Longer Life and Population Growth

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RECENT SUCCESSES in prolonging the life spans of laboratory animals have raised the possibility of large increases in human longevity (Carey et al. 1998; Lin et al. 1997; Biddle et al. 1997). The prospect of longer life is often greeted by fears of overpopulation (Kevles 1999; Kolata 1999; Gavrilov and Gavrilova 1991; Bova 1998). Kevles's concerns, which appeared on the opinion page of the *New York Times*, are typical. He wrote that "forestalling death would inevitably worsen many of the social crises that we already see looming. It would increase population, further burdening the planet—and might well create a generation gap of titanic proportions." In this article, we use a simple mathematical model to show that longer life need not—and, if current trends continue, will not—lead to population growth.

We distinguish between two types of post-reproductive life extension. Life-cycle telescoping occurs when death is postponed without affecting the timing of childbearing. The alternative is life-cycle stretching, in which longer life is accompanied by delays in the timing of reproduction. Our model shows that population growth will result from life-cycle telescoping, but not from stretching. Stretching appears to be the more likely scenario, judging from animal experiments, evolutionary and behavioral theory, and recent human experience. We conclude thus that current forecasts of an end to world population growth before the end of the twenty-first century (Lutz, Sanderson, and Scherbov 1997) may not be upset even by quite dramatic increases in human longevity. Similarly, differential access to life-extension technology (Silver 1997) may not alter the population composition in favor of those who live longer. Life-cycle stretching may itself be an evolutionarily adaptive mechanism.

Population growth consequences of different scenarios for increased longevity

To study the effects of increased longevity on population size, we consider stationary populations in which mortality declines occur in post-reproduc-

tive ages. Near zero population growth rates are typical of most developed countries and are forecast for the world population by the end of the twenty-first century (e.g., Lutz, Sanderson, and Scherbov 1997). In stationary populations, an identity relates population size K to years of life expectancy at birth e and the annual number of births B:

$$K = Be. \tag{1}$$

Any change in life expectancy that leaves the number of births unchanged, such as life-cycle telescoping, will produce a proportional change in total population size.

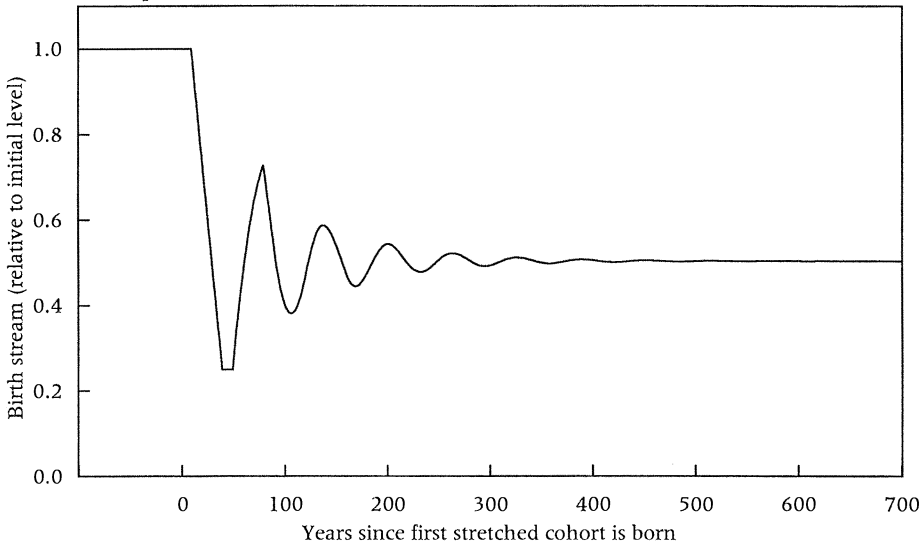
Consider now the case where a population undergoes a transition in which the timing of reproduction is allowed to vary with the timing of death. Let the change in demographic regimes occur from one cohort to the next, such that everyone born before a given moment in time has the original demographic regime, and everyone born after this time has the longer-life regime. Replacement fertility holds for all cohorts. Denote the expectation of life e' and the mean age of reproduction μ' under the new regime. We find that

$$\lim_{t\to\infty} K'(t) = K \cdot \frac{\mu}{\mu'} \cdot \frac{e'}{e}, \tag{2}$$

where $K'(t)$ is the size of the population t years after the change in regime. This result provides the conditions under which life expectancy can be increasing without causing population growth: namely, when the ratio of life expectancy to the mean age of reproduction is kept constant across demographic regimes (i.e., $\frac{e'}{\mu'} = \frac{e}{\mu}$). This is the scenario we call life-cycle stretching. Telescoping is a special case of (2) where $\mu' = \mu$. More generally, population will increase whenever longevity increases faster than the mean age of reproduction ($\frac{e'}{e} > \frac{\mu'}{\mu}$), while population declines will be produced if the opposite occurs ($\frac{e'}{e} < \frac{\mu'}{\mu}$).

The dynamics of stretching the life cycle can be illustrated by simulation. Figure 1 shows the birth stream that results from a simple form of stretching in which the mean age of reproduction was doubled by shifting the onset and end of childbearing to older ages. After an initial period of oscillation, the birth stream settles down to a new equilibrium equal to one-half of the previous equilibrium. The existence of an equilibrium is a well-known consequence of demography's strong ergodic theorem (Sharpe and Lotka 1911). What is remarkable is that the level of this equilibrium de-

FIGURE 1 Simulated birth stream following a stretching transformation of the life cycle



NOTE: The original net maternity function is defined uniformly at 0.025 for ages 10 through 49. The stretched maternity function has the same value, but the age range has been shifted to ages 40 through 79. The simulation shows that the stream of births declines during the first few years following the change in demographic regimes as the births of the "stretched" cohorts are postponed. This decline is reversed as the new cohorts occupy the full range of ages of their reproductive span. Oscillations follow as the original dip in births is echoed.

pends only on the shift in mean age of reproduction.[1] It is also possible to derive this result as a consequence of the renewal theorem (Feller 1971). Li and Tuljapurkar (1999) use related methods to study population momentum.

Evidence for life-cycle stretching

While it is not possible to specify the form that future extensions of life will take, there are a number of reasons to believe that increases in longevity will be accompanied by delays in childbearing. The biological link between reproductive timing and mortality has been demonstrated repeatedly. The same animal experiments that have succeeded in extending longevity in Mediterranean fruit flies (Carey et al. 1998), drosophila (Finch 1990: 304–310), mice (Biddle et al. 1997), and nematode worms (Lin et al. 1997) also resulted in postponing the timing of reproduction. In humans, historical studies of the British peerage (Westendorp and Kirkwood 1998) and con-

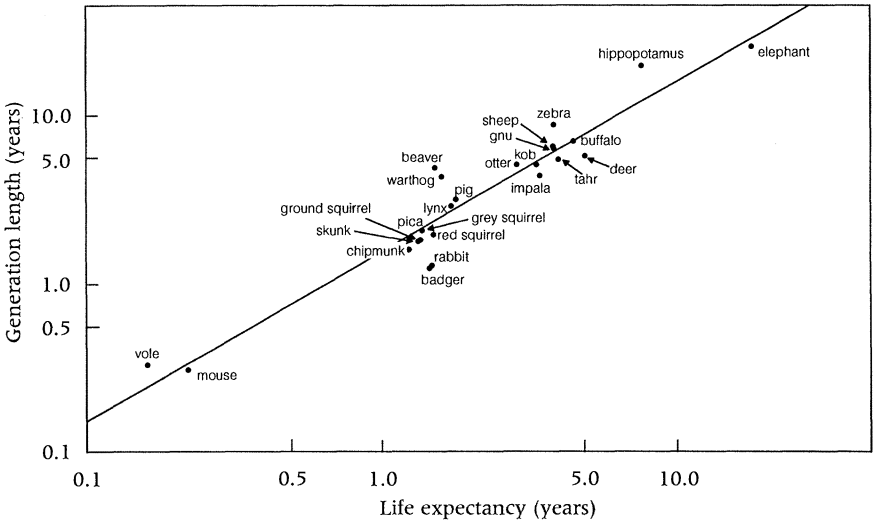
[1]A self-contained proof of equation (2) using elementary methods is available from the authors <http://opr.princeton.edu/~josh/stretchproof.pdf>.

temporary epidemiological studies (Perls and Silver 1999) have found a positive association between longevity and late childbearing.

Contemporary variation across species provides a proxy measure of evolutionary history, although ideally one would want to study change within species. The correlation between life expectancy and age at sexual maturity is very strong both across mammalian species (Harvey and Zammuto 1985) and across primates in particular (Harvey and Clutton-Brock 1985), a relationship often attributed largely to differences in body weight. Figure 2 shows the relationship between life expectancy and mean age at reproduction (generation length) in 25 mammalian species for which data are available. The correlation coefficient is large (r = 0.95) and the slope of the logarithmic regression line through these data is 1.01 (s.e. = 0.07). The regression line thus indicates that a doubling of life expectancy is accompanied by a 101 percent increase in the mean age of reproduction.

There are several explanations for the connection between reproductive timing and mortality (Charlesworth 1994). The costs of early reproduction may be high both in terms of subsequent survival and in terms of the survival of offspring. For density-dependent populations the linkage between longevity and age of reproduction may be evolutionarily adaptive because it allows increases in longevity without placing larger demands on the local environment. Life-cycle stretching may also be adaptive in the con-

FIGURE 2 Relationship between life expectancy at birth and mean age at reproduction (generation length) for 25 mammalian species (logarithmic scale)



NOTE: Logarithmic regression line has a slope of 1.01 (s.e. = 0.07); r = 0.95 (r = 0.94 in original scale).
SOURCE: Millar and Zammuto 1983.

text of environmental variation (Tuljapurkar 1997). There may also be an evolutionary argument for the ideal number of generations that are simultaneously alive. Grandparents may be able to contribute to the fitness of their offspring by assisting their grandchildren. On the other hand, if too many generations are alive at the same time, the fitness of the youngest generation may be diminished through competition for resources. Evolution may have introduced a mechanistic biological link between the timing of birth and death, a link that may mean that the same technological advances that postpone death will also, however inadvertently, postpone reproduction.

Although the future life-cycle demography of humans may be influenced in part by biological constraints, choices will also play a role in determining when long-lived humans, using their own free will, will decide to bear children. Behavioral theories such as economic theories of human capital investment (Becker 1983) support the proposition that delayed childbearing is a rational response to longer life spans. Kaplan and Lam (1999) have shown theoretically that increased productivity at older ages creates incentives for postponing childbearing. Life-course stretching may thus result as much from the optimizing choices of individuals facing increased longevity as from more-deterministic biological processes.

Empirical support for the link between longer life and postponement of childbearing can be found in the low-mortality populations of North America, Europe, and Asia, where reproductive ages have been rising in recent decades. As shown in Table 1, the mean age at childbearing has been increasing at approximately the same pace as life expectancy over the last two decades in the United States, Japan, and Sweden. Ages at first birth have been increasing slightly faster than mean ages at childbearing because of a decline in higher-order births to older women (Bongaarts and Feeney 1998). Later onset of reproduction appears to be driven by changes in behavior rather than changes in biology, since the age at menarche has been getting earlier during most of the twentieth century (Eveleth and Tanner 1990).

TABLE 1 Annual rates of change (in percent) in life expectancy and women's reproductive timing in selected low-mortality populations, 1975 to 1995

Country	Life expectancy at birth (females)	Mean age at first birth	Mean age at childbearing
United States	0.1	0.4	0.2
Japan	0.4	0.3	0.3
Sweden	0.2	0.5	0.4

NOTES: United States maternal ages at birth are medians and available from 1975 through 1993. Swedish female life expectancy in 1975 estimated from 1970 to 1979 average. Swedish maternal mean age at childbearing data available from 1978 to 1995.
SOURCES: National Center for Health Statistics 1999: 108; Japan Ministry of Health and Welfare 1998: Table 4.19; Statistics Sweden 1996: Tables 3.23, 3.24, and 4.17.

Life-cycle stretching appears to be a feasible scenario if we place it in the context of currently forecast improvements in human longevity. Lee and Carter (1992) forecast a joint-sex life expectancy of 86.05 years by 2065, an increase of 13.5 percent from 1990. The same proportional increase in the timing of reproduction would imply a mean age at childbearing of 30.0 years instead of the current value of 26.4 years. Such levels are clearly possible without biological innovations; in Japan, the current mean age at childbearing is already 29.2 years (Japan Ministry of Health and Welfare 1998). Whether reproductive timing is as elastic as longevity for very large changes, like a doubling of life expectancy, is not yet known. While animal experiments suggest that this may be the case, it may turn out to be easier to postpone death than menopause. Nonetheless, it is clear that reproductive timing in human populations has not yet begun to approach biological limits.

Conclusion

Fears that extension of the human life span will lead to population growth in replacement-level populations may be misplaced. As long as later ages at death are accompanied by proportional delays in the timing of childbirth, a shrinking birth stream will exactly offset increases in longevity. Current forecasts, which omit the possibility of dramatic increases in longevity, suggest that world population growth will cease toward the end of the twenty-first century. Our results suggest that these forecasts can still hold, even if longevity is greatly increased.

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References

Becker, G. S. 1975. *Human Capital: A Theoretical and Empirical Analysis, with Special Reference to Education.* 2nd ed. New York: Columbia University Press.

Biddle, F. G., S. A. Eden, J. S. Rossler, and B. A. Eales. 1997. "Sex and death in the mouse: Genetically delayed reproduction and senescence," *Genome* 40: 229–235.

Bongaarts, J. and G. Feeney. 1998. "On the quantum and tempo of fertility," *Population and Development Review* 24: 271–291.

Bova, B. 1998. *Immortality: How Science Is Extending Your Life Span—and Changing the World.* New York: Avon.

Carey, J. R. et al. 1998. "Dual modes of aging in Mediterranean fruit fly females," *Science* 281: 996–998.

Charlesworth, B. 1994. *Evolution in Age-Structured Populations.* 2nd ed. Cambridge: Cambridge University Press.

Eveleth, P. B. and J. M. Tanner. 1990. *Worldwide Variation in Human Growth.* 2nd ed. Cambridge: Cambridge University Press.

Feller, W. 1971. *An Introduction to Probability Theory and Its Applications, Volume II.* 2nd ed. New York: Wiley.

Finch, C. E. 1990. *Longevity, Senescence, and the Genome.* Chicago: University of Chicago Press.

Frauenthal, J. C. 1975. "Birth trajectory under changing fertility conditions," *Demography* 12: 447–454.

Gavrilov, L. A. and N. S. Gavrilova. 1991 [1986]. *The Biology of Life Span: A Quantitative Approach,* translated by J. Payne and L. Payne. Chur, Switzerland: Harwood.

Harvey, P. H. and T. H. Clutton-Brock. 1985. "Life history variation in primates," *Evolution* 39: 559–581.

Harvey, P. H. and R. M. Zammuto. 1985. "Patterns of mortality and age at first reproduction in natural populations of mammals," *Nature* 315: 319–320.

Japan Ministry of Health and Welfare. 1998. *Vital Statistics of Japan 1996, Volume 1.*

Kaplan, H. and D. Lam. 1999. "Life history strategies: The tradeoff between longevity and reproduction," paper presented at the Annual Meeting of the Population Association of America, New York, March.

Kevles, D. 1999. "Life on the far side of 150," *New York Times,* 16 March, Section A, p. 27.

Keyfitz, N. 1971. "On the momentum of population growth," *Demography* 8: 71–80.

Kolata, G. 1999. "Pushing limits of the human life span," *New York Times,* 9 March, Section F, p. 1.

Lee, R. D. and L. Carter. 1992. "Modeling and forecasting U.S. mortality," *Journal of the American Statistical Association* 87(419): 659–671.

Li, N. and S. Tuljapurkar. 1999. "Population momentum for gradual demographic transitions," *Population Studies* 53: 255–262.

Lin, K., J. B. Dorman, A. Rodan, and C. Kenyon. 1997. "*daf-16*: An HNF-3/forkhead family member that can function to double the life-span of *Caenorhabditis elegans*," *Science* 278: 1319–1322.

Lutz, W., W. Sanderson, and S. Scherbov. 1997. "Doubling of world population unlikely," *Nature* 387: 803–805.

Millar, J. S. and R. M. Zammuto. 1983. "Life histories of mammals: An analysis of life tables," *Ecology* 64: 631–635.

National Center for Health Statistics. 1999. *Vital Statistics 1993, Volume 1, Natality.* Hyattsville, MD: US Department of Health and Human Services.

Perls, T. T. and M. H. Silver. 1999. *Living to 100: Lessons to Living to Your Maximum Potential at Any Age.* New York: Basic Books.

Sharpe, F. R. and A. J. Lotka. 1911. "A problem in age-distribution," *Philosophical Magazine* 21: 435–438.

Silver, L. M. 1997. *Remaking Eden: Cloning and Beyond in a Brave New World.* New York: Avon.

Statistics Sweden. 1996. *Population Statistics 1995, Part 4, Vital Statistics.*

Tuljapurkar, S. 1997. "The evolution of senescence," in *Between Zeus and the Salmon: The Biodemography of Longevity,* ed. K. W. Wachter and C. E. Finch. Washington, DC: National Academy Press, pp. 65–77.

Westendorp, R. G. J. and T. B. L. Kirkwood. 1998. "Human longevity at the cost of reproductive success," *Nature* 396: 743–746.