Mean and variability of lifetime reproduction: individual stochasticity and the fertility transition

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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 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, Sobotka, and Jasilioniene, 2009; Wilson, 2004). In recent years fertility has started to increase again. Myrskylä, Kohler, and Billari (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 and Kaplan, 1999; Kirk, 1996; Bryant, 2007; Goldstein, Sobotka, and Jasilioniene, 2009). Biodemographic explanations have been proposed that explain reduced fertility as a (perhaps mistaken) evolved response to increased costs of offspring (Hill and 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, Sobotka, and Jasilioniene, 2009; Myrskylä, Kohler, and Billari, 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, Kohler, and Billari (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, Steiner, and Orzack, 2009; Steiner and 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, Sobotka, and Jasilioniene, 2009; Myrskylä, Kohler, and Billari, 2009). Following Myrskylä, Kohler, and Billari (2009), we also investigate the relationship between the statistics of LRO and the UNDP Human Development Index (HDI). However, where Myrskylä, Kohler, and Billari (2009) focus on the the effect of an increasing HDI on TFR, we assess the effect of HDI on multiple statistics of lifetime reproduction.

2 Methods: Markov chains with rewards

Notation. Matrices are denoted by upper-case bold symbols (e.g., **P**), vectors by lower-case bold symbols (e.g., ρ). Vectors are column vectors by default. The transpose of **P** is **P**^T. The inverse of **P** is **P**⁻¹. The vector **1** is a vector of ones, and the matrix **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 **x** on the diagonal and zeros elsewhere is denoted $\mathcal{D}(\mathbf{x})$. The expected value is denoted by $\mathbf{E}(\cdot)$. The Hadamard, or element-by-element, product of matrices **A** and **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.

2.1 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

$$\mathbf{P} = \begin{pmatrix} \mathbf{U} & \mathbf{0} \\ \hline \mathbf{m}^{\mathsf{T}} & 1 \end{pmatrix} \tag{1}$$

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

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

$$r_{ij} = \begin{cases} 1 \text{ with probability } f_j \\ 0 \text{ with probability } (1 - f_j) \end{cases}$$
(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 kth moments of the transition-specific rewards r_{ij} . The first moment matrix is

$$\mathbf{R}_{1} = \begin{pmatrix} f_{1} & \dots & f_{\omega} & 0\\ \vdots & \ddots & \vdots & \vdots\\ \underline{f_{1}} & \dots & f_{\omega} & 0\\ \hline f_{1} & \dots & f_{\omega} & 0 \end{pmatrix}$$
(4)

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

$$\mathbf{R}_1 = \mathbf{R}_2 = \mathbf{R}_3 \tag{5}$$

2.1.1 Lifetime accumulated rewards

We define ρ 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 ρ describes the accumulation over the remaining lifetime of an individual of age *i*. The vector of *k*th moments of ρ is denoted ρ_k , where

$$\boldsymbol{\rho}_{k} = \left(E\left[\rho_{i}^{k} \right] \right) \tag{6}$$

From the recursion equations presented in Caswell (2011), we obtain equations for the equilibria of ρ_k (Caswell and 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 subjctor $\tilde{\rho}$ giving the accumulation of rewards in the ω transient states. To this end, we define a matrix Z

$$\mathbf{Z} = \left(\begin{array}{c|c} \mathbf{I}_{\omega} & \mathbf{0}_{\omega \times 1} \end{array} \right) \tag{7}$$

Multiplying ρ_i by 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:

$$\tilde{\boldsymbol{\rho}}_{1} = \mathbf{N}^{\mathsf{T}} \mathbf{Z} \left(\mathbf{P} \circ \mathbf{R}_{1} \right)^{\mathsf{T}} \mathbf{1}_{\omega+1}$$
(8)

$$\tilde{\boldsymbol{\rho}}_{2} = \mathbf{N}^{\mathsf{T}} \left[\mathbf{Z} (\mathbf{P} \circ \mathbf{R}_{2})^{\mathsf{T}} \mathbf{1}_{\omega+1} + 2 (\mathbf{U} \circ \mathbf{R}_{1})^{\mathsf{T}} \tilde{\boldsymbol{\rho}}_{1} \right]$$
(9)

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

$$V(\tilde{\boldsymbol{\rho}}) = \tilde{\boldsymbol{\rho}}_2 - \tilde{\boldsymbol{\rho}}_1 \circ \tilde{\boldsymbol{\rho}}_1 \tag{11}$$

$$SD\left(\tilde{\boldsymbol{\rho}}\right) = \sqrt{V\left(\tilde{\boldsymbol{\rho}}\right)}$$
 (12)

$$CV(\tilde{\boldsymbol{\rho}}) = \mathcal{D}(\tilde{\boldsymbol{\rho}}_1)^{-1} SD(\tilde{\boldsymbol{\rho}})$$
(13)

$$Sk\left(\tilde{\boldsymbol{\rho}}\right) = \mathcal{D}\left[V(\tilde{\boldsymbol{\rho}})\right]^{-3/2} \left(\tilde{\boldsymbol{\rho}}_{3} - 3\tilde{\boldsymbol{\rho}}_{1} \circ \tilde{\boldsymbol{\rho}}_{2} + 2\tilde{\boldsymbol{\rho}}_{1} \circ \tilde{\boldsymbol{\rho}}_{1} \circ \tilde{\boldsymbol{\rho}}_{1}\right).$$
(14)

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).

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 and Kaplan (2007), Blurton Jones (2011), and Hill and 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 and 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 and 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 and Mayer, 1953). We used Hutterite fertility rates from a study by Eaton and 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.

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: 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^{-3}	Lithuania	1959 - 2010	$52^{}$	HMD. HFD
$\frac{-}{22}$	Luxembourg	1966 - 2009	44	HMD. HFC
23	Netherlands	1950-2009	60	HMD, HFD
$\frac{-9}{24}$	New Zealand	1948 - 2008	61	HMD HFC
25	Northern Ireland	1974 - 2009	36	HMD HFD
$\frac{20}{26}$	Norway	1967 - 2009	43	HMD HFD
$\frac{20}{27}$	Poland	1970 - 2000	40	HMD HFC
28	Portugal	1940 - 2009	70	HMD HFD
20	Russia	$1940 \ 2000 \ 1959 \ 2010$	52	HMD, HFD
30	Scotland	1938-2010	65	HMD, HFD
31	Slovakia	1950-2009	60 60	HMD, HFD
35	Slovenia	1983_2009	27	HMD, HFD
0⊿ 33	Snain	1022-2009	∠ 1 88	$\begin{array}{c} \text{HMD}, \text{HFD} \\ \text{HMD}, \text{HFC} \end{array}$
00 24	Sweden	1801_2010	190	$\frac{11110}{1110}, \frac{1110}{1110}$
94 35	Sweden	1091 - 2010 1039 - 9011	120 80	HMD HFD
20 26	Taiwan	1992-2011	00 95	1 1 1 1 1 1 1 1 1 1
ა0 97		1970-2010 1050 2000	30 E 1	HMD, HFD
31 20	Ukraine	1939-2009	16	IMD, HFD
38 20	United Kingdom	1974-2009	30	HMD, HFD
39	USA	1933-2010	78	HMD, HFD
40	west Germany	1956 - 2010	55	HMD, HFD



Figure 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, Kohler, and Billari (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 nonrandom relationships among themselves. We examine these by looking for correlations among the statistics and examining temporal trajectories in the statistics.

3 Results

3.1 LRO patterns over age

In Figure 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.



Figure 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 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 of 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 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.

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, Sobotka, and Jasilioniene, 2009; Myrskylä, Kohler, and Billari, 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 $CV.^2$

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.

²The similarity of values of the coefficient of variation and of skewness was noted in several species by Caswell (2011); it is possibly related to the statistical distribution of lifetime reproduction; if LRO followed a Poisson distribution, the CV would equal the skewness.







Figure 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 and Wagner (1995) and Adler (1997).

3.3 Relationship to HDI

The HDI is a synthetic index designed to describe socioeconomic living conditons. The decline in TFR during fertility transition has been associated with improvement in standards of living. Myrskylä, Kohler, and Billari (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, Kohler, and Billari (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 5(a)). Furthermore, we find a similar reversal in the relationship between HDI and the other statistical properties of LRO (see Figure 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,

Figure 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 2009. The regression line equations are presented in Table A1 in the Appendix.

(d) Skewness over HDI

(c) CV over HDI



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

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 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 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 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 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.

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 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 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 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 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 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 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 and Tuljapurkar, 2012). Adding heterogeneity to the model may increase the variance in LRO (Steiner and 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 and 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 and Kluge, 2014).

$\mathbf{5}$ Acknowledgements

Appendix Α

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 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	5.					

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

	Skewness	$\rho_1 = 3.9 - 3.3Sk$	V = 3.5 - 2.9Sk	SD = 2.1 - 1.2Sk	CV = 0.14 + 0.91Sk	
in 2000	CV	$\boldsymbol{\rho}_1 = 4.4 - 3.6 CV$	V = 3.9 - 3.2 CV	SD = 2.2 - 1.3CV		Sk = 0.14 + 1.1CV
al properties for LRO	Standard Deviation	$\boldsymbol{\rho}_1 = 1.7 + 2.7SD$	V = 1.4 + 2.4SD		CV = 1.7 - 0.74SD	Sk = 1.7 - 0.81SD
nship among statistic	Variance	$\rho_1 = 0.093 + 1.1V$		$SD = 0.6 \pm 0.42V$	CV = 1.2 - 0.31V	Sk = 1.2 - 0.34V
Relatio	Mean		$V = 0.085 + 0.88 \boldsymbol{\rho}_1$	$SD = 0.63 + 0.37 \rho_1$	$CV = 1.2 - 0.27 \rho_1$	$Sk = 1.2 - 0.3 \boldsymbol{ ho}_1$
	Regression lines	Mean	Variance	Standard Deviation	CV	Skewness

Dolotionship among statical among for LDA is 2000

Table A2: Table of regression lines drawn through the scatterplot data in Figure 6. All lines showed an R^2 of around 0.98-0.99.

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