

DEMOGRAPHIC CONSEQUENCES OF NATURAL SELECTION

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. . . .
Let's have a bloody good cry.
And always remember the longer you live,
The sooner you'll bloody well die.

(from an old Irish ballad)

INTRODUCTION

From the standpoint of most people's interests and perspectives, little need be added to the simple and elegant statement above. From the special perspective of a student of evolution, the statement seems a trifle parochial, and some qualifications and additions seem justified. It seems parochial in three respects, which we will call the dimensional, the ontogenetic, and the phylogenetic.

By dimensional parochialism we mean that the usual view of mortality rates focuses on those pertaining to animals of the order of 10^1 to 10^2 kg. Variation in this narrow range is trivial compared to that between the sizes over which organisms vary, from less than a nanogram to hundreds of tons. Over these many orders of magnitude there is a simple relationship between size and the death rates and birth rates that jointly determine demography: the smaller the size the greater the rates. The exact relation can be read from data summarized by Bonner (1957) and Sheldon, Prakash, and Suttcliffe (1972), who documented the size dependence of productivity. Their data show that the potential doubling time for an organism, with mass (m) measured in grams is about $100m^{-.25}$ days. Since all such populations, in fact, remain finite, we assume that their environments have the capability of removing them as fast as they are produced, removing the small organisms faster than the large. A formulation for population doubling time must work equally well for cohort half life.

The immense diversity in sizes and attendant mortality rates of organisms were produced by evolution. Natural selection almost always favors lower

mortality, but at any given moment in the history of life, it favored larger size for some organisms, smaller for others. We assume that this is the main way in which natural selection has shaped rates of birth and death, as an incidental consequence of selection for size. The prevailing average rates at particular sizes are scaling problems resolvable by physical principles such as surface-volume relations. It is for variation within a size category that we need the biological principle of natural selection.

The usual view of human mortality is ontogenetically parochial in its adult chauvinism. Children, at least in their early years, currently have higher mortality rates than adolescents or young adults. With the markedly higher mortality at all ages, which prevailed for most of human evolution, almost no one would survive to adult ages of higher mortality than those of the first few years. Mean or median life expectancy for a two-year-old could be greater than for either a newborn or a patriarch. The truth of our opening statement, on the relation between length of life and imminence of death, may be technically questionable even for modern populations. We suspect that if we gathered the necessary data and calculated an annual mortality rate for the first ten minutes of life, we might find it higher than that of centenarians. If you are a baby in your first minute of extra-uterine life, the longer you live the more remote your death is likely to be.

Perspectives are often phylogenetically parochial in their concentration on a single species. Ours is a species much closer to the upper than the lower end of the size scale. Our intuitive perspective relates to large organisms, with life expectancies in years, rather than the hours or days characteristic of much of the size spectrum. We are also an unusual species in the close similarity of size, and therefore mortality, of young and adult. The 15-fold increase in size between neonate and adult is trivial compared to the size contrast in other organisms between different stages in the development of a single individual. Consider the difference between a redwood seed and the mature tree. Among unitary animals (those without vegetative proliferation), it may be that the bluefin tuna is an extreme example of ontogenetic size change. A large adult may have about a billion times the mass of a newly hatched larva. Ontogenetic size changes imply ontogenetic changes in the mortality rates characteristic of the sizes of the different stages. Students of marine fish populations commonly find per-day losses among larvae that exceed per-year losses among adults. The narrowly limited size change in human development means that we experience only a narrow range of mortality rates, compared to such organisms as the redwood or tuna.

AGE AND MORTALITY AMONG HUMAN ADULTS

The rest of this presentation will be dimensionally, ontogenetically, and phylogenetically parochial. From adolescence on, a human age cohort experiences an ever rising mortality rate, and our intent here is to explore the possibility of deducing, from basic evolutionary postulates, a quantitative description of this change. Medawar's (1952) was the first valid statement of the relationship between age and selection for the maintenance of viability. We believe that the validity and fruitfulness of Medawar's theory was convincingly established by comparative evidence cited in his paper and later in Williams (1957). Experimental work has more recently added new confirmation (Bell, 1984; Charlesworth, 1984; Luckinbill et al, 1984; Rose, 1983).

The logic of the theory got detailed mathematical development by Hamilton (1966), but neither he nor anyone else has produced a conclusion in the form of an explicit $\mu = f(x)$, with μ being the mortality rate and x being age. We think it unlikely that any such formulation will be derived, because of mathematical difficulties that circumvent any attempt to use the theory in an axiomatic way. It may still be possible to use the theory to

generate theoretical demographies by computer simulation. Theoretical age structures would be of value, because it is normal scientific practice to compare expectations with observations, in order to check the validity of the reasoning used in generating the expectations.

The observations needed, for checking the theorizing below, would be detailed and accurate demographic data on Stone-age populations. Such observations are not available, but we hope that our project can be rescued to some extent by a contrived alternative. Hamilton (1966) published demographic data on Chinese women living in Taiwan about 1906 to illustrate his account of the evolution of senescence. The data as published depart from average Stone-age demography in one conspicuous respect: the population was growing at a rapid rate, despite what would be considered heavy mortality by current standards. The mean condition for the Stone Age must have averaged very close to zero growth, or human numbers would not have stayed finite for so long. A growth rate of one percent per century would suffice for replacing the present population of the earth from a single pair in less than a quarter of the Pleistocene.

We presume that Stone-age mortality rates averaged greater than those of the Taiwan population, and fertility rates lower. Lower fertility may have resulted from the same sorts of stresses that caused mortality, but also from the apparent tendency for mothers in hunter-gatherer societies to nurse their babies to a greater age than in agricultural societies. The Taiwan population would conform to the zero growth requirement if it had about a 0.239 increase in mortality rate and a 0.239 decrease in birth rate at all ages (Figure 1). With this demographic schedule, girls at birth would have an average expectation of living to produce one daughter. At adolescence (age 15) about half would have died, and the remainder would now have an expectation of producing two daughters before the termination of reproduction by death or menopause or obstetrical malfunction. We would welcome suggestions as to what might be better than our derived curve (Figure 1) for use as data on Stone-age demography.

The simplest plausible expectation for a schedule of mortality rates expected from natural selection would have mortality vary inversely according to each age's importance to fitness. Using \underline{x} for age, \underline{l}_x for the probability of survival to \underline{x} , \underline{V}_x for reproductive value at \underline{x} , and μ_x for instantaneous mortality at \underline{x} , the expectation is that

$$\mu_x = k / \underline{l}_x \underline{V}_x$$

Reproductive value at age \underline{x} measures the mean future reproductive output for individuals of that age. The formulation implies some genetic assumptions, in particular that proportionately equal increases in mortality are equally likely to arise by mutation. A stage with a mortality rate of 0.010 per year would be as likely to change to 0.011 by mutation as one with 0.10 would be to change to 0.11. The same must hold for decreases, although the rate of occurrence of a given decrease is expected to be much less than that of a proportionately similar increase. Under these conditions the formulation describes an Evolutionarily Stable Strategy (ESS), a state which, once attained, could not be altered by selection for a different state. A different assumption on the nature of the genetic variation may lead to a different ESS. For example, if mutational changes of equal absolute magnitude were equally frequent, the population would evolve semelparity, with a single bout of reproduction followed by death.

There are several levels of difficulty in using the equation above for deriving the equilibrium demography expected from natural selection. The first is mathematical and results from complex recursive dependencies among the terms. Survival (\underline{l}) at age \underline{x} depends on all previous values of μ , which in turn are functions of previous \underline{l} -values. Reproductive value depends on all

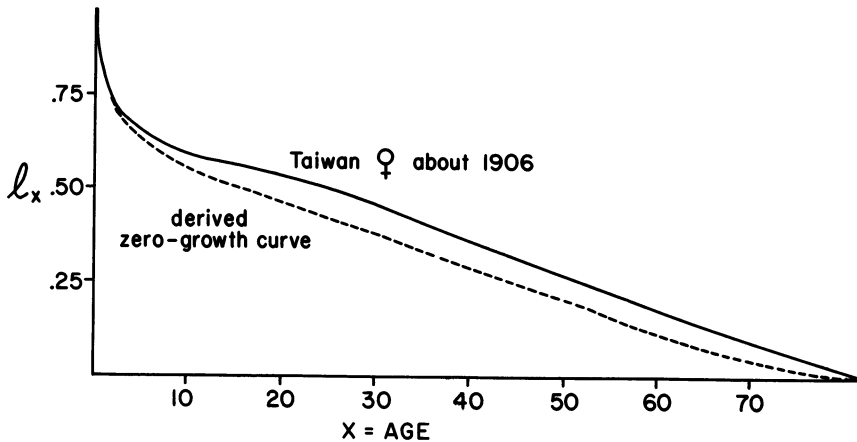


Fig. 1. The solid line shows cohort attrition over time for Chinese women in Taiwan about 1906 (from Hamilton, 1966). The dashed line shows the result of dividing observed mortality rates and multiplying birth rates by 0.761. This change results in zero population growth and is proposed as an approximation to Stone-age demography.

future mortality and birth rates. We see no hope for any precise analytical derivation of a theoretical age structure. A still more serious difficulty lies in the evolutionary irrelevance of any facile measure of reproductive value. A demographer normally measures the fertility of an age class by counting the number of babies that it produces. Human reproduction requires that babies not only be produced but nurtured and tended for many years. A woman past menopause is conventionally considered postreproductive, but she may still be contributing to the welfare of her descendants and other relatives. If so she is acting in a way that enhances the proliferation of her own genes. She is reproductively active from the standpoint of natural selection. We presume that it is for this reason alone that a woman may be able to live beyond menopause. By conventional measure, her \bar{V} drops to zero at this stage and the woman drops dead, according to our rule for mortality rate. The fallacy here lies in the conventional formulation of reproductive value.

Our solution to the problem of analytical intractability is to abandon mathematics and rely on computer simulation (Appendix). Our solution to the problem of defining reproduction is to see what can be accomplished by guesswork. In our simulation the reproductive value declines each year as a function of the expected fertility of the previous year, but only by a fraction of the expected decline. In this way a woman still has some reproductive value left at menopause, a value that represents a guess as to how effective she then might be in enhancing the survival of her own genes represented in relatives. If a plausible guess allows the generation of an age structure closely similar to that of our modified Taiwan data, the exercise shows that theory and observation are potentially compatible. If no plausible guess has that result, the finding is more instructive. In the simulation illustrated, we represent effects of kin selection by having the reproductive value of a woman at menopause equal to a third of what it was at age fifteen. We think this an extreme assumption, and believe that a smaller value would be more realistic.

It is a simple matter, with these rules of the game, to use trial-and-error simulations (Appendix) to produce theoretical demographies consistent with the rules and with the requirement of zero population growth

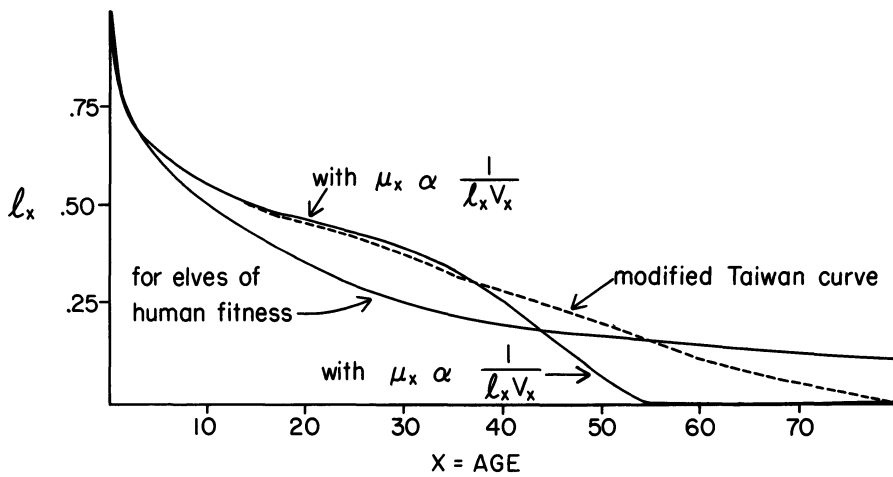


Fig. 2. The dashed line repeats the reconstruction of Stone-age demography shown in Figure 1. The solid lines show the Stone-age demography predicted by our theory, and the demography expected of eternal youth purchased at the cost of developmental retardation (Tolkien's elves).

(Figure 2). Note that senescence in the theoretical curve is much more abrupt than in that based on the Taiwan data. A number of considerations bear on the interpretation of this result. The theoretical curve is for a homogeneous cohort with optimal tradeoffs of viability among ages but with all fertility values and minimum mortality (age 15) uniformly altered from the Taiwan values so as to achieve zero population growth. The fitness homogeneity of the population is manifest in the low variability of life span. Any real Stone-age human cohort would be heterogeneous in fitness. Some girls at puberty would have great vigor of body and mind and a lofty social status. They would be expected to have much greater than average longevity and reproductive performance. Others may be crippled or chronically ill outcasts with little likelihood of rearing even one child.

Unfortunately, no degree of fitness heterogeneity is sufficient to excuse the discrepancy between theory and what we are using as observation (modified Taiwan age structure). If we simulate an extreme heterogeneity by giving half the cohort four times the fitness of the other half, but with the total having the same mean fitness as the homogeneous cohort, we still get only a small percentage of survivors beyond age sixty and none beyond age sixty-six. It must also be realized that the simulation uses what we regard as an unrealistically high reproductive value for a woman after menopause. Lower values result in earlier and more abrupt attrition.

The outcome of our simulation is not surprising. Our formula for relating mortality to reproductive value and survival is a formula for explosive positive feedback. Declining survival and reproductive value cause increase in mortality rate which causes a greater decline in survival and reproductive value in the next year and so on in an ever steeper cycle until mortality shows a catastrophic increase in a single year and the cohort vanishes. It should also be noted that all fertility values used in the simulation are empirically based on the data from Taiwan. In future work we plan to simulate fertility senescence along with viability senescence. Fertility can be expected to show the same sort of sudden collapse as viability, because it also would have a positive-feedback relation with survival. A more sudden decline in fertility would increase the rate of decline in viability and produce an even steeper end to the cohort than appears in Figure 2.

We conclude that our simulation does not give a realistic picture of what we are using as primitive human demography, despite the use of numerical constants chosen to be unfairly favorable to a match between theory and observation. Either there is some flaw in our reasoning or the modified Taiwan data are grossly unrepresentative of primitive human populations. Perhaps the most probable error is conceptual, our simple assumption of an equal likelihood for proportionately equal mutational changes at different ages. This implies an absolute equivalence between developmental and absolute time, which would be clearly unrealistic for development through a broad range of sizes. Developmental processes can be expected to take place much more rapidly in the small sizes early in life than later on.

In defense of our genetic assumption we can point out that there are no important size changes in human development after age fifteen. Moreover, there are many examples of morphogenetic change at constant absolute rates during adulthood in many mammals. Those with an annual cycle of change in coat color, gonads, or secondary sexual characters would be obvious examples. We do not really view these observations as justifying the use of our simple model of the genetics of mortality rates. Our simulation (Appendix) assumes that, for instance, a mutation that lowers mortality by one percent in the tenth year only, is neither more nor less likely to arise than one that would lower it by one percent in the twentieth only. There is no reason to rule out the possibility that the twentieth and twenty-first year together would be the developmental equivalent of the tenth. Annual cycles of morphogenesis at similar rates could be exceptional, and not indicative of a general tendency for rates of development to remain uniform during adulthood. Resolution of this difficulty may have to await a more advanced understanding of developmental constraints on the evolutionary process.

DEMOGRAPHY OF TOLKIEN'S ELVES

The elves of Middle Earth, according to J. R. R. Tolkien in The Silmarillion and several prior works, were essentially human in most respects. A difference that Tolkien stressed was the elves' eternal youth. As adults they suffered no deterioration of adaptive performance with increasing age. This major biological advantage must have evolved at some compensating cost, otherwise they would have rapidly displaced their competitors. The co-existence of elven and human populations in approximate equilibrium for many centuries shows that neither could have had a net competitive advantage over the other.

It is clear from Tolkien's works that elves had a normal childhood in most respects, but he is silent on its duration. This raises the possibility that their freedom from senescence was purchased at the cost of developmental retardation. If this were the only cost, its magnitude must have been very nearly whatever is needed to reduce elven fitness to human fitness. The required retardation in development can be found with simulations using, throughout elven adulthood, the previously determined adolescent minimum of mortality and third-decade maximum of birth rate, with various degrees of prolongation of childhood and of childhood mortality rates. This method shows that an approximate doubling of the childhood years would give elves the required zero population growth.

The resulting elven age structure (Figure 2), after sexual maturity at about age 30, is simply determined by a constant exponential decay of each age cohort. Fertility increases gradually to its maximum after age 40 (as in the human population after age 20) and keeps this maximum value thereafter. It is clear that the elves utterly fail to conform to our postulated inverse proportionality between mortality and the product of survival and reproductive value. They may well conform to models of tradeoffs between speed of

attainment of maturity and levels of adaptive performance after maturity (Taylor and Williams, 1984).

The lesson for us from this simulation of elven life history is this: If our evolution had been somehow forbidden to use fitness tradeoffs between adult ages, but had instead favored age-independent adult fitness at the cost of slower development, and had achieved the same lifetime fitness under Stone-age conditions, we would now be like Tolkien's elves. Each of us would have taken about 30 years to produce the phenotype we actually reached in 15, but we would thereafter have a 15-year-old's mortality rate. We would live until struck by lightning, appendicitis, a terrorist, or other stress that might be lethal to a fifteen-year-old.

Elves are not the only zoological example of freedom from senescence. Evolution effectively forbids senescence in any tissues that will be passed on in either sexual or asexual reproduction. So animals with limited life spans belong to potentially immortal populations, and genetically defined individuals from single zygotes can persist indefinitely in species with modular modes of development (Jackson and Coates, 1986). There may be coral colonies many millenia in age (Potts, 1984).

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APPENDIX

Our Turbo Pascal program appears below. The output shown is for stone age equal to 0.761 and cost equal to 0.666. These values give zero population growth and the reproductive value of one (daughter) per newborn or per half adolescent (age 15). They also give the population structure that would result from everyone having average fitness but ideal tradeoffs in viability among adult ages. This ideal would be stabilized by natural selection if genetic variation is as explained in the text. Values for stone age other than 0.761 can be used to show the demography of groups of other-than-average fitness, but the output will be realistic only if the age-15 repr value is made to equal the final girl sum. This compatibility can be achieved by successive approximation. The program of course could be used as a module in a larger program that finds the compatible pairs of values, simulates plausible patterns of fitness variation, &c.

```
program dieoff (output);

const
  start_age = 15;
  stop_age = 65;
  start_survival = 0.5;
  Taiwan_mortality = 0.0100;
type
  age_range = start_age..stop_age;
  column = array [age_range] of real;
var
  survival, mortality, repr_value, birthrate, girls, girl_sum :
    column; { Sons don't count here for repr_value. }
  age : integer;
  last_age : integer;
  cost : real; { Cost would be 1.0 without aid to relatives. }
  stone_age : real; { This measures stone-age prospects, relative to
    those of Taiwan in 1906 }

  yesno : char;
  diskout, diskopen : boolean;
  diskfile : text;

procedure init_birthrate; { modified from Taiwan in 1906 (Hamilton, 1966) }
const
  Taiwan_birthrate : column = (
    0.0036, {15}
    0.0120, 0.0260, 0.0450, 0.0700, 0.0950, {16..20}
    0.1170, 0.1302, 0.1640, 0.1720, 0.1733, {21..25}
    0.1733, 0.1733, 0.1670, 0.1631, 0.1600, {26..30}
    0.1570, 0.1552, 0.1515, 0.1494, 0.1420, {31..35}
    0.1378, 0.1320, 0.1290, 0.1250, 0.1100, {36..40}
    0.0930, 0.0800, 0.0600, 0.0386, 0.0320, {41..45}
    0.0207, 0.0020, 0.0003, 0.0001, 0.0000, {46..50}
    0.0000, 0.0000, 0.0000, 0.0000, 0.0000, {51..55}
    0.0000, 0.0000, 0.0000, 0.0000, 0.0000, {56..60}
    0.0000, 0.0000, 0.0000, 0.0000, 0.0000); {61..65}
var
  age : integer;
```



```

begin {init_birtrate}
  for age := start_age to stop_age do
    birtrate[age] := stone_age * Taiwan_birtrate[age];
end; {init_birtrate}

procedure make_table;
begin {make_table}
  init_birtrate;
  survival[start_age] := start_survival;
  mortality[start_age] := Taiwan_mortality / stone_age;
  repr_value[start_age] := 1.0; { expected number of future daughters per }
  girls[start_age] := 0.0; { half woman at age 15 }
  girl_sum[start_age] := 0.0;
  age := start_age;
  repeat
    age := age+1;
    repr_value[age] := { approximately }
      (repr_value[age-1]) - cost * survival[age-1] * birtrate[age-1];
    if mortality[age-1] > 5.0
    then survival[age] := 0.0
    else survival[age] := survival[age-1] * exp( -mortality[age-1] );
    if survival[age] > 0.0
    then mortality[age] :=
      (mortality[age-1] * survival[age-1] * repr_value[age-1]) /
      (survival[age] * repr_value[age])
    else mortality[age] := 1.0;
    girls[age] := survival[age-1] * birtrate[age-1];
    girl_sum[age] := girl_sum[age-1] + girls[age];
    last_age := age;
  until (age = stop_age ) or (survival[age] <= 0.0) or
    (repr_value[age] <= 0.0);
end; {make_table}

procedure write_table;
begin {write_table}
  clrscr;
  writeln('cost = ', cost:6:4, ', stone_age = ', stone_age:6:4 );
  writeln(' X    l(x)  mu(x)   V(x)   b(x)   g(x)   G(x)');
  if diskout then begin
    writeln(diskfile,'cost = ', cost:6:4, ', stone_age = ', stone_age:6:4 );
    writeln(diskfile,' X    l(x)  mu(x)   V(x)   b(x)   g(x)   G(x)');
  end;
  for age := start_age to last_age do begin
    writeln( age:2, ' ', survival[age]:6:4,
      ' ', mortality[age]:6:4,
      ' ', repr_value[age]:6:4, ' ',
      ' ', birtrate[age]:6:4, ' ', girls[age]:6:4,
      ' ', girl_sum[age]:6:4);
    if diskout then writeln( diskfile, age:2, ' ', survival[age]:6:4,
      ' ', mortality[age]:6:4,
      ' ', repr_value[age]:6:4, ' ',
      ' ', birtrate[age]:6:4, ' ', girls[age]:6:4,
      ' ', girl_sum[age]:6:4);
    if (age - start_age + 1) mod 20 = 0 then begin
      gotoxy( 20, 24 );
      write('Press any key to continue');
      repeat until keypressed;
      window(1,3,80,25); clrscr;
      window(1,1,80,25); gotoxy(1,3);
    end;
  end;
end;

```

```

if last_age < stop_age then begin
    writeln( 'Simulation terminated at age ',last_age:2,
            ' because survival or repr. value reached 0. ');
    if diskout then writeln( diskfile,
        'Simulation terminated at age ',last_age:2,
        ' because survival or repr. value reached 0. ');
    end;
end; {write_table}

begin {main}
    diskopen := false;
    assign(diskfile,'die.out');
    repeat
        clrscr;
        write('Enter a value for "cost": ');
        readln(cost);
        write('Enter a value for "stone_age": ');
        readln(stone_age);
        write('Log this run to disk? [y/n]:');
        read(kbd,yesno);
        diskout := (yesno = 'Y') or (yesno = 'y');
        if diskout and not diskopen then begin
            rewrite(diskfile);
            diskopen := true;
        end;
        make_table;
        write_able;
        write('Do another run? [y/n]:');
        read(kbd,yesno);
    until (yesno <> 'Y') and (yesno <> 'y');
    close(diskfile);
end. {main}

```

SAMPLE OUTPUT [X is age in years, l(x) survivorship, mu(x) mortality rate, g(x) fertility (births of daughters) and G(x) cumulative daughters.]
The output is for cost = 0.666 and stone age = 0.761.

X	l(x)	mu(x)	V(x)	b(x)	g(x)	G(x)
15	0.5000	0.0131	1.0000	0.0027	0.0000	0.0000
16	0.4935	0.0133	0.9991	0.0091	0.0014	0.0014
17	0.4869	0.0135	0.9961	0.0198	0.0045	0.0059
18	0.4804	0.0138	0.9897	0.0342	0.0096	0.0155
19	0.4738	0.0142	0.9787	0.0533	0.0165	0.0320
20	0.4671	0.0146	0.9619	0.0723	0.0252	0.0572
21	0.4603	0.0152	0.9394	0.0890	0.0338	0.0910
22	0.4534	0.0159	0.9121	0.0991	0.0410	0.1320
23	0.4463	0.0167	0.8822	0.1248	0.0449	0.1769
24	0.4389	0.0177	0.8451	0.1309	0.0557	0.2326
25	0.4312	0.0189	0.8068	0.1319	0.0574	0.2900
26	0.4231	0.0202	0.7690	0.1319	0.0569	0.3469
27	0.4146	0.0217	0.7318	0.1319	0.0558	0.4027
28	0.4058	0.0233	0.6954	0.1271	0.0547	0.4574
29	0.3964	0.0251	0.6610	0.1241	0.0516	0.5089
30	0.3866	0.0270	0.6283	0.1218	0.0492	0.5581
31	0.3763	0.0293	0.5969	0.1195	0.0471	0.6052
32	0.3654	0.0317	0.5670	0.1181	0.0450	0.6502
33	0.3540	0.0345	0.5382	0.1153	0.0432	0.6933
34	0.3420	0.0376	0.5111	0.1137	0.0408	0.7342

X	l(x)	mu(x)	V(x)	b(x)	g(x)	G(x)
35	0.3294	0.0411	0.4852	0.1081	0.0389	0.7730
36	0.3162	0.0450	0.4614	0.1049	0.0356	0.8086
37	0.3022	0.0495	0.4394	0.1005	0.0332	0.8418
38	0.2876	0.0545	0.4191	0.0982	0.0304	0.8721
39	0.2724	0.0603	0.4003	0.0951	0.0282	0.9004
40	0.2565	0.0669	0.3831	0.0837	0.0259	0.9263
41	0.2399	0.0743	0.3688	0.0708	0.0215	0.9478
42	0.2227	0.0825	0.3575	0.0609	0.0170	0.9647
43	0.2051	0.0920	0.3485	0.0457	0.0136	0.9783
44	0.1870	0.1026	0.3422	0.0294	0.0094	0.9877
45	0.1688	0.1150	0.3386	0.0244	0.0055	0.9932
46	0.1505	0.1300	0.3358	0.0158	0.0041	0.9973
47	0.1321	0.1488	0.3342	0.0015	0.0024	0.9996
48	0.1138	0.1727	0.3341	0.0002	0.0002	0.9998
49	0.0958	0.2053	0.3341	0.0001	0.0000	0.9999
50	0.0780	0.2521	0.3341	0.0000	0.0000	0.9999
51	0.0606	0.3244	0.3341	0.0000	0.0000	0.9999
52	0.0438	0.4487	0.3341	0.0000	0.0000	0.9999
53	0.0280	0.7028	0.3341	0.0000	0.0000	0.9999
54	0.0139	1.4191	0.3341	0.0000	0.0000	0.9999
55	0.0034	5.8659	0.3341	0.0000	0.0000	0.9999
56	0.0000	1.0000	0.3341	0.0000	0.0000	0.9999

Simulation terminated at age 56 because survival or repr. value reached 0.