

Statistics of inter-individual variation in lifetime fertility: a Markov chain approach^{*†}

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Abstract

Lifetime fertility is the total number of children (or sometimes of female children) to which a woman gives birth over her lifetime. The net reproductive rate R_0 is the expectation of lifetime fertility. The total fertility rate (TFR) is the expectation conditional on the woman surviving through her childbearing years. Both R_0 and TFR can be calculated from age- or stage-classified demographic models. Because it is an expectation, R_0 provides no information on variability. Here, I present and apply a new approach, based on the theory of Markov chains with rewards, that provides all the moments of the distribution of lifetime reproduction. The approach applies to age- or stage-classified models, to constant, periodic, or stochastic environments, and to any kind of reproductive schedule. As examples, I calculate and compare these statistics for models in which fertility depends on age, or on age and parity, using data from Sweden in 1970 and the Czech Republic in 1950.

1 Introduction

1.1 Lifetime fertility

Lifetime fertility is the total number of children, or sometimes the number of female children, a woman has over her lifetime. The net reproductive rate R_0 measures the expectation of lifetime fertility. As is well known (Cushing and Zhou, 1994; Caswell, 2001, 2009), R_0 expressed as female offspring per female is also the population growth rate per generation (not per unit of time), and is an indicator function for population growth, in that population growth is positive if and only if $R_0 > 1$. It is calculated from age-classified models as

$$R_0 = \int_0^{\infty} \ell(x)m(x)dx, \quad (1)$$

where $\ell(x)$ is survivorship to age x and $m(x)$ is fertility at age x (Rhodes, 1940), and from stage classified models as

$$R_0 = \max \text{eig} \left[\mathbf{F} (\mathbf{I} - \mathbf{U})^{-1} \right], \quad (2)$$

where \mathbf{F} is a matrix of stage-specific fertilities and \mathbf{U} is a matrix giving transition probabilities of individuals among stages (Cushing and Zhou, 1994; Caswell, 2001, 2009; de Camino-Beck and Lewis, 2007). In evolutionary demography, R_0 is sometimes used as a measure of fitness, although

26 this works only under certain circumstances (Metz, 2008). In epidemiology, R_0 gives the expected
 27 number of secondary infections following the introduction of a single infectious individual into a
 28 susceptible population (Heesterbeek, 2002). The infection can spread and produce an outbreak if
 29 and only if $R_0 > 1$.

30 Because it is an expectation, R_0 provides no information on that baseline level of variability.
 31 My goal here is to present a general and tractable calculation of all the moments of lifetime fer-
 32 tility, applicable to stage- or age-classified populations, for arbitrary distributions of stage-specific
 33 reproduction. Although I will not address it here, it applies to constant, periodic, and stochas-
 34 tic environments (Caswell, 2011). The calculations use a mathematical framework (Markov chains
 35 with rewards) that has many potential applications to questions in addition to lifetime reproductive
 36 output.

37 **Notation.** Matrices are denoted by upper-case bold symbols (e.g., \mathbf{P}), vectors by lower-case bold
 38 symbols (e.g., $\boldsymbol{\rho}$). Some block-structured matrices are denoted by, e.g., \mathbb{P} . Vectors are column
 39 vectors by default. The transpose of \mathbf{P} is \mathbf{P}^\top . The vector $\mathbf{1}$ is a vector of ones. The diagonal
 40 matrix with the vector \mathbf{x} on the diagonal and zeros elsewhere is denoted $\mathcal{D}(\mathbf{x})$. The expected value
 41 is denoted by $E(\cdot)$, the variance by $V(\cdot)$, the coefficient of variation by $CV(\cdot)$ and the skewness
 42 by $Sk(\cdot)$. The Hadamard, or element-by-element, product of matrices \mathbf{A} and \mathbf{B} is denoted by
 43 $\mathbf{A} \circ \mathbf{B}$. Transition matrices of Markov chains are written in column-to-row orientation, and hence
 44 are column-stochastic.

45 1.2 The approach: Markov chains with rewards

46 The method used here was introduced in Caswell (2011) and applied there to a variety of species.
 47 We use an absorbing Markov chain to describe the life cycle, and associate a “reward” with each
 48 possible transition among the states of the Markov chain. Death appears in the model as an
 49 absorbing state, or possibly multiple absorbing states (e.g., representing causes of death). The
 50 transition matrix of this absorbing chain can be written

$$\mathbf{P} = \left(\begin{array}{c|c} \mathbf{U} & \mathbf{0} \\ \hline \mathbf{M} & \mathbf{I} \end{array} \right) \quad (3)$$

51 where \mathbf{U} is the transient matrix (dimension $s \times s$) and \mathbf{M} is a matrix of mortality rates. I will
52 assume throughout that the dominant eigenvalue of \mathbf{U} is less than 1, so that an individual beginning
53 in any transient state will eventually be absorbed (i.e., will eventually die) with probability 1.

54 In a Markov chain with rewards, an individual moving from state j to state i collects a reward r_{ij} .
55 In the present application, the reward corresponds to reproduction. Markov chains with rewards
56 were introduced by Howard (1960) to analyze Markov decision processes. In his development, the
57 reward r_{ij} was a fixed quantity. Here, however, I will consider the r_{ij} to be random variables with
58 specified statistical properties (Benito, 1982). Fixed rewards follow as a special case.

59 **1.3 Reproduction as a reward**

60 In age-classified demographic models, reproduction between t and $t + 1$ is a function of the age at
61 time t , independent of the transition made by the individual between t and $t + 1$. If this is so, the r_{ij}
62 will depend only on j . In an age-parity model, reproduction is associated with the transition from
63 one parity state to the next. In this case, r_{ij} will depend explicitly on both i and j . The analysis
64 here also assumes that the dead do not reproduce, so $r_{ij} = 0$, for all j that represent absorbing
65 states.

66 **2 Analytical methods**

67 As an individual moves through the stages of the life cycle, it accumulates reproductive rewards.
68 The goal of our analysis is to calculate the statistical properties (mean, variance, skewness) of
69 the accumulated lifetime reward. The solution to this problem is provided by an simple set of
70 recurrence relations (Caswell, 2011).

71 Define $\boldsymbol{\rho}$ as the vector (dimension $(s + 1) \times 1$) of accumulated rewards as a function of the initial
72 stage of the individual. The vector of k th moments of the entries of $\boldsymbol{\rho}$ is denoted $\boldsymbol{\rho}_k$, where

$$\boldsymbol{\rho}_k = \left(E [\rho_i^k] \right). \quad (4)$$

73 The rewards r_{ij} are random variables. The matrix of the k th moments of the r_{ij} is denoted \mathbf{R}_k :

$$\mathbf{R}_k = \left(E \left[r_{ij}^k \right] \right). \quad (5)$$

74 Caswell (2011) proved that the moment vectors $\boldsymbol{\rho}_i$ can be calculated recursively as follows.
 75 Let \mathbf{P} be the transition matrix of the Markov chain, let \mathbf{R}_k be the matrix of k th moments of
 76 the transition-specific rewards. Calculations are referenced to a terminal time T . The first three
 77 moments of the accumulated reward satisfy

$$\boldsymbol{\rho}_1(t+1) = (\mathbf{P} \circ \mathbf{R}_1)^\top \mathbf{1} + \mathbf{P}^\top \boldsymbol{\rho}_1(t) \quad (6)$$

$$\boldsymbol{\rho}_2(t+1) = (\mathbf{P} \circ \mathbf{R}_2)^\top \mathbf{1} + 2(\mathbf{P} \circ \mathbf{R}_1)^\top \boldsymbol{\rho}_1(t) + \mathbf{P}^\top \boldsymbol{\rho}_2(t) \quad (7)$$

$$\boldsymbol{\rho}_3(t+1) = (\mathbf{P} \circ \mathbf{R}_3)^\top \mathbf{1} + 3(\mathbf{P} \circ \mathbf{R}_2)^\top \boldsymbol{\rho}_1(t) + 3(\mathbf{P} \circ \mathbf{R}_1)^\top \boldsymbol{\rho}_2(t) + \mathbf{P}^\top \boldsymbol{\rho}_3(t) \quad (8)$$

78 for $t = 0, \dots, T-1$, with $\boldsymbol{\rho}_1(0) = \boldsymbol{\rho}_2(0) = \boldsymbol{\rho}_3(0) = 0$. In general, the m th moments of accumulated
 79 rewards are given by

$$\boldsymbol{\rho}_m(t+1) = \sum_{k=0}^m \binom{m}{k} (\mathbf{P} \circ \mathbf{R}_{m-k})^\top \boldsymbol{\rho}_k(t) \quad (9)$$

80 with $\boldsymbol{\rho}_m(0) = 0$. The combination of the assumptions that \mathbf{P} has the structure (3) and that $r_{ij} = 0$
 81 for all absorbing states j means that every individual will eventually be absorbed in a state in which
 82 future rewards are zero; thus $\boldsymbol{\rho}_1(t)$ will converge to a limit as $T \rightarrow \infty$; this limit is the expectation
 83 of lifetime rewards calculated over the entire lifetime of every individual. See Caswell (2011) for
 84 proofs and further references.

85 The first moment $\boldsymbol{\rho}_1$ gives the mean lifetime reproductive output. The variance, standard
 86 deviation, coefficient of variation, and skewness of lifetime reproductive output are calculated from
 87 the moment vectors

$$V(\boldsymbol{\rho}) = \boldsymbol{\rho}_2 - \boldsymbol{\rho}_1 \circ \boldsymbol{\rho}_1 \quad (10)$$

$$SD(\boldsymbol{\rho}) = \sqrt{V(\boldsymbol{\rho})} \quad (11)$$

$$CV(\boldsymbol{\rho}) = \mathcal{D}(\boldsymbol{\rho}_1)^{-1} SD(\boldsymbol{\rho}) \quad (12)$$

$$Sk(\boldsymbol{\rho}) = \mathcal{D}[V(\boldsymbol{\rho})]^{-3/2} (\boldsymbol{\rho}_3 - 3\boldsymbol{\rho}_1 \circ \boldsymbol{\rho}_2 + 2\boldsymbol{\rho}_1 \circ \boldsymbol{\rho}_1 \circ \boldsymbol{\rho}_1). \quad (13)$$

88 The variance is useful because it can be partitioned additively among sources. The standard
 89 deviation cannot be partitioned in this way, but it has the advantage of appearing in the same units
 90 as ρ . The CV scales the standard deviation relative to the mean, and hence is dimensionless. The
 91 CV is also the square root of Crow’s (1958) index of the opportunity for selection; this provides a
 92 upper bound on the rate of increase of mean fitness, if fitness is measured by lifetime reproduction
 93 and all the variance in reproduction is genetic. Finally, the skewness, which is dimensionless,
 94 measures the symmetry of the distribution of rewards. Positive skewness implies a long tail of
 95 positive values, and vice versa.

96 The i th element of the vector ρ gives the lifetime reproductive output of an individual of age i ;
 97 this can be referred to as the *remaining lifetime* accumulation.

98 Several authors in the widely scattered literature on Markov chains with rewards have addressed
 99 the variance, but not the complete set of moments, of accumulated rewards. (e.g., Sladkỳ and van
 100 Dijk, 2005; Benito, 1982).

101 **3 Analysis of age-dependent fertility**

102 Age-dependent fertility is parameterized by the vector \mathbf{p} of age-specific survival probabilities and
 103 the vector \mathbf{f} of age-specific fertilities. The model follows the standard structure of an age-classified
 104 Leslie matrix. A surviving individual moves to the next age class, hence the transition matrix \mathbf{U}
 105 contains survival probabilities on the subdiagonal and zeros elsewhere (Figure 1a):

$$\mathbf{U} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{pmatrix} \quad (14)$$

106 (here written for 4 age classes).

107 The reward matrices are defined from the vector \mathbf{f} of age-specific fertilities. Ignoring multiple
 108 births, the number of offspring at age j is a Bernoulli random variable with moments

$$E[r_{ij}] = f_j \quad (15)$$

$$E[r_{ij}^2] = f_j \quad (16)$$

$$E[r_{ij}^3] = f_j. \quad (17)$$

109 Thus the reward matrices containing the moments of offspring production are

$$\mathbf{R}_k = \left(\begin{array}{cccc|c} f_1^k & f_2^k & f_3^k & f_4^k & 0 \\ f_1^k & f_2^k & f_3^k & f_4^k & 0 \\ f_1^k & f_2^k & f_3^k & f_4^k & 0 \\ f_1^k & f_2^k & f_3^k & f_4^k & 0 \\ \hline f_1^k & f_2^k & f_3^k & f_4^k & 0 \end{array} \right) \quad k = 1, 2, 3 \quad (18)$$

110 (again, for the case with four age classes).

111 As an example, I analyze a historical sequence of mortality and fertility for the human population
 112 of Sweden from 1891 to 2007 (Human Mortality Database, 2013; Human Fertility Database, 2013).
 113 This period included two world wars, the 1916 flu epidemic, and a health transition sufficient to
 114 raise female life expectancy at birth from 53 to 83 years.

115 4 Analysis of fertility dependent on age and parity

116 The life cycle graph for a population in which individuals are classified by age and parity is shown
 117 in Figure 1b. The Markov chain matrix appropriate to this classification is derived using the
 118 vec-permutation methodology (Hunter and Caswell, 2005; Caswell, 2011).

119 We begin by defining age classes $1, \dots, \omega$ and parity states $1, \dots, s$. Transitions among parity
 120 states for age class i are described by a $s \times s$ matrix given by

$$\mathbf{B}(i) = \left(\begin{array}{cccc} 1 - q_1(i) & 0 & 0 & 0 \\ q_1(i) & 1 - q_2(i) & 0 & 0 \\ 0 & q_2(i) & 1 - q_3(i) & 0 \\ 0 & 0 & q_3(i) & 1 \end{array} \right) \quad i = 1, \dots, \omega \quad (19)$$

121 (shown here for $s = 4$ parity classes). The quantity $q_j(i)$ is the probability of transition from parity

122 class j to $j + 1$ for an individual in age class i .

123 For ages less than the age at first reproduction, $\mathbf{B}(i) = \mathbf{I}_s$, and it is impossible to advance to
 124 the next parity class. The entry in the bottom right corner corresponds to an open final parity
 125 class. The parity transition probabilities q_i are available for parity 0, 1, 2, 3, 4, and 5+ from the
 126 age-parity fertility tables in the Human Fertility Database Human Fertility Database (2013).

127 Transitions from one age class to the next for parity state j are given by a $\omega \times \omega$ matrix

$$\mathbf{M}(j) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ p_1(i) & 0 & 0 & 0 \\ 0 & p_2(i) & 0 & 0 \\ 0 & 0 & p_3(i) & 0 \end{pmatrix} \quad i = 1, \dots, s \quad (20)$$

128 (shown here for $\omega = 4$ age classes). The matrix entry $p_i(j)$ is the survival probability of an individual
 129 in age class i and parity class j . In the absence of parity-specific mortality data, all the $\mathbf{M}(j)$ will
 130 be equal.

131 The Markov chain describing the joint dynamics of age and parity is created from the block
 132 diagonal matrices

$$\mathbb{B} = \begin{pmatrix} \mathbf{B}(1) & & \\ & \ddots & \\ & & \mathbf{B}(\omega) \end{pmatrix} \quad \text{parity state transitions} \quad (21)$$

$$\mathbb{M} = \begin{pmatrix} \mathbf{M}(1) & & \\ & \ddots & \\ & & \mathbf{M}(s) \end{pmatrix} \quad \text{age transitions} \quad (22)$$

133 The transient matrix $\tilde{\mathbf{U}}$ and the transition matrix $\tilde{\mathbf{P}}$ are then

$$\tilde{\mathbf{U}} = \mathbf{K}^\top \mathbb{M} \mathbf{K} \mathbb{B} \quad (23)$$

$$\tilde{\mathbf{P}} = \left(\begin{array}{c|c} \tilde{\mathbf{U}} & 0 \\ \hline \mathbf{1}^\top - \mathbf{1}^\top \tilde{\mathbf{U}} & 1 \end{array} \right) \quad (24)$$

134 Where the row vector $\mathbf{1}^\top - \mathbf{1}^\top \tilde{\mathbf{U}}$ contains the age- and parity-specific probabilities of death. The
 135 matrix \mathbf{K} is the vec-permutation matrix (also called the commutation matrix) of order (s, ω) (Hen-
 136 derson and Searle, 1981; Magnus and Neudecker, 1979; Hunter and Caswell, 2005).

137 Rewards, in the form of reproduction, are obtained when an individual advances from one parity
 138 state to the next (Figure 1b). The reward matrices corresponding to the parity transition matrix
 139 (19) are

$$\mathbf{R}_j(i) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & q_s(i) \end{pmatrix} \quad \begin{array}{l} i = 1, \dots, \omega \\ j = 1, 2, 3 \end{array} \quad (25)$$

140 The entry $q_s(i)$ in the lower right corner is the reward obtained by treating reproduction in the
 141 open parity interval as a Bernoulli random variable.

142 The reward matrix corresponding to age-parity transition matrix $\tilde{\mathbf{P}}$ is a block-structured matrix
 143 constructed from the $\mathbf{R}_j(i)$:

$$\tilde{\mathbf{R}}_j = \left(\begin{array}{ccc|c} \mathbf{R}_j(1) & \cdots & \mathbf{R}_j(\omega) & 0 \\ \vdots & & \vdots & \vdots \\ \mathbf{R}_j(1) & \cdots & \mathbf{R}_j(\omega) & 0 \\ \hline \mathbf{0}_{s \times 1} & \cdots & \mathbf{0}_{s \times 1} & 0 \end{array} \right) \quad (26)$$

144 The analysis of lifetime reproduction now proceeds using (6)–(13), using the Markov chain
 145 matrix $\tilde{\mathbf{P}}$ and the reward matrices $\tilde{\mathbf{R}}_1$, $\tilde{\mathbf{R}}_2$, and $\tilde{\mathbf{R}}_3$.

146 The result is a set of moment vectors $\boldsymbol{\rho}_i$, of dimension $(s\omega + 1) \times 1$, that give the moments of
 147 lifetime reproduction as a function of current age and parity.

148 5 Applications: Sweden and Czech Republic

149 The results of the age-specific and the age-parity-specific fertility models can be examined in several
 150 different ways. One of these, the analysis of temporal trends, will be presented elsewhere (van
 151 Daalen and Caswell in prep.). Here, I examine the age patterns of the mean and variation in
 152 lifetime fertility, for two countries, selected (more or less arbitrarily) to represent two different

153 mortality and fertility situations. Sweden in 1970 had a period female life expectancy at birth of
154 77.2 years, and a TFR of 1.9. The Czech Republic in 1950 had a life expectancy of 66.8 years and a
155 TFR of 2.8. The results may hint at patterns to be expected comparing countries in the earlier and
156 the later stages of a fertility transition. Period life tables were obtained from the Human Mortality
157 Database (2013), and age-parity fertility tables from the Human Fertility Database (2013).

158 The results are shown in a series of figures, organized as follows:

- 159 1. Age trajectories of the mean, standard deviation, coefficient of variation, and skewness of
160 lifetime reproduction for Sweden 1970 (Figure 2).
- 161 2. Age trajectories of the mean, standard deviation, coefficient of variation, and skewness of
162 lifetime reproduction for Czech Republic 1950 (Figure 3).
- 163 3. Bar plots showing the interaction of age and parity in determining the statistics of lifetime
164 reproduction for selected ages, for Sweden 1970 (Figures 4 and 6).
- 165 4. Bar plots showing the interaction of age and parity in determining the statistics of lifetime
166 reproduction for selected ages, for Czech Republic 1950 (Figures 5 and 8).

167 A few patterns are obvious from these comparisons. In both Sweden and Czech Republic, the
168 mean and standard deviation of remaining lifetime reproduction decline with age (no surprise in
169 the former; the latter is not as easily predictable). When variation is measured relative to the
170 mean, there is a dramatic increase in the CV with age. The skewness follows the same pattern. In
171 both countries, then, remaining lifetime reproduction becomes more uncertain and highly positively
172 skewed at ages greater than about 35 (Figures 2 and 3).

173 The age-parity-specific model shows similar patterns, but there is a striking difference between
174 Sweden and Czech Republic. For Sweden, the mean, standard deviation, CV, and skewness in
175 lifetime reproduction are highest for parity 0, and lower for higher parity states. The pattern is
176 the opposite in the Czech Republic; higher parity women have a higher expectation and standard
177 deviation of lifetime reproduction.

178 The effects of parity are far from trivial. At the same age, differences in parity may change
179 the mean, standard deviation, and CV of lifetime reproduction by a factor of 3 or more, and the
180 skewness by a factor of 5.

181 6 Discussion

182 6.1 Variability and heterogeneity are not the same thing

183 Empirical measurements of lifetime fertility (in any species) typically reveal variation — often
184 large amounts of variation — among individuals. The distribution is often positively skewed, with
185 a long tail of rare individuals producing more than the average number of offspring; e.g., many
186 examples in Clutton-Brock (1988) and Newton (1989). The observed variability and skewness of
187 lifetime fertility is sometimes interpreted as evidence of heterogeneity among individuals. However,
188 variability in lifetime fertility is to be expected even in the absence of heterogeneity.

189 Demographic variation in lifetime fertility arises from three sources. One source is individual
190 stochasticity: stochastic variation among individuals in the pathways they take through the life
191 cycle (Caswell, 2009). A cohort of identical individuals, experiencing identical vital rates at every
192 stage, will differ in how long they live and how long they spend in each stage (Caswell, 2009). A
193 second source of variation is within-stage variation in reproduction. A cohort of identical individu-
194 als, in the same stage, experiencing the same probability distribution of stage-specific reproduction,
195 will differ in how many offspring they produce. The analysis here includes both sources. These
196 stochastic processes are collectively called *individual stochasticity* Caswell (2009, 2011). They pro-
197 duce variation even if all individuals are absolutely identical, experiencing the same vital rates
198 at every age or stage. The results presented here obtained in exactly this way; every individual
199 experiences the same probabilities as captured in \mathbf{P} and the \mathbf{R}_j . Thus these results provide cannot
200 be used to infer differences among women due to heterogeneity.

201 Of course, *unobserved heterogeneity* does exist; individuals are genuinely different from each
202 other in ways not captured by age, or by age and parity. If individuals are different, they will expe-
203 rience different transition probabilities (\mathbf{P}) and/or rewards (\mathbf{R}_i). Heterogeneity may reflect fixed
204 differences (e.g., genetic differences, or differences in local environment among individuals of sessile
205 species), or differences that develop over time (e.g., accumulated damage caused by environmental
206 factors). In order to compare the contributions of heterogeneity and individual stochasticity, the
207 heterogeneity must be incorporated into the Markov chain model. This has been done for mortality
208 models based on heterogeneous frailty (Caswell, 2014), and will be pursued for fertility in a future
209 paper.

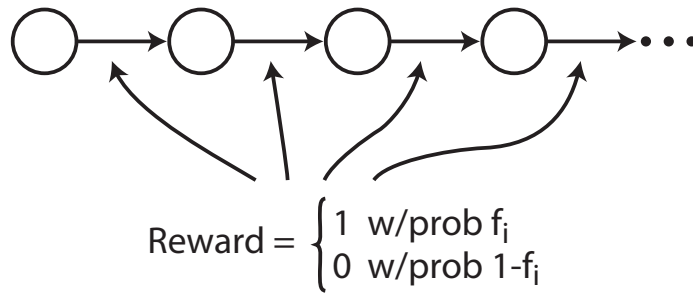
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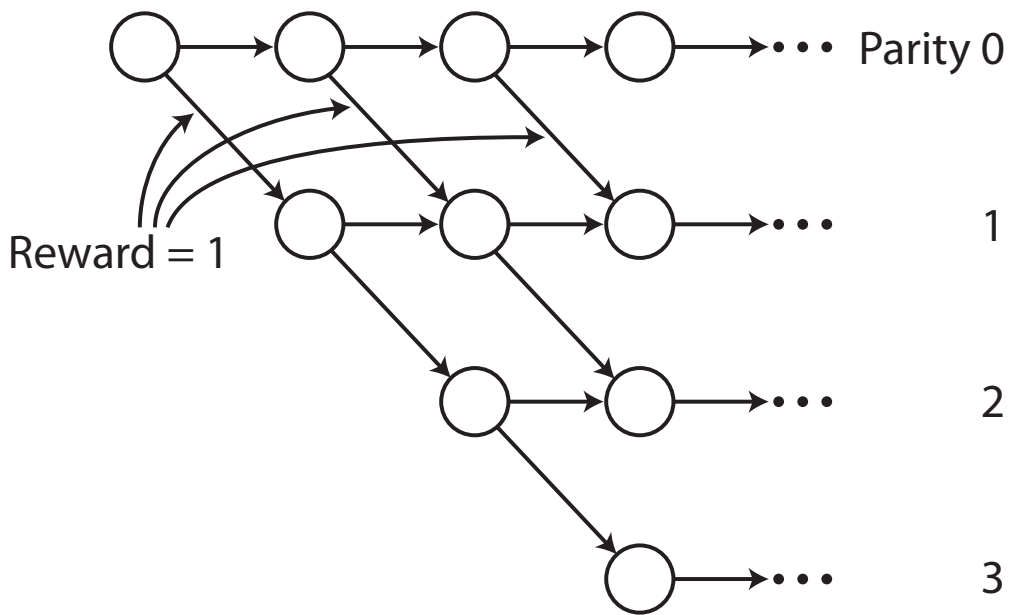
215 **References**

- 216 Benito, F. 1982. Calculating the variance in Markov-processes with random reward. *Trabajos de*
217 *estadística y de investigación operativa* **33**:73–85.
- 218 Caswell, H. 2001. *Matrix Population Models*. 2nd edition. Sinauer Associates, Sunderland, MA.
- 219 Caswell, H. 2009. Stage, age and individual stochasticity in demography. *Oikos* **118**:1763–1782.
- 220 Caswell, H. 2011. Beyond R_0 : demographic models for variability of lifetime reproductive output.
221 *PloS one* **6**:e20809.
- 222 Caswell, H. 2014. A matrix approach to the statistics of longevity in the gamma-Gompertz and
223 related models. Submitted .
- 224 Clutton-Brock, T. H. 1988. *Reproductive success: studies of individual variation in contrasting*
225 *breeding systems*. University of Chicago Press, Chicago, Illinois.
- 226 Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. *Human Biology*
227 pages 1–13.
- 228 Cushing, J., and Y. Zhou. 1994. The net reproductive value and stability in matrix population
229 models. *Natural Resources Modeling* **8**:297–333.
- 230 de Camino-Beck, T., and M. A. Lewis. 2007. A new method for calculating net reproductive rate
231 from graph reduction with applications to the control of invasive species. *Bulletin of Mathematical*
232 *Biology* **69**:1341–1354.
- 233 Heesterbeek, J. A. P. 2002. A brief history of R_0 and a recipe for its calculation. *Acta biotheoretica*
234 **50**:189–204.

- 235 Henderson, H. V., and S. Searle. 1981. The vec-permutation matrix, the vec operator and Kronecker
236 products: A review. *Linear and Multilinear Algebra* **9**:271–288.
- 237 Howard, R. A. 1960. *Dynamic programming and Markov processes*. Wiley, New York, New York.
- 238 Human Fertility Database, 2013. Max Planck Institute for Demographic Research (Germany) and
239 the Vienna Institute of Demography (Austria). URL www.humanfertility.org.
- 240 Human Mortality Database, 2013. University of California, Berkeley (USA), and Max Planck
241 Institute for Demographic Research (Germany). URL www.mortality.org.
- 242 Hunter, C. M., and H. Caswell. 2005. The use of the vec-permutation matrix in spatial matrix
243 population models. *Ecological modelling* **188**:15–21.
- 244 Magnus, J. R., and H. Neudecker. 1979. The commutation matrix: some properties and applica-
245 tions. *The Annals of Statistics* pages 381–394.
- 246 Metz, J. A. J., 2008. Fitness. Pages 1599–1612 *in* *Encyclopedia of Ecology*, volume 2. Amsterdam:
247 Elsevier.
- 248 Newton, I. 1989. *Lifetime reproductive success in birds*. Academic Press, San Diego, California.
- 249 Rhodes, E. C. 1940. Population Mathematics. I. *Journal of the Royal Statistical Society* **103**:61–89.
- 250 Sladký, K., and N. M. van Dijk, 2005. Total reward variance in discrete and continuous time
251 Markov chains. Pages 319–326 *in* *Operations Research Proceedings 2004*. Springer.



(a) Age-dependent fertility



(b) Age-parity-dependent fertility

Figure 1: Life cycle structures for (a) age-dependent fertility and (b) age-parity-dependent fertility, showing the rewards dependent on stages (for the first case) and on transitions (for the second case).

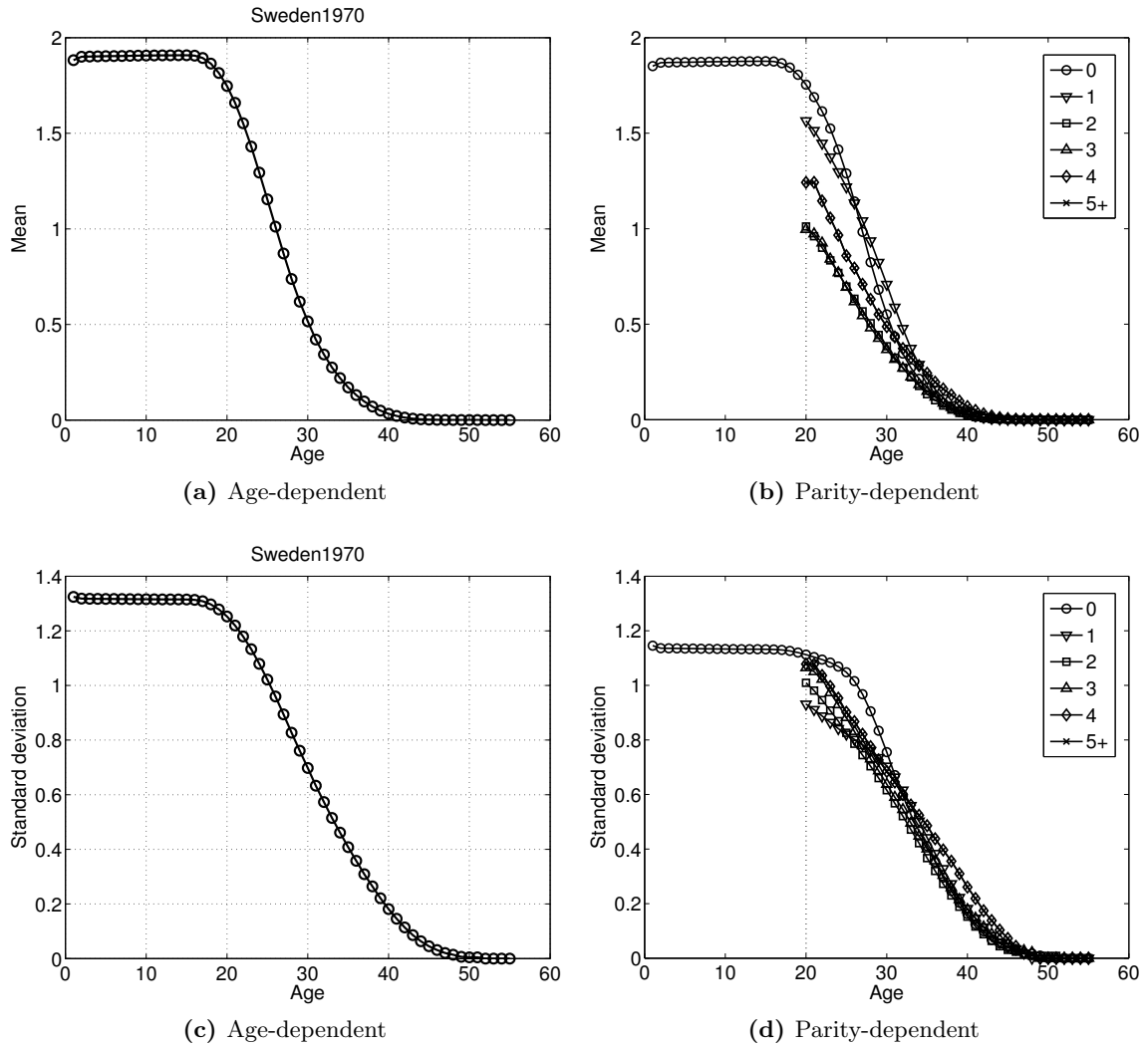


Figure 2: The mean (above) and standard deviation (below) of lifetime reproductive out put for Sweden in 1970. Graphs in the left column show statistics of *age-specific* lifetime reproduction. The right column shows *age-parity-specific* lifetime reproduction. Values for parity states greater than 0 are shown from age 20 onwards. Continued on next figure.

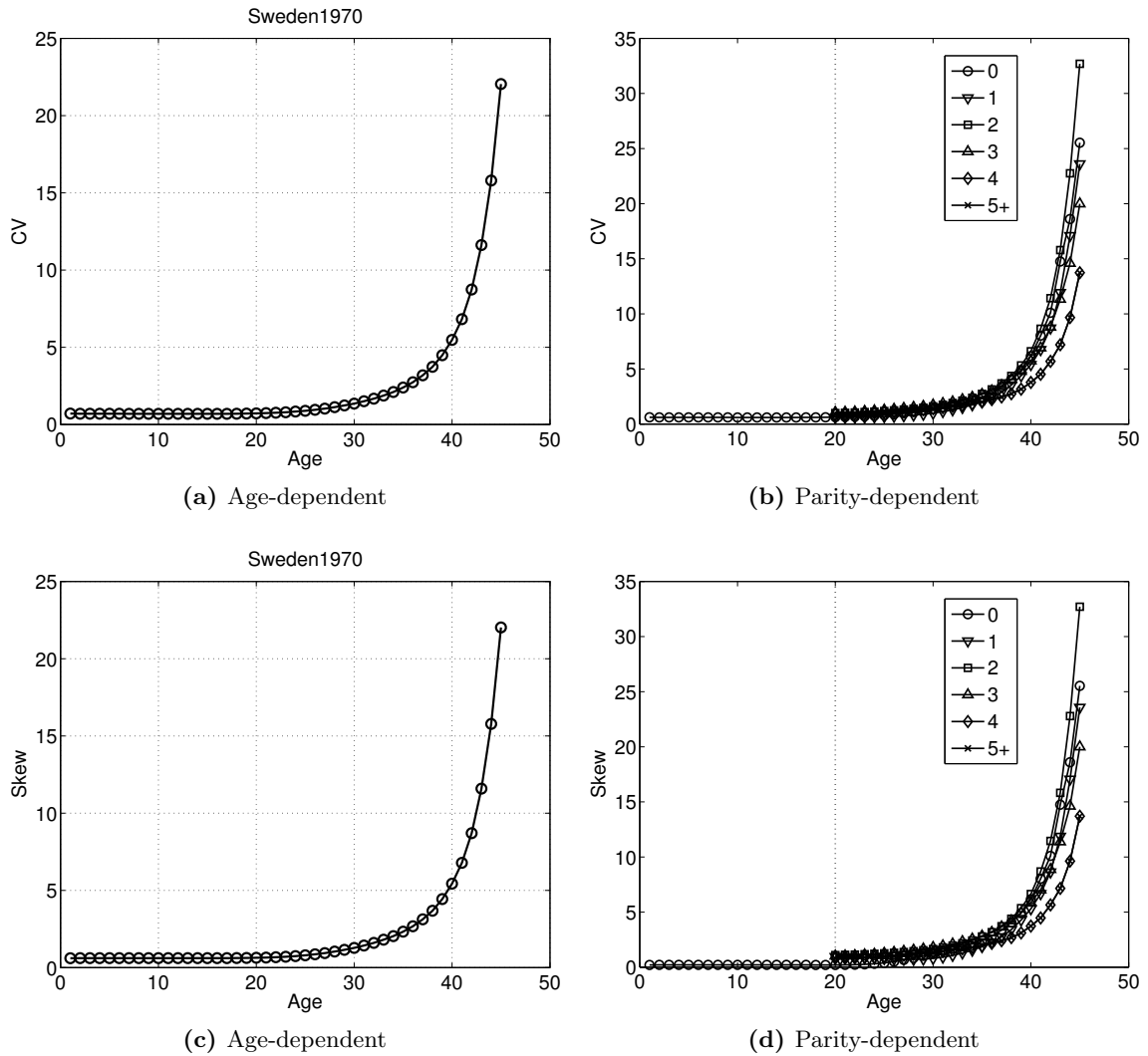


Figure 2: (continued) The coefficient of variation (above) and skewness (below) of lifetime reproductive output for Sweden in 1970. Graphs in the left column show statistics of *age-specific* lifetime reproduction. The right column shows *age-parity-specific* lifetime reproduction. Values for parity states greater than 0 are shown from age 20 onwards.

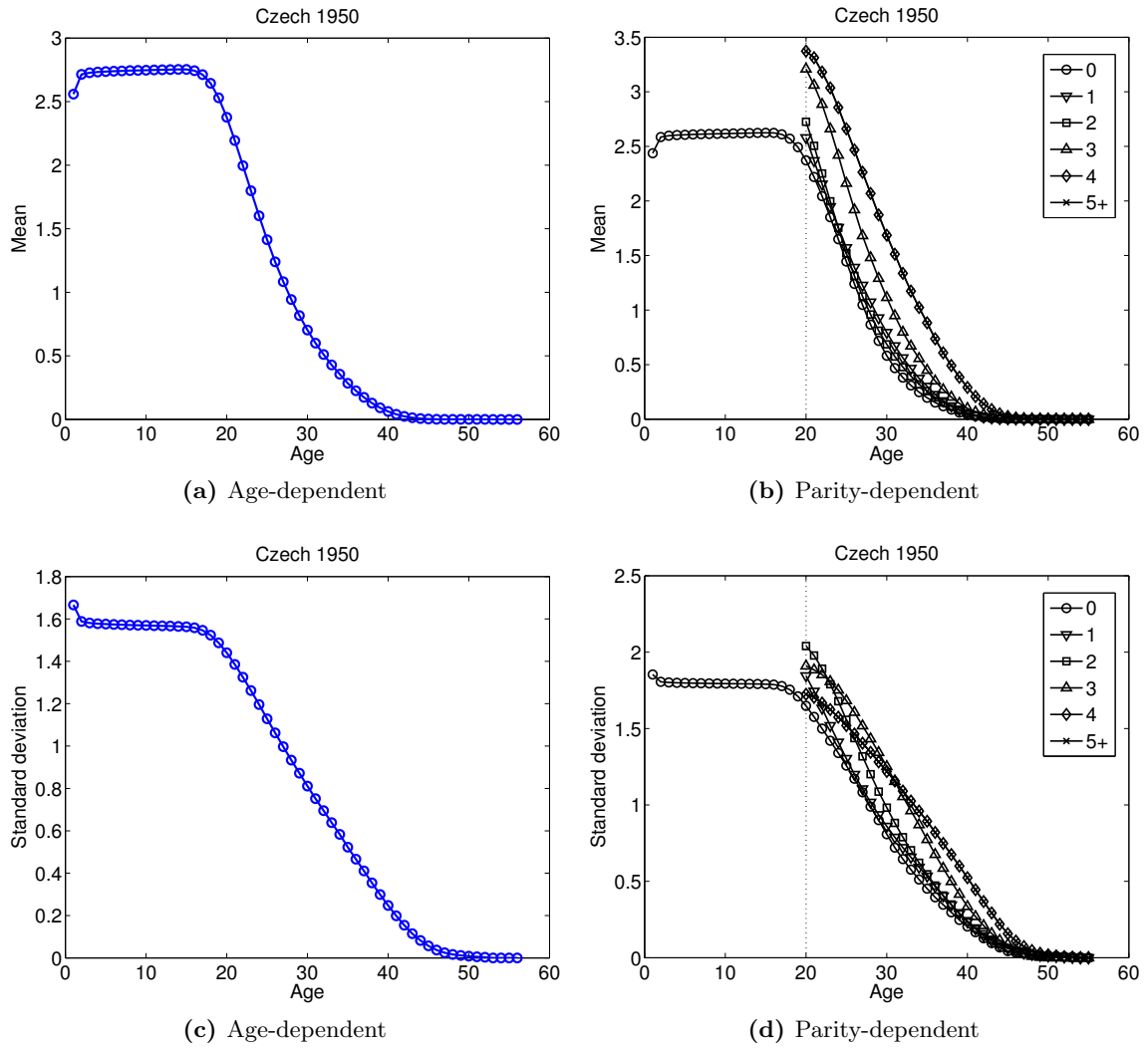


Figure 3: The mean (above) and standard deviation (below) of lifetime reproductive out put for Czech Republic in 1950. Graphs in the left column show statistics of *age-specific* lifetime reproduction. The right column shows *age-parity-specific* lifetime reproduction. Values for parity states greater than 0 are shown from age 20 onwards. Continued on next figure.

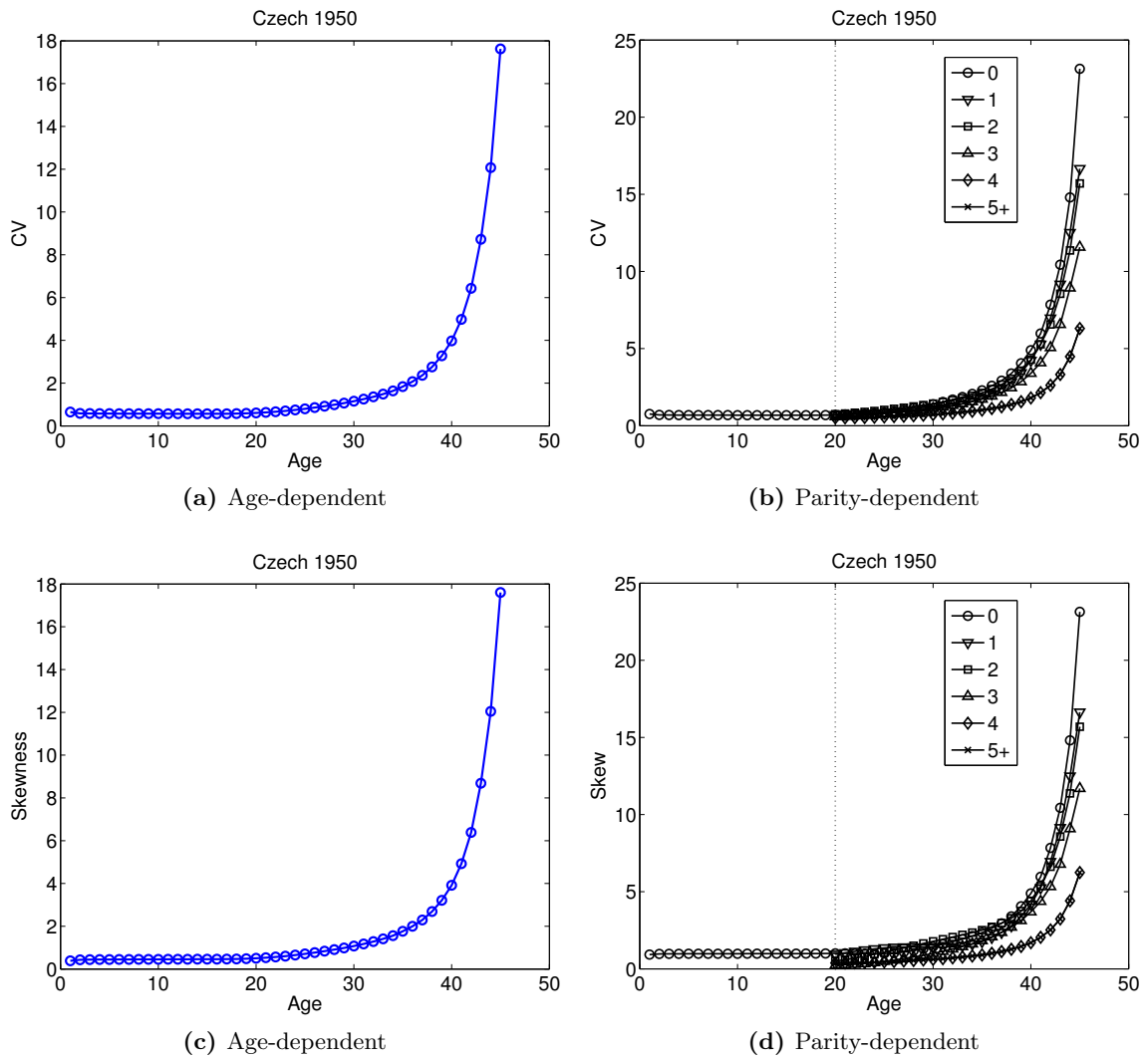


Figure 3: (continued) The coefficient of variation (above) and skewness (below) of lifetime reproductive output for Czech Republic in 1950. Graphs in the left column show statistics of *age-specific* lifetime reproduction. The right column shows *age-parity-specific* lifetime reproduction. Values for parity states greater than 0 are shown from age 20 onwards.

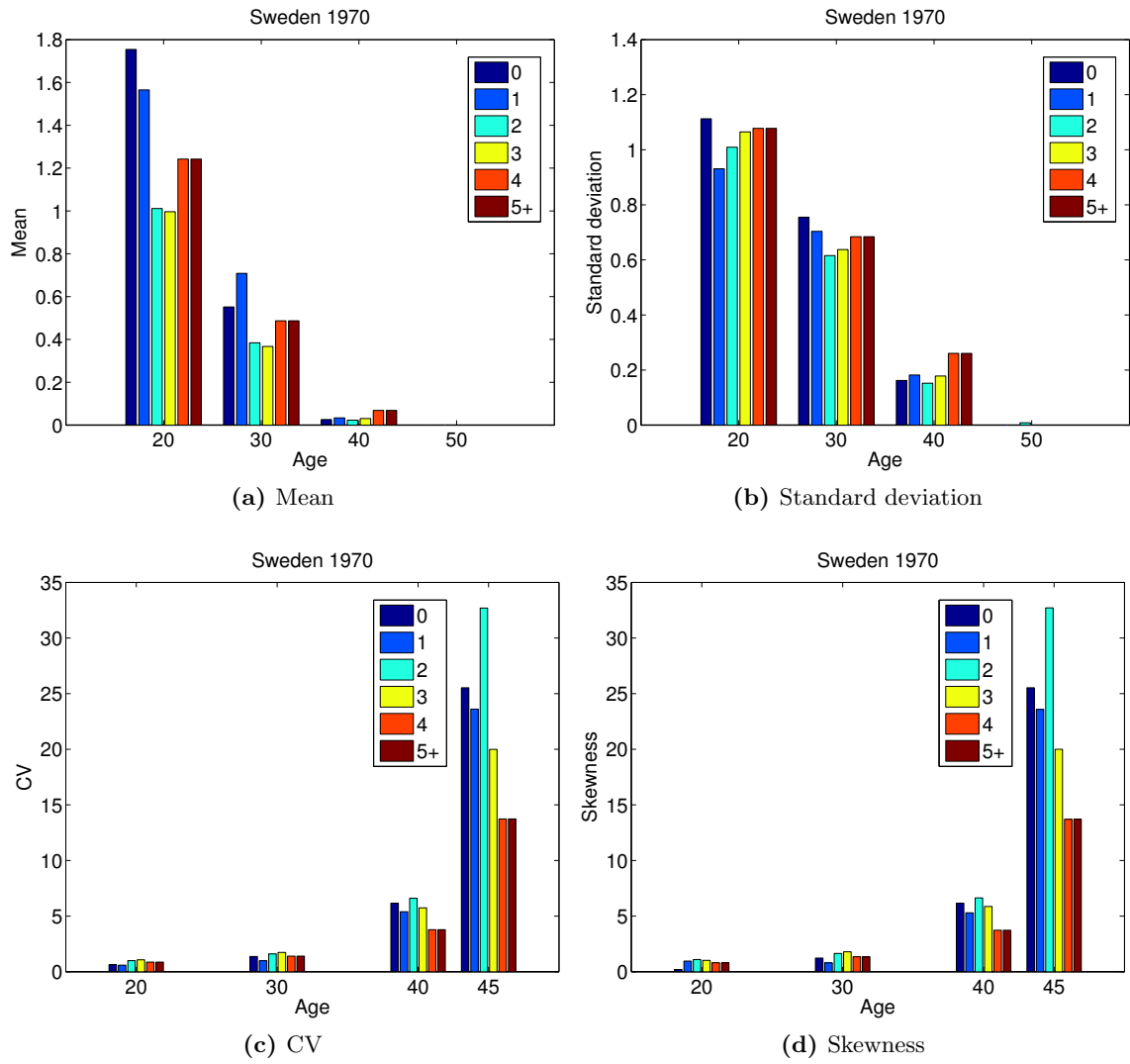


Figure 4: Statistics of lifetime reproduction as a function of age and parity for Sweden in 1970.

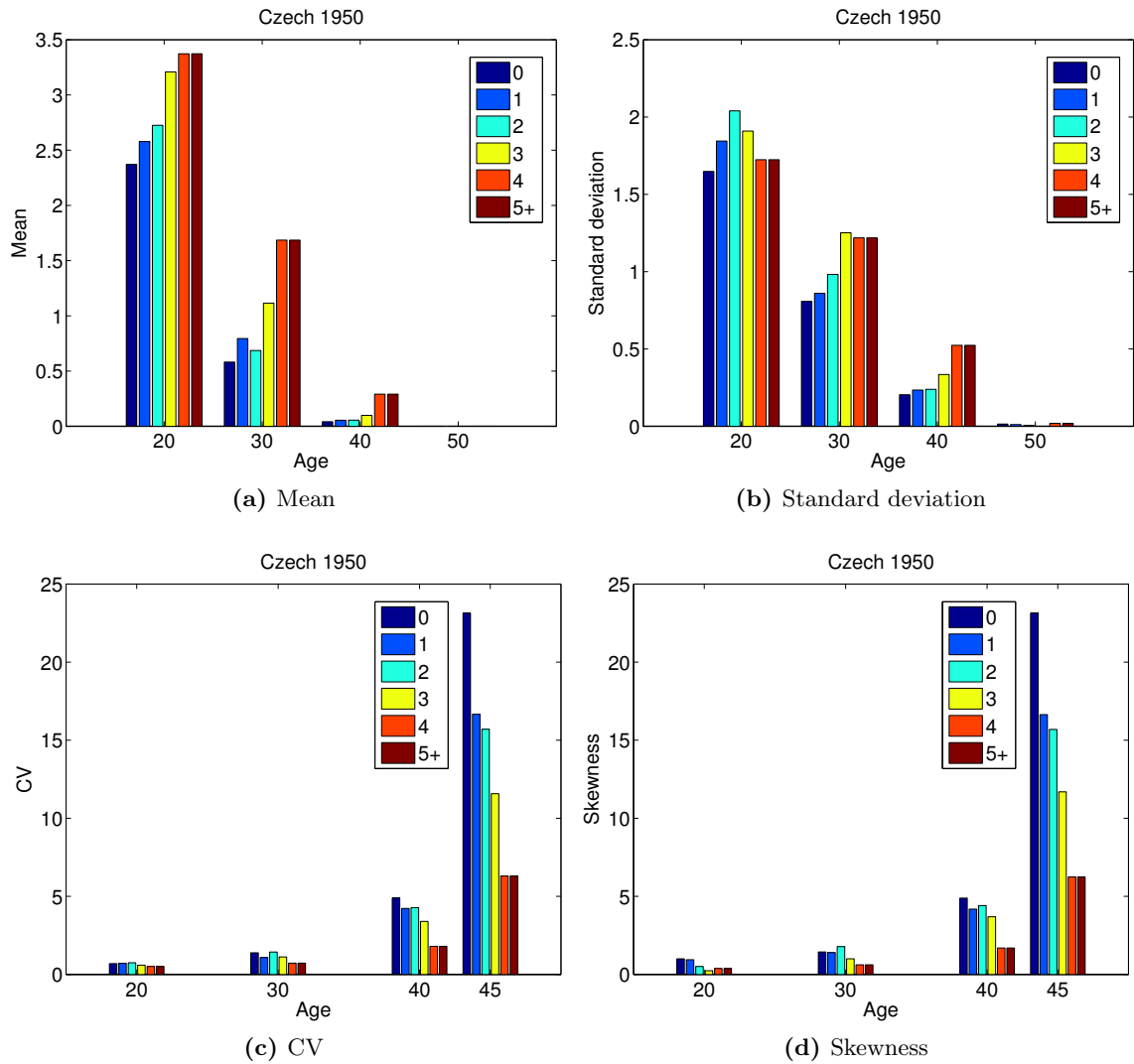


Figure 5: Statistics of lifetime reproduction as a function of parity and age for Czech Republic in 1950.

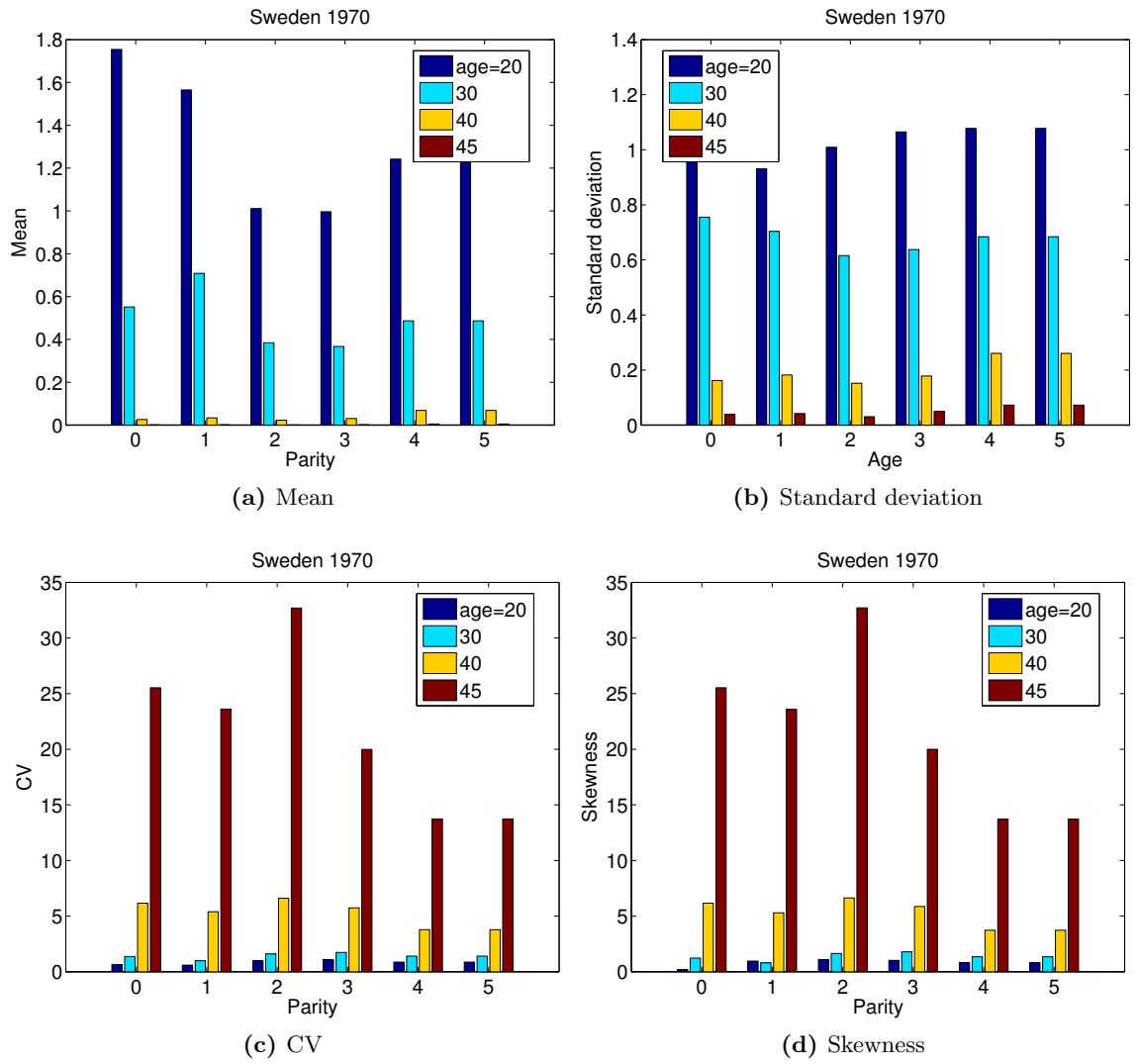


Figure 6: Statistics of lifetime reproduction as a function of parity and age for Sweden in 1970.

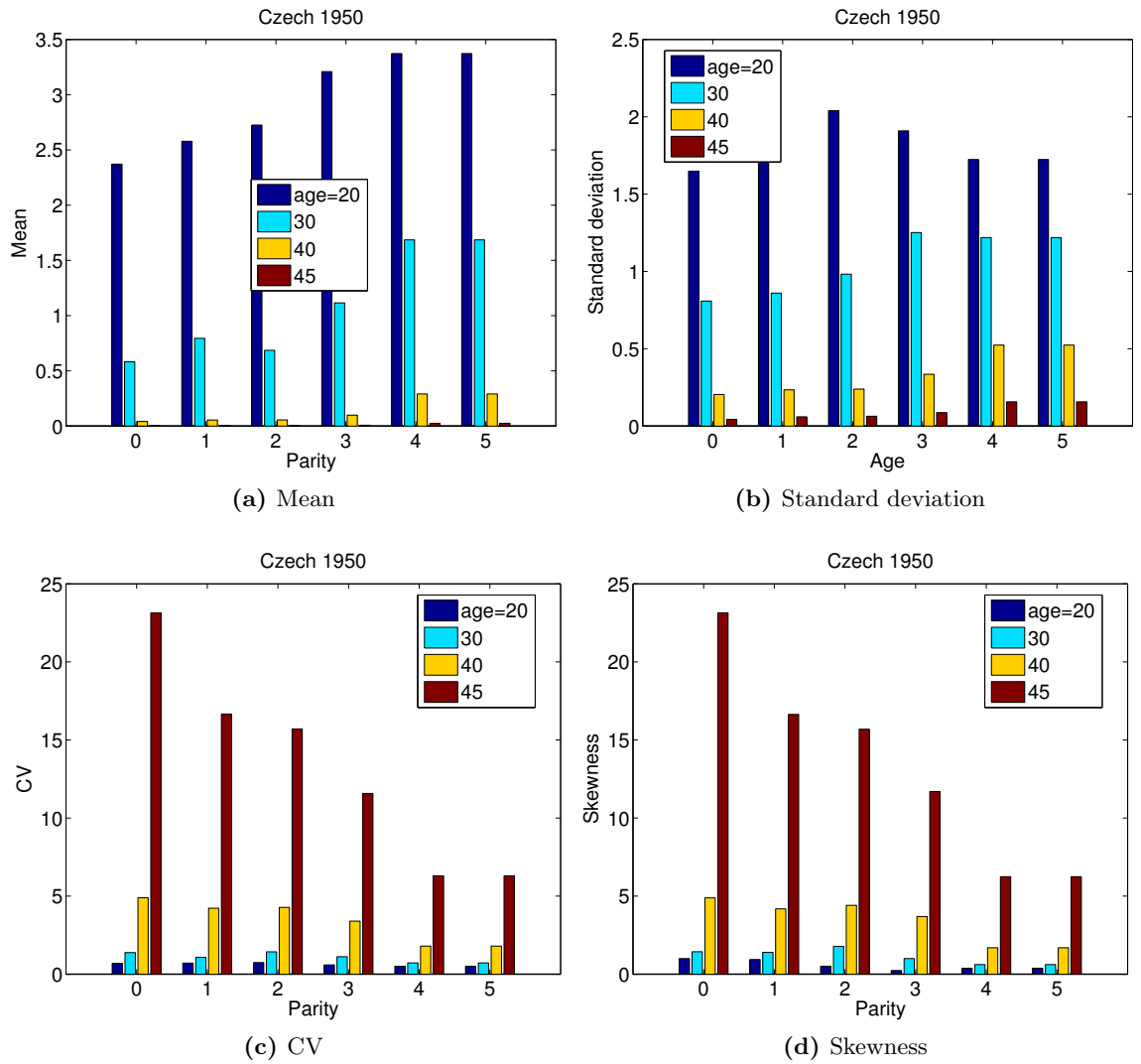


Figure 7: Czech Republic 1950

Figure 8: Statistics of lifetime reproduction as a function of parity and age for Czech Republic in 1950.