SI for chapter 13. The outcome variables: fertility, child survival, and reproductive success.

SI 13.1. Regressions to show fit of child death x age.

SI 13.2. Procedure. Program to score RS data procedure

SI 13.3. Standard scores are independent of age at final observation (“endage”) standardscores

SI 13.4. More reasons why early RS may not predict final RS. reasonotpredict

SI 13.5 Testing the measures of reproductive success. testing

- **SI 13.5.1. Correlations between standard scores at adjacent 5 year age points.**
- **SI 13.5.2. Women ss matrices womenssmatrices**
- **SI 13.5.3. Women PCA**
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- **SI 13.5.5. Men correlation matrices mensssmatrices**
- **SI 13.5.6. Men PCA mensspca**

SI 13.6. Standard scores at end age predicted from earlier ages. ssfreendage

SI 13.7. Rate of early reproduction x rate of later reproduction. brt

SI 13.8. A note on STDs and variance in female RS. STDS

SI 13.9. Sources for Table 13.1. stdzvariance

SI 13.10. The relative importance of different components of reproductive success. components stepwise

SI 13.11. Age at first birth as predictor of lifetime RS. agefirstb

SI 13.12. Reproductive value by age for Hadza men and women reprodvalue

SI 13.13. Adult sex ratios of Hadza and others. asr

SI 13.14. Thinking about desertion. Opportunities for conception versus unclaimed wives. wivesmates

SI 13.1. Regressions to show fit of child death to age.

Entire sample, all fathers, all ages recorded. 243 child deaths in 5519 child years of data.

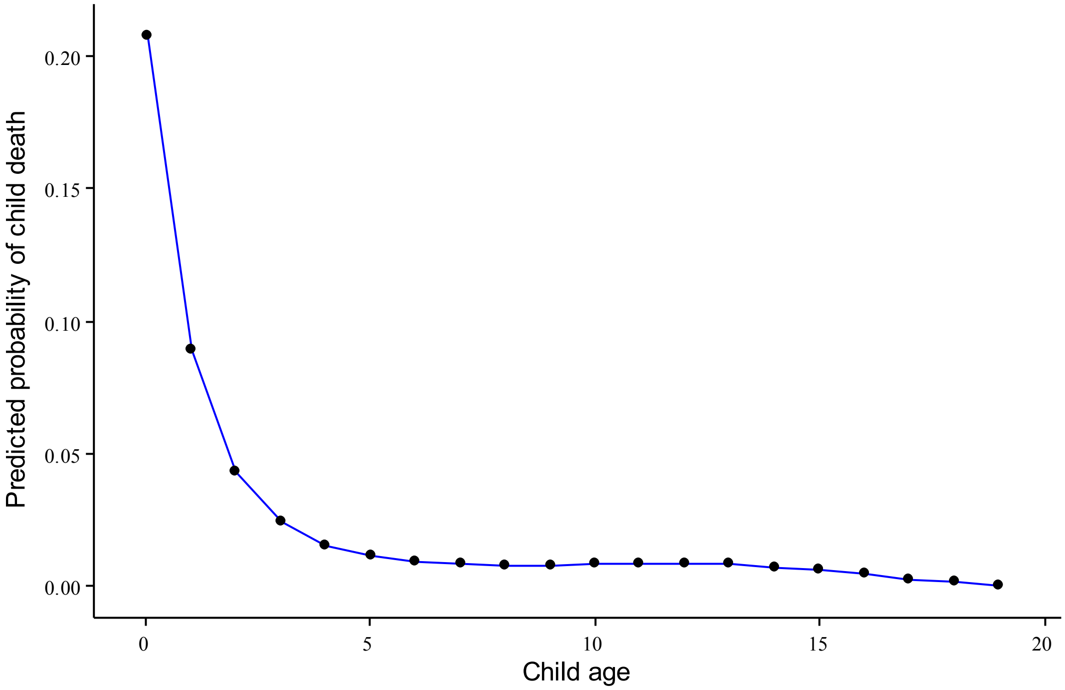
	Intecept	Beta	P	LL
age	-1.837	-0.3385	.000	-846.26
Age Age^2	-1.638	-0.5392 0.0154	.000 .000	-820.23
Age Age^2 Age^3	-1.508	-.7579 .0458 -.00081	.000 .000 .002	-812.41
Age Age^2 Age^3 Mo age birth	-0.776	-.7606 .0456 -.00081 -.0289	.000 .000 .002 .012	-809.18

Sample restricted to under 20 years old, children of Hadza fathers:-

Binary Logistic Regression: live/died versus child age, agesqd, ...
Link Function: Logit
205 deaths in 4341 child-years
Log-Likelihood = -653.966
“OR” = odds ratio.

	Beta coefficent	se	z	p	OR	95% CI of OR
Child age	-1.0867	.1209	-8.99	.000	0.34	0.27-0.43
Age^2	0.1111	.0238	4.66	.000	1.12	1.07-1.17
Age^3	-.00370	.0011	-3.24	.001	1.0	.99-1.0
Mother age at birth	-.0269	.0123	-2.20	.028	.97	.95-1.0
Constant	-.6561	.3224	-2.03	.042		

Probability of child death x age predicted by above regression.



SI 13.2. Procedure. Program to score RS data. Data handling and calculation of measures.

Program selects the eligible men and women. Their record must not be a duplicate (thus "m" or "f") must have an age estimate (YOB). Women must have been interviewed and scored as use = 1. Men were restricted to those seen mostly in the study area (inarea >= 60) and in 3 or more censuses, and alive in 2000.

The reproductive record of both sexes are built the same way, by finding all children for whom they are listed as parent, sorting the children into age order, calculating parent's age at birth of each child, recording in an array for each parent by parent age, the parent's age in the year of the child's birth, checking for age at death if any, and accumulating the number of children born, alive, and the % surviving during each year of the parent's life.

The next routines read this array, and for each age of parent scores the number of births, cumulative N of births, N of cases, the mean , sample size, sd, for N of births, N alive, % surviving. Finally a routine calculates the standard scores at each age for each parent as observed score / standard deviation.

These are written to an Access file which can be saved as an Excel file and read into Minitab. The file can also be combined with other such data files.

I wanted to derive measures of RS of men as well as women. The reproductive success of each sex depends in part on the RS of the opposite sex, and average RS should be the same in each sex (if the adult sex ratio is approximately equal). But when marriages are even slightly unstable, the distributions of men's RS cannot be scored from those of their current wives. Hadza marriages break up quite often (Woodburn 1968 b, and see chapter 15). The reproductive output of any particular woman has been achieved with between one and eight men. The reproductive output of a particular man will have been achieved with a number of women, again varying from a lifelong marriage between one man and one woman, to a succession of wives, any one of whom we may or may not have interviewed.

SI 13.3. Standard scores are independent of age at final observation

I extracted reproductive achievement up to each of the following ages: 15, 20, 25, 30, 35, … to 55 for women, and ages 20, 25, 30 … 80 for men. The measures were number of children alive, number of births, % of those born who were alive at each of these ages. I computed the mean number of births etc. accumulated by men and women by age 20, 23, 25, 30, 35 and so on. Some have more than the average number of births, some fewer, or even none. I then computed the deviation of each individual from this mean at each of these ages. Because the raw deviations are larger at greater ages, I expressed the individuals' deviations as standard scores - the deviation divided by the standard deviation for the respective age. The sign is preserved in the standard score.

Some individuals fall below the mean, some above it. I did the same thing for the number of live children, and for number ever born. For those who have had any births, I computed the mean and the individual deviations for the percentage of children kept alive. A score was also derived for “endage”. For women this is the age at her last interview. For men, Endage is the last year in which the man was observed, taken from his marriage file. The endage was usually not at a five-year age point.

The means of number of children born by each age grew in a relatively smooth fashion (graphs below, Figure SI 13.3a and b), only among the oldest people were there indications of fluctuation due to the declining sample size and poor information.

I set no criterion child age for child survival. At each age of mother it is possible that one of the children will be less than a year old, and thus at quite some risk of failing to survive. At younger parental ages this vulnerable latest infant will comprise a larger portion of the still small, accumulated surviving family.

SI Table 13.3. Standard scores are not correlated with age at end of observation. Correlations for women shown below. Regressions show 0% of variance in standard score is accounted for by “endage”. Pearson correlation coefficient and p value.

Measure	Correlation coefficient	P value
Ss live end	-.026	.731
Ss born end	-.037	.634
Ss surv end	-.005	.956

Figure SI 13.3a. Interviewed women's mean number of births by age x and average number of live children at age x. Family size accumulates fairly steadily until the sample size diminishes at higher ages.

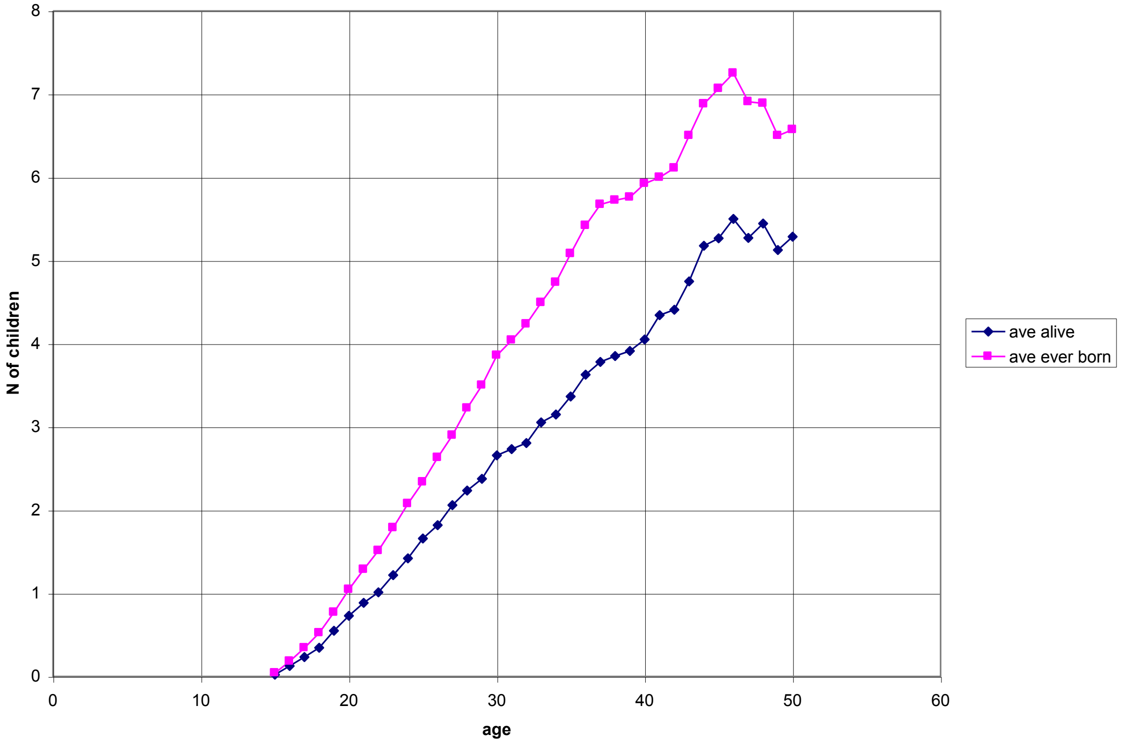
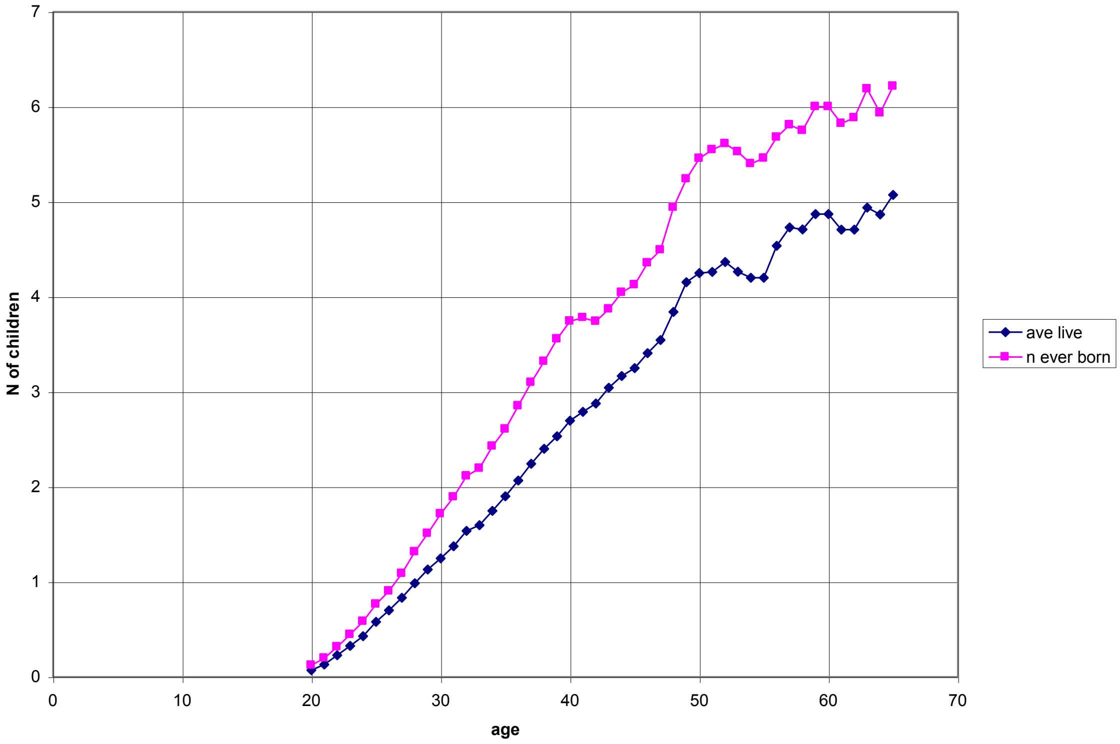


Figure SI 13.3b. Men. Average number of births and average number of live children accumulated by age x. Note that men's families continue to grow until the man is around 60.



SI 13.4. More reasons why early RS may not predict final RS. "random" disasters.

I looked to see whether the measures from early ages predict the score at each later 5-year point, and at the final age at which an individual was observed. But in a small population living a hard life with difficult access to modern medicine, misfortune can fall at any time, and forcefully. A family with a productive early trajectory can be wiped out by an infection in the space of a couple of years. Some of these events may not be so random. Such a family might have escaped their fate had they lived exclusively in the bush instead of near a village with tourist money, purchasable food, alcohol, and more TB. In a population with a high divorce rate like the Hadza, a change of spouses may bring about a marked change in reproductive capacity, presumably this is one of the "motivators" of divorce, the hope, or belief in having found a better partner.

SI 13.5 Testing the measures of reproductive success.

SI 13.5.1. Correlations between scores at adjacent 5 year age points.

Note: when we compare our standard score measures between one age and a later age, we are not comparing independent measures. The final measure of accumulated reproduction cannot be completely independent of measures of reproduction accomplished at earlier ages. Thus the first results that I present may exaggerate the efficiency with which measurements from young women represent their eventual, final reproductive success.

SI table 13.5.2a. WOMEN, standard score of living children accumulated by each age x standard score for each later age.

	Sslive20	Sslive25	Sslive30	Sslive35
Sslive25	0.651 0.000			
Sslive30	0.503 0.000	0.810 0.000		
Sslive35	0.443 0.000	0.634 0.000	0.846 0.000	
Sslive40	0.352 0.028	0.601 0.000	0.758 0.000	0.900 0.000

SI table 13.5.2b. WOMEN, standard scores of children ever born by each age x scores at later ages.

	Ssborn20	Ssborn25	Ssborn30	Ssborn35
Ssborn25	0.749 0.000			
Ssborn30	0.810 0.000	0.825 0.000		
Ssborn35	0.473 0.000	0.704 0.000	0.920 0.000	
Ssborn40	0.239 0.143	0.638 0.000	0.882 0.000	0.933 0.000

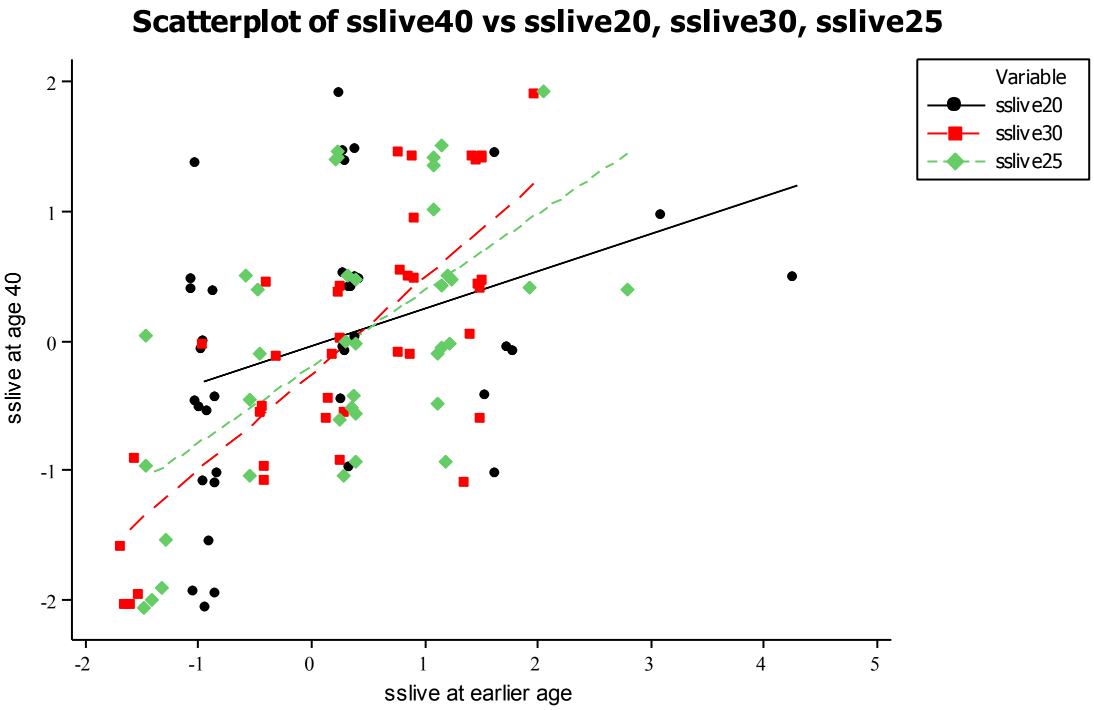
SI table 13.5.2c. WOMEN. ss survive. Proportion of those born who are alive at mother's age x.

	Ss surv20	Ss surv25	Ss surbv30	Ss surv35
Ss surv 25	0.683 0.000			
Ss surv30	0.714 0.000	0.798 0.000		
Ss surv35	0.605 0.000	0.678 0.000	0.825 0.000	
Ss surv40	0.685 0.000	0.530 0.001	0.729 0.000	0.888 0.000

SI table 13.5.3. Women. Result of Principal Component Analysis of cumulative number of children born by each age. Only the first 2 components account for amounts of variance (proportion, and cumulative) worth considering. 38 cases used, 135 cases contain missing values.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	4.541	1.054	0.233	.0898	.0640	.018
Proportion	0.757	0.176	.039	.015	.011	.003
Cumulative	0.757	0.933	.971	.986	.997	1.00
Ssborn20	.242	.794	-.536	-.100	-.093	-.067
Ssborn25	.398	.395	.625	.485	.234	.069
Ssborn30	.450	-.028	.362	-.515	-.631	.050
Ssborn 35	.449	-.157	-.062	-.511	.712	.035
Ssborn 40	.438	-.308	-.203	.309	-.103	-.752
ssborn	.432	-.305	-.382	.364	-.144	.649

SI figure 13.5.4. Color version of text figure 13.1.



SI table 13.5.5a. MEN standard scores of number alive at age x.

	Ss live20	Ss live 25	Sslive30	Sslive35	Sslive40	Sslive45	Sslive50
Sslive25	0.370 0.000						
Sslive30	0.303 0.000	0.695 0.000					
Sslive35	0.253 0.008	0.653 0.000	0.867 0.000				
Sslive40	0.186 0.081	0.491 0.000	0.734 0.000	0.900 0.000			
Sslive45	0.059 0.645	0.394 0.001	0.716 0.000	0.878 0.000	0.963 0.000		
Sslive50	0.027 .863	0.432 0.003	0.629 0.000	0.792 0.000	0.901 0.000	0.968 0.000	
Sslive55	0.088 0.616	0.368 0.030	0.523 0.001	0.728 0.000	0.852 0.000	0.928 0.000	0.975 0.000

SI table 13.5.5b. MEN, standard scores of number of children born by age x.

	Ssborn 20	Ssborn 25	Ssborn 30	Ssborn 35	Ssborn 40	Ssborn 45	Ssborn 50
Ssborn 25	0.615 0.000						
Ssborn 30	0.489 0.000	0.785 0.000					
Ssborn 35	0.363 0.000	0.669 0.000	0.903 0.000				
Ssborn 40	.261 0.014	0.571 0.000	0.792 0.000	0.943 0.000			
Ssborn 45	0.229 0.069	0.469 0.000	0.782 0.000	0.907 0.000	0.970 0.000		
Ssborn 50	0.207 0.178	0.512 0.000	0.736 0.000	0.841 0.000	0.924 0.000	0.980 0.000	
Ssbonr 55	0.288 0.093	0.497 0.002	0.692 0.000	0.800 0.000	0.909 0.000	0.965 0.000	0.990 0.000

SI table 13.5.5c. MEN, standard scores of child survival to age x.

	Sssurv 20	Ss surv 25	Ss surv 30	Ss surv 35	Ss surv 40	Ss surv 45	Ss surv 50
Ss surv 25	0.737 0.001						
Ss surv 30	0.714 0.009	0.648 0.000					
Ss surv 35	0.657 0.077	0.677 0.000	0.687 0.000				
Ss surv 40	0.000 1.000	0.347 0.026	0.645 0.000	0.820 0.000			
Ss surv 45		0.172 0.392	0.569 0.000	0.696 0.000	0.887 0.000		
Ss surv 50		0.053 0.824	0.538 0.002	0.714 0.000	0.788 0.000	0.939 0.000	
Ss surv 55			0.322 0.117	0.639 0.000	0.625 0.000	0.839 0.000	0.919 0.000

SI 13.5.6. Table a. Men. Result of Principal Components analysis of cumulative number of children alive at each age.
All available data. 64 cases used, 124 cases contain missing values

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	3.975	1.148	.5235	.2474	.0729	.0335
Proportion	.662	.191	.087	.041	.012	.006
Cumulative	.662	.854	.941	.982	.994	1.00
Sslive20	.154	.803	-.553	-.161	-.015	.012
Sslive25	.337	.420	.789	-.285	-.077	.027
Sslive30	.454	.084	.022	.816	-.347	.020
Sslive35	.485	-.086	-.042	.104	.860	.076
Sslive40	.468	-.254	-.164	-.294	-.195	-.752
Sslive45	.451	-.317	-.207	-.360	-.311	.654

SI 13.5.6 Table b. Men. Results of Principal components analysis of cumulative number of children born at each age.
64 cases used, 124 cases contain missing values

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	4.225	.9386	.5884	.1836	.0421	.0224
Proportion	.704	.156	.098	.031	.007	.004
Cumulative	.704	.861	.959	.989	.996	1.00
Ssborn20	.187	.902	-.388	-.007	-.035	.011
Ssborn25	.347	.283	.818	.361	-.013	-.013
Ssborn30	.453	-.049	.155	-.765	-.425	-.048
Ssborn35	.475	-.098	-.077	-.181	.834	-.175
Ssborn40	.463	-.203	-.222	.243	-.089	.792
Ssborn45	.446	-.233	-.318	.439	-.338	-.582

SI 13.6. Standard scores at end age predicted from earlier ages.

Table 13.6 a. Predicting Women's final accumulated reproductive performance from earlier measures of RS. Correlations (r) of standard score at final observation ("endage") with standard scores at earlier ages.

ss at early age	N	r with ss Live children at end age	r with ss N born by end age	r with ss % survive at end age
20	172	0.556 p < .000	0.612 p <.000	0.703 p <.000
25	139	0.724 p <.000	0.789 p <.000	0.667 p <.000
30	98	0.800 p <.000	0.914 p <.000	0.761 p <.000
35	73	0.927 p <.000	0.955 p <.000	0.893 p <.000
40	38	0.956 p <.000	0.978 p <.000	0.900 p <.000

Table 13.6 b. Predicting Men's final measurement of RS from earlier measures of RS. Correlations (r) of standard score at endage with standard scores at earlier ages.

ss at early age	N	r with ss N born x final obs	r with ss live children x final obs	r with ss % survive at final obs
20	188	0.420 p <.000	0.189 p = .010	-0.151 p =.537
25	156	0.645 p <.000	0.607 p <.000	0.453 p <.000
30	129	0.792 p <.000	0.711 p <.000	0.553 p <.000
35	108	0.899 b <.000	0.829 p <.000	0.606 p <.000
40	88	0.943 p <.000	0.886 p <.000	0.710 p <.000
45	64	0.966 p <.000	0.912 p <.000	0.733 p <.000
50	44	0.982 p <.000	0.938 p <.000	0.758 p <.000
55	35	0.988 p <.000	0.977 p <.000	0.803 p <.000

SI 13.7. Rate of early reproduction x rate of later reproduction.

I also used the longer reproductive histories to compare rates of reproduction early and late in the career. In this exercise I computed the number of births in each five-year period for each man and woman. In contrast to the cumulative standard scores discussed in the previous section and in the text, these scores of quinquennial reproduction at an early age are not statistically dependent on scores at another age. They can better show us whether there is a tendency toward slow early reproduction to be followed by fast later reproduction, or vice versa. These scores were not standardized. The sample and data sources were the same as above.

The results are shown below in Tables SI 13.7 tables 1a and b. There are significant and positive correlations between adjacent quinquienna but a much less consistent pattern across longer time periods. The results are less distinct than for cumulative reproductive achievement. In this situation principal components analysis should be more useful. Its results are shown in SI 13.7 tables 2a and b. For both men and women the first component (the component that accounts for most variance) is one on which birth rates at each age load positively. There is one exception -–birth rate for men aged 15-19 loads negatively. For men, the second component, accounting for 17% of the variance, has negative loadings for the younger ages and positive for the older. This is compatible with the idea of early restraint being followed by later success. But it may reflect the lengthy reproductive careers of a few men. The first component, which accounts for 41% of the variance, shows a clearer picture of consistent success or failure. Among women the first component accounts for 34% of the variance and has positive loadings for all ages. The women's second component, accounting for 25%, is not obviously compatible with an early versus late dimension, it presents a contrast between the prime childbearing years (20-34) with the younger and older tails (15-19 and over 35.). The younger and older tails will turn out to be important when we investigate effects of grandmothers and teenage helpers. A problem with these analyses is that the sample size is limited by the oldest age group included, because the older age groups include fewer individuals. If women aged 40 are included the sample size is reduced and the second component becomes smaller.

The principal component results are compatible with a pattern in which both men and women are either consistently successful reproducers, or consistently unsuccessful. The evidence for a subsidiary tendency toward a trade off between early and late reproduction is weak, although slightly more clear for men than for women. This result is similar to that of Sear et al (2003). The results do not appear obviously compatible with the view that fast early reproduction will be compensated for by slower later reproduction or vice versa. They appear more compatible with the idea that there are some lastingly successful reproducers and some less successful. The result is good support for using standard scores at endage as a measure of ultimate RS. This analysis does not directly address whether the average woman's reproductive effort or output is increased with age, the standard scores render this invisible.

SI table 13.7.1a. Women. Early birth rates by later birth rates. “brt15” is number of births between age 15 and 19. The table shows correlation coefficients (for example birth rate age 25 to 29, correlates with birth rate age 20-24 with a coefficient of .337, which gives probability less than .000).

	Brt 15	Brt 20	Brt 25	Brt 30	Brt 35	Brt 40
Brt 20	-0.022 .772					
Brt 25	0.028 .745	0.337 .000				
Brt 30	0.027 .790	0.189 .060	0.270 .007			
Brt 35	0.348 .002	0.096 .414	0.341 .003	0.241 .039		
Brt 40	-0.160 .329	0.137 .406	0.343 .033	0.104 .529	0.343 .032	
N	223	173	140	99	74	39

SI table 13.7.1b. Men. Early birth rates by later birth rates. “brt15” is number of births between age 15 and 19. The table shows correlation coefficients (for example birth rate age 25 to 29, correlates with birth rate age 20-24 with a coefficient of .225, which gives probability of .004).

	Brt15	Brt20	Brt25	Brt30	Brt35	Brt40	Brt45	Brt50	Brt55
Brt20	.218 .002 **								
Brt25	.213 .007 **	.225 .004 **							
Brt30	.160 .068	.260 .003 **	.363 .000 **						
Brt35	-.086 .372	.126 .193	.278 .003 **	.406 .000 **					
Brt40	-.109 .308	.105 .326	.269 .011 **	.267 .012 **	.466 .000 **				
Brt45	-.037 .769	-.031 .805	.544 .000 **	.448 .000 **	.441 .000 **	.577 .000 **			
Brt50	-.134	.087	.493	.423	.350	.454	.621		

	.385	.576	.001 **	.004 **	.020 *	.002 **	.000 **		
Brt55	-.058 .743	.163 .350	.343 .044 *	.259 .133	-.121 .489	.107 .540	.123 .481	.218 .209	
N	194	194	160	131	109	89	64	44	35

SI table 13.7.2a. Women Principle components for birth rates. 74 cases.

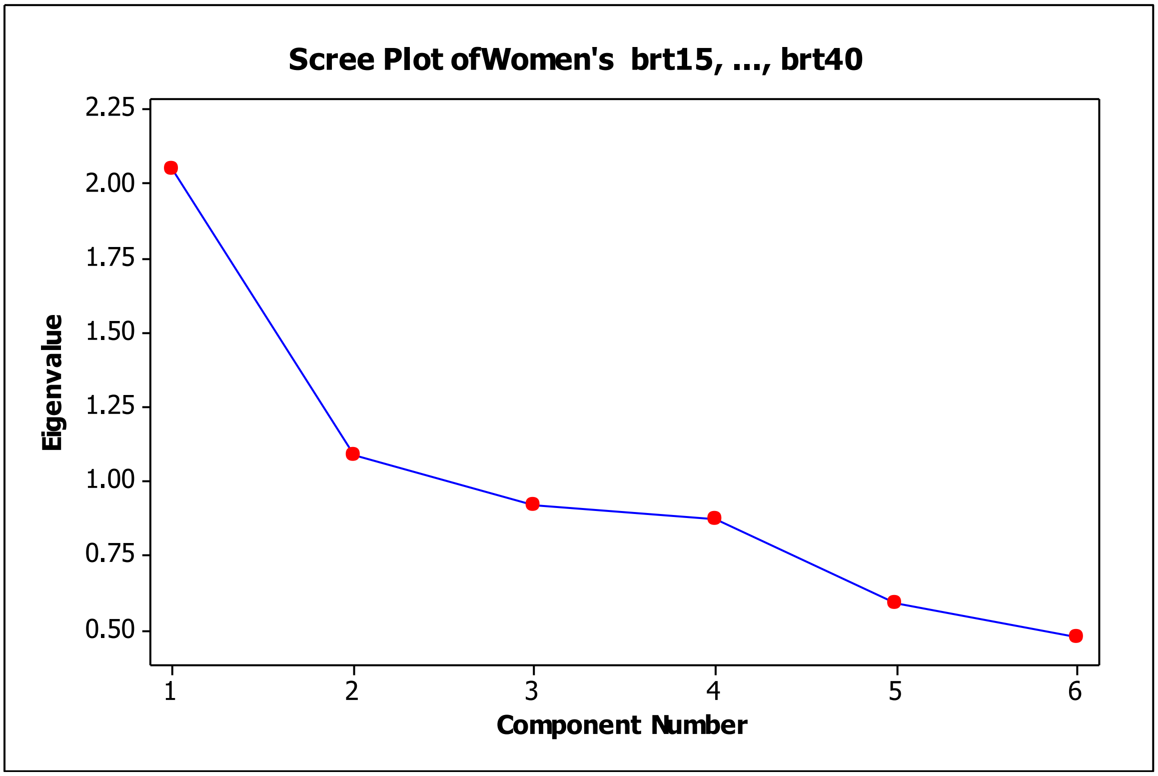
If brt40 is included the sample size is reduced to 38 cases. Results are then similar but the scree plot steeper - the second factor accounts for less variance.

	PC1	PC2
% of variance	34.1	24.7
Brt 15	.225	.736
Brt 20	.299	-.478
Brt 25	.538	-.182
Brt 30	.486	-.267
Brt 35	.578	.354

SI table 13.7.2b. Men. Principal components. Birth rate. 64 cases.

	PC1	PC2
% of variance	40.7	16.6
Brt 15	-.021	-.765
Brt 20	.135	-.432
Brt 25	.436	-.242
Brt 30	.407	-.250
Brt 35	.416	.214
Brt 40	.479	.219
Brt 45	.473	.118

Scree plot for principal components analysis of women's quinquennial birth rates. First component accounts for 34% of the variance.



SI 13.8. A note on STDs and variance in female RS.

The pattern of sex difference is common but not totally universal (Brown et al 2009).

We may expect variance in women's RS to be higher in populations with frequent sterilizing infections of the reproductive system. The opportunity for selection of means of avoiding or resisting infection is obvious. Populations with a low incidence may have already found successful avoidance strategies, as by avoiding larger more infected populations, or by reducing the number of sexual partners. We may wonder whether avoidance strategies generally have a higher pay off for women than for men.

SI 13.9. Sources for Table 13.1.

Standardized variance in RS for some human populations. [variance/ (mean^2)].

	Births - men	Births - women	RS - men	RS - women
Hadza	.4508	.1428	.6122	.2665
!Kung	.3255	.2215	.3227	.2147
Ache			.5347	.1885
Yanomamo	.9154	.5547		
Kipsigis		.1067	.4975	.25
Gainj	.5218	.2171		
Dogon			.2835	.2210

Hadza. See text. Exact values vary slightly with age sample used.

!Kung, men: Howell 1979 Table 16.2, women: Table 16.1 p335. Howell (1979: 269) reports variance 8.60 in CFS for men over 50 with mean 5.14, and women variance as 4.87, with mean CFS 4.69. These give standardized variance ($I_{fertility}$) 0.3255 for males and 0.2215 for females.

Ache: Hill & Hurtado (1996 p 411 Fig 12.5). Mean for 3 cohorts of females = 4.49, mean squared = 20.16. Mean of Variance (sd^2) = 3.8, Standardized variance = .1885. Mean for 3 cohorts of males = 4.017, mean of variance = 8.63, standardized variance = .5347

Yanomamo: Chagnon 1979 p 383 Table 14-2; Chagnon 1974:131.

Kipsigis: women mean of 3 cohorts (.1, .1, .12), Borgerhoff-Mulder 1988

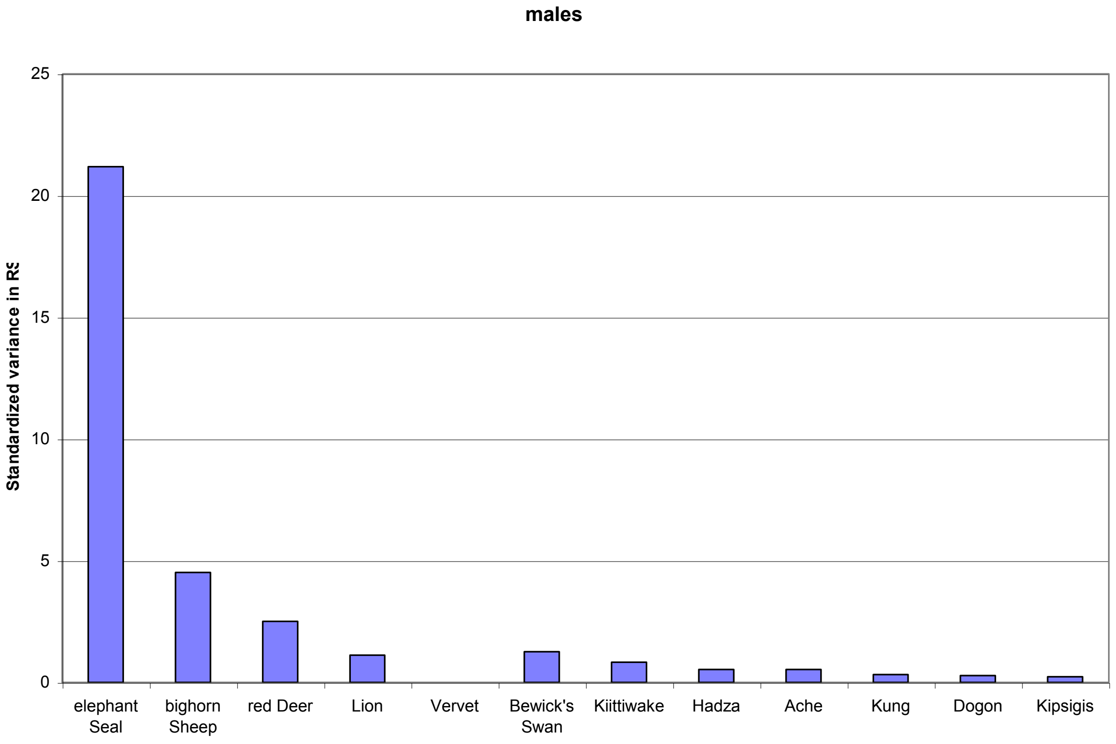
Gainj from Wood Johnson & Campbell (1985 Table 2) and see Wood (1987 for a more complete treatment) average of index for each 5 year age block ages 30-60+. Wood notes that the sex difference is almost entirely due to polygyny.

Dogon: Strassman (2003) Fig 12.1, men mean rs 6.14 sd 3.27. Women mean rs 3.19 sd 1.5

Small differences arise from differences in age between sub-samples used. Thus my Hadza results differ from figures in the recently published compendia. So do my figures for other populations. It is difficult to account for these differences because limited information is available in these accounts. The differences in the published Hadza figures arise from 2 sources: use of samples at different times from Marlowe's steadily accumulating data, and perhaps the use in the published compendia of counts from individuals not yet at the end of their reproductive careers. (Brown pers.comm attributes the much higher figure for Ache in Brown et al 2009 to a clerical error).

We should also not overlook the difficulties of obtaining these data in the first place. Even determining adult sex ratios is less simple than might appear. Choice of age ranges makes a difference, and sometimes we may determine the age range in a way that makes the result resemble OSR.

Besides clerical errors we should note that RS based on genotyping offspring will probably give higher variance for males than RS based on women's attributions of paternity (which will be greatly influenced by their societal norms). Most of the non-human cases in Table 13.1 were from studies before genetic data were widely used. Similar discrepancies will arise if RS is based on counts of co-resident children, numbers married or unmarried, and so on. The published accounts are not all clear on their criteria.



SI 13.10. The relative importance of different components of reproductive success.

Contributions to reproductive success from fertility, and from offspring survival.

Having derived our measures of individual differences in RS we can do some interesting preliminary analyses. How much do variation in fertility, or variation in offspring survival contribute to reproductive success of Hadza men and women? This topic can get quite complicated (Brown ch 27, Grafen ch 28 in Clutton-Brock 1988) but a simple approach is just to look at what happens in a multiple regression model predicting RS from fertility and survivorship. Note that, except in so far as the measure is missing for individuals that had no births, our measure of survivorship is independent of fertility. The relative importance of these variables can be further examined with stepwise regression.

It is difficult to rigorously compare the sexes in the relative contribution to RS from different components of fitness such as number of births and child survival because births and survival are in a multiplicative relationship: number of live children = number born x proportion who survive. The methods that have been used in the literature all give the same results on the Hadza data. 3D surface plots of the three standard score measures are suggestive. They suggest (as do regressions and stepwise regressions) that men can most increase RS by increases in the number of children they father, and women can better increase their RS by increased child survival.

Brown (1988: 441) gives a basic equation for partitioning variance in RS into a contribution from variation in say fertility, and variation into another variable, in our case child survivorship. I applied this equation to data on women aged 40+, and men aged 45+ and 50+ (Table below). The results suggest that over 80% of the variance in men's RS is contributed by variance in number of births, and only about 15% by variation in child survival. For women the percentage contribution of fertility was 54% and for child survival 40%. This result distinguishes the sexes slightly more than stepwise regression.

Table for Brown calculations.

Subjects	Women 40+	Men 45+	Men 50+
Mean live Cs	4.3158	3.5625	4.1818
Variance	5.4111	10.5992	10.8034
Mean births	6.3158	5.0156	5.8636
Variance	6.6003	16.8728	16.4461
Mean % child survival	66.49	73.344	73.573
Variance	5.405	5.534	5.727
% N births contribution	53.9	85.6	82.4
% child survival contribution	39.9	13.1	18.2

In regression and stepwise regression, not surprisingly, for both men and women, the number of children born accounts for the largest amount of variance in number alive. For women, the adjusted r-squared for standard score of number born was 51.8%. For men the adjusted r-squared was 70.2%. (The r^2 reflects the proportion of variance accounted for, beta coefficients attempt to represent slope – for example, the effect on RS of unit increase in standard score of fertility). Stepwise regressions, in which fertility (SSBORN) is added to the regression model at the first step, show the additional amount of variance accounted for by adding child survival (SS SURV) at the second step. These show the greater contribution of offspring survival to female RS (36.2%) and lesser contribution to variance in male RS (21.1%). In both cases p-values were below .001 and the Mallows Cp tests shows that offspring survival makes a very substantial contribution to predicting RS.

Regression analysis of the relationship between RS and number of births suggests another difference between men and women. In the text, figure 13.3 a and b plots RS against "ssborn" and shows the strong contribution of births to RS. But the plot for women suggests a slight leveling, or diminishing returns to increased fertility, at the highest fertilities. This can be supported by the significant contribution of ssbirth squared and cubed to predicting women's RS and their negligible (and non-significant) contribution to men's RS. Text figure 13.3 shows the data points and fitted curves for each sex to RS = ssborn + ssborn squared + ssborn cubed.

Women. Regression analysis predicting sslive at final observation from ssborn and sssurv

The regression equation is
sslive = - 0.0047 + 0.709 ssborn + 0.508 sssurv
153 cases. S = 0.333845 R-Sq = 88.2% R-Sq(adj) = 88.0%

Predictor	Beta coefft	se	t	p
Ss born	0.7092	.0297	23.86	.000
Ss surv	0.5082	.0238	21.38	.000
Constant	-.0047	.0275	-.017	0.863

Table. Women. Stepwise regression of RS (standard score of live children at endage) on its component fertility and offspring survival. ss surv improves R-sq by 36.22%

Stepwise Regression: sslive = ssborn, sssurv
Alpha-to-Enter: 0.15 Alpha-to-Remove: 0.15
N = 153

	Step 1	Step 2
Constant	-.0916	-.0047
Ss born	0.762	0.709
T value	12.83	23.86
p	0.000	0.000
Ss surv		0.508
T value		21.38
P		.000
S	0.669	0.334
R-sq	52.15	88.18
R-sq adjusted	51.83	88.02
Mallows Cp	458.1	3.0

Men. Regression analysis: sslive at final observation = ssborn + sssurv

sslivend = - 0.0044 + 0.908 ssbornend + 0.412 sssurvend
125 cases. S = 0.297077 R-Sq = 91.4% R-Sq(adj) = 91.3%

Predictor	Beta coefft	se	t	p
Ss born	0.9079	.0274	33.14	.000
Ss surv	.4121	.0239	17.26	.000
Constant	-0.0044	.0302	-0.15	0.883

Table. Men. Stepwise regression of RS (standard score of live children at end of observation) on its ccomponent fertility and offspring survival. Men.
Child survival (sssurvend) improves R-sq by 21.09%.

Stepwise Regression: sslive = ssborn, sssurv
Alpha-to-Enter: 0.15 Alpha-to-Remove: 0.15
Response is sslive on 2 predictors, with N = 125

	Step 1	Step 2
Constant	-0.1559	-.0044
Ss born	0.862	0.908
T value	17.11	33.14
p	.000	.000
Ss surv		0.412
T value		17.26
P		0.000
S	0.549	0.297
R-sq	70.43	91.41
R-sq adjusted	70.18	91.27
Mallows Cp	299.0	3.0

More discussion on variance measure and “opportunity for sexual selection”.

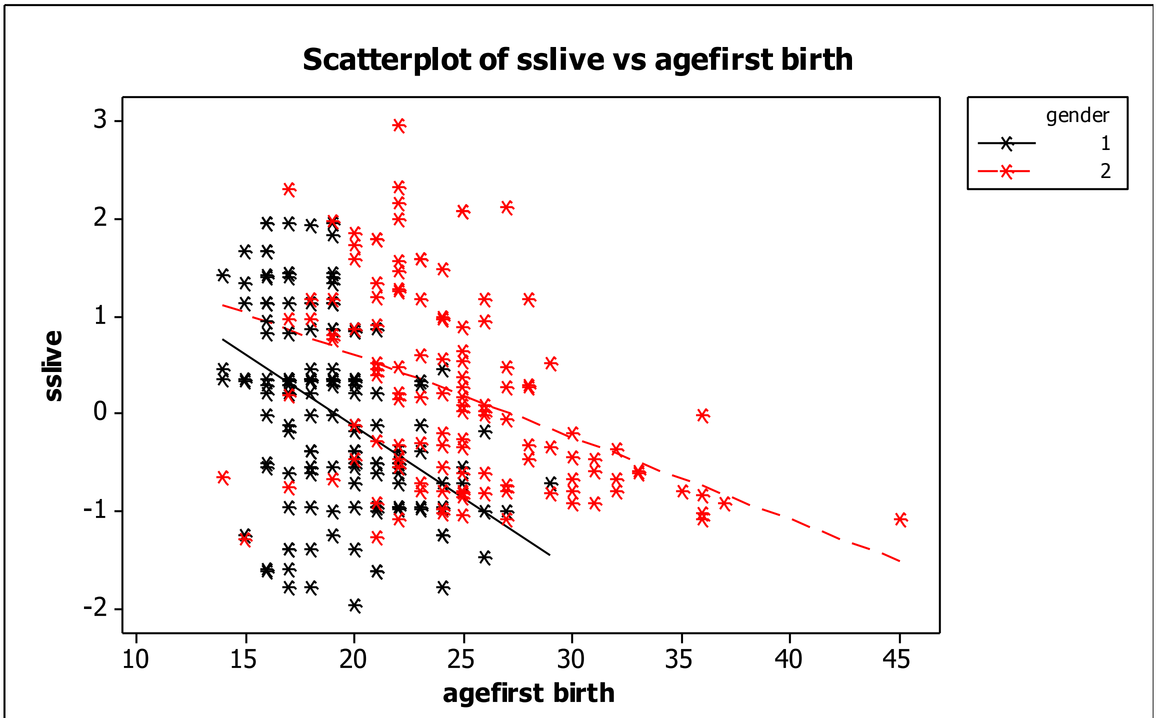
Grafen (1988) discusses the meaning for behavioral ecologists of the variance studies of the “Chicago School”. He differentiates between the Wade & Arnold (1980) group’s interest in measuring selection in progress, whence their term “opportunity for selection”, and the behavioral ecologists interest in whether a behavior or structure is an adaptation. Thus low variation in antler size would not tell us that antlers were not a result of selection. But variation might tell us about why some stags succeed and others fail. In hunter-gather studies an example might be the idea that toddler clinginess was an adaptation against predation. We see almost no actual predation on children (cases have been known), thus have no variance to work with. But it is easy to believe that an unattended toddler would be quickly scarfed up by an eager Hyena or patient Leopard. A similar example may be provided by the observations on Hadza RS and age at first birth (next section). Among women, age at first birth varies little but is a stronger predictor of eventual RS than it is among men. We may also suggest that women's age at first birth has been subject to stronger "stabilizing selection" than has male age at first birth.

The variance measures imply that if there are genes that affect, say fertility, there is variation on which selection can act. In our context a more interesting implication is at the phenotypic level. If there is something a man can do to obtain more paternities, it will increase his fitness relative to other men. The lesser variance in child survival implies he can get less far ahead of other men by improving his children's survival. The results for women imply that they can gain more of an advantage over other women by improving the survival of their children.

SI 13.11. Age at first birth as predictor of lifetime RS.

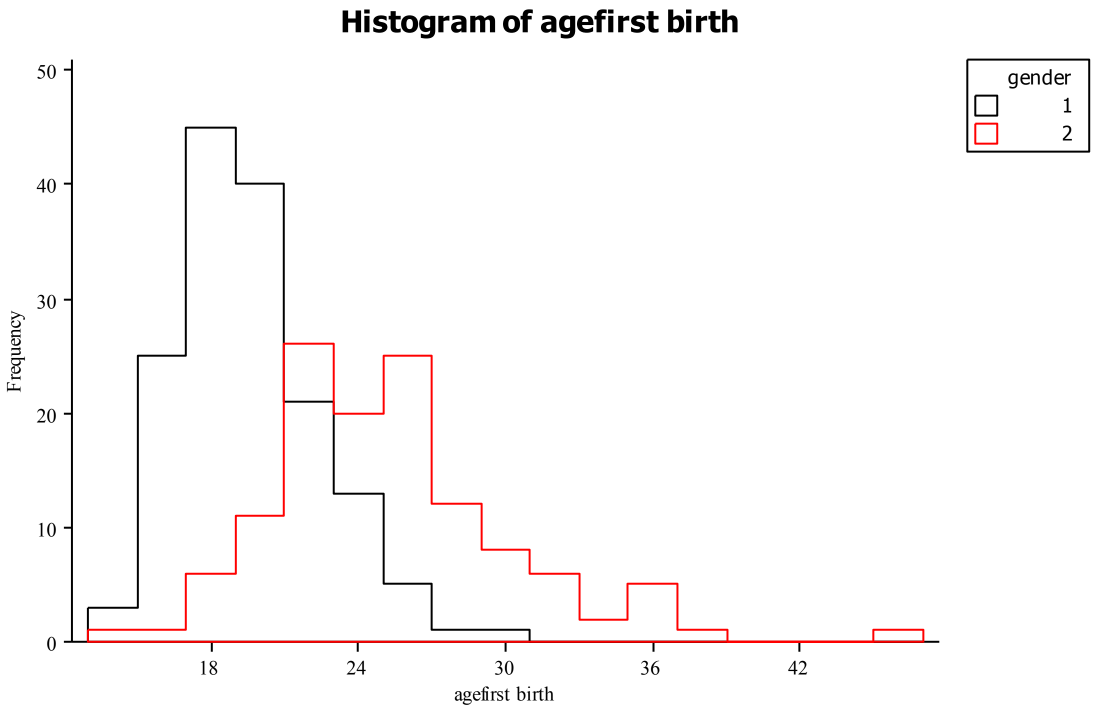
Using the women aged 25 and older at final observation, and men aged 30 and older (to remove any possible confounding effect of those whose observations ended before they had a birth) we find the relationship is again linear, and significant for both sexes. The fit line is steeper for women than for men. The regression coefficient for men (b = -0.0677, p = .000) is smaller than that for women (b = -0.1307, p.000). An early start to reproduction seems to have a greater influence on RS among women than among men (Figure 3).

A lowess plot for the whole sample of men shows an increase in RS as age at first birth climbs from 15 to 20, suggesting that a very early start may be detrimental to men's RS. Young men in our own society (often acclaiming their resistance to early marriage) seem acutely aware of this possibility. But adding the square of age at first birth which should approximate the curve suggested by lowess, fails to add significantly to r-squared.

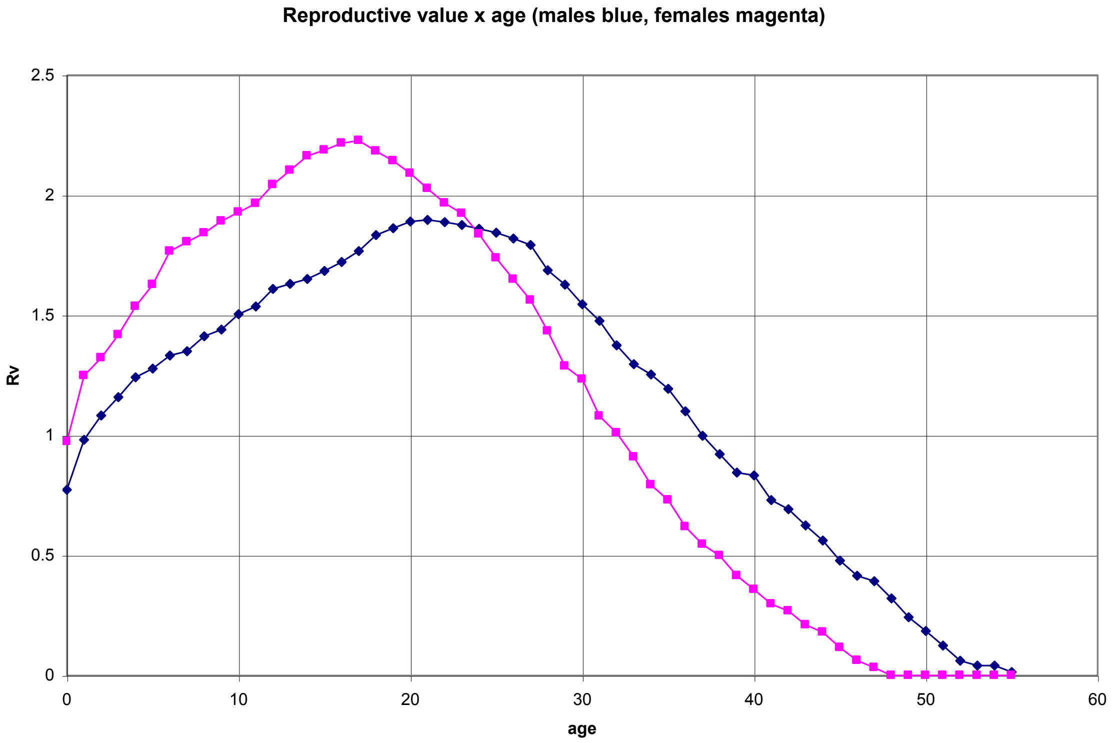


Minitab-men-newRS-ss-agefirstbirth-09-2-6-sheet5-with-women-11-10-17

Scatter of age at first birth for men (gender = 2 = red line) and women (gender = 1 = blue line). Men’s mean is 24.76, median 24, variance 24.33. Women’s mean is 19.1, median 19, variance 8.27. Thus while standardized variance is greater for men than for women, the “selection gradient” (slope of RS x age at first birth) is steeper for women than for men.



SI 13.12. Reproductive value by age for Hadza men and women



age	males	females
0	0.77289	0.973419
1	0.981575	1.248298
2	1.082342	1.322115
3	1.159301	1.418204
4	1.241829	1.536536
5	1.278159	1.627398
6	1.332889	1.766456
7	1.35033	1.804997
8	1.41215	1.842468
9	1.440352	1.891973
10	1.504596	1.92856
11	1.536364	1.964896
12	1.610005	2.043549
13	1.631071	2.103325
14	1.650548	2.163279
15	1.684657	2.187143
16	1.721555	2.216484
17	1.767348	2.227242

18	1.833928	2.183341
19	1.862641	2.142781
20	1.890394	2.091022
21	1.896726	2.027777
22	1.88725	1.966698
23	1.875752	1.924096
24	1.859711	1.838228
25	1.843544	1.737415
26	1.819276	1.648914
27	1.792206	1.562368
28	1.686912	1.433268
29	1.627003	1.287673
30	1.546039	1.232915
31	1.476222	1.079763
32	1.374654	1.009989
33	1.296524	0.90969
34	1.253731	0.793273
35	1.193571	0.729976
36	1.099983	0.619104
37	0.998502	0.545652
38	0.921836	0.498603
39	0.84444	0.415583
40	0.832896	0.357876
41	0.730339	0.297455
42	0.692572	0.268375
43	0.625067	0.210194
44	0.561816	0.179877
45	0.478163	0.11659
46	0.415018	0.062443
47	0.392502	0.03264
48	0.320944	0
49	0.242691	0
50	0.185438	0
51	0.124864	0
52	0.061233	0
53	0.04092	0
54	0.041455	0
55	0.014542	0

SI 13.13. Adult sex ratios of Hadza and others.

Data table for text Figure 13.5.
“Observed sum females in age” is sum of females of age x seen in all censuses.
“Predicted females in age” is number read out from final year of population simulation that uses observed Hadza fertility and mortality.

age	Observed sum females in age	Observed sum males in age	Observed m/f	Predicted females in age	Predicted males in age	Predicted m/f
0	112	109	0.973214	27740.3	29812.19	1.074689
1	88	92	1.045455	21393.93	23399.55	1.093747
2	75	96	1.28	19734.94	21156.8	1.072047
3	74	74	1	18824.05	19691.07	1.046059
4	65	81	1.246154	17825.54	18324.94	1.028016
5	53	70	1.320755	16932.62	17747.79	1.048142
6	58	70	1.206897	16349.33	16967.03	1.037781
7	46	67	1.456522	15984.01	16694.75	1.044466
8	61	63	1.032787	15513.61	15914.32	1.02583
9	65	59	0.907692	14731.92	15552.46	1.055698
10	71	57	0.802817	14394.04	14843.79	1.031246
11	68	45	0.661765	13855.71	14490.2	1.045793
12	44	53	1.204545	13535.2	13782.89	1.0183
13	45	42	0.933333	13124.88	13561.71	1.033282
14	49	48	0.979592	12816.11	13344.07	1.041195
15	67	48	0.716418	12510.82	13018.33	1.040566
16	69	52	0.753623	12211.57	12700.54	1.040041
17	69	47	0.681159	11914.68	12276.78	1.030392
18	70	47	0.671429	11617.96	11751.2	1.011468
19	62	55	0.887097	11431.52	11453.93	1.00196
20	58	50	0.862069	11023.11	11051.48	1.002574
21	39	52	1.333333	10739.93	10874.14	1.012496
22	43	39	0.906977	10368.91	10586.22	1.020958
23	44	46	1.045455	10202.51	10304.88	1.010034
24	52	51	0.980769	10038.78	10026.96	0.998822
25	65	41	0.630769	9877.687	9640.12	0.975949
26	61	42	0.688525	9719.174	9262.512	0.953014
27	55	41	0.745455	9563.205	9008.15	0.941959
28	42	44	1.047619	9194.255	8863.591	0.964036
29	33	38	1.151515	9046.71	8721.352	0.964036
30	43	36	0.837209	8798.274	8471.554	0.962865
31	36	42	1.166667	8558.393	8335.606	0.973969
32	49	39	0.795918	8421.051	8096.856	0.961502
33	49	41	0.836735	8285.914	7966.921	0.961502
34	44	27	0.613636	8061.632	7627.417	0.946138

age	Observed sum females in age	Observed sum males in age	Observed m/f	Predicted females in age	Predicted males in age	Predicted m/f
35	50	39	0.78	7932.263	7396.943	0.932514
36	34	32	0.941176	7804.969	7278.24	0.932514
37	41	40	0.97561	7457.775	7161.442	0.960265
38	29	32	1.103448	7338.096	7046.519	0.960265
39	31	30	0.967742	7104.09	6723.356	0.946406
40	29	33	1.137931	6736.346	6300.567	0.935309
41	23	24	1.043478	6498.331	6199.458	0.954008
42	22	29	1.318182	6261.053	5982.853	0.955567
43	22	21	0.954545	6160.578	5773.815	0.93722
44	12	28	2.333333	6061.716	5681.159	0.93722
45	20	26	1.3	5964.44	5589.991	0.93722
46	17	18	1.058824	5726.115	5500.285	0.960561
47	16	26	1.625	5378.431	5100.287	0.948285
48	17	17	1	5292.121	4907.03	0.927233
49	9	16	1.777778	5207.195	4718.682	0.906185
50	21	25	1.190476	5001.69	4642.959	0.928278
51	16	17	1.0625	4921.425	4568.451	0.928278
52	23	30	1.304348	4627.443	4401.639	0.951203
53	20	12	0.6	4444.818	4048.622	0.910863
54	12	17	1.416667	4274.211	3983.651	0.93202
55	27	27	1	4112.256	3826.434	0.930495
56	18	16	0.888889	3970.194	3673.539	0.925279
57	21	24	1.142857	3906.482	3244.092	0.830438
58	22	6	0.272727	3774.219	2872.829	0.761172
59	10	11	1.1	3713.652	2748.426	0.740087
60	38	24	0.631579	3583.899	2479.051	0.691719
61	24	10	0.416667	3455.858	2217.539	0.641675
62	28	26	0.928571	3319.471	2113.875	0.636811
63	14	9	0.642857	3266.201	2010.69	0.615605
64	10	14	1.4	3071.094	1780.581	0.579787
65	32	15	0.46875	3021.811	1752.007	0.579787
66	11	5	0.454545	2973.318	1723.892	0.579787
67	17	16	0.941176	2609.346	1570.707	0.601954
68	8	1	0.125	2496.354	1486.154	0.59533
69	13	11	0.846154	2456.293	1228.336	0.500077
70	21	11	0.52381	2183.164	1153.753	0.528477

Marlowe (2010:137) reports a sex ratio of 0.97 in the 916 people in his censuses (450 males, 465 females). He reported as an Operational sex ratio, the ratio of males aged 18-60 to females aged 16-49 as 1.14 (273 males, 239 females).

Recent interest in the potential effect of Adult Sex Ratio on mating systems, rates of extra-pair mating in birds and mammals, and affairs, and divorces in people has outpaced the difficulties of measurement.

1. In studies of simple societies the numbers are small and the ratio varies by only small amounts.

2. In humans (if you look at Coale & Demeny 1983 and compare mortality levels) the ratio also depends on mortality level. At lower mortality there are more males.

3. The ratio depends strongly on the definitions of “adult”.

4. The definition of relevant age range may involve circularity. Usually they are based on a belief about reproductive capacity, and the resulting ratio is used to explain the reproductive capacity.

5. This is probably more of an issue for men than for women. The ages at which women are capable of conceiving are rather well known. We would all be satisfied using 15-44 or 15-49. But the ages at which men are capable of conceiving children is more difficult. They produce viable sperm from say the late mid-teens (among Hadza perhaps, earlier among others) until at least the mid or late 60s or beyond. But they rarely father children at the extremes of these ages, probably partly because they cannot out compete men in the “prime ages”.

6. The aim is to measure effect of ASR on costs of competition for mates, or costs of desertion. ASR will be one factor influencing these costs. But competition will shape the careers, particularly of males. This may shape the age span we decide to score.

7. Among animals investigators mainly consider single breeding seasons or episodes, in which once pregnant a female is in “time out” and not available for further matings. Their use among humans tempts us to confuse time scales. A pregnant woman cannot be immediately fertilized again, and is removed from the current pool of available mates. But a deserted wife is added to the pool of available wives. She will become fertile again before long.

It seems widely acknowledged that when we measure adult sex ratio, we have to define “adult”. When we measure operational sex ratio, the matter of definition becomes still more obvious. We have in mind the number of males and females competing for reproductive opportunities. We also have in mind some feasible minimum and maximum age when individuals can be plausibly regarded as in competition with some chance of success.

Clutton-Brock & Isvaran (2007), used a criterion for choosing the ages to count in order to measure OSR which he called Duration of Effective Breeding, defined as the ages at which fertility was greater than 25% of peak fertility. This suggests ages 20-52 for Hadza men. It is useful to have a rule that we might all use. But it is also possible that the plausibly reproductive ages are determined by the level of competition.

8. Inclusion or exclusion of the younger age groups has a big effect on the final ratio, especially in populations with a "young" age pyramid, and in populations with high adult male mortality.

9. Hurtado & Hill's (1992) measure "fertility units per male" should also improve comparative study because it measures exactly what we are interested in, and takes account of variation in fertility from one population to another. It does not help with deciding which males to count.

Possibly also important is the demographer's problem: where did all the men go to? Coast (2001) found this to be a striking puzzle in Maasai demography. It may apply to many African, and other rural populations where migration to town is common, and transport expensive and communications poor. The length of reproductive careers of men, and the extent of migration to cities, may both vary in response to factors of interest, including sex ratio but also in response to local economy, particularly traditions of land tenure and mechanisms for controlling access to land and mediating competition between men for crucial resources. Non-human primate adult sex ratios may suffer from similar problems. In many species males emigrate from their natal group and only in some do they join an easily observed "bachelor herd". Migration as a single young adult may be especially dangerous, either from predators, or from competitors when the young male tries to join another group. We need to think about when ASR tells us about causes of competition and when it shows results of competition.

In the Hadza data we can derive the scores from censuses, censuses plus anthropometry turnout, or from the population register (so long as we exclude the dead and the not yet born and count only those alive at a particular time).

ASR scored year by year is extremely variable. But all my records are affected by the (primarily female) trough in the age structure, a shortage of women born between around 1946 and 1957 - this would increase ASR, would not account for the observed very low ASR, an apparent excess of women. They account for the big rise in ASR among older age groups.

The secular variation in ASR, from over 1 to around 0.8, remaining below 1 for my entire study period, suggests that men are exposed to varying selection pressure, within the lifetime of some, and from one generation to another. A man's appropriate responses would best be based not on head counts but on more immediate, direct, and local indications of competition.

If ASR truly differed between 1967 and the 1990s we might expect some differences in men's behavior. Is it too speculative to link this to the apparent difference between the divorce rate noted by Woodburn (1968b) and the higher rate that I calculated in chapter 15. As noted in chapter 15, there are many less interesting ways to account for the apparent difference in divorce rates. But we should be encouraged to continue to think about opportunistic variability in men’s reproductive strategies.

SI 13.14. Thinking about desertion. Opportunities for conception versus unclaimed wives.

If we are thinking only about a context such as Hadza men looking for wives, then each deserted wife is an opportunity for another man, even if he must wait a while before she becomes ready for her next pregnancy. When we think about desertion much may depend on whether we think men are waiting for a wife, or for a next pregnancy.