

UNIVERSITY OF AMSTERDAM

MSC RESEARCH PROJECT

IN THEORETICAL ECOLOGY

**Comparative estimates of lifetime
reproductive output using Markov chains
with rewards**

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April 8, 2015



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Foreword

An important measure in demography and ecology is lifetime reproductive output (Heesterbeek, 2002; Caswell, 2011). Lifetime reproductive output (LRO) is defined as the estimated number of offspring an individual produces during its entire life. As such, LRO can be a measure of fitness. The relationship between mean LRO and fitness has been extensively studied, but mean LRO equals fitness only under a specific set of circumstances (Grafen, 1988; Partridge, 1989; Newton; 1989). Mean LRO can be calculated as R_0 . The net reproductive rate R_0 represents not only the expected number of offspring per individual, but also the population growth rate per generation and indicates whether populations persist, grow, or decline (Caswell, 2009; 2011). Unfortunately, R_0 provides no information on inter-individual variation in LRO. Variation in LRO is important because selection operates on variation. Using measures on both mean and variance in LRO, one can calculate the Opportunity for Selection. Furthermore, the partitioning of variance in LRO can elucidate the factors that determine lifetime reproductive output.

This document presents different analyses of variation in lifetime reproductive output using Markov chains with rewards. In Chapter 1 the statistics of LRO are analyzed for human population during a prominent demographic transition in developed countries. This is the most detailed study in this document. Chapter 2 compares the variation in LRO arising solely from individual stochasticity with observed variation in LRO for a set of vertebrate species. This comparison provides insight on the contribution of heterogeneity to observed variation in lifetime reproductive output. Chapter 3 contains some mathematical notes on the derivation of the equilibrium equations of LRO and some results on the sensitivity analysis of LRO.

Chapter 1

Mean and Variability in Human Lifetime Reproductive Output

Individual Stochasticity and the Fertility Transition

Abstract

BACKGROUND: In the last half of the previous century many developed countries went through a period of decreasing fertility rates, referred to as the fertility transition. The fertility transition is often measured using the Total Fertility Rate (TFR), which gives the mean number of children produced by a woman surviving through her reproductive years. The TFR ignores effects of mortality and, as a mean, provides no information on variability among individuals in lifetime reproduction.

OBJECTIVES: Our goal is to quantify the statistics (mean, variance, standard deviation, coefficient of variation, and skewness) during the fertility transition. We compare these statistical properties as functions of age, time, and developmental indices.

METHODS: We used Markov chains with rewards to compute the moments of lifetime reproductive output (LRO) based on age-specific mortality and fertility rates for 40 developed countries, two hunter-gatherer populations and North-American Hutterites. The analysis uses a Markov chain to model individual survival, and treats reproduction as a Bernoulli-distributed reward with probability equal to the age-specific fertility.

RESULTS: All statistical properties of lifetime reproduction changed during the fertility transition. The mean and standard deviation of LRO declined, and the coefficient of variation and skewness increased. By 2000, these statistics were tightly correlated across countries, suggesting that the entire distribution of LRO shifted, not just the mean.

CONCLUSIONS: We find that developed countries adhere to a seemingly universal distribution in LRO, during and after the fertility transition. This distribution becomes more apparent when development improves health circumstances and decreases mortality.

Key words: Fertility, lifetime reproduction, fertility transition, individual stochasticity, Markov chains with rewards.

1.1 Introduction

During the twentieth century, many countries experienced the so-called fertility transition, showing sharp declines in the population’s fertility level. The fertility transition is said to be part of a larger demographic transition, in which reductions in mortality during the past two centuries are followed by declines in fertility in the last century (Lee, 2003). More recently, after the Second World War, fertility started declining more sharply, resulting in an increasing number of countries dropping below replacement level (2.1 children per female) (Lee, 2003). In 2003, more than 50% of the world’s population lived in countries with below replacement fertility (Wilson, 2004). Countries in Southern and Eastern Europe and in East Asia have reached even lower levels of fertility, dropping below 1.3 (i.e. “lowest-low fertility”) (Goldstein et al., 2009; Wilson, 2004). In recent years fertility has started to increase again. Myrskylä et al. (2009) show that, although the relationship between Total Fertility Rate and the Human Development Index was negative in the past, this relationship has become positive in highly developed countries, resulting in increasing fertilities.

Explanations for the fertility transition include the effects of improving socioeconomic circumstances, tempo effects related to postponement of childbearing, better access to methods of fertility control, and diffusion of ideas about family planning at the population level (Hill & Kaplan, 1999; Kirk, 1996; Bryant, 2007; Goldstein et al., 2009). Biodemographic explanations have been proposed that explain reduced fertility as a (perhaps mistaken) evolved response to increased costs of offspring (Hill & Kaplan, 1999). Recent reports of recovering fertility provide similar explanations for rising fertility levels; the effect of even further improvement in socioeconomic circumstances, decreased tempo effects and perhaps, in some cases, effect of government policies to raise national fertility (Goldstein et al., 2009; Myrskylä et al., 2009).

Studies of the fertility transition usually measure fertility as Total Fertility Rate (TFR). TFR is the expected lifetime reproduction that would take place if a woman were to survive through her reproductive years, ignoring the possibility of death (Le Bras, 2008). Our goal here is to go beyond the TFR in two ways. First, we focus on lifetime reproduction, where lifetime is defined as years lived between birth and death; this incorporates mortality, which is ignored by the TFR. The net reproductive rate R_0 is the expectation of lifetime reproductive output (LRO), and can be calculated from the mortality and fertility rates. The net reproductive rate is also the population growth rate per generation and it is used to indicate whether populations persist, grow, or decline (Lotka, 1936; Caswell, 2009, 2011).

Neither R_0 nor the TFR provide any information on variation among individuals in lifetime reproductive output. Yet, variation in LRO can have important demographic and evolutionary consequences (Heesterbeek, 2002; Caswell, 2011), and it is presently unknown how variation in fertility changed during the fertility transition. Could a change in mean be accompanied by a change in variability of reproductive output? If this is the case, variability in LRO may also respond to changes in socioeconomic conditions (e.g. Myrskylä et al. (2009)). Our second goal is to examine statistics of the variation in LRO during the fertility transition. These statistics are calculated from mortality and fertility schedules as are R_0 and TFR, but are not yet widely used in demography (Caswell, 2011, 2014a).

Variability in lifetime reproductive output can be quantified by several statistics. The variance and standard deviation measure variation on an absolute scale. The coefficient of variation (CV) scales the standard deviation relative to the mean. The standardized variance, also known as Crow’s I , scales the variance relative to the square of the mean (Crow, 1958). Crow’s I measures the opportunity for selection on a varying trait and provides an upper limit to the strength of selection. Of course, Crow’s I measures actual, rather than potential, selection only if reproductive output is heritable (Clutton-Brock, 1988). Skewness in LRO measures the asymmetry of the distribution. If skewness is positive, as is often the case with fertility in animal studies (Clutton-Brock, 1988), many individuals produce few children, and

a long tail of individuals producing many children.

The sources of variance in LRO are important. Variance arises from both heterogeneity (differences in the vital rates among individuals within the same age or stage) and from random outcomes among identical individuals experiencing the same vital rates. The latter source of variation is *individual stochasticity* (Caswell, 2009, 2011, 2014a), and it has been found to be a major contributor to variance in LRO in many species (Caswell, 2011; Tuljapurkar et al., 2009; Steiner & Tuljapurkar, 2012)

Individual stochasticity contributes to variation between individuals in LRO in two ways. First, individuals will differ in the pathways they follow throughout the life cycle; by chance some will live longer and some die sooner. Second, individuals of a given age will experience stochasticity in their reproductive output; given a probability of reproduction, by chance some will produce a child and some will not. The overall variance in LRO is a combination of these two sources.

Caswell (2011) presents a method to calculate the mean, variance and other statistical properties of LRO due to the individual stochasticity implied by a mortality and fertility schedule. The method uses a Markov chain description of the life cycle, assigns a random reward (in our case, reproduction) to each transition, and then accumulates this reward over the life cycle (Howard, 1960; Caswell, 2011).

In this paper, we will assess changes in the statistics of LRO during the fertility transition, based on period mortality and fertility data from 40 developed countries, covering the years 1891 to 2011. We compute the mean, variance, standard deviation, coefficient of variation (CV), and skewness of LRO. These are assessed over age, over time, in relation to human development, and in relation to the other statistical properties. We will compare the statistics of LRO for our sample of developed countries with those for several populations without fertility control. The latter include the hunter-gatherer populations of the Ache and the Hadza, and the high-fertility population of the Hutterites.

Over time, we assess the changes in all statistics during the fertility transition, focusing on the period between 1960 and 2011, which saw the steepest declines, lowest levels of fertility, and the start of a possible fertility recovery (Goldstein et al., 2009; Myrskylä et al., 2009). Following Myrskylä et al. (2009), we also investigate the relationship between the statistics of LRO and the UNDP Human Development Index (HDI). However, where Myrskylä et al. (2009) focus on the effect of an increasing HDI on TFR, we assess the effect of HDI on multiple statistics of lifetime reproduction.

1.2 Methods: Markov chains with rewards

Notation. Matrices are denoted by upper-case bold symbols (e.g., \mathbf{P}), vectors by lower-case bold symbols (e.g., $\boldsymbol{\rho}$). Vectors are column vectors by default. The transpose of \mathbf{P} is \mathbf{P}^\top . The inverse of \mathbf{P} is \mathbf{P}^{-1} . The vector $\mathbf{1}$ is a vector of ones, and the matrix \mathbf{I} is the identity matrix. Where necessary to avoid confusion, dimensions are indicated by subscripts; e.g., the $\omega \times \omega$ identity matrix is \mathbf{I}_ω . The diagonal matrix with the vector \mathbf{x} on the diagonal and zeros elsewhere is denoted $\mathcal{D}(\mathbf{x})$. The expected value is denoted by $E(\cdot)$. The Hadamard, or element-by-element, product of matrices \mathbf{A} and \mathbf{B} is denoted by $\mathbf{A} \circ \mathbf{B}$. Transition matrices of Markov chains are written in column-to-row orientation, and hence their columns sum to one.

1.2.1 Markov chains with rewards

Our analysis describes the life cycle as an absorbing Markov chain (e.g., Caswell 2001, 2006, 2009; see Feichtinger 1973 for an early example). It is applicable to age-structured and stage-structured models and to models incorporating various types of temporal or environmental variation. In our case, age-structured population projection matrices are transformed into a

Markov chain to represent the human life cycle. Let ω denote the number of age classes. Death is incorporated into the model as an absorbing state. The Markov chain transition matrix is

$$\mathbf{P} = \left(\begin{array}{c|c} \mathbf{U} & \mathbf{0} \\ \hline \mathbf{m}^\top & 1 \end{array} \right) \quad (1.1)$$

where \mathbf{U} is a $\omega \times \omega$ matrix of transition probabilities among transient (i.e., living) states, and \mathbf{m}^\top is a $1 \times \omega$ vector of mortality rates. The matrix \mathbf{U} contains survival probabilities on the subdiagonal and zeros elsewhere; e.g., for $\omega = 3$,

$$\mathbf{U} = \begin{pmatrix} 0 & 0 & 0 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}. \quad (1.2)$$

Reproduction appears as a “reward” associated with the transitions between the states of the Markov chain. Individuals moving from age j to age i collect the reward r_{ij} (Howard, 1960; Caswell, 2011). In demography (e.g., in population projections and the Euler-Lotka equation) age-specific fertility depends only on the current age; thus r_{ij} depends on j but not on the transition made between j and i .¹ We consider r_{ij} to be a random variable with a Bernoulli distribution (Caswell, 2011), thus ignoring multiple births:

$$r_{ij} = \begin{cases} 1 & \text{with probability } f_j \\ 0 & \text{with probability } (1 - f_j) \end{cases} \quad (1.3)$$

where the probabilities f_j are age-specific fertilities. We assume that individuals in the absorbing state accrue no rewards (i.e., the dead do not reproduce).

Calculating the statistical properties of lifetime reproductive output requires a set of matrices giving the moments of the reward for each transition; we call these *reward matrices*. That is, \mathbf{R}_k is a matrix of the k th moments of the transition-specific rewards r_{ij} . The first moment matrix is

$$\mathbf{R}_1 = \left(\begin{array}{ccc|c} f_1 & \dots & f_\omega & 0 \\ \vdots & \ddots & \vdots & \vdots \\ f_1 & \dots & f_\omega & 0 \\ \hline f_1 & \dots & f_\omega & 0 \end{array} \right) \quad (1.4)$$

where the upper right block is of dimension $\omega \times \omega$. Under the Bernoulli assumption, the higher-order moments are equal:

$$\mathbf{R}_1 = \mathbf{R}_2 = \mathbf{R}_3 \quad (1.5)$$

1.2.1.1 Lifetime accumulated rewards

We define $\boldsymbol{\rho}$ as a vector, of dimension $(\omega + 1) \times 1$, of accumulated rewards for each initial age. The entries in the first age class (age 0) refer to accumulated reproduction over the entire lifetime of the individual. The i th entry of $\boldsymbol{\rho}$ describes the accumulation over the remaining lifetime of an individual of age i . The vector of k th moments of $\boldsymbol{\rho}$ is denoted $\boldsymbol{\rho}_k$, where

$$\boldsymbol{\rho}_k = \left(E \left[\boldsymbol{\rho}_i^k \right] \right) \quad (1.6)$$

From the recursion equations presented in Caswell (2011), we obtain equations for the equilibria of $\boldsymbol{\rho}_k$ (Caswell & van Daalen, 2014, in prep.) Because the absorbing state accumulates

¹See Caswell (2014b) for a multistate model in which reproduction depends on age and parity, and rewards are explicitly associated with transitions among parity states.

no rewards, we are interested only in the subector $\tilde{\rho}$ giving the accumulation of rewards in the ω transient states. To this end, we define a matrix \mathbf{Z}

$$\mathbf{Z} = \left(\mathbf{I}_\omega \mid \mathbf{0}_{\omega \times 1} \right) \quad (1.7)$$

Multiplying ρ_i by \mathbf{Z} cleaves off the rewards for the absorbing states, leaving only the rewards for the transient states of the Markov chain. The equilibria for the first three moments of accumulated rewards are as follows:

$$\tilde{\rho}_1 = \mathbf{N}^\top \mathbf{Z} (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1}_{\omega+1} \quad (1.8)$$

$$\tilde{\rho}_2 = \mathbf{N}^\top \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1}_{\omega+1} + 2(\mathbf{U} \circ \mathbf{R}_1)^\top \tilde{\rho}_1 \right] \quad (1.9)$$

$$\tilde{\rho}_3 = \mathbf{N}^\top \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1}_{\omega+1} + 3(\mathbf{U} \circ \mathbf{R}_2)^\top \tilde{\rho}_1 + 3(\mathbf{U} \circ \mathbf{R}_1)^\top \tilde{\rho}_2 \right] \quad (1.10)$$

where $\mathbf{N} = (\mathbf{I}_\omega - \mathbf{U})^{-1}$ is the fundamental matrix of the Markov chain. The entries of the first moment vector $\tilde{\rho}_1$ give the mean remaining lifetime reproductive output of each age class. The other statistical properties of variance, standard deviation, coefficient of variation, and skewness of lifetime reproductive output are calculated from the moment vectors in the following way:

$$V(\tilde{\rho}) = \tilde{\rho}_2 - \tilde{\rho}_1 \circ \tilde{\rho}_1 \quad (1.11)$$

$$SD(\tilde{\rho}) = \sqrt{V(\tilde{\rho})} \quad (1.12)$$

$$CV(\tilde{\rho}) = \mathcal{D}(\tilde{\rho}_1)^{-1} SD(\tilde{\rho}) \quad (1.13)$$

$$Sk(\tilde{\rho}) = \mathcal{D}[V(\tilde{\rho})]^{-3/2} (\tilde{\rho}_3 - 3\tilde{\rho}_1 \circ \tilde{\rho}_2 + 2\tilde{\rho}_1 \circ \tilde{\rho}_1 \circ \tilde{\rho}_1). \quad (1.14)$$

1.2.2 Data: fertility and mortality

We obtained data on period survival and fertility from the Human Mortality Database (Human Mortality Database, 2014), the Human Fertility Database (Human Fertility Database, 2014) and the Human Fertility Collection (Human Fertility Collection, 2014). These age-specific data were available for 40 developed countries for varying numbers of years (Table 1.1).

For comparison with these developed countries, we analyzed two hunter-gatherer populations: the Hadza of Tanzania and the Ache of Paraguay, using mortality and fertility data from Gurven & Kaplan (2007), Blurton Jones (2011), and Hill & Hurtado (1996). The Hadza live in the sub-Saharan wooded savanna near Serengeti National Park. Women reproduce after marriage, starting from age 14 and peaking in their reproductive output around age 30 (Blurton Jones, 2011). The Ache live in the subtropical Paraná watershed of Eastern Paraguay. Ache women start reproducing at age 12 and reach a peak in reproduction around age 30-35 (Hill & Hurtado, 1996). Both Ache and Hadza populations are exposed to higher mortality than countries in the developed world, resulting in life expectancies of 37 and 34, respectively (Gurven & Kaplan, 2007). We also analyzed the ethnic Hutterites of North America, an Anabaptist religious sect with unregulated fertility reported to have the highest TFR of any known population (Eaton & Mayer, 1953). We used Hutterite fertility rates from a study by Eaton & Mayer (1953) covering the period of 1946-1950. We follow Eaton and Mayer in assuming that Hutterite mortality was similar to the overall U.S. rates during this period.

1.2.3 Characterizing patterns of LRO

The computation of LRO statistics from the available data permits many different comparisons. We will consider LRO by age, LRO over time, LRO in relation to socio-economic indicators, and the relationship among the different statistics in LRO. Here, we provide more detail of what each of these comparisons entails.

We will present the mean, standard deviation (SD), coefficient of variation (CV), and skewness (Sk) of remaining LRO as a function of age, for a fixed year. Over time, we will

Table 1.1: Table of countries used in our analyses. Sources refer to the databases from which we collected the data; HMD for the Human Mortality Database, HFD for the Human Fertility Database and HFC for the Human Fertility Collection.

| # | Country | Data Range | Years | Sources |
|----|-------------------|------------|-------|----------|
| 1 | Australia | 1921–2009 | 89 | HMD, HFC |
| 2 | Austria | 1951–2010 | 60 | HMD, HFD |
| 3 | Belarus | 1960–2008 | 47 | HMD, HFC |
| 4 | Belgium | 1952–2009 | 58 | HMD, HFC |
| 5 | Bulgaria | 1947–2009 | 63 | HMD, HFD |
| 6 | Canada | 1921–2009 | 89 | HMD, HFD |
| 7 | Czech Republic | 1950–2011 | 62 | HMD, HFD |
| 8 | Denmark | 1901–2011 | 111 | HMD, HFC |
| 9 | East Germany | 1956–2010 | 55 | HMD, HFD |
| 10 | England and Wales | 1938–2009 | 72 | HMD, HFD |
| 11 | Estonia | 1959–2010 | 52 | HMD, HFD |
| 12 | Finland | 1939–2009 | 71 | HMD, HFD |
| 13 | France | 1946–2010 | 65 | HMD, HFD |
| 14 | Germany | 1990–2010 | 21 | HMD, HFD |
| 15 | Hungary | 1950–2009 | 60 | HMD, HFD |
| 16 | Iceland | 1963–2009 | 47 | HMD, HFC |
| 17 | Ireland | 1955–2009 | 55 | HMD, HFC |
| 18 | Italy | 1930–2009 | 80 | HMD, HFC |
| 19 | Japan | 1947–2009 | 63 | HMD, HFD |
| 20 | Latvia | 1970–2011 | 42 | HMD, HFC |
| 21 | Lithuania | 1959–2010 | 52 | HMD, HFD |
| 22 | Luxembourg | 1966–2009 | 44 | HMD, HFC |
| 23 | Netherlands | 1950–2009 | 60 | HMD, HFD |
| 24 | New Zealand | 1948–2008 | 61 | HMD, HFC |
| 25 | Northern Ireland | 1974–2009 | 36 | HMD, HFD |
| 26 | Norway | 1967–2009 | 43 | HMD, HFD |
| 27 | Poland | 1970–2009 | 40 | HMD, HFC |
| 28 | Portugal | 1940–2009 | 70 | HMD, HFD |
| 29 | Russia | 1959–2010 | 52 | HMD, HFD |
| 30 | Scotland | 1938–2009 | 65 | HMD, HFD |
| 31 | Slovakia | 1950–2009 | 60 | HMD, HFD |
| 32 | Slovenia | 1983–2009 | 27 | HMD, HFD |
| 33 | Spain | 1922–2009 | 88 | HMD, HFC |
| 34 | Sweden | 1891–2010 | 120 | HMD, HFD |
| 35 | Switzerland | 1932–2011 | 80 | HMD, HFD |
| 36 | Taiwan | 1976–2010 | 35 | HMD, HFD |
| 37 | Ukraine | 1959–2009 | 51 | HMD, HFD |
| 38 | United Kingdom | 1974–2009 | 36 | HMD, HFD |
| 39 | USA | 1933–2010 | 78 | HMD, HFD |
| 40 | West Germany | 1956–2010 | 55 | HMD, HFD |

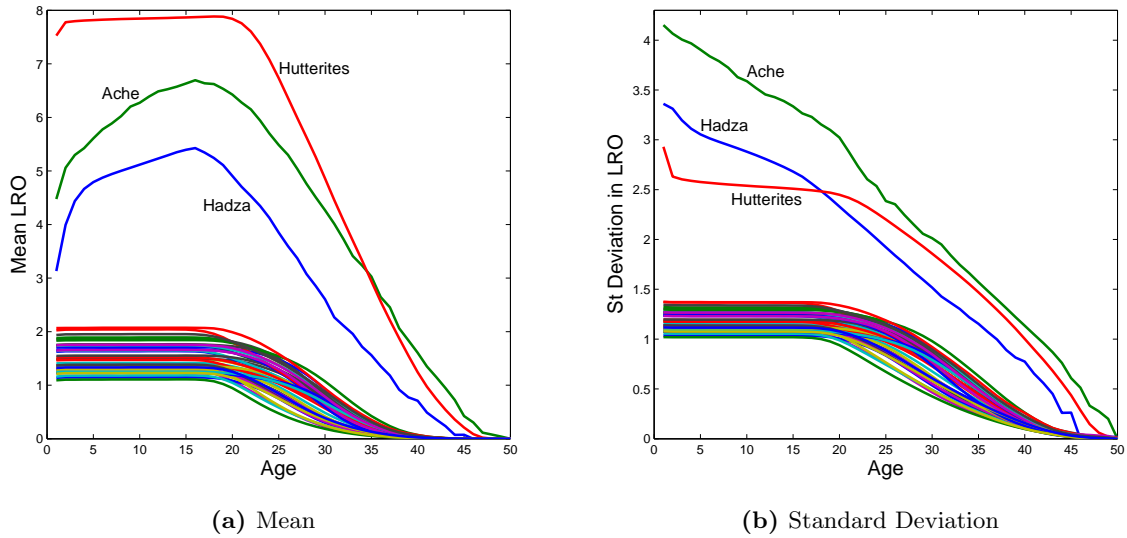


Figure 1.1: Mean and standard deviation of age-specific remaining lifetime reproductive output for 40 developed countries in the year 2000, 2 hunter-gatherer populations (the Ache and the Hadza), and a population of Hutterites.

show the patterns in mean LRO, standard deviation, coefficient of variation and skewness in LRO at birth for each country. Our focus lies on the period from 1965 to 2010, the period characteristically associated with the fertility transition. We assess whether our results for LRO are similar to known results using TFR and whether similar patterns arise in the other statistics of LRO.

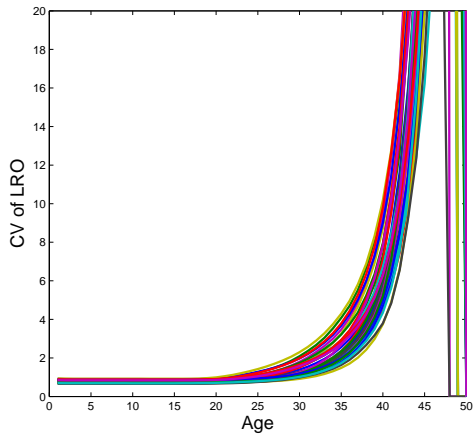
The relationship between LRO and socio-economic indicators is investigated using the Human Development Index, as LRO presumably responds to the conditions in which individuals find themselves. The HDI, as employed by the United Nations Development Programme, measures a country’s health, education and standard of living. These measures are assigned equal weight and combined into a broad-scale indicator of human development (UNDP, 2014). Myrskylä et al. (2009) found a relationship between period TFR and the human development index (HDI). Increases in the HDI up to ~ 0.9 were associated with declines in TFR, but above that point, they found evidence that the TFR began to increase. To evaluate such changes for the mean and variation, we regressed the statistics of LRO for all countries, at age 0, against the HDI for the years 1980 and 2009.

When viewed across countries or over time, the statistics of LRO show clear and non-random relationships among themselves. We examine these by looking for correlations among the statistics and examining temporal trajectories in the statistics.

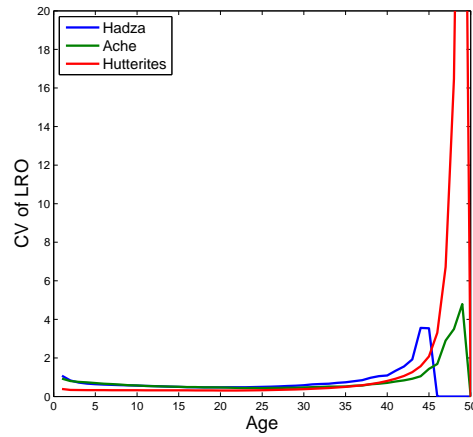
1.3 Results

1.3.1 LRO patterns over age

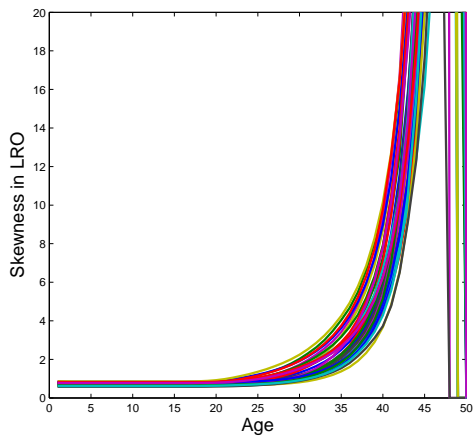
In Figure 1.1 the mean and standard deviation of remaining LRO are shown as a function of age. After age 20 all populations show a decline in both mean and SD, until women reach the age of infertility around age 45–50. The Hutterites show a slight increase in mean LRO between age 0 and age 1. In the two hunter-gatherer populations, mean remaining LRO increases with age between birth and age 20. These increases reflect the high infant mortality rates in these populations. The SD of remaining LRO decreases almost linearly with age for Ache and Hadza.



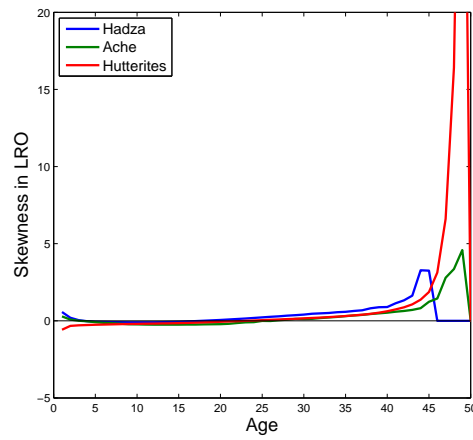
(a) CV for developed countries



(b) CV for hunter-gatherers and Hutterites



(c) Skewness for developed countries



(d) Skewness for hunter-gatherers and Hutterites

Figure 1.2: Coefficient of variation and skewness of age-specific remaining lifetime reproductive output for 40 developed countries in the year 2000, 2 hunter-gatherer populations (the Ache and the Hadza), and a population of Hutterites.

In Figure 1.2 the coefficient of variation (CV) and skewness (Sk) in remaining LRO are shown separately for developed countries and for the hunter-gatherers and Hutterites. The relative variation in remaining LRO, as measured by the CV, is between 0.5 and 1 at birth for the developed countries, but rises rapidly with age after age 25. The remaining LRO of women over age 40 is extremely variable; by age 45 the CV peaks at values between 40 and a little over 300. Hutterite lifetime CV is the lowest measured, falling just below 0.4. Ache lifetime CV is just below 1, whereas the Hadza are the only population with a CV at birth over 1.

The skewness of remaining LRO follows a similar pattern. Skewness at birth in the developed countries is slightly positive (between 0.5 and 1) and increases dramatically at older ages. Skewness in LRO at birth is slightly negative for the Hutterites, and remains so until after age 20. For the Hadza and Ache, skewness starts off between 0 and 1, drops to slightly negative values, then becomes positive again around age 20. Hadza and Ache women show lower peaks in CV and skewness around age 45, whereas Hutterites show variability comparable to developed countries at this age.

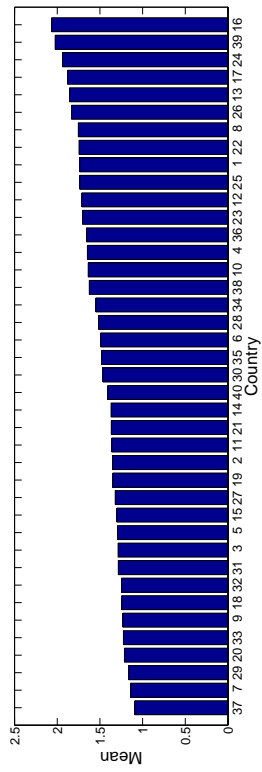
In Figure 1.3, the lifetime values for mean, standard deviation, CV and skewness of LRO at birth are shown for all 40 countries in the year 2000, corresponding to the values in the age dependent graphs at age 0. Mean LRO was below replacement (2.1) in 2000 for all countries.

1.3.2 Patterns over time

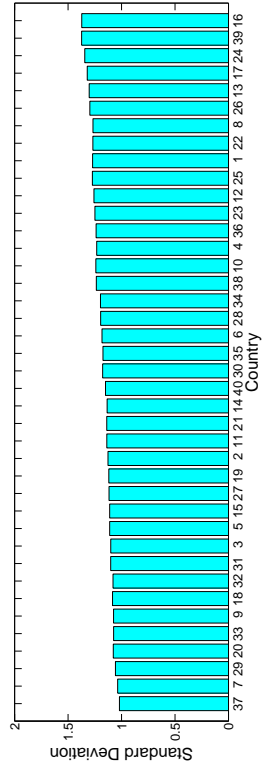
We focus on the period during which most developed countries experienced the fertility transition (1965-2010). Our results for mean LRO agree with other well-known results concerning the fertility transition: LRO declines sharply and then begins to rise again in recent years (Goldstein et al., 2009; Myrskylä et al., 2009). Measures of variability, however, display different patterns. The standard deviation of LRO also declines sharply from 1965 to about 2000, and shows signs of beginning to recover from 2000–2010. The coefficient of variation increases from 1965, levelling off after 2000. The skewness does the same, showing a very similar pattern to the CV.

The magnitude of increase or decrease in statistical properties of LRO differs between different countries. Moreover, not all countries show a reversal in pattern in the last 5-10 years. The time series for mean and standard deviation appear similar for all countries, and also inversely similar to CV and skewness.

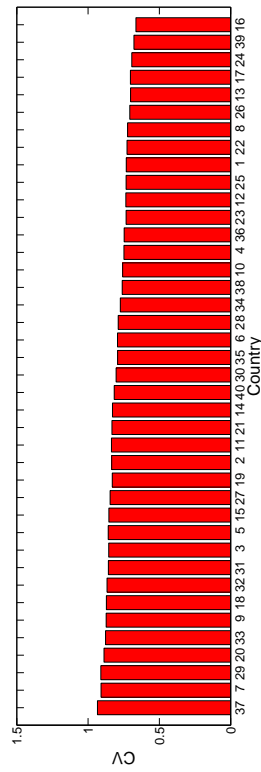
We have included a gallery showing the time series of the statistics of LRO at selected ages, for all 40 developed countries, in an Online Appendix.



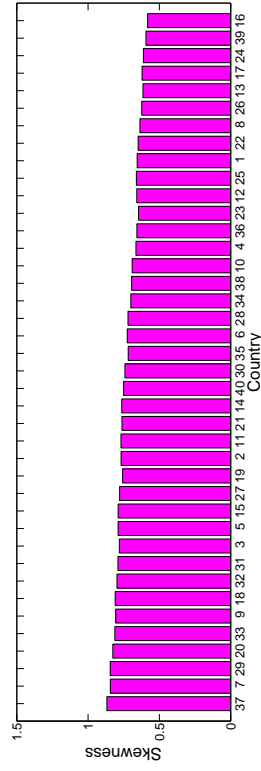
(a) Mean in the year 2000



(b) Standard Deviation in the year 2000



(c) CV in the year 2000



(d) Skewness in the year 2000

Figure 1.3: Statistics of LRO in the developed countries in the year 2000. The numbers on the x axis refer to the countries' number in Table 1.1.

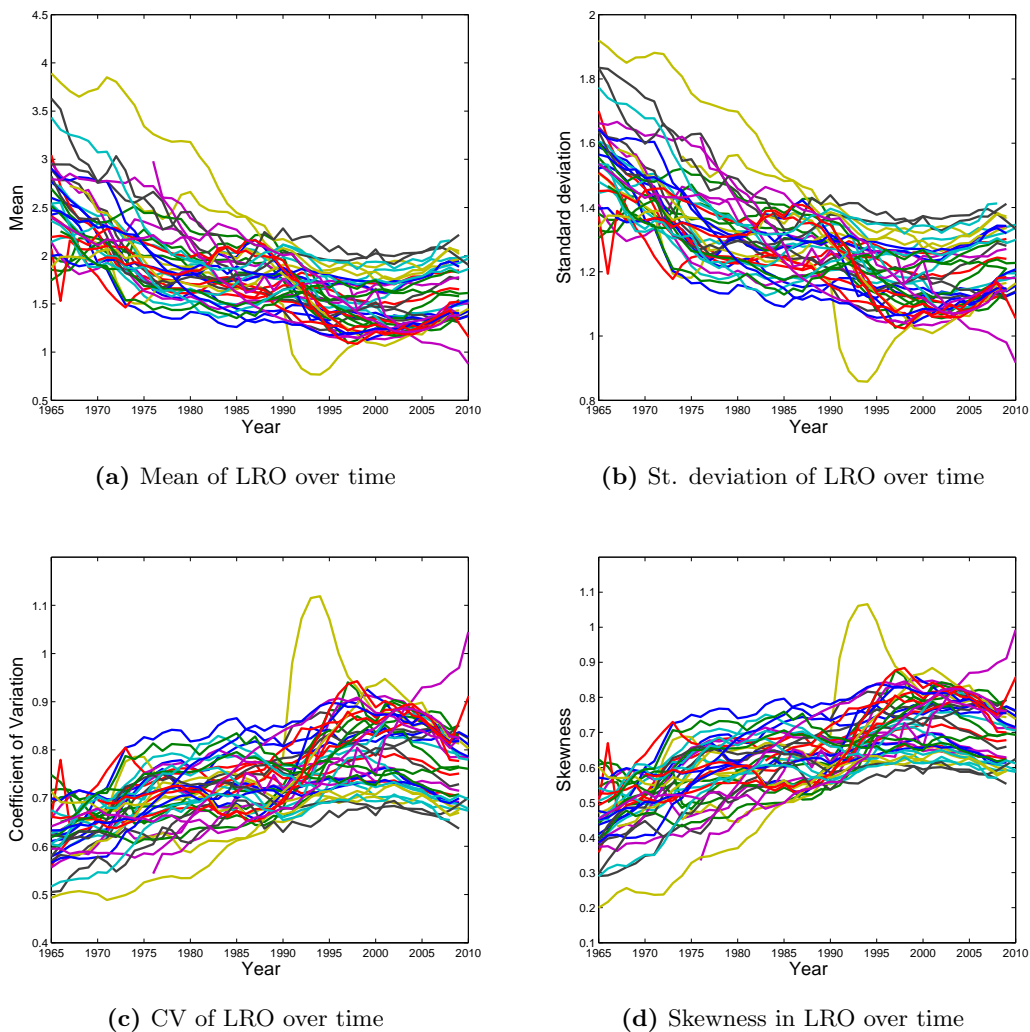
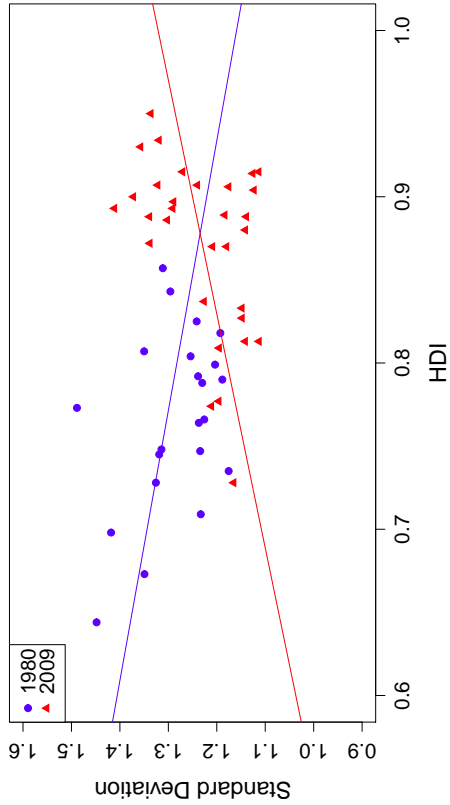


Figure 1.4: Mean, standard deviation, CV and skewness of lifetime reproduction over time for 40 developed countries. The yellow line is East Germany; reasons for its unusual trajectory have been discussed by Witte & Wagner (1995) and Adler (1997).

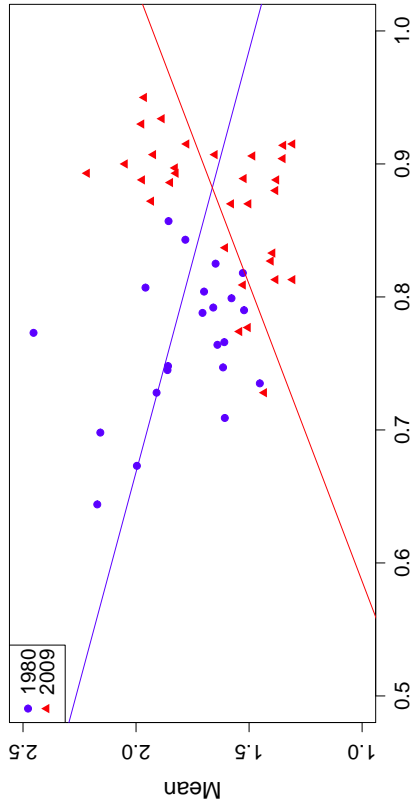
1.3.3 Relationship to HDI

The HDI is a synthetic index designed to describe socioeconomic living conditions. The decline in TFR during fertility transition has been associated with improvement in standards of living. Myrskylä et al. (2009) found that TFR declined with increases in the HDI up to a point, but that further increases in the HDI were associated with increases in TFR.

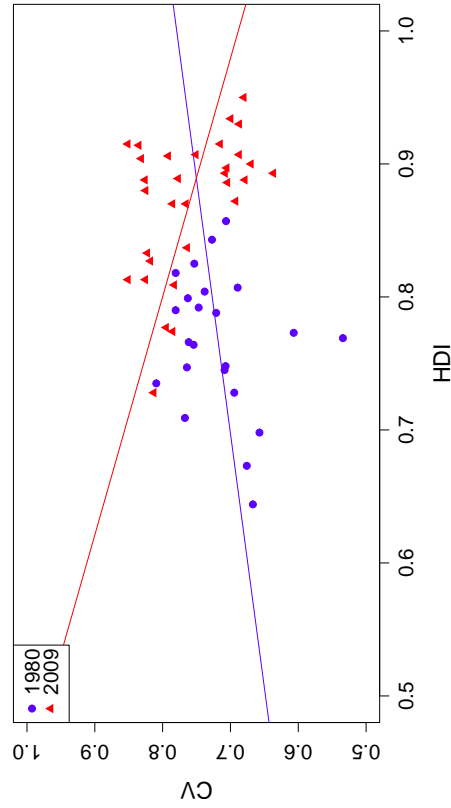
We analyzed the relation between the HDI and all four statistics of LRO in 1980 and again in 2009, at which point the HDI had increased notably. Similar to Myrskylä et al. (2009), we find a negative relationship between mean LRO and HDI in the year 1980, but a positive relationship in the year 2009 (see Figure 1.5(a)). Furthermore, we find a similar reversal in the relationship between HDI and the other statistical properties of LRO (see Figure 1.5(b-d)). The standard deviation decreased with HDI in the 1980, but increased with HDI in 2009. The CV and skewness show opposite patterns to mean and SD, as both increased with HDI in 1980 and decreased with HDI in 2009. In earlier years, with lower values of HDI, improvements in economic and living conditions led to reduced mean LRO and SD, but increased relative variability as measured by the CV and increased skewness. In later years, the slopes are



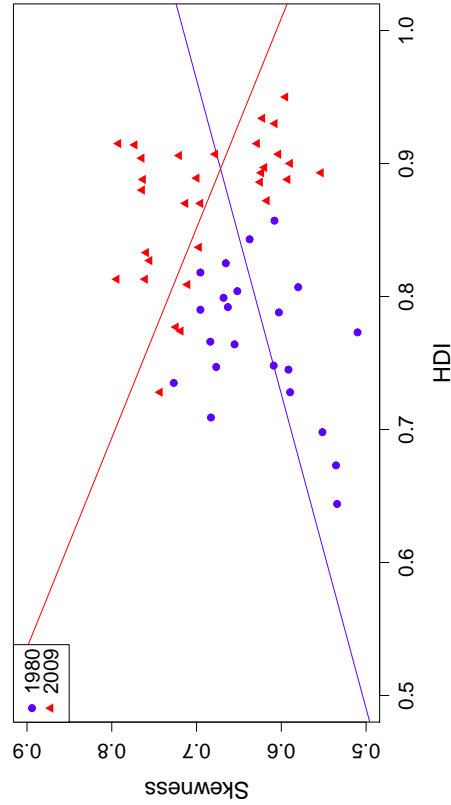
(a) Mean over HDI



(b) St. deviation over HDI



(c) CV over HDI



(d) Skewness over HDI

Figure 1.5: Relationship of mean, standard deviation, CV and skewness with the Human Development Index (HDI). Blue dots and lines represent this relationship in the year 1980, red triangles and lines represent the relationship in the year 2009. The regression line equations are presented in Table A1 in the Appendix.

reversed (see Table A1 for the regression line equations).

1.3.4 Relationships among the statistics of LRO

The mean, variance, coefficient of variation, and skewness provide a statistical characterization of the LRO implied by the life table and the fertility schedule. When compared across developed countries, a general relationship between these statistics exists. The scatterplot in Figure 1.6 shows the relationships among all statistics for all countries in the year 2000. The mean and standard deviation of LRO are positively related to each other, as are CV and skewness. The former statistics are, however, negatively related to the latter (see Table A2 for regression line equations).

When we added data from two additional years (1990 and 2005), the statistics of LRO became slightly less tightly distributed (van Daalen and Caswell, unpublished data). To further explore changes over time, we created phase portraits showing the dynamics of the mean and SD over the historical records available for the countries. Figure 1.7 shows the time trajectories for 4 countries (Bulgaria, Canada, Japan, and Sweden). The dotted line in the figures is the regression line relating the mean and SD in the scatterplot in Figure 1.6.

In all four countries, the mean and SD of lifetime reproduction converge to the inter-country regression line. Before the convergence statistics of LRO were more variable both within and between countries. After this convergence countries moved along the line, with both the mean and SD declining at first, before increasing again, as is also shown in Figure 1.4. The fact that the countries practically “retrace their steps” along the line reinforces the idea of the existence of a universal distribution of LRO to which developed countries appear to converge. Similar patterns were found in all 40 countries we examined.

1.4 Discussion

Markov chains with rewards provide valuable information on the statistical properties of lifetime reproduction during the fertility transition. Among a sample of 40 developed countries, repeated patterns were shown to occur over both age and time. In three high fertility populations (the Ache in Paraguay, the Hadza in Tanzania and the Hutterites of North America) mean lifetime reproductive output is, unsurprisingly, higher than in developed countries, but the Ache and Hadza also show a substantial increase in mean remaining LRO between age 0 and age 20 due to high childhood mortality rates. Once individuals have this period of high mortality behind them, mean remaining LRO is higher. The effects of this high childhood mortality on the age patterns of variance and skewness remains to be investigated.

The similarity in patterns among the 40 developed countries suggests a relationship among the statistical properties of lifetime reproduction. Whenever mean LRO changes, the other moments change along with it. Therefore, during the fertility transition, not only mean LRO, but the entire distribution of lifetime reproductive output changed. The fertility transition was characterized by a decreasing mean lifetime reproductive output, a decreasing standard deviation (so a decreasing spread in values), an increasing CV (i.e. an increase in the measure of relative variation) and an increasing, positive skewness (an increase in the degree of asymmetry characterizing the distribution).

Our estimates of the statistics of LRO do not incorporate any kind of heterogeneity among individuals. The calculations, like all life table calculations, assume that all individuals experience the same rates of mortality and reproduction at any age. Variation arises only due to individuals taking different trajectories through life (by dying at different ages) or succeeding or failing at reproduction at a given age due to chance. Together, these two sources are termed individual stochasticity.

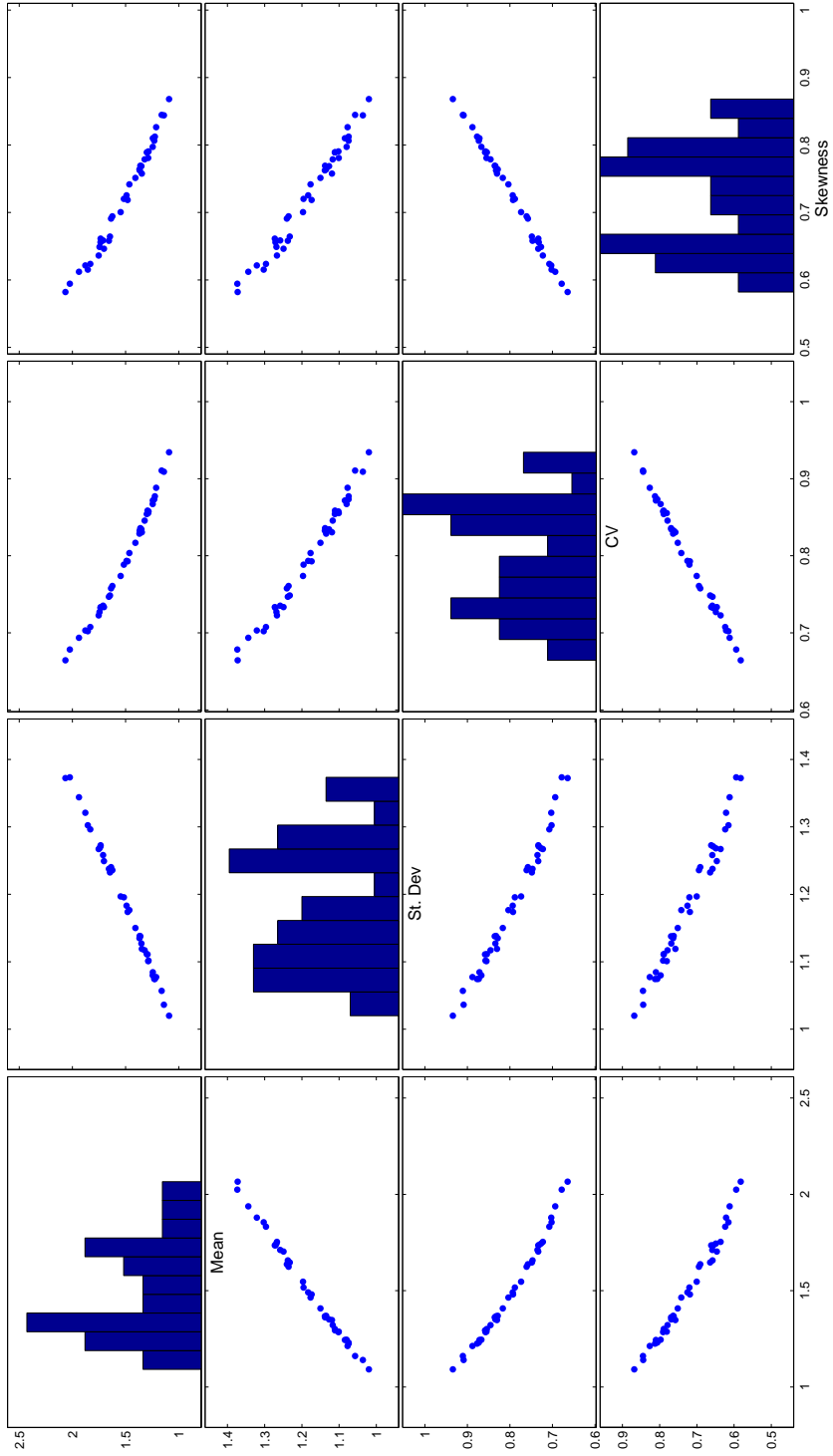
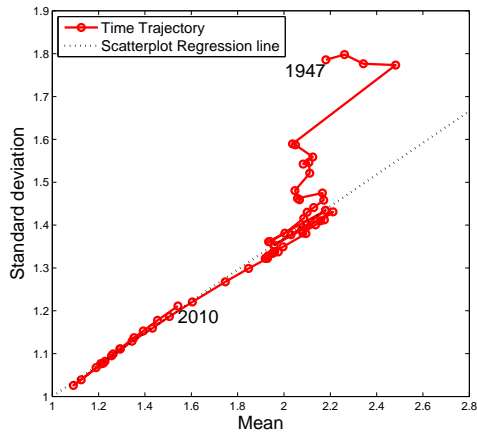
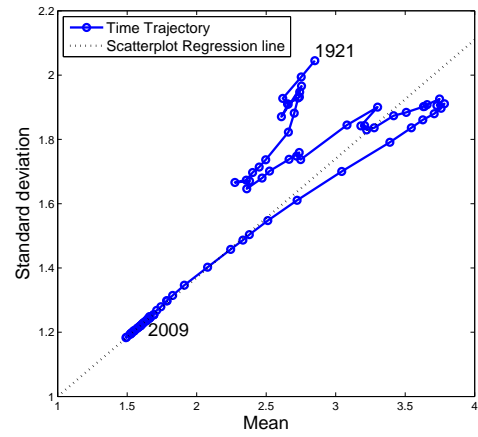


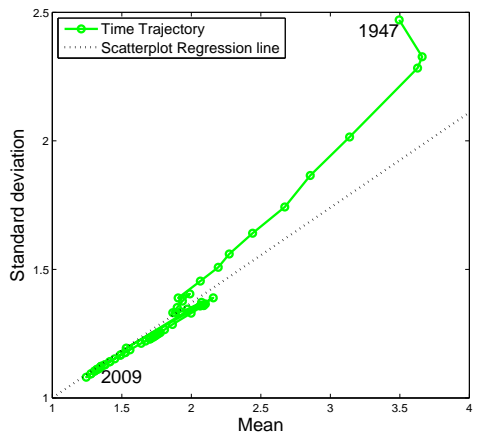
Figure 1.6: Scatterplot of the mean, standard deviation, CV and skewness of LRO for 40 developed countries in the year 2000.



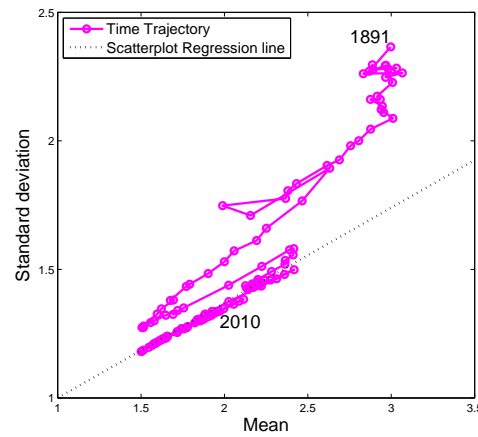
(a) Bulgaria



(b) Canada



(c) Japan



(d) Sweden

Figure 1.7: Trajectories of the mean plotted against standard deviation over time. The starting and ending years are indicated for each trajectory. The dotted lines represent the regression line through the scatterplot of mean and SD shown in Figure 1.6.

They can be partitioned by comparing the variance from the full model with the results of a model with fixed rewards. In a fixed reward model (Caswell, 2011) a fertility of f_i implies that every individual of age i produces a fraction f_i of a child, rather than producing one or zero children with probabilities f_i and $1 - f_i$.

Figure 1.8 shows the fraction of the variance in LRO due to the variance in rewards, as a function of life expectancy, for the developed countries in our dataset. These countries have high levels of social security and highly developed health care, and thus low mortality. As life expectancy increases, the proportion of variance explained by the randomness in the rewards approaches 1. We conclude that improvement of health and life expectancy, and the subsequent reduction of the influence of mortality, plays a crucial role in determining the distribution of lifetime reproduction of developed countries.

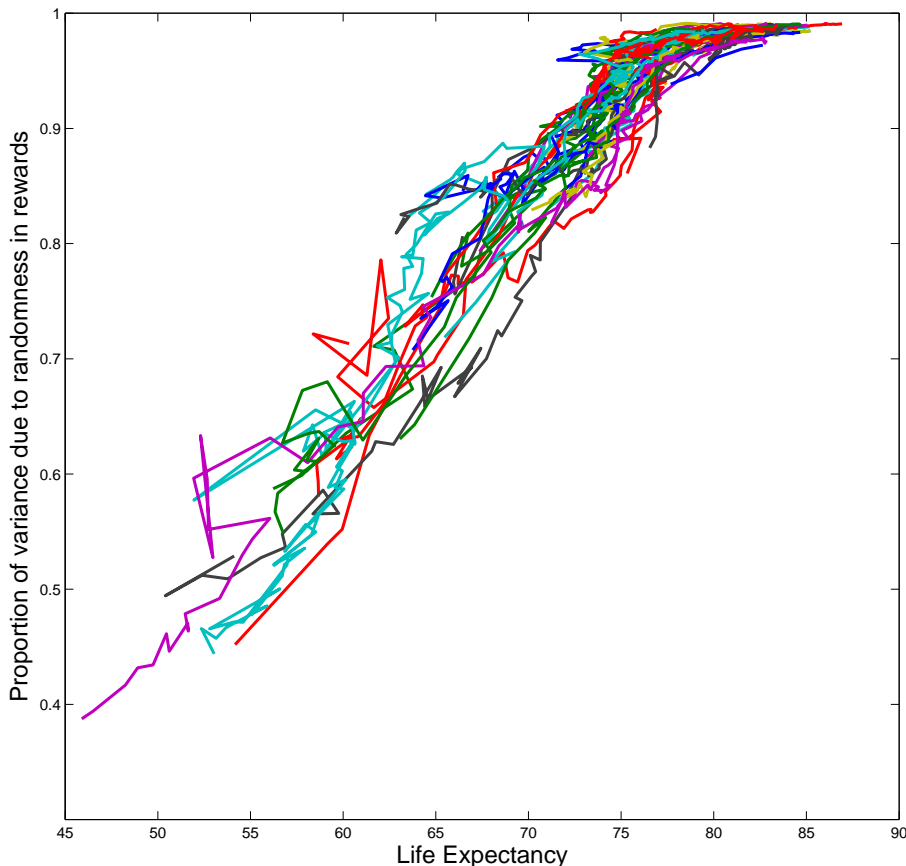


Figure 1.8: The contribution of the randomness of the reward to variance in LRO, as a function of life expectancy, both calculated at every point in time for all 40 developed countries.

The tight link between statistical properties of LRO across different developed countries in the year 2000 (Figure 1.6) suggests a universal distribution of LRO. If mortality were so low that all individuals survived through their reproductive years, then LRO would be the sum of 50 Bernoulli trials, with a different probability at each age. Such a sum is a random variable with a Poisson-binomial distribution. If the probabilities are small enough, the Poisson-binomial distribution is well approximated by the Poisson distribution (Le Cam, 1960; Steele, 1994).

The mean and variance of the Poisson distribution are equal, the coefficient of variation is a function of the mean, and the coefficient of variation and skewness are equal. We observe

these relationships to some extent in Figure 1.6 when mortality has become very low in these countries. In earlier years, or in the fixed reward model, the relationships among the statistics of LRO are much looser (van Daalen and Caswell, unpublished data).

The inter-individual variation in LRO shown here is a function of individual stochasticity alone. Our results do not incorporate heterogeneity among individuals in mortality or fertility. They could be interpreted as baseline results in comparison to measurements of actual lifetime reproduction (Caswell, 2011; Steiner & Tuljapurkar, 2012). Adding heterogeneity to the model may increase the variance in LRO (Steiner & Tuljapurkar, 2012). However, incorporating dynamic heterogeneity may also reduce the variance in LRO, as in a case where heterogeneity due to parity is added to a fertility model (Caswell, 2014b). The overall effect of heterogeneity on LRO is an open problem.

The analysis of fertility patterns using Markov chains with rewards provides new insight into the demographic factors influencing lifetime reproductive output. Our approach makes it possible to explore the addition of heterogeneity to the model. This can be achieved by developing multistate models that include more details in the reproductive process (Caswell, 2014b) or by linking the results to Markov chain models incorporating heterogeneous frailty (Caswell, 2014a). Sensitivity analysis of these models will show how the statistics of LRO respond to changes in the parameters of the mortality and fertility schedules (Caswell & van Daalen, 2014). Finally, we note that the approach can be applied to rewards other than reproductive output, including health and longevity (Caswell and Zarulli, unpublished data) and lifetime accumulation of economic rewards (Caswell & Kluge, 2014).

Chapter 2

Lifetime Reproductive Output in Birds and Mammals

Contributions of Heterogeneity and Individual Stochasticity to Variance in LRO

2.1 Introduction

Variation in lifetime reproductive output has important demographic and evolutionary properties Caswell (2011). Crow (1958) describes a method to calculate the opportunity for selection from the variance in LRO. Crow's Index of Total Selection is calculated as $I = \text{variance}/\text{mean}^2$, which also provides an upper limit to the strength of selection. This index, often referred to as the *standardized variance*, is utilized to investigate the contribution of different components of reproductive success (i.e. survival, longevity, fecundity and offspring survival; Brown (1988)) to LRO. For example, in gorillas male lifetime reproductive output is mostly determined by offspring survival, while female LRO shows little variance due to low environmental variability (Breuer et al., 2010; Robbins et al., 2011).

Variance in lifetime reproductive output, however, arises from different underlying sources of variation. Variation can be due to stochasticity or due to heterogeneity between individuals. Heterogeneity can be thought of as individuals experiencing different vital rates during their lifetime, whereas stochasticity refers to individuals experiencing the same vital rates, but due to chance and luck, individuals differ in their reproductive output (Tuljapurkar et al., 2009; Caswell, 2011). Increasingly, studies have argued that the largest part of variation in LRO is caused by these stochastic factors and is therefore non-heritable (e.g. Newton (1989); Steiner & Tuljapurkar (2012)). In order to identify the relative contributions of both sources of variation it is necessary to separate the processes of heterogeneity and stochasticity. It is now possible to calculate lifetime reproductive output when only incorporating stochasticity and leaving out heterogeneity (Caswell, 2011). Stochasticity contributes to variation in LRO in two ways. Firstly, individuals experiencing the same vital rates can differ in the trajectories they follow through the life cycle (individual stochasticity sensu Caswell (2011)). Secondly, individuals of a given age or stage can experience stochasticity in their reproductive output (Caswell, 2011).

Caswell (2011) presents a novel method to calculate the mean and variance of LRO that incorporates stochastic variation and is generally applicable. Using Markov chains with rewards, any species that is described by a projection matrix can be assessed. Markov chains model the transitions of individuals within the life cycle. As individuals transition, they accumulate rewards, which, in this case, constitutes reproduction (Howard, 1960; Caswell, 2011). The Markov chain with rewards method identifies potentially interesting patterns in LRO within

and between species. Furthermore, it produces a baseline level of variance (without fixed heterogeneity) to which observed variances can be compared to investigate what proportion of variance is heritable and what proportion of variance is mainly due to luck.

This study investigates the contributions of individual stochasticity and heterogeneity to the variance in lifetime reproductive output in several species of birds and mammals. Should the modeled estimates be equal to the observed estimates, it can be concluded that all the variation in lifetime reproduction in that species is caused by individual stochasticity and, as such, heterogeneity does not contribute to the variation in LRO. Previous studies have shown that for *C. elegans* and kittiwakes most, if not all, of the variance in reproductive success is due to individual stochasticity (Caswell, 2011; Steiner & Tuljapurkar, 2012; Steiner et al., 2010). The current study aims to provide more comparisons of this kind in order to investigate the generality of these findings.

2.2 Methods

Notation. Matrices are denoted by upper-case bold symbols (e.g., \mathbf{P}), vectors by lower-case bold symbols (e.g., $\boldsymbol{\rho}$). Vectors are column vectors by default. The transpose of \mathbf{P} is \mathbf{P}^\top . The inverse of \mathbf{P} is \mathbf{P}^{-1} . The vector $\mathbf{1}$ is a vector of ones, and the matrix \mathbf{I} is the identity matrix. Where necessary to avoid confusion, dimensions are indicated by subscripts; e.g., the $\omega \times \omega$ identity matrix is \mathbf{I}_ω . The diagonal matrix with the vector \mathbf{x} on the diagonal and zeros elsewhere is denoted $\mathcal{D}(\mathbf{x})$. The expected value is denoted by $E(\cdot)$. The Hadamard, or element-by-element, product of matrices \mathbf{A} and \mathbf{B} is denoted by $\mathbf{A} \circ \mathbf{B}$. Transition matrices of Markov chains are written in column-to-row orientation, and hence their columns sum to one.

2.2.1 Markov chains with rewards explained

Markov chains with rewards can be used to model the life cycles of organisms (Caswell, 2001, 2009, 2011). Individuals from a given species can transition from one state to the next, where the state can represent age or stage (e.g. developmental or breeding stage). The probabilities of an individual moving between ages/stages are captured in the Markov chain. Individuals also have a probability of dying. Therefore, death is included as an absorbing state in the Markov chain:

$$\mathbf{P} = \left(\begin{array}{c|c} \mathbf{U} & \mathbf{0} \\ \hline \mathbf{m}^\top & 1 \end{array} \right) \quad (2.1)$$

The number of states is denoted by ω . The matrix \mathbf{U} (dimension $\omega \times \omega$) contains the transition probabilities from one state to the next. In the case of age-structured populations transition probabilities are found only on the subdiagonal of the matrix;

$$\mathbf{U} = \begin{pmatrix} 0 & 0 & 0 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}. \quad (2.2)$$

In the case of stage-structured populations where, for example, transitions between breeding stages take place, it could be possible to get from any stage to any other stage. In that case every entry in \mathbf{U} could contain a transition probability.

Reproduction appears in the model as a “reward”. For a given transition between state j to state i an individual can collect reward r_{ij} . The rewards are random variables. Given that the moments of the distribution of reproduction are often not reported in empirical studies, we calculated the moments of the rewards using an assumed distribution. Depending on the species and the type of reproduction taking place, either a Bernoulli or a Poisson distribution is assumed. The former applies to species that exhibit a probability of producing a single offspring, whereas the latter is suitable for species that produce multiple offspring at a single

reproductive event. We assume that individuals in the absorbed state cannot collect any rewards (i.e., the dead do not reproduce).

Transition-specific rewards can be collected into *reward matrices*. Different reward matrices contain the different moments of the reward for each transition. Thus, \mathbf{R}_k collects the k th moments of the rewards r_{ij} . The first moment matrix is

$$\mathbf{R}_1 = \left(\begin{array}{ccc|c} f_1 & \dots & f_\omega & 0 \\ \vdots & \ddots & \vdots & \vdots \\ f_1 & \dots & f_\omega & 0 \\ \hline f_1 & \dots & f_\omega & 0 \end{array} \right) \quad (2.3)$$

where f_j is the fertility rate or number for the current state. The upper left block is of dimension $\omega \times \omega$. Under the Bernoulli assumption, the higher-order moments are equal:

$$\mathbf{R}_1 = \mathbf{R}_2 = \mathbf{R}_3 \quad (2.4)$$

Under the Poisson assumption, \mathbf{R}_2 and \mathbf{R}_3 are calculated as follows:

$$\mathbf{R}_2 = \left(\begin{array}{ccc|c} f_1(1+f_1) & \dots & f_\omega(1+f_\omega) & 0 \\ \vdots & \ddots & \vdots & \vdots \\ f_1(1+f_1) & \dots & f_\omega(1+f_\omega) & 0 \\ \hline f_1(1+f_1) & \dots & f_\omega(1+f_\omega) & 0 \end{array} \right) \quad (2.5)$$

$$\mathbf{R}_3 = \left(\begin{array}{ccc|c} f_1(1+3f_1+f_1^2) & \dots & f_\omega(1+3f_\omega+f_\omega^2) & 0 \\ \vdots & \ddots & \vdots & \vdots \\ f_1(1+3f_1+f_1^2) & \dots & f_\omega(1+3f_\omega+f_\omega^2) & 0 \\ \hline f_1(1+3f_1+f_1^2) & \dots & f_\omega(1+3f_\omega+f_\omega^2) & 0 \end{array} \right) \quad (2.6)$$

We define a vector $\boldsymbol{\rho}$ (dimension $(\omega + 1) \times 1$) of accumulated rewards over the lifetime for every initial state. That is, the first entry of this vector is the lifetime reproductive output of an individual that starts accumulating rewards starting from age 0. The i th entry of $\boldsymbol{\rho}$ contains the reproductive output of an individual in stage/age i . As individuals in the dead stage do not reproduce, we can define a subvector $\tilde{\boldsymbol{\rho}}$, which contains the accumulated rewards for the ω transient states. We define

$$\tilde{\boldsymbol{\rho}}_i = \mathbf{Z}\boldsymbol{\rho}_i \quad (2.7)$$

where

$$\mathbf{Z} = \left(\mathbf{I}_\omega \mid \mathbf{0}_{\omega \times 1} \right). \quad (2.8)$$

The equilibria for the first three moments of accumulated reproductive output then become

$$\tilde{\boldsymbol{\rho}}_1 = \mathbf{N}^\top \mathbf{Z} (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1}_{\omega+1} \quad (2.9)$$

$$\tilde{\boldsymbol{\rho}}_2 = \mathbf{N}^\top \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1}_{\omega+1} + 2(\mathbf{U} \circ \mathbf{R}_1)^\top \tilde{\boldsymbol{\rho}}_1 \right] \quad (2.10)$$

$$\tilde{\boldsymbol{\rho}}_3 = \mathbf{N}^\top \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1}_{\omega+1} + 3(\mathbf{U} \circ \mathbf{R}_2)^\top \tilde{\boldsymbol{\rho}}_1 + 3(\mathbf{U} \circ \mathbf{R}_1)^\top \tilde{\boldsymbol{\rho}}_2 \right] \quad (2.11)$$

where

$$\mathbf{N} = (\mathbf{I}_\omega - \mathbf{U})^{-1}. \quad (2.12)$$

\mathbf{N} is the fundamental matrix of the Markov chain.

The first moment reward vector $\boldsymbol{\rho}_1$ gives the mean remaining lifetime reproductive output (LRO) for each age class. Additional statistical properties of LRO, such as the variance and standardized variance, can be calculated as

$$V(\tilde{\boldsymbol{\rho}}) = \tilde{\boldsymbol{\rho}}_2 - \tilde{\boldsymbol{\rho}}_1 \circ \tilde{\boldsymbol{\rho}}_1 \quad (2.13)$$

$$SV(\tilde{\boldsymbol{\rho}}) = \mathcal{D}(\tilde{\boldsymbol{\rho}}_1)^{-2} V(\tilde{\boldsymbol{\rho}}) \quad (2.14)$$

2.2.2 Empirical and modeled measures of LRO

Robbins et al. (2011) tabulated empirical measures of LRO and standardized variance for 22 species of vertebrate animals. We searched for demographic models for each species, from which we could calculate the statistics of LRO, to compare with the empirical measurements. We were able to find the necessary models for 16 species (see Table 2.1). Unless stated otherwise, model data was retrieved from the same location as empirical data. In two cases, models could not be created for the exact same species and a closely related species was used instead.

Mountain gorilla (*Gorilla beringei beringei*): Robbins et al. (2011) monitored a set of 13 breeding females for their entire adult lifespan. Gorillas are typically considered adults at age 8. The study took place in the Virunga Volcano region of Uganda, Rwanda and the Democratic Republic of Congo. LRS was defined as the total number of offspring (both sexes) that survived until weaning age (3 years). (p. 584)

The age-structured model for Mountain gorillas is parameterized using survival data ($\ell(x)$) from Robbins & Robbins (2004) (Table 2) and fertility data ($m(x)$) from Robbins et al. (2011) (Supporting information, Text S1, section B). A very low probability of breeding before age 8 is included, and individuals do not grow older than 44 years. Bernoulli distributed rewards were assumed.

Ache hunter-gatherers (*Homo sapiens*): Hill & Hurtado (1996) studied a cohort of Ache hunter-gatherers born between 1890-1909. Cohort size is unspecified. These cohort members were at least 60 years old at time of first contact and had thus completed their reproductive career before the contact period. LRS was measured as offspring (both sexes) that survived to age 15. The study took place in Alto Parana, Paraguay. (description on p. 386, bottom part of figure 12.5, p. 411).

Age-specific fertility rates were obtained from the same source (Hill & Hurtado, 1996) (p. 261). Age-specific mortality was from an unknown source, very similar to the rates reported by Hill & Hurtado (1996) on page 196. Rewards were assumed to be Bernoulli distributed.

African lion (*Panthera leo*): Packer et al. (1988) studied several prides of lions in the Ngorongoro crater and on the Serengeti plains of Tanzania. 54 female lions that reached 8 years of age were included in the study. Reproductive success is the number of offspring (both sexes) that reach 12 months of age. Upon reaching 4 years of age individuals become reproductive. (p. 368, table 23.1 on p. 370).

The model was parameterized using mx data from the supplementary material from Jones et al. (2014). We used 2 different sources of $\ell(x)$: $\ell(x)$ reported by Jones et al. (2014), based on Packer et al. (1998) and an $\ell(x)$ we calculated from data in the supplementary material from Jones et al. (2014), using a more simple calculation. Poisson distributed rewards were used.

Red deer (*Cervus elaphus*): Kruuk et al. (2000) studied red deer on the Isle of Rhum, Scotland. Breeding success of 202 females was defined as the number of offspring of both sexes produced over their lifetime. (Table 1, p. 699, description p. 700).

The model was parameterized using $\ell(x)m(x)$ data from Lowe (1969) (Tables 8 and 13). Fertility data was presented as the number of daughters per hind. In order to be able to compare the modeled LRO estimates to the measured LRS, production of both sexes was calculated. This was done by multiplying $m(x)$ by 2 for young and old hinds, and by 1.616 for hinds in their prime, as prime hinds were shown to have a significantly skewed offspring sex ratio. We assumed Bernoulli distributed rewards.

Chacma baboon (*Papio ursinus griseipes*): Cheney et al. (2004) studied a population of gray-footed chacma baboons in the Okavanga Delta of Botswana. 42 females (of which only 24 had died and, thus, completed their reproductive lifespan) were assessed. LRS was the number of offspring (both sexes) that survived to age 1. (p. 420, table II)

Age-specific mortality and fertility data for Chacma baboons could not be found, so instead, we calculated LRO for another species of baboon, the Yellow Baboon (*Papio cynocephalus*) in Amboseli park, Kenya. The model was parameterized with data from Altmann & Alberts (2003) (Table 6-1). Bernoulli distributed rewards were assumed.

Rhesus Macaque (*Mulatta mulatta*): Blomquist (2009) studied rhesus macaques on the island Cayo Santiago near Puerto Rico. LRS was calculated as the number of offspring produced by 208 females that reproduced. (Females that failed to reproduce before dying were excluded, although values for all females are reported: mean 3.23, ofs 1.5035, n=377).

Several different models were investigated for rhesus macaques. We obtained life table data from Sade et al. (1975)(table 1, p. 258) and matrix models from Hernández-Pacheco et al. (2013)(table 1, page 4). The matrices from Hernández-Pacheco et al. (2013) included a high-density and a low-density situation. These matrices were transformed from a partly age-specific matrix with a final breeding stage into a completely age-specific matrix, with breeding stage probabilities of survival and reproduction simply copied for the next age. We expanded the matrix until it had 25 age classes, as female go into menopause at age 25. For both the life table data from Sade et al. and the matrix models, the production of females per female was measured. To be able to compare to the empirical estimates we multiplied this output by 2. Rewards were assumed to be Bernoulli distributed.

Tawny Owl (*Strix aluco*): Millon et al. (2010) studied a population of Tawny owls in Kielder forest, northern England. 41 females born in Kielder forest were observed. LRS was measured as lifetime production of fledglings (both sexes). (p. 428)

For Tawny Owls, we also included several different models. Francis & Saurola (2004, Table 6) report projection matrices for Tawny Owls in Finland for different points in the Vole cycle, the tawny owls' primary prey. Matrices for low, medium, and high vole abundances and one for the mean over the entire cycle were retrieved. Furthermore, 2 additional sources of life table data were used. Both Southern (1970, table III(b)) and Dempster (1975) provide survival rates and mean offspring number over all years of breeding for Tawny owls in Wytham woods, England. All models were run with Poisson distributed rewards.

Roe deer (*Capreolus capreolus*): Vanpé et al. (2008) studied a population of roe deer in Bogesund, Sweden. 28 does of known age were followed through a 10-year period and only those deer that completed their life span naturally were included. LRS was based on observations of weaned fawns of both sexes (p. 313). The mean was not reported.

A life table for Roe deer in Chize, France, was acquired from the supplementary material of Jones et al. (2014). We analyzed the resulting matrix model in two ways: with Poisson distributed rewards and using an empirical calculation of the higher moment rewards. This new way required knowledge of the probability of roe deer females producing either 1, 2, or 0 offspring at any age.

Eastern Kingbird (*Tyrannus tyrannus*): Murphy & Sandercock (2007, p. 1014) studied Eastern Kingbirds in Charlotte valley in Delaware and Otsego counties in New York. 136 females with complete breeding data were included in the analysis. LRS was calculated as the number of young (both sexes) fledged over a lifetime.

The model for eastern kingbird was composed of vital rates mentioned on page 1013 of Murphy & Sandercock (2007). The model includes non-breeders, successful breeders, failed

breeders and replacement breeders (failed breeders who manage to replace their first nest). Rewards were assumed to be Poisson distributed.

Chimpanzee (*Pan troglodytes*): Nishida et al. (2003) studied a large group of Chimpanzees in the Mahale Mountains National Park, Tanzania. 26 females that were observed from a young age until their deaths provided complete birth records. LRS was measured as the number of weaned offspring (both sexes). (p. 111)

The data that was used for modelling chimpanzees came from a synthetic life table, that is, a life table composed of survival and fertility rates from several populations of chimpanzees from Tanzania, Uganda, Guinea and Cote d'Ivoire (fertility from SI material of Emery Thompson et al. (2007), survival from Hill et al. (2001)). A second model was tested for which the exact source was unknown. Rewards were assumed to be Bernoulli distributed.

Common Buzzard (*Buteo buteo*): Krüger & Lindström (2001) studied a population of Common buzzard in Westphalia, Germany, in an 11-year study. LRS is (most likely) calculated as the mean number of offspring of both sexes produced over the lifetime of a female. (p. 262)

As Krüger & Lindström (2001) used a matrix model in their original analysis, we could use this same matrix model after receiving the parameters through personal communication with the author. We used the Poisson assumption for the distribution of rewards.

Subantarctic fur seal (*Arctocephalus tropicalis*): Beauplet & Guinet (2007) studied a colony of subantarctic fur seals on Amsterdam Island in the southern Indian Ocean. Females had a reproductive lifespan of around 10 years. 126 females were included in the study, each contributing at least 5 years of reproduction. LRS was measured as the number of offspring weaned (both sexes) that had a sufficient growth rate to be likely to survive the post-weaning period. (p. 1879)

A matrix model for Antarctic fur seals on Bird Island, South Georgia was used (Forcada & Hoffman, 2014). As this model focused solely on female offspring, fertility was doubled, assuming 0.5 as the sex ratio, to model production of offspring of both sexes. We received the parameters of the model through personal communication. Bernoulli distributed rewards were used.

Cheetah (*Acinonyx jubatus*): Kelly et al. (1998) studied Cheetahs on the Serengeti plains, Tanzania, for a period of 25 years. 108 independent females were followed. The mean age at independence was 17.1 months. LRS was determined as the average number of cubs raised to independence over the mothers lifetime. (methods p. 476, Independence p. 477, and results of LRS p. 479)

Lubben et al. (2008) provided a matrix model of the Serengeti cheetah. As they modeled only female offspring, fertility was multiplied by 2. Also, in order to match the requirement that individuals aren't followed until independence, we multiplied all fertilities by the product of the survival rates of the first 3 stages in Lubben et al. (2008) (the fourth being Independent cheetahs). Lifetime reproductive output became the reproductive output of a stage 4 individual. Poisson distributed rewards were used.

Great Tit (*Parus major*): McCleery & Perrins (1988) studied Great tits in Wytham woods, Oxford, U.K., where 50 years of data has been collected on this species. LRS is measured as the number of offspring (both sexes) that is recruited into the breeding population. (Table 2, p. E65)

The life table from the study mentioned above was used to parameterise the matrix model (McCleery & Perrins, 1988, p. 140). We assumed rewards were Poisson distributed.

Table 2.1: Table of species used in our analyses.

| # | Empirical Species | Nr. of matrices | Notes |
|----|------------------------|-----------------|---|
| 1 | Mountain Gorilla | 1 | - |
| 2 | Ache | 1 | - |
| 3 | African Lion | 2 | Diff. mortality rates |
| 4 | Red Deer | 1 | - |
| 5 | Chacma Baboon | 1 | Modeled Yellow Baboon |
| 6 | Rhesus Macaque | 3 | High and low density plus 2nd source |
| 7 | Tawny Owl | 6 | 4 points in Vole cycle, 2 other sources |
| 8 | Roe Deer | 2 | Extra run with empirical moments |
| 9 | Eastern Kingbird | 1 | Model from the same study |
| 10 | Chimpanzee | 2 | Synthetic life table + unknown source |
| 11 | Common Buzzard | 1 | Output by color morph (3), same study |
| 12 | Subantarctic Fur Seal | 1 | Modeled Antarctic Fur Seal |
| 13 | Cheetah | 1 | Lifetime starting from independence |
| 14 | Great Tit | 1 | Model from the same study |
| 15 | European Badger | 1 | Lifetime starting from independence |
| 16 | Northern Elephant Seal | 2 | High and low density |

European badger (*Meles meles*): Dugdale et al. (2010) studied a high-density badger population for 18 years. The study was performed in Wytham woods, near Oxford, U.K.. LRS was calculated for independent individuals of known age that had died before the end of the study. Using microsatellite markers, offspring of both sexes that had survived to independence (12-15 weeks) were assigned parentage (from the pool of individuals described above). (Description, p. 284, values, p. 285)

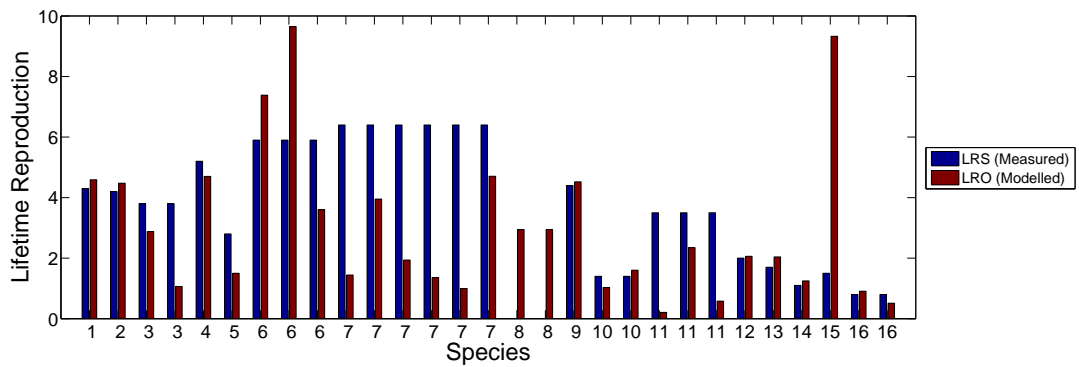
A life table from Macdonald & Newman (2002, p. 128) was used for the matrix model. Fertility was multiplied by 2 to model production of both sexes and by the survival rate of 1-year old badgers. 2-year old badgers become independent and so in this way our model matched the requirement of the Dugdale study of only considering independent individuals. Therefore, lifetime reproduction was also assessed starting from 2 years of age. Rewards were assumed to be Poisson distributed.

Northern elephant seal (*Mirounga angustirostris*): Le Boeuf & Reiter (1988) presented data on 204 known-age female elephant seals born on Ao Nuevo island, California, USA. LRS was measured as the number of pups weaned successfully. (p. 358, table 22.5 and text)

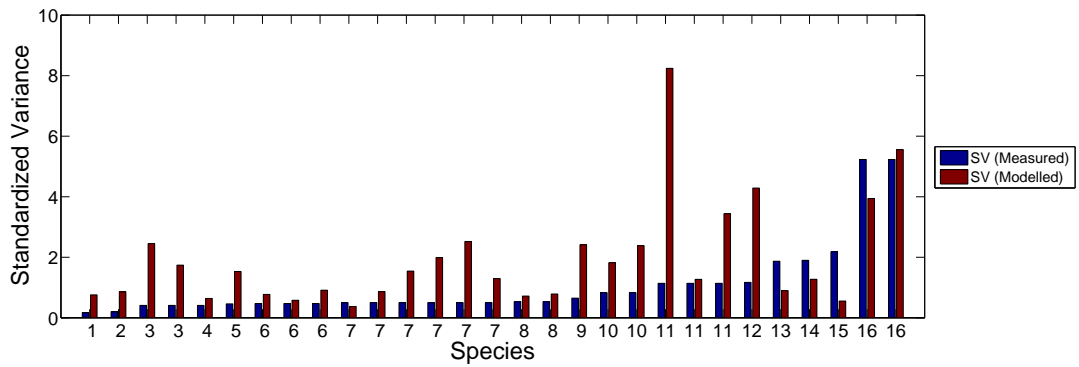
Survival rates from Condit et al. (2014, Table 3) were used. We retrieved 2 sets of fertility rates from Reiter & Le Boeuf (1991), one for low density populations and one for high density populations (figure 3, p. 156). Two matrix models were created for both density situations. Bernoulli distributed rewards were assumed.

2.3 Results

Overall, the modeled estimates of mean lifetime reproductive output were similar to the empirical estimates (Figure 2.1(a)). In some cases the blue bars show the same value, as we had 1 empirical estimate, but multiple model estimates for a given species. The extremely high model estimate of LRO shown by species 15 is the European badger. The empirical estimates



(a) Mean LRO comparisons



(b) Variance comparisons

Figure 2.1: Empirical estimates (blue bars) compared to model estimates (red bars) of mean LRO (a) and variance in LRO (b). Numbers on the x-axis correspond to the species presented in Table 2.1.

for Roe Deer (species 8) were not reported.

The estimates of the standardized variance in LRO are shown in Figure 2.1**(b)**. Most of the modeled estimates of standardized variance exceeded the empirical estimates. The identifiers of the species can be found in Table 2.1. Species 11, the Common Buzzard, is a single species with 3 separate color morphs. The less successful color morphs have a very low mean, which can lead to a very high standardized variance. As these color morphs are inherently different in their reproductive success, estimates for the total population are difficult to come by and the comparison is less easily interpretable.

2.4 Discussion

In most of the species investigated here, variance in lifetime reproductive output is either completely or mostly due to individual stochasticity as opposed to heterogeneity. The models include only individual stochasticity, the luck that individuals experience in their survival and reproduction. The empirical estimates, on the other hand, are composed of all underlying sources of variation, including both individual stochasticity and other differences between individuals, what we refer to as heterogeneity. Figure 2.1**(b)** shows that in many cases, the estimates of standardized variance from the models are higher than the empirical estimates. It can therefore be concluded that these observed variances are due to individual stochasticity.

Recall that the models we have shown here are baseline models. As discussed by Steiner & Tuljapurkar (2012) adding heterogeneity to these kinds of models explicitly can only further increase the variance. There are exceptions to this statement, as additional *dynamic* heterogeneity has been shown to reduce the variance in human reproductive output (Caswell, 2014b). When considering fixed heterogeneity, though, the variance can only increase. Although the effect of adding heterogeneity to the model will depend on the type of heterogeneity, the fact remains that the baseline model can account for all the variance in most cases. We maintain that individual stochasticity has caused most, if not all, of the variance in most of the species presented here.

Indeed, the species that show higher observed variances than model variances appear to be the exception and not the rule. These species include Tawny Owls when vole abundances are low, Cheetahs, Great Tits, European Badgers and Elephant Seals in low density populations. In the case of Tawny Owls and Elephant Seals, other circumstances can lead to measured variances that are entirely explained by stochasticity. This indicates that the environment of the species can play a significant role in determining whether heterogeneity is an underlying cause of variation in LRO. In the case of Cheetahs and Badgers early stages of the life cycle were left out in both the observed mean and variance of LRO and in the modeled calculations of these quantities. It is not clear how the use of these post-independence life cycles affects the comparison between measured and modeled variances, but it is worth noting that the only species with these life cycles do show a greater contribution of heterogeneity to variation in LRO.

Comparing empirical estimates of mean LRO and variance in LRO with estimates generated by Markov chains with rewards is a robust way of assessing the contribution of individual stochasticity and heterogeneity to the variance in lifetime reproductive output. We have shown that in most of the species investigated here individual stochasticity is the sole generator of variance in LRO. We expect this to be a general trend, but analyses of additional species, especially those with different life histories (e.g. plants, invertebrates), are required before this can be proven. The rarity of studies with enough detail and length that allow both empirical estimates of LRO and model building, complicates the creation and analysis of these data for very large numbers of species. For now, we advise that researchers interested in studying the underlying causes of variance in lifetime reproductive output create baseline models to assess contributions of both heterogeneity and individual stochasticity.

Chapter 3

Sensitivity Analysis

Of Mean LRO and Variance in LRO

3.1 Background

Sensitivity analysis describes how sensitive some outcome of the model is to a slight change in an underlying parameter. The analytical solutions of sensitivity analysis for Markov chains with results are shown below. Sensitivity of the first and second moments of the accumulated reward vectors of lifetime reproductive success to changes in mortality and fertility rates are shown for a population of humans in the Netherlands in 1950. First, the derivations of the equilibria of the moment vectors of the rewards are presented.

3.2 Equations

Notation. Matrices are denoted by upper-case bold symbols (e.g., \mathbf{P}), vectors by lower-case bold symbols (e.g., $\boldsymbol{\rho}$). Vectors are column vectors by default. The transpose of \mathbf{P} is \mathbf{P}^\top . The inverse of \mathbf{P} is \mathbf{P}^{-1} . The vector $\mathbf{1}$ is a vector of ones, and the matrix \mathbf{I} is the identity matrix. Where necessary to avoid confusion, dimensions are indicated by subscripts; e.g., the $\omega \times \omega$ identity matrix is \mathbf{I}_ω . The diagonal matrix with the vector \mathbf{x} on the diagonal and zeros elsewhere is denoted $\mathcal{D}(\mathbf{x})$. The expected value is denoted by $E(\cdot)$. The Hadamard, or element-by-element, product of matrices \mathbf{A} and \mathbf{B} is denoted by $\mathbf{A} \circ \mathbf{B}$. Transition matrices of Markov chains are written in column-to-row orientation, and hence their columns sum to one.

3.2.1 Equilibrium equations

These are the equations for the moments of future rewards:

$$\boldsymbol{\rho}_1(t) = (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{P}^\top \boldsymbol{\rho}_1(t-1) \quad (3.1)$$

$$\boldsymbol{\rho}_2(t) = (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2(\mathbf{P} \circ \mathbf{R}_1)^\top \boldsymbol{\rho}_1(t-1) + \mathbf{P}^\top \boldsymbol{\rho}_2(t-1) \quad (3.2)$$

$$\boldsymbol{\rho}_3(t) = (\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{P} \circ \mathbf{R}_2)^\top \boldsymbol{\rho}_1(t-1) + 3(\mathbf{P} \circ \mathbf{R}_1)^\top \boldsymbol{\rho}_2(t-1) + \mathbf{P}^\top \boldsymbol{\rho}_3(t-1) \quad (3.3)$$

It is important to note that $\boldsymbol{\rho}$ is a vector of the future rewards per state (stage), and that these states include one or multiple absorbing states. In this case, a single absorbing state is included, representing death, but multiple absorbing states, due to multiple causes of death, are possible as well. In either case, it is clear that individuals that have reached this absorbing state are no longer capable of accumulating rewards (i.e. dead individuals cannot reproduce). As such, the future rewards in the absorbing state is always zero, and therefore of

no importance to the calculation of the equilibrium. We can introduce a matrix \mathbf{Z} that cleaves of the absorbing state rewards, leaving us with only the rewards for the transient states:

$$\tilde{\rho}_1 = \mathbf{Z}\rho_1 \quad (3.4)$$

where

$$\mathbf{Z} = \left(\mathbf{I} \mid \mathbf{0} \right) \quad (3.5)$$

which is equal to

$$\mathbf{Z} = \left(\begin{array}{cccc|c} 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 & 0 \end{array} \right) \quad (3.6)$$

in the case of a single absorbing state.

For a simple two-stage example, equation (3.4) gives

$$\begin{pmatrix} \rho_j \\ \rho_a \end{pmatrix} = \left(\begin{array}{cc|c} 1 & 0 & 0 \\ 0 & 1 & 0 \end{array} \right) \begin{pmatrix} \rho_j \\ \rho_a \\ \rho_d \end{pmatrix} \quad (3.7)$$

As ρ_d , the rewards for the dead stage, always equal zero, the following is true as well;

$$\mathbf{Z}^\top \tilde{\rho}_1 = \rho_1 \quad (3.8)$$

as \mathbf{Z}^\top , in this case, just adds a zero to $\tilde{\rho}_1$:

$$\begin{pmatrix} 1 & 0 \\ 0 & 1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \rho_j \\ \rho_a \end{pmatrix} = \begin{pmatrix} \rho_j \\ \rho_a \\ 0 \end{pmatrix} \quad (3.9)$$

Now, the recursion equations can be rewritten for $\tilde{\rho}_1$ in order to calculate the equilibrium for the future rewards of the transient states. First, note that the following relations are true for a Markov chain with multiple absorbing states, i.e.

$$\mathbf{P} = \begin{pmatrix} \mathbf{U} & \mathbf{0} \\ \mathbf{M} & \mathbf{I} \end{pmatrix} \quad (3.10)$$

Applying both \mathbf{Z} and \mathbf{Z}^\top cuts off all elements in \mathbf{P} save for \mathbf{U} :

$$\mathbf{Z}\mathbf{P}\mathbf{Z}^\top = \mathbf{U} \quad (3.11)$$

$$\mathbf{Z}\mathbf{P}^\top\mathbf{Z}^\top = \mathbf{U}^\top \quad (3.12)$$

The first-moment equation (3.1) can be multiplied by \mathbf{Z} :

$$\mathbf{Z}\rho_1(t) = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{Z}\mathbf{P}^\top \rho_1(t-1) \quad (3.13)$$

If we apply equation (3.4), we get

$$\tilde{\rho}_1(t) = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{Z}\mathbf{P}^\top \rho_1(t-1) \quad (3.14)$$

Rewriting ρ_1 as (3.8), along with the use of (3.12), results in

$$\tilde{\rho}_1(t) = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{Z}\mathbf{P}^\top\mathbf{Z}^\top \tilde{\rho}_1(t-1) \quad (3.15)$$

$$= \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{U}^\top \tilde{\rho}_1(t-1) \quad (3.16)$$

Now, we are trying to solve for the equilibrium of $\tilde{\rho}_1(t)$ and we can find it by looking for the $\tilde{\rho}_1$ where the recursion equation no longer changes the value of $\tilde{\rho}_1$, so we need a $\tilde{\rho}_1$ where the LHS and the RHS of the equation are equal:

$$\tilde{\rho}_1 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{U}^\top \tilde{\rho}_1 \quad (3.17)$$

Bringing all terms containing $\tilde{\rho}_1$ to the left-hand side:

$$(\mathbf{I} - \mathbf{U}^\top) \tilde{\rho}_1 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} \quad (3.18)$$

Then $\tilde{\rho}_1$ is equal to:

$$\tilde{\rho}_1 = (\mathbf{I} - \mathbf{U}^\top)^{-1} \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} \quad (3.19)$$

This is an actual answer, since $(\mathbf{I} - \mathbf{U}^\top)$ is invertible. If, however, \mathbf{Z} had not been applied to the equations and, more importantly, to \mathbf{P}^\top , a similar equation with \mathbf{P}^\top in the place of \mathbf{U}^\top would have been acquired. $\mathbf{I} - \mathbf{P}^\top$ is not invertible, though, and this answer would, thus, not have made any sense.

The same operations can be applied to find the equilibria for the 2nd and 3rd moments of ρ . Note that the following statements are true:

$$\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1} \quad (3.20)$$

$$\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{Z}^\top = (\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \quad (3.21)$$

Equation (3.20) is true because the fundamental matrix \mathbf{N} represents the number of visits to the transient states present in \mathbf{U} (Iosifescu, 1980), thus:

$$\mathbf{N} = \sum \mathbf{U}^k \quad (3.22)$$

$$\mathbf{N} = \mathbf{I} + \mathbf{U} + \mathbf{U}^2 + \mathbf{U}^3 + \dots + \mathbf{U}^\infty \quad (3.23)$$

$$\mathbf{U}\mathbf{N} = \mathbf{U} + \mathbf{U}^2 + \mathbf{U}^3 + \mathbf{U}^4 + \dots + \mathbf{U}^\infty \quad (3.24)$$

$$\mathbf{N} = \mathbf{I} + \mathbf{U}\mathbf{N} \quad (3.25)$$

$$\mathbf{I}\mathbf{N} - \mathbf{U}\mathbf{N} = \mathbf{I} \quad (3.26)$$

$$(\mathbf{I} - \mathbf{U})\mathbf{N} = \mathbf{I} \quad (3.27)$$

$$\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1} \quad (3.28)$$

Equation (3.21) is true, because (3.11) is true and \mathbf{Z} and \mathbf{Z}^\top applied to \mathbf{R}_1 , does the same thing; it cleaves off the absorbing states and their rewards.

Then, the equilibrium for $\tilde{\rho}_2$ is found, mainly by using equation (3.4) and (3.8):

$$\rho_2 = (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2(\mathbf{P} \circ \mathbf{R}_1)^\top \rho_1 + \mathbf{P}^\top \rho_2 \quad (3.29)$$

$$\tilde{\rho}_2 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{Z}^\top \tilde{\rho}_1 + \mathbf{Z}\mathbf{P}^\top \mathbf{Z}^\top \tilde{\rho}_2 \quad (3.30)$$

All that remains now, is to get all $\tilde{\rho}_2$'s on the LHS of the equation and rewrite some of the terms:

$$\tilde{\rho}_2 - \mathbf{U}^\top \tilde{\rho}_2 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{Z}^\top \tilde{\rho}_1 \quad (3.31)$$

$$\tilde{\rho}_2 = (\mathbf{I} - \mathbf{U}^\top)^{-1} \left[\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2(\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tilde{\rho}_1 \right] \quad (3.32)$$

$$\tilde{\rho}_2 = \mathbf{N}^\top \left[\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2(\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tilde{\rho}_1 \right] \quad (3.33)$$

The equilibrium for $\tilde{\rho}_3$ is derived similarly:

$$\rho_3 = (\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{P} \circ \mathbf{R}_2)^\top \rho_1 + 3(\mathbf{P} \circ \mathbf{R}_1)^\top \rho_2 + \mathbf{P}^\top \rho_3 \quad (3.34)$$

$$\tilde{\rho}_3 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_2)^\top \tilde{\rho}_1 + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tilde{\rho}_2 + \mathbf{U}^\top \tilde{\rho}_3 \quad (3.35)$$

$$(\mathbf{I} - \mathbf{U}^\top) \tilde{\rho}_3 = \mathbf{Z}(\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_2)^\top \tilde{\rho}_1 + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tilde{\rho}_2 \quad (3.36)$$

$$\tilde{\rho}_3 = \mathbf{N}^\top \left[\mathbf{Z}(\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_2)^\top \tilde{\rho}_1 + 3(\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tilde{\rho}_2 \right] \quad (3.37)$$

3.2.2 Sensitivity of mean LRO

The equilibrium vector for the first moment rewards of LRO is

$$\tilde{\rho}_1 = \mathbf{N}^\top \mathbf{Z} (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1}_{\tau+1} \quad (3.38)$$

where τ is the number of transient states and s the number of transient plus absorbing states. In this case, s is equal to $\tau + 1$.

The sensitivity of $\tilde{\rho}_1$ to a given parameter becomes:

$$\frac{d\tilde{\rho}_1}{d\theta^\top} = \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{N}} \frac{d\text{vec } \mathbf{N}}{d\theta^\top} + \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{P}} \frac{d\text{vec } \mathbf{P}}{d\theta^\top} + \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{R}_1} \frac{d\text{vec } \mathbf{R}_1}{d\theta^\top} \quad (3.39)$$

We will consider an age-classified model for humans, parameterized in terms of $\boldsymbol{\mu}$ and \mathbf{f} , the mortality and fertility rate, respectively. The rates used here are based on mortality and fertility data from the Netherlands in 1950, obtained from the Human Mortality Database (Human Mortality Database, 2014) and the Human Fertility Database (Human Fertility Database, 2014).

The Markov chain produced from these data depends only on two sets of parameters, the age-specific mortality rates and age-specific fertility rates. Since not all of the matrices in Equation (3.38) depend on both of these parameter sets several terms disappear if we focus on either one of these sets. The sensitivity of $\tilde{\rho}_1$ to the mortality rate $\boldsymbol{\mu}$ and fertility rate \mathbf{f} , respectively, is

$$\frac{d\tilde{\rho}_1}{d\boldsymbol{\mu}^\top} = \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{N}} \frac{d\text{vec } \mathbf{N}}{d\boldsymbol{\mu}^\top} + \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{P}} \frac{d\text{vec } \mathbf{P}}{d\boldsymbol{\mu}^\top} \quad (3.40)$$

$$\frac{d\tilde{\rho}_1}{d\mathbf{f}^\top} = \frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{R}_1} \frac{d\text{vec } \mathbf{R}_1}{d\mathbf{f}^\top} \quad (3.41)$$

The derivatives of $\tilde{\rho}_1$ to the matrices \mathbf{N} , \mathbf{P} , and \mathbf{R}_1 are calculated by taking the derivative of Equation (3.38), applying the vec operator and Roth's theorem, and simplifying.

$$\frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{N}} = [\mathbf{1}_s^\top (\mathbf{P} \circ \mathbf{R}_1) \mathbf{Z}^\top \otimes \mathbf{I}] \mathbf{K}_{\tau,\tau} \quad (3.42)$$

$$\frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{P}} = (\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{R}_1) \quad (3.43)$$

$$\frac{\partial \tilde{\rho}_1}{\partial \text{vec}^\top \mathbf{R}_1} = (\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{P}) \quad (3.44)$$

The derivatives of \mathbf{N} and \mathbf{P} with respect to $\boldsymbol{\mu}$ are

$$\frac{d\text{vec } \mathbf{N}}{d\boldsymbol{\mu}^\top} = (\mathbf{N}^\top \otimes \mathbf{N}) \frac{d\text{vec } \mathbf{U}}{d\boldsymbol{\mu}^\top} \quad (3.45)$$

$$\frac{d\text{vec } \mathbf{P}}{d\boldsymbol{\mu}^\top} = [\mathbf{C}_1 - \mathbf{C}_2 (\mathbf{I} \otimes \mathbf{1}^\top)] \frac{d\text{vec } \mathbf{U}}{d\boldsymbol{\mu}^\top} \quad (3.46)$$

with

$$\mathbf{C}_1 = \begin{pmatrix} \mathbf{I}_\tau \\ \mathbf{0}_{1 \times \tau} \end{pmatrix} \otimes \begin{pmatrix} \mathbf{I}_\tau \\ \mathbf{0}_{1 \times \tau} \end{pmatrix} \quad (3.47)$$

$$\mathbf{C}_2 = \begin{pmatrix} \mathbf{I}_\tau \\ \mathbf{0}_{1 \times \tau} \end{pmatrix} \otimes \begin{pmatrix} \mathbf{0}_{\tau \times 1} \\ \mathbf{I}_1 \end{pmatrix} \quad (3.48)$$

That leaves us to define the derivative of \mathbf{U} with respect to $\boldsymbol{\mu}$.

$$\frac{d\text{vec } \mathbf{U}}{d\boldsymbol{\mu}^\top} = -\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p}) \quad (3.49)$$

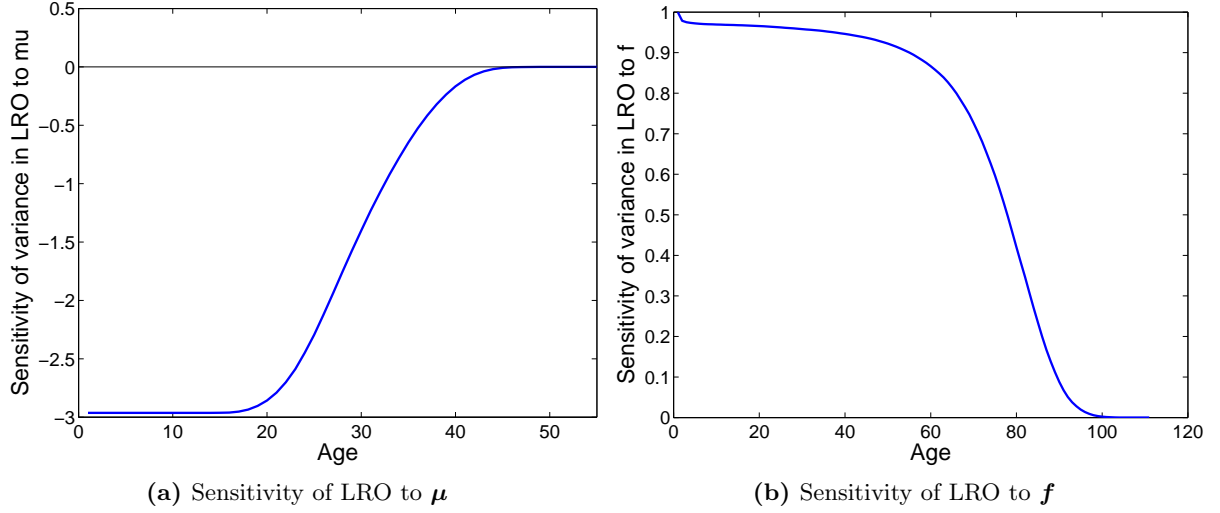


Figure 3.1: The sensitivity of mean lifetime reproductive output to a change in vital rates at any age for a population of humans in the Netherlands in 1950.

where

$$\mathbf{W} = \begin{pmatrix} 0 & 0 & \dots & 0 & 0 \\ 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & 1 & 0 \end{pmatrix} \quad (3.50)$$

and

$$\mathbf{p} = e^{-\mu}. \quad (3.51)$$

Now all the terms in Equation (3.40) can be substituted to give the analytical solution

$$\begin{aligned} \frac{d\tilde{\rho}_1}{d\boldsymbol{\mu}^\top} &= [\mathbf{1}_s^\top (\mathbf{P} \circ \mathbf{R}_1) \mathbf{Z}^\top \otimes \mathbf{I}] \mathbf{K}_{\tau,\tau} (\mathbf{N}^\top \otimes \mathbf{N}) (-\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p})) \\ &+ (\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{R}_1) [\mathbf{C}_1 - \mathbf{C}_2 (\mathbf{I} \otimes \mathbf{1}^\top)] (-\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p})) \end{aligned} \quad (3.52)$$

We can do the same for the sensitivity of $\tilde{\rho}_1$ with respect to \mathbf{f} .

$$\frac{d\text{vec } \mathbf{R}_1}{d\mathbf{f}^\top} = \mathbf{V}^\top \otimes \mathbf{1}_s \quad (3.53)$$

where

$$\mathbf{V} = \begin{pmatrix} \mathbf{I}_\tau & \mathbf{0}_{\tau \times 1} \end{pmatrix} \quad (3.54)$$

Then, Equation (3.41) becomes

$$\frac{d\tilde{\rho}_1}{d\mathbf{f}^\top} = (\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{P}) (\mathbf{V}^\top \otimes \mathbf{1}_s) \quad (3.55)$$

Equations (3.52) and (3.55) are matrices giving the sensitivity of the remaining reproductive output at any age to a change at any age in mortality rate and fertility rate, respectively. The effect of changes in mortality or fertility rates at any age on lifetime reproductive output is obtained by assessing only the first row of the matrix (see Figure 3.1).

Figure 3.1(a) shows that a positive change in mortality rate at early ages has a negative effect on lifetime reproductive output. After age 20 this effect diminishes until it reaches 0 around age 45. This is to be expected as after this age women do not produce children anymore. Figure 3.1(b) shows that a positive change in fertility rate positively affects lifetime reproductive output. The effect slowly declines with age, as older women have a greater chance of dying, as well as fewer reproductive years remaining, which will make a greater chance of reproducing have little effect.

3.2.3 Sensitivity of variance in LRO

Variance in LRO is calculated as

$$V(\tilde{\rho}) = \tilde{\rho}_2 - \tilde{\rho}_1 \circ \tilde{\rho}_1. \quad (3.56)$$

Differentiating this gives

$$\frac{dV(\tilde{\rho})}{d\theta^\top} = \frac{d\tilde{\rho}_2}{d\theta^\top} - 2\mathcal{D}(\tilde{\rho}_1) \frac{d\tilde{\rho}_1}{d\theta^\top}. \quad (3.57)$$

The equilibrium equations for $\tilde{\rho}_1$ and $\tilde{\rho}_2$ are

$$\tilde{\rho}_1 = \mathbf{N}^\top \mathbf{Z} (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1}_s \quad (3.58)$$

$$\tilde{\rho}_2 = \mathbf{N}^\top \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1}_s + 2(\mathbf{U} \circ \mathbf{R}_1)^\top \tilde{\rho}_1 \right] \quad (3.59)$$

The sensitivities of $\tilde{\rho}_1$ are given above. Just as $\tilde{\rho}_1$, $\tilde{\rho}_2$ can change due to a change in mortality rate or due to a change in fertility rate. The equations that represent this change are, respectively,

$$\frac{d\tilde{\rho}_2}{d\mu^\top} = \frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{N}} \frac{d\text{vec} \mathbf{N}}{d\mu^\top} + \frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{P}} \frac{d\text{vec} \mathbf{P}}{d\mu^\top} + \frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{U}} \frac{d\text{vec} \mathbf{U}}{d\mu^\top} + \frac{\partial \tilde{\rho}_2}{\partial \tilde{\rho}_1} \frac{d\tilde{\rho}_1}{d\mu^\top} \quad (3.60)$$

$$\frac{d\tilde{\rho}_2}{d\mathbf{f}^\top} = \frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{R}_2} \frac{d\text{vec} \mathbf{R}_2}{d\mathbf{f}^\top} + \frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{R}_1} \frac{d\text{vec} \mathbf{R}_1}{d\mathbf{f}^\top} + \frac{\partial \tilde{\rho}_2}{\partial \tilde{\rho}_1} \frac{d\tilde{\rho}_1}{d\mathbf{f}^\top} \quad (3.61)$$

Then, the derivatives of $\tilde{\rho}_2$ with respect to \mathbf{N} , \mathbf{P} , \mathbf{U} , and $\tilde{\rho}_1$ can be obtained by differentiating Equation (3.59), applying the vec operator and Roth's theorem, and simplifying.

$$\frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{N}} = [\mathbf{1}_s^\top (\mathbf{P} \circ \mathbf{R}_2) \mathbf{Z}^\top \otimes \mathbf{I}] \mathbf{K}_{\tau, \tau} + \left[2\tilde{\rho}_1^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1) \otimes \mathbf{I} \right] \mathbf{K}_{\tau, \tau} \quad (3.62)$$

$$\frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{P}} = [\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}] \mathbf{K}_{s, s} \mathcal{D}(\text{vec} \mathbf{R}_2) \quad (3.63)$$

$$\frac{\partial \tilde{\rho}_2}{\partial \text{vec}^\top \mathbf{U}} = [\tilde{\rho}_1^\top \otimes 2\mathbf{N}^\top] \mathbf{K}_{\tau, \tau} \mathcal{D}(\text{vec} \mathbf{R}_1) \quad (3.64)$$

$$\frac{\partial \tilde{\rho}_2}{\partial \tilde{\rho}_1} = 2\mathbf{N}^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \quad (3.65)$$

Now the derivatives of \mathbf{N} , \mathbf{P} , \mathbf{U} , and $\tilde{\rho}_1$ with respect to μ can be calculated. We'll see that \mathbf{N} and \mathbf{P} can be rewritten as functions of $d\text{vec} \mathbf{U}$;

$$\frac{d\text{vec} \mathbf{N}}{d\mu^\top} = (\mathbf{N}^\top \otimes \mathbf{N}) \frac{d\text{vec} \mathbf{U}}{d\mu^\top} \quad (3.66)$$

$$\frac{d\text{vec} \mathbf{P}}{d\mu^\top} = [\mathbf{C}_1 - \mathbf{C}_2 (\mathbf{I} \otimes \mathbf{1}^\top)] \frac{d\text{vec} \mathbf{U}}{d\mu^\top} \quad (3.67)$$

with the sensitivity of \mathbf{U} with respect to μ being

$$\frac{d\text{vec} \mathbf{U}}{d\mu^\top} = -\mathcal{D}(\text{vec} \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p}) \quad (3.68)$$

Note that these equations are the same as the ones defined for the sensitivity of $\tilde{\rho}_1$. The sensitivity of $\tilde{\rho}_1$ with respect to $\boldsymbol{\mu}$ has also been defined previously (see Equation (3.52)).

Now, we can fill in equation 3.60 to find the sensitivity of $\tilde{\rho}_2$ to mortality rates $\boldsymbol{\mu}$.

$$\begin{aligned}
\frac{d\tilde{\rho}_2}{d\boldsymbol{\mu}^\top} = & \left\{ \left[\mathbf{1}_s^\top (\mathbf{P} \circ \mathbf{R}_2) \mathbf{Z}^\top \otimes \mathbf{I} \right] \mathbf{K}_{\tau,\tau} + \left[2\tilde{\rho}_1^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1) \otimes \mathbf{I} \right] \mathbf{K}_{\tau,\tau} \right] (\mathbf{N}^\top \otimes \mathbf{N}) \\
& + \left[\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z} \right] \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{R}_2) [\mathbf{C}_1 - \mathbf{C}_2 (\mathbf{I} \otimes \mathbf{1}^\top)] \\
& + \left[\tilde{\rho}_1^\top \otimes 2\mathbf{N}^\top \right] \mathbf{K}_{\tau,\tau} \mathcal{D}(\text{vec } \mathbf{R}_1) \right\} (-\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p})) \\
& + \left[2\mathbf{N}^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \right] \left(\left[\mathbf{1}_s^\top (\mathbf{P} \circ \mathbf{R}_1) \mathbf{Z}^\top \otimes \mathbf{I} \right] \mathbf{K}_{\tau,\tau} (\mathbf{N}^\top \otimes \mathbf{N}) (-\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p})) \right. \\
& \left. + (\mathbf{1}_s^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{R}_1) [\mathbf{C}_1 - \mathbf{C}_2 (\mathbf{I} \otimes \mathbf{1}^\top)] (-\mathcal{D}(\text{vec } \mathbf{W})(\mathbf{I}_\tau \otimes \mathbf{1}_\tau) \mathcal{D}(\mathbf{p})) \right)
\end{aligned} \tag{3.69}$$

This is obviously not the most convenient equation and we will therefore not substitute the equation above in Equation (3.57). Equation (3.57) represents the final product: replace $\boldsymbol{\theta}$ with $\boldsymbol{\mu}$ and you have the sensitivity of the variance in LRO to changes in mortality rates. We have presented all the necessary parts to calculate and plot this quantity.

Before we do so, let's also derive the sensitivity of $V(\tilde{\rho})$ to changes in the fertility rate \mathbf{f} . We know the sensitivity of $\tilde{\rho}_1$ to \mathbf{f} , that was shown in the section above. To derive Equation (3.61), we will need the following pieces; sensitivity of $\tilde{\rho}_2$ to \mathbf{R}_2 , \mathbf{R}_1 (in this case $\tilde{\mathbf{R}}_1$), and $\tilde{\rho}_1$, as well as sensitivities of \mathbf{R}_2 , $\tilde{\mathbf{R}}_1$, and $\tilde{\rho}_1$ to \mathbf{f} . The first are retrieved by differentiating, applying the vec operator and Roth's theorem to Equation (??):

$$\frac{\partial \tilde{\rho}_2}{\partial \mathbf{R}_2^\top} = (\mathbf{1}_S^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{P}) \tag{3.70}$$

$$\frac{\partial \tilde{\rho}_2}{\partial \tilde{\mathbf{R}}_1^\top} = (\tilde{\rho}_1^\top \otimes 2\mathbf{N}^\top) \mathbf{K}_{\tau,\tau} \mathcal{D}(\text{vec } \mathbf{U}) \tag{3.71}$$

$$\frac{\partial \tilde{\rho}_2}{\partial \tilde{\rho}_1} = 2\mathbf{N}^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top \tag{3.72}$$

As under Bernoulli assumptions $\mathbf{R}_2 = \mathbf{R}_1$ the sensitivity of \mathbf{R}_2 to \mathbf{f} is

$$\frac{d\mathbf{R}_2}{d\mathbf{f}^\top} = \mathbf{V}^\top \otimes \mathbf{1}_s, \tag{3.73}$$

which is identical to the equation for \mathbf{R}_1 in the previous section.

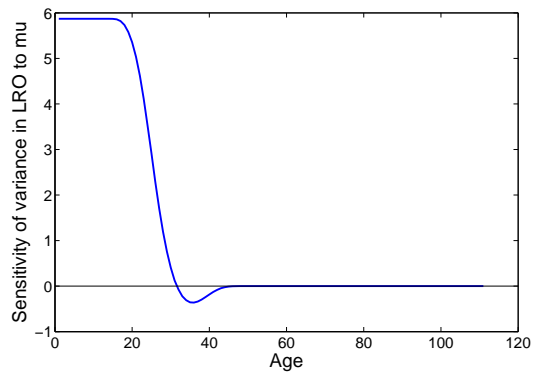
The sensitivity of $\tilde{\mathbf{R}}_1$ to \mathbf{f} is only slightly different:

$$\frac{d\tilde{\mathbf{R}}_1}{d\mathbf{f}^\top} = \mathbf{I} \otimes \mathbf{1}_\tau. \tag{3.74}$$

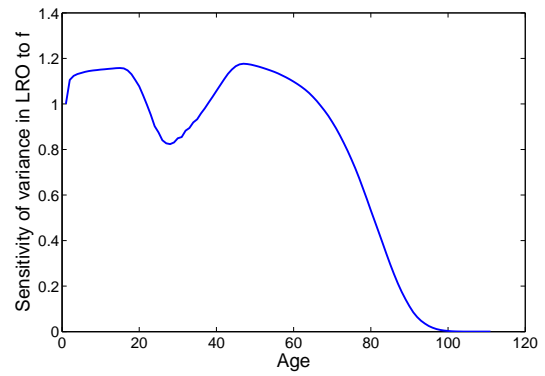
We know the sensitivity of $\tilde{\rho}_1$ to \mathbf{f} from the previous section, so now we can substitute the terms in Equation (3.61) to give us

$$\begin{aligned}
\frac{d\tilde{\rho}_2}{d\mathbf{f}^\top} = & (\mathbf{1}_S^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{P}) (\mathbf{V}^\top \otimes \mathbf{1}_s) + (\tilde{\rho}_1^\top \otimes 2\mathbf{N}^\top) \mathbf{K}_{\tau,\tau} \mathcal{D}(\text{vec } \mathbf{U}) (\mathbf{I} \otimes \mathbf{1}_\tau) \\
& + 2\mathbf{N}^\top (\mathbf{U} \circ \tilde{\mathbf{R}}_1)^\top (\mathbf{1}_S^\top \otimes \mathbf{N}^\top \mathbf{Z}) \mathbf{K}_{s,s} \mathcal{D}(\text{vec } \mathbf{P}) (\mathbf{V}^\top \otimes \mathbf{1}_s)
\end{aligned} \tag{3.75}$$

This equation and Equation (3.55) can be put into Equation (3.57), assuming $\boldsymbol{\theta}$ is \mathbf{f} , to give the sensitivity of the variance to changes in fertility rates.



(a) Sensitivity of LRO to μ



(b) Sensitivity of LRO to f

Figure 3.2: The sensitivity of variance in lifetime reproductive output to a change in vital rates at any age for a population of humans in the Netherlands in 1950.

If we now consider the first row of the matrices for sensitivities of variance to both μ and f , we have the sensitivity of variance in lifetime reproductive output to mortality and fertility, as shown in Figure 3.2.

Figure 3.2(a) shows that a positive change in mortality rate at any age will have a positive effect on the variance in lifetime reproductive at early ages, a slightly negative effect on variance in LRO around age 35-40, and no effect on the variance at later, non-reproductive ages. Once the reproductive period truly starts (around age 18) additional mortality has an increasingly smaller effect on variance in LRO, which is likely due to the fact that at older ages individuals will already have had the opportunity to reproduce and are thus more similar in their reproductive output. The small excursion to negative sensitivities around age 35-40 may be due to the fact that individuals don't survive to reproduce at age 40 and up. Since reproduction late in life increased the variance, the prevention of this happening due to increased mortality in ages right before this time could reduce the variance in lifetime reproductive output. Another possible explanation refers to the fact that variance in longevity becomes negative under additional mortality at these ages (Van Raalte & Caswell, 2013). Reduced variance in longevity could underlie a reduction in variance in lifetime reproduction.

Figure 3.2(b) shows that a positive change in fertility at any age will have a positive effect on the variance in lifetime reproductive output. The fact that the effect is greater at earlier and later ages than at intermediate ages is likely due to the fact that at intermediate ages the fertility rate is already high and an increase in fertility will generate higher variances at ages where fertility rate is lower.

Acknowledgements

I would like to thank my supervisor, Hal Caswell, and my Assessor, André de Roos, and the entire Theoretical Ecology group at the University of Amsterdam. I thank my fellow students: Peter van Wechem, Rachid Chafi and Adjani Peralta for useful discussions, and Boris Berkhout for the occasional help with R. Furthermore, I thank Oskar Burger, Mikko Myrskylä, and Greg Roth for more helpful discussions. This research was partially supported by ERC Advanced Grant 322989 to Hal Caswell.

A.1 Appendix

In Table A1, equations are shown for the regression of several statistics of LRO as functions of HDI. These lines, for the year 1980 and the year 2009, are drawn in Figure 1.5 as well. Table A2 shows the regression lines for the relationships among the statistical properties of LRO.

Table A1: Regression lines for the statistics of LRO as functions of HDI for the years 1980 and 2009, as shown in Figure 1.5.

| Regression of the different statistics as a function of HDI | | |
|---|-----------------------------------|------------------------------------|
| Statistic | 1980 | 2009 |
| Mean | $3.054 - 0.578 \times \text{HDI}$ | $-0.312 + 2.239 \times \text{HDI}$ |
| Standard Deviation | $1.775 - 0.616 \times \text{HDI}$ | $0.611 + 0.71 \times \text{HDI}$ |
| CV | $0.517 + 0.262 \times \text{HDI}$ | $1.247 - 0.558 \times \text{HDI}$ |
| Skewness | $0.293 + 0.423 \times \text{HDI}$ | $1.240 - 0.634 \times \text{HDI}$ |

The following figures (**A1-A10**) show how the lifetime remaining reproductive output changed over time for humans of 4 different age classes for 40 developed countries.

Table A2: Table of regression lines drawn through the scatterplot data in Figure 1.6. All lines showed an R^2 of around 0.98-0.99.

| Relationship among statistical properties for LRO in 2000 | | | | | |
|---|--------------------------|-------------------------|------------------------|------------------------|------------------------|
| Regression lines | Mean | Variance | Standard Deviation | CV | Skewness |
| Mean | x | $\rho_1 = 0.093 + 1.1V$ | $\rho_1 = 1.7 + 2.7SD$ | $\rho_1 = 4.4 - 3.6CV$ | $\rho_1 = 3.9 - 3.3Sk$ |
| Variance | $V = 0.085 + 0.88\rho_1$ | x | $V = 1.4 + 2.4SD$ | $V = 3.9 - 3.2CV$ | $V = 3.5 - 2.9Sk$ |
| Standard Deviation | $SD = 0.63 + 0.37\rho_1$ | $SD = 0.6 + 0.42V$ | x | $SD = 2.2 - 1.3CV$ | $SD = 2.1 - 1.2Sk$ |
| CV | $CV = 1.2 - 0.27\rho_1$ | $CV = 1.2 - 0.31V$ | $CV = 1.7 - 0.74SD$ | x | $CV = 0.14 + 0.91Sk$ |
| Skewness | $Sk = 1.2 - 0.3\rho_1$ | $Sk = 1.2 - 0.34V$ | $Sk = 1.7 - 0.81SD$ | $Sk = 0.14 + 1.1CV$ | x |

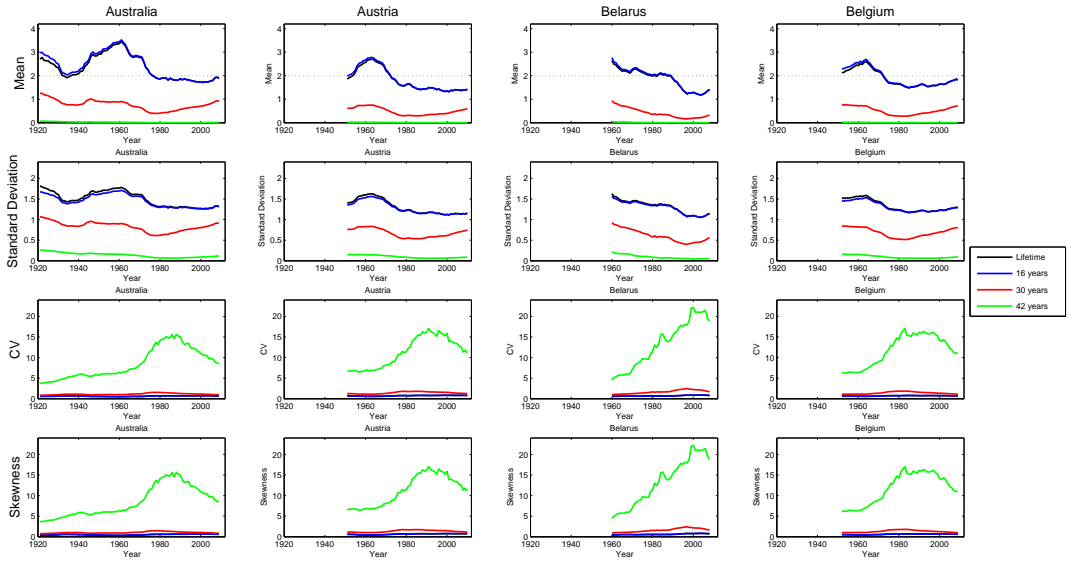


Figure A1: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Australia, Austria, Belarus, and Belgium.

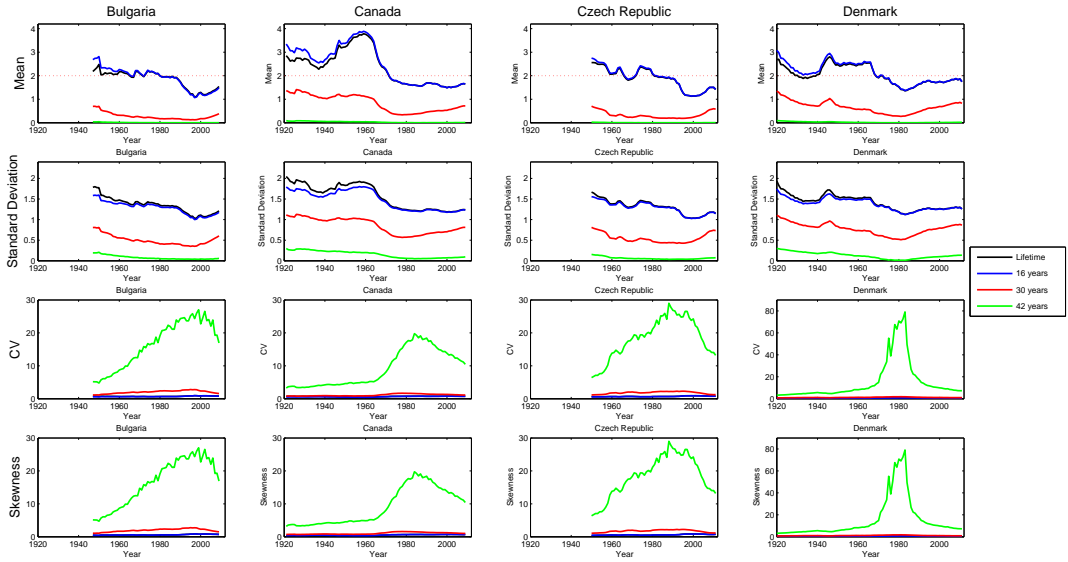


Figure A2: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Bulgaria, Canada, the Czech Republic, and Denmark.

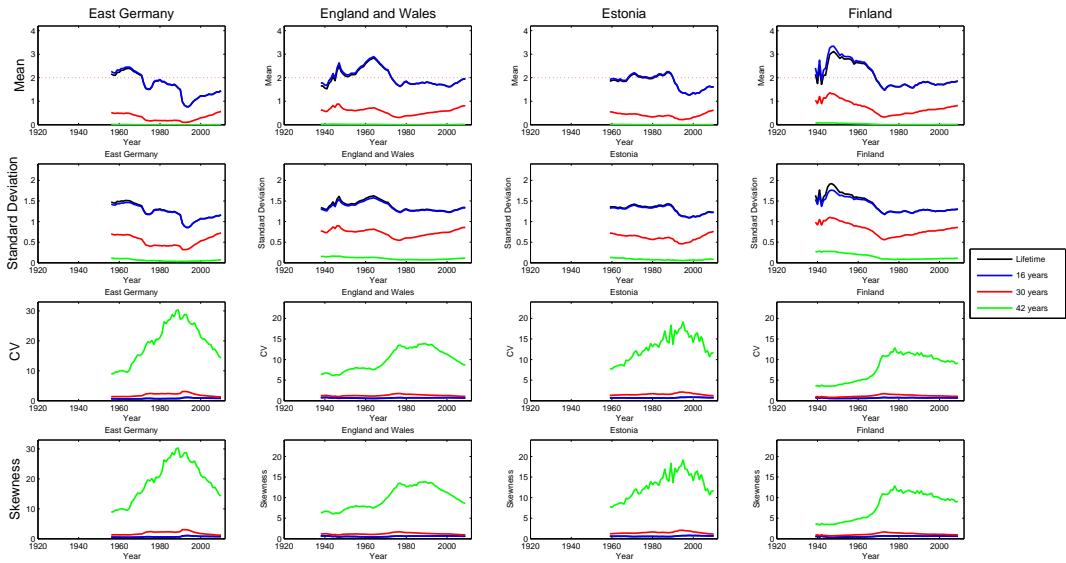


Figure A3: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are East Germany, England and Wales, Estonia, and Finland.

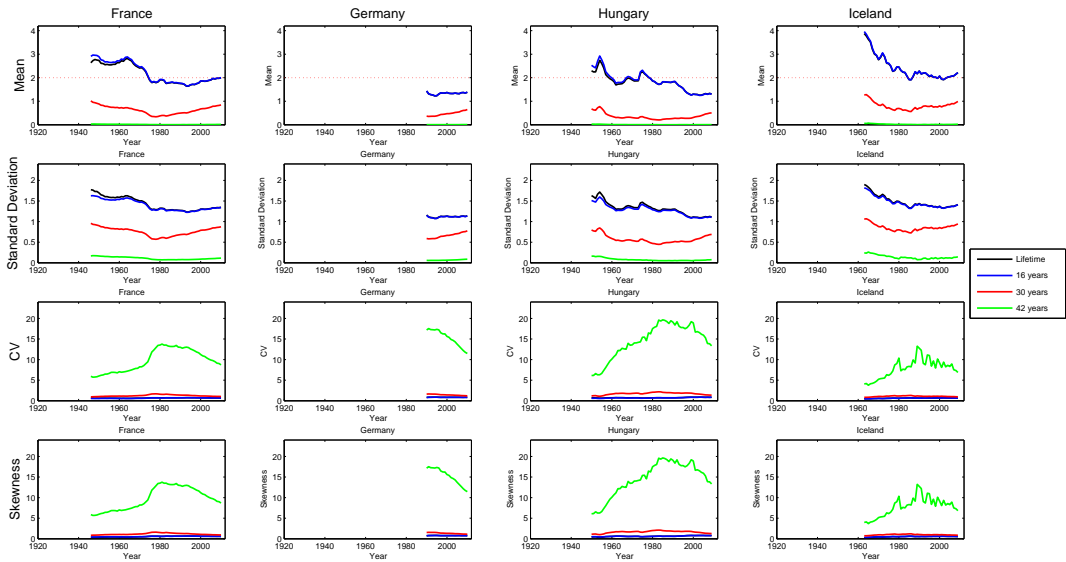


Figure A4: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are France, Germany, Hungary, and Iceland.

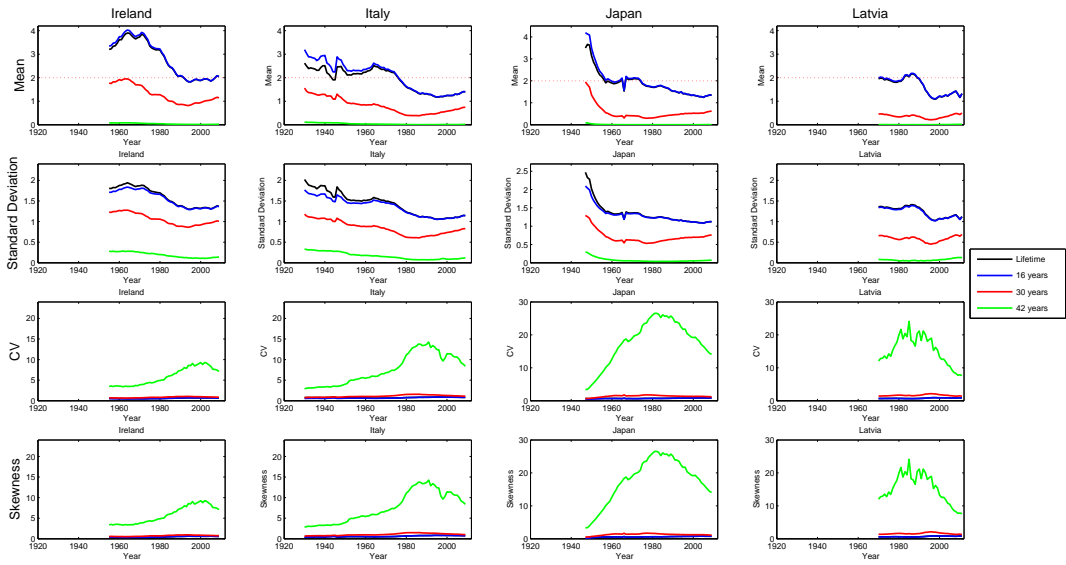


Figure A5: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Ireland, Italy, Japan, and Latvia.

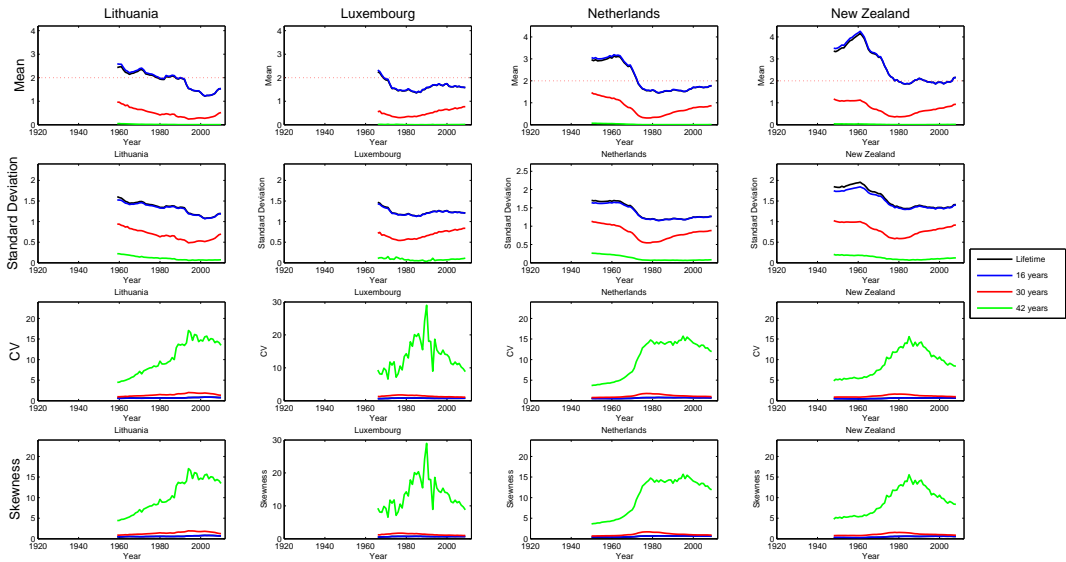


Figure A6: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Lithuania, Luxembourg, the Netherlands, and New Zealand.

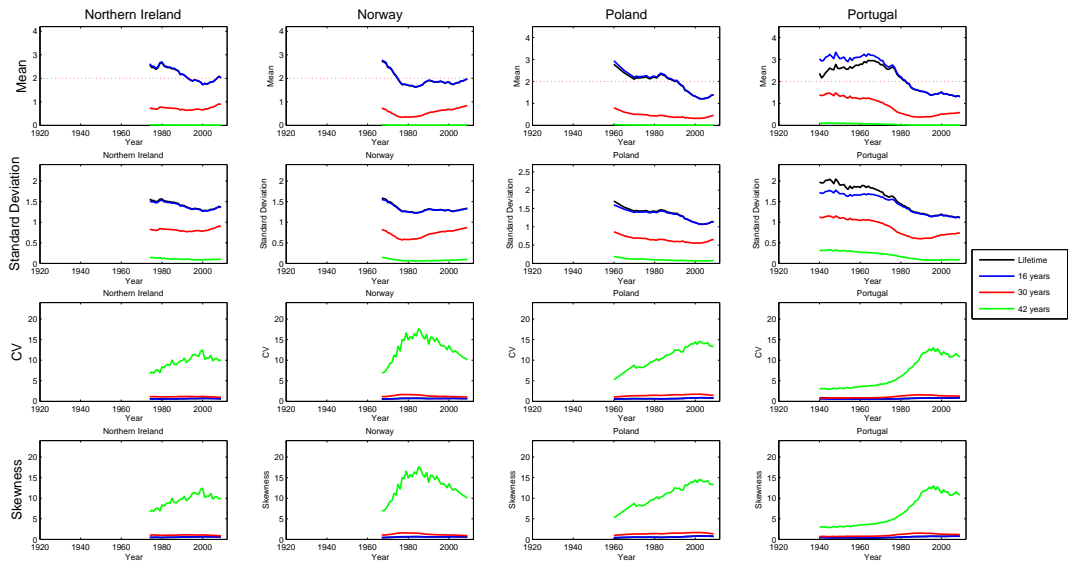


Figure A7: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Northern Ireland, Norway, Poland, and Portugal.

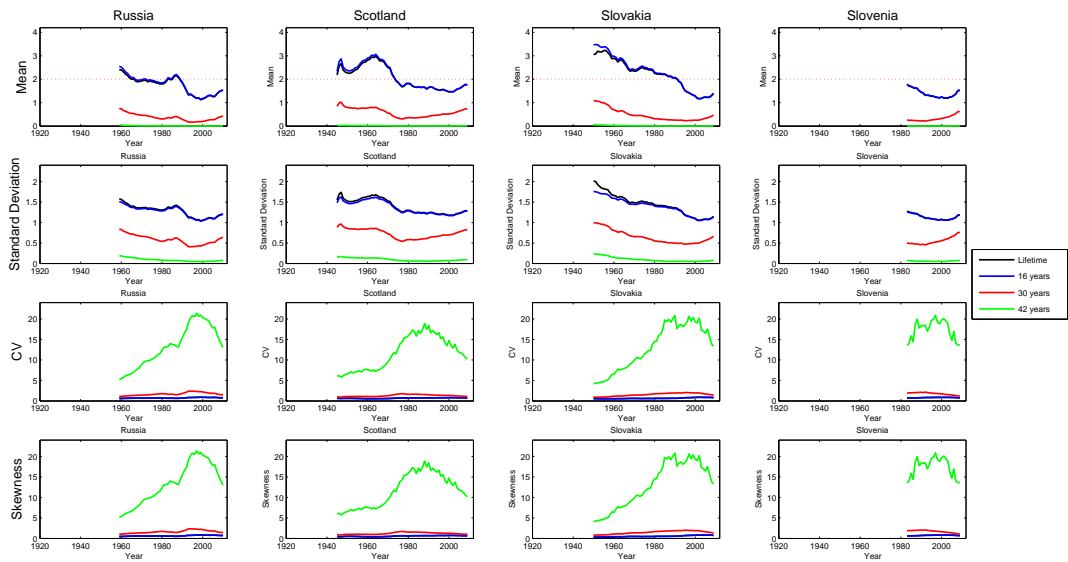


Figure A8: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Russia, Scotland, Slovakia, and Slovenia.

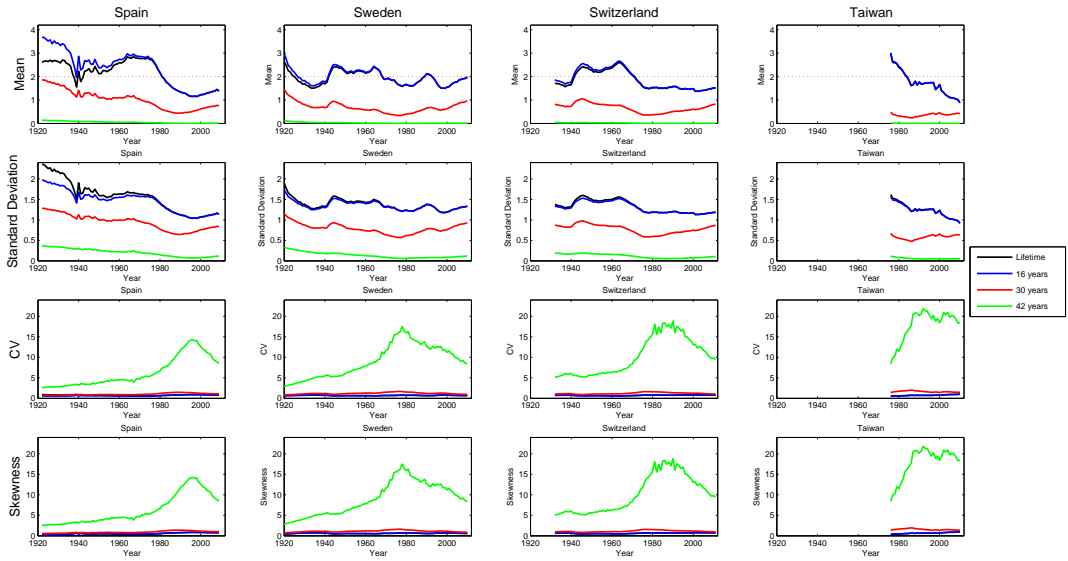


Figure A9: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Spain, Sweden, Switzerland, and Taiwan.

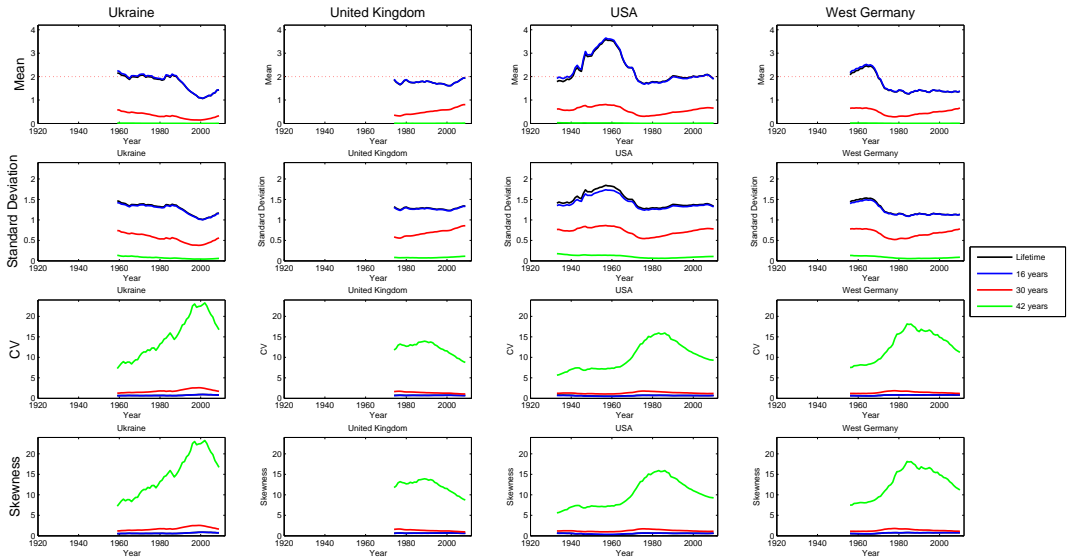


Figure A10: Mean, standard deviation, CV and skewness of lifetime reproductive output (black line) and remaining reproductive output at age 16 (blue line), age 30 (red line), and 42 years (green line). Countries shown are Ukraine, the United Kingdom, the USA, and West Germany.

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