reaching an analogous state of reproductive decline. Therefore S, unlike the other measures presented here, can meaningfully be zero or negative in some populations.

We performed simple micro-simulations in Microsoft Excel (see Appendix 1) to determine S for theoretical populations in which actuarial senescence exactly parallels reproductive senescence, (and mortality risk is not temporally associated with individual reproductive events). Our simulated populations (Appendix 1) have values of S very close to zero. A $S \leq 0$ indicates that the population should not be considered to have biologically significant post-reproductive lifespan. Variance in S increases with smaller sample sizes, coarser demographic data and more gradual senescence. Biological significance can be assessed for any one population through comparison to a null distribution of outputs from this micro-simulation using the demographic characteristics of that population. Alternatively, the distribution of S values for a group of populations can be directly compared to the null expectation that their mean value is zero.

A final parameter we calculate is the sexual dimorphism in S, which we denote ${}_dS$.

$${}_dS = \frac{S_{females} - S_{males}}{S_{females}}$$

A positive ${}_dS$ indicates that S for females is greater than S for males.

Data Sources

We gathered life tables for populations of humans, and non-humans. We excluded populations with sample sizes for females of fewer than 60 individual*years sampled per year of age, as data exploration with data on males, and our micro-simulations (Appendix 1), suggested that samples smaller than this gave occasional estimates of PFS and PRLS with unacceptably high errors. While G and S did not vary with simulated sample sizes above 60, the non-normal distribution of errors lead to increased mean estimates of G with decreasing sample sizes below 60. Our analysis focuses on females, as the debate around the significance of PFS centers on the longevity, social role and physiology of

females, and female age-specific fertility rates are more available and more reliable than the same data for males.

Human Data

Our human populations are divided into five groups varying according to state of economic development. These are: Hunter-Gatherers, pre-modern Sweden 1751-1755, UN Least Developed Nations, UN Less Developed Nations and UN More Developed Nations.

Our sample of human hunter-gatherers includes the Forest Period Ache (27), Dobe !Kung (28) and the Eastern Hadza (29).

Our data for the demographics of UN member nations are drawn from UN World Population Program data for 2001 (30), and because these data are given in five-year intervals, spline interpolated (31) to single year intervals. We compared the outcome of this method to single year data from the national statistical bureaus of the United States (32, 19), Japan (19, 33) and Sweden (19, 34), and found no meaningful differences. We followed UN Development Agency categories in classifying countries and regions as "More Developed," "Less Developed" or "Least Developed."

As hunter-gatherers are the closest sample we can attain of humans living in a natural habitat, we use these populations as our samples of realized human demography in the absence of modern conveniences. Arguments both for and against this simplifying assumption have filled many pages (see 35). We argue only that if the assumption is not entirely valid, it is close enough to not substantially alter our conclusions.

At the opposite end of this economic development spectrum are the UN Most Developed Nations. These human populations benefit from life-extending technologies and environments and usually are not food limited. Mortality in these populations is artificially lowered substantially, leading us to treat longevity in these populations as the potential not frequently realized in a more natural setting. Fertility in these populations is also substantially altered, with individuals usually capable of increased reproductive lifespans but realizing decreased reproductive lifespans.

Non-human Data

We found sufficiently large datasets on only two species of primates living in the wild, *Pan troglodytes* (36, 37) and *Papio hamadrayas* (38). Additionally, we found fertility (39) and mortality (40) data for semi-wild troops of *Macaca fuscata*. Many wild primate populations were excluded because of insufficient sample sizes. Collecting enough data to build a reliable life-table on a population of wildlife, particularly species as long-lived, far-ranging and difficult to observe as are most primates, is several lifetimes' work. (See Wich et al. (41) for a life table with extremely small sample-sizes based on an enormous amount of effort).

We added to this data on the survival and reproduction of 63 species of primates in zoo populations and one species in 'semi-free ranging' captive populations. Zoo data were obtained from the International Species Information System (ISIS; 42), an organization that compiles data from zoos around the world, primarily to aid in management of captive populations. ISIS member organizations, the source of these data, are mostly also members of the Association of Zoos and Aquariums or similar organizations overseas, requiring them to maintain high standards in both record-keeping and animal care. Like the populations of the Most Developed UN member nations, but unlike the three hunter-gatherer populations included in this study, the captive primates in ISIS's database receive the benefits of a high level of medical care, nutritionally planned diets, modern sanitation techniques and protection from other environmental dangers. It is certainly true that quality of care varies between institutions, and between species, and that management practices can directly influence mortality and reproductive schedules. However, we believe these data are appropriate for this use based on two lines of reasoning.
First, for the limited number of primate species for which wild longevity data are available, primates seem to live longer in ISIS member institutions than in the wild (current study). Second, while best methods for keeping some species are probably unclear, leading to a low quality of care, these species tend not to be widely kept, leading to low sample sizes. In excluding populations for which our sample sizes are small, we likely also exclude those species for which management practices are least well developed. Species in which several hundreds or thousands of individuals are kept by ISIS institutions can safely be assumed to have been the subjects of detailed management plans.

Data quality is another potential limitation of ISIS data, and we have done our best to deal with this by removing small samples and unrealistic outliers (e.g. a chimpanzee whose birth date was reported as being in the 1690s rather than the 1960s), and by using measures that are relatively robust to individual false records.

A final limitation to ISIS data is that the dataset is not public, and while ISIS generously allowed us to use life-tables for their captive primates, the individual-level data used to construct those life-tables could not be shared beyond ISIS staff and members. For a fuller discussion of the benefits and limitations of captive life-table data, see Kohler et al. (43).

We include two published datasets on populations of long-lived non-primates, the Short-finned Pilot Whale (*Globicephala macrorhynchus; 44*) and the African Elephant (*Loxodonta africana; 45).*

Comparative analysis of PFS

We calculated each of the above-described variables for the females and males for each population for which we had sufficient data. These parameters are presented in Appendix 2.

These data allow us to ask direct comparative questions important to understanding the evolution of PFS. Using both traditional analyses and phylogenetically controlled independent contrasts, they paint a more nuanced and quantitative picture of PFS than was possible using traditional measures of PRLS.

PFS as measured by S is significantly above the null expectation (zero) in captive primate populations (Mean=0.105, N=63, t=5.34, p<.0001) all human populations and our whale sample. This indicates that the capacity for biologically significant PFS is widespread. In contrast, PFS in wild populations of primates does not rise to the level of biological significance (both S values being negative), indicating that realized PFS in natural habitats is likely a rarer event, arising in humans and some whales. Indicating that potential for PFS is a trait widespread among female primates, more so than males, ${}_{d}S$ is positive for almost every species of primates examined.

Directly comparing these various populations to each other using G values, we find that PFS for all human populations under a wide range of circumstances is significantly greater than for any non-human primates in the wild or in captivity (Figure 3). These differences are particularly striking when comparing populations in their natural habitats. G values for hunter-gatherers range from 0.42 to 0.48, while G values for our sample of wild primates are below 0.02.

G does not vary significantly between women of Least Developed Countries, Historical Sweden and Hunter-Gatherer groups, perhaps indicating that a threshold level of development must be reached to expand PFS. However, it is clear when comparing among UN member nations that PFS expands rapidly as one examines increasingly developed nations. Japan is the extreme case in this regard, with G above 0.67.

Many life-history evolution questions relating to PFS will require parameterizations specific to the questions (For this purpose, Appendix 2 presents a table with the intermediate parameters used in the calculation of G and S). For example, it has been proposed that the extraordinary extent of human life-expectancy at reproductive cessation has evolved in response to our extended pre-reproductive period. This raises the question of whether pre-reproductive period, measured here as age B, is correlated with post-reproductive lifespan. In making such a comparison, one again must control for the scale of the life-history. Using our sample of zoo primates, we test for correlation of $e_M/(M-B)$ to $B/(M-B)$. That is, we ask whether there is a correlation between PRLS and pre-reproductive lifespan once one controls for the length of reproductive lifespan. We find that there is no such relationship. While this does not invalidate the possibility that extended PRLS results from the extended juvenile period in humans, it indicates that if such a connection does exist, it is peculiar to humans. The one wild population in our dataset to approach humans in PFS is the short-finned pilot whales. Given that humans and whales realize significant PFS in natural habitats, but African elephants and non-

human primates do not, humans and whales likely experienced distinct originations of this trait, suggesting that failure to find a particular selective pressure for PFS in a whale (46) may not greatly impact our thinking on why PFS evolved in humans.

Discussion

PRLS has long been the dominant means of measuring PFS, and few efforts have been made to critically examine the usefulness of this measurement to the questions evolutionary biologists ask about PFS, or offer alternatives. In examining PRLS, we have found it lacking both in its comparability between populations and in its usefulness in addressing relevant evolutionary questions in a quantitatively rigorous fashion.

Life-table methodologies, the foundational methods of demography, allow us to generate parameters useful in comparative contexts and appropriate to the questions we wish to answer. Using these parameters, we have clarified that capacity for PFS is a widespread trait among female, but not male primates, and that realized PFS in the absence of modern life-extension is not a common primate trait, but is found in humans and also in some whales. This suggests separate evolutionary originations of realized PFS in humans and whales, indicating that the selective forces acting in each origination may have been different. While all of these findings have previously been suggested, this understanding is far from universally accepted, in large part because quantitative comparisons between truly comparable measures of PFS have been lacking.

The field of demography is in large part the quantitative study of life-histories. As such, demographers have refined specific quantitative methods for addressing many of the same variables of interest to biologists studying life-history evolution. For studying a trait as complex and inherently demographic as post-fertile survival, the tools of demography are vital to the evolutionary biologist. We urge biologists interested in life-history evolution to make use of the methods of demography, both by presenting survival and fertility data in the standard demographic formats, and by employing the computational methods of demography to put these data to good use.

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Appendix 1: Microsimulation

We used a simple microsimulation to determine the expectation for our parameter S (see text) under the null hypothesis that reproductive senescence exactly parallels actuarial senescence. The microsimulation, in the form of a Microsoft Excel spreadsheet takes three inputs: a q_x series, a sample size, and a "fertility denominator." The series of up to 101 q_x values can be input to reflect the demography of the population in question. Sample size can be set anywhere from 1 to 2000 by copying and pasting the appropriate number of rows, each representing the life-history of a single individual. The fertility denominator (FD) sets the probability of reproduction of each surviving individual such that $m_x=(1-q_x)/FD$.

The survival of each individual is determined randomly for each individual for each year, such that if the individual survived to age x, the probability of survival to age $x+1=(1-q_x)$. The reproductive output of each individual for each year is determined such that if the individual is alive at age x, the individual will have one offspring with probability of m_x and have zero offspring with probability of $1-m_x$.

We then calculate ages M and Z as described in the text, and calculate S=(M-Z)/Z.

We applied this method to a variety of qx schedules, sample sizes and fertility denominators. In general, the variance of S decreases with increasing population size, and in long-lived populations. This correlation of variance of S with longevity arises from the graininess of the data, and does not represent a biological reality. This effect can be counteracted simply by using shorter units of time to measure shorter lifespans.

Across all variations mean S values approximated zero. As population sizes or number of replicates increased, simulated mean S values strayed less far from zero.

Appendix 2:

A table of demographic parameters for the populations included in our analyses is attached as a separate file.

Figure 1. Age specific survival for populations with identical post-reproductive lifespans

Populations A (red) and B (blue) Both begin reproducing at age=2, reach reproductive cessation at age=10, and both experience 50% annual mortality at all ages above ten. Population *A* experiences no adult mortality prior to reproductive cessation, while Population *B* experiences higher predation upon reproductive adults. *A* will include many post-fertile individuals, while *B* will include almost none. However, calculating PRLS for each population will yield the same result, with life expectancy at reproductive cessation being one year for both populations. For both these populations the ratio of PRLS to fertile lifespan is 1/8.

Population A
Population B

Figure 2. Post-reproductive lifespan over life expectancy at birth.

A measure of PRLS (e_M) plotted against life expectancy at birth (e_0) for 63 species of captive primates. Data are from the International Species Information System. The majority of information in these interspecies comparisons of PRLS is attributable to the overall longevity of the organisms (t ratio= 10.76, r2= 0.65, $p<0.0001$ $e_M= 1.5626+0.3554*e_0$), not to variation in the representation of post-fertile individuals in the populations, indicating that PRLS is of limited value for comparisons between species with different overall longevities.

Figure 3. Post-fertile survival for human and non-human primate populations.
G (T_M/T_B, see text) represent post-fertile survival for humans (top) and non-human primates (bottom) under varying circumstances. Human populations are: hunter-gatherers, Sweden 1751-1755, United Nations Least Develop Nations, UN Less Developed Nations and UN more Developed Nations. Primate populations are wild (*Pan troglodytes* and *Papio cyanocephalus*), Semiwild (*Macaca fuscata*) and 63 zoo populations.