# Serial monogamy increases reproductive success in men but not in women 

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#### Abstract

Evolutionary theory predicts that males seek more sexual partners than females because of their higher fitness benefits from such a reproductive strategy. Accordingly, variance in numbers of partners and offspring is expected to be greater and association between mating and reproductive success to be stronger in males. Studies testing key predictions of this hypothesis in humans are lacking. Using data of 3700 men and 4010 women living in contemporary United States, we examined sex differences in the variance of number of spouses and offspring and in the association between spouse number and number of offspring. The results suggested a stronger selective advantage of serial monogamy in men than in women. Variance in spouse and offspring number was, respectively, $5 \%$ and $10 \%$ higher in men. In addition, the association between mating and reproductive success was stronger in men, so that men with 3 or more consecutive spouses had $19 \%$ more children than men with only spouse, whereas spouse number beyond the first partner was not associated with number of children in women. When the sample was stratified by ethnic group, the sex differences were stronger among Black and Hispanic participants than among White participants. Key words: humans, mating system, remarriage, reproductive strategy, sexual selection. [Behav Ecol]


Amating system (or breeding system) of a species or a population characterizes how individuals obtain mates, how many mates they interact with during their lifespan, how long these interactions last, and how individuals take care of their offspring (Emlen and Oring 1977; Clutton-Brock 1989; Reynolds 1996). These systems may vary from monogamy to polygyny or polyandry to promiscuity (Marlowe 2000). The evolution of mating systems depends on the payoffs associated with different reproductive strategies, determined by parental investment and prevailing socioecological circumstances, for example, local sex ratio or the ability of males to monopolize and guard females from other males (Emlen and Oring 1977; Arnold and Duvall 1994). Variation in the structure of mating systems has important implications for understanding the evolution of social behaviors, such as parental care and intrasexual competition (Kokko and Jennions 2008).

One of the crucial factors influencing the structure of mating systems is the sex difference in the costs and benefits of alternative reproductive strategies. The sexes invest different amounts of resources in fertilization and gestation, which enables the less investing sex (usually the males) to increase their offspring count by mating with several partners, whereas the other sex (usually the females) does not benefit from such a reproductive strategy to the same degree (Trivers 1972). Differences in post-zygotic parental investment and socioecological conditions may further influence the sex difference in the variance of mating and reproductive success (Trivers 1972; Kokko and Jennions 2008).

Sex differences in the benefits of multiple mating were first demonstrated in fruit flies (Drosophila melanogaster) by Bateman (1948), who postulated that the variance in the num-

[^0]ber of 1) mates and 2) offspring should be greater, and 3) the relationship between mating success and number of offspring should be stronger in males relative to females (Arnold 1994; Tang-Martinez and Ryder 2005; Snyder and Gowaty 2007). The Bateman's third prediction is particularly relevant for evolution. The stronger the association between mating and reproductive success, the stronger the influence of sexual selection is predicted to be on characteristics enhancing mating success and multiple mating (Arnold 1994).

Sex-specific benefits of multiple mating in the evolutionary past have also been suggested to explain sex differences in human behavior (Buss and Schmitt 1993; Buss 1998; Gangestad and Simpson 2000; Schmitt et al. 2001). Evolutionary psychological research of phenomena, such as mate choice (Buss and Schmitt 1993), sexual behavior (Schmitt 2003, 2005), marriage (Pollet and Nettle 2008; Kruger and Schlemmer 2009), and extrapair sexual relations (Brand et al. 2007), rest heavily on the assumptions that Bateman's predictions have operated for the large part of human evolution (Schmitt 2003, 2005). A recent review of Bateman's predictions in contemporary and historical nonindustrialized human populations (Brown et al. 2009) suggested a higher overall variance in both mating and reproductive variance in men compared with women, particularly in polygynous societies, whereas in monogamous societies, the variances were relatively similar in the 2 sexes.

Bateman's third prediction, that having multiple partners increases reproductive success more strongly in males than in females, has rarely been tested in humans (Brown et al. 2009). Studies in nonindustrialized societies have reported a positive association between partner number and reproductive success in men among the polygynous Brazilian Xavante (Salzano et al. 1967) and Kenyan Kipsigis (Borgerhoff Mulder 1987) and in the monogamous Sami (Käär et al. 1998) but a negative association in the Tanzanian Pimbwe (Borgerhoff Mulder 2009). In women, partner number has been reported to have a positive association with reproductive success in the

Pimbwe (Borgerhoff Mulder 2009) but no association in the Finnish Sami (Käär et al. 1998). However, few of these studies have specifically compared the effects of multiple partners on reproductive success in both sexes within the same population and also included individuals who never marry.

In polygynous societies, some men are able to have several wives simultaneously and thereby increase their offspring number (Borgerhoff Mulder 1987). In societies with socially imposed monogamy but a possibility of divorce and remarriage, men and women can have several consecutive partners. Such serial monogamy may effectively resemble polygyny in its reproductive consequences if some men are able to utilize more than one woman's reproductive lifespan through repeated marriages. Furthermore, in societies with low child mortality, the relationship between paternal investment and offspring reproductive success is relaxed; in such circumstances, men may gain greater fitness returns by allocating energy to mating effort rather than to paternal investment (Sear and Mace 2008). Forsberg and Tullberg (1995) observed a positive association between remarriage and fertility in the 20th century Sweden in men but not in women, suggesting that Bateman's third prediction may hold in contemporary socially monogamous societies. However, it is unknown whether these findings generalize to other postindustrial populations. In addition, the Swedish study had some methodological limitations (no data on children beyond the third child in women and too small a sample size to examine the effect of third or later partner) that restrict the conclusions that can be drawn from it.

Our aim is to investigate Bateman's 3 predictions in contemporary United States characterized by a monogamous mating system. First, we examine sex differences in the variance of numbers of spouses and offspring from the start of reproductive life until ages $40-47$ years. Second, we investigate whether serial monogamy is associated with the number of children differently in men and women. In accordance with Bateman's predictions, we hypothesize that remarrying men have more children than men who marry only once, whereas this association is absent in women. Finally, we examine whether these associations are similar in different ethnic groups.

Comparisons with the Bateman's predictions between separate subpopulations are of interest because they advance our understanding of the possible socioecological variation in reproductive strategies (Brown et al. 2009). In the United States of America, different ethnic groups exhibit differences in reproductive characteristics. On average, Black and Hispanic people have higher rates of overall fertility, multipartnered fertility (i.e., having children with 2 or more partners; (Guzzo and Furstenberg 2006; Manlove et al. 2008), and nonmarital fertility (Wu 2005) than do White people. Furthermore, White and Hispanic people have lower divorce risk than Blacks (Bulanda and Brown 2007). Thus, different ethnic groups face somewhat different reproductive environments. Given that more than $94 \%$ of marriages in the late 20th century USA have been between partners with shared ethnic origin (Harris and Ono 2005), it is possible to examine Bateman's predictions separately by ethnic groups.

We use data from a nationally representative sample of American men $(n=3700)$ and women $(n=4010)$ born between 1957 and 1964 and participating in the ongoing US National Longitudinal Survey of Youth study. Our data have several benefits in addressing our aims. First, it includes detailed marital and reproductive history data for a large number of participants from a nationally representative sample who were followed until the average age of 44 years. The vast majority of participants were followed until they had reached their completed fertility; men and women older than 44 years account only for $3 \%$ and $<1 \%$, respectively, of the population's sex-specific fertility rate (Martin et al. 2004). These data
allow us to examine not only achieved fertility at this age but also to model age- and parity-specific childbearing over the life course. Second, the sample includes not only reproductively successful individuals but also those who did not marry or reproduce, so the estimates are not biased by family-based sampling used in some of the previous studies in preindustrial societies. Finally, the multiethnic sample provides us with an opportunity to examine potential intrapopulation differences in the association between serial monogamy and reproductive success based on ethnic group differences.

## MATERIALS AND METHODS

## Participants

The participants were 3700 men and 4010 women (total $n=$ 7710) from the ongoing US National Longitudinal Survey of Youth. In this study, a nationally representative sample of individuals born between 1957 and 1964 has been followed annually since 1979 and biannually after 1994. The original sample ( $n=12686$ ) consists of 3 subsamples aged 14-22 years at baseline in 1979: a representative sample of noninstitutionalized civilian youths ( $n=6111$ ); a supplemental sample designed to oversample civilian Hispanic, Black, and economically disadvantaged nonblack/non-Hispanic youths ( $n=5295$ ); and a military sample ( $n=1280$ ). Details of the sampling process have been reported elsewhere (http:// www.bls.gov/nls/nlsy79.htm). Due to funding constraints, the number of interviewed military sample and supplemental sample members were limited after years 1984 and 1990, respectively. The main sample in the present study consisted of participants who provided data at follow-up phase in 2004 when the participants were 40-47 years of age.

Appropriate cross-sectional or longitudinal sampling weights taking into account sex, ethnicity, year of birth, sample type, and location were applied in the statistical analysis in order to adjust for differential probabilities of selection into the sample and for attrition. Thus, the sample yielded representative estimates for the US population born between years 1957 and 1964. The survey is sponsored and directed by the US Bureau of Labor Statistics and conducted by the Center for Human Resource Research at The Ohio State University. Interviews are conducted by the National Opinion Research Center at the University of Chicago. The study was approved by institutional review boards of the institutions conducting the surveys, and informed consent was obtained complying with Federal law and the policies of the US office of Management and Budget.

## Measures

"Fertility history" was constructed from all available data of born children reported by the participants at each follow-up phase. Only biological children of the participants were included in the analyses. Marital status history was likewise constructed from all available data collected over the follow-up period. At each follow-up phase, current marital status of the participant and the order of participants' current spouse, if any, have been recorded. From these data, 2 measures of marital history were derived. "Spouse number" was defined as the number of spouses the participant had had by the end of the follow-up period. There were only few individuals reporting more than 3 spouses, so this variable was top coded at a group of 3 or more. In survival analysis, spouse number was coded as a time-varying covariate, which indicated that for each followup year separately 1) whether or not the participant had a spouse and 2) the order of this spouse in the participant's relationship history.
"Ethnic background" in the cohort is commonly categorized into 3 groups (Black, Hispanic, and White/Other) on the basis of participants' self-reported data (details are given in section 4.32 of the study user's guide; http://www.bls.gov/nls/ nlsy79.htm). In order to have a relatively homogenous group of Whites in ethnicity-stratified analyses, we excluded from the White/other group individuals who were Asian of origin and those for whom ethnicity could not be determined because of missing data or because of being categorized in a residual category of "other" ( $n=145$ men and 130 women). However, these individuals were included in all ethnicity-combined analyses. Lastly, as the total sample consists of different subsamples (see above), subsample membership was included as a categorical covariate $(0=$ main sample, $1=$ supplementary sample, and $2=$ military sample).

Socioeconomic status, education in particular, is known to be an important factor in fertility behavior (Skirbekk 2008). We included parental education (a measure of early socioeconomic status) and participant's own education (a measure of adult socioeconomic status) as covariates. Parental education was assessed at baseline in 1979 on the basis of education level of the more educated parent of the participant (range from $0=$ no education to $20=$ eight year of college or more). Participant's own education was assessed using the highest completed grade in adulthood on a 20-point scale (range from $0=$ no education to $20=$ eight year of college or more).

## Statistical analysis

Statistical analysis was performed using the STATA 9.2 statistical program. Sex differences in the variances of the number of children and number of spouses were expressed as male-tofemale ratios of the variances (squared standard deviations) of these variables, and statistical differences were determined using Levene's test. The association between lifetime number of spouses and number of children at the final follow-up phase was assessed using linear regression analysis. The time-dependent associations between time-varying spouse number and probability of having children during the follow-up period were assessed with discrete-time survival analysis fitted separately for the birth of the first, second, third, fourth, fifth, and sixth child. In these models, missing values of marital status were imputed with data from the previous phase because the survival analysis model requires full data of covariates across the follow-up period. All models were fitted separately for men and women and also by ethnicity, adjusted for subsample membership and birth year. Sex differences in the associations were tested with sex $\times$ predictor interaction effects.

## RESULTS

Table 1 shows the descriptive statistics for the sample. First, to test the prediction that variance in mating success is higher in men than in women, we calculated the variance in the total number of spouses of men and women at age 40-47 years (Figure 1). In the total sample, the male-to-female variance ratio for spouse number was 1.05 (variances for men and women was, respectively, 0.67 vs. $0.64 ; 95 \%$ confidence interval $[\mathrm{CI}]=1.01-1.10, P$ value for sex difference in variances $=0.05)$, indicating that the variance in number of partners was $5 \%$ higher in men. This variance ratio was significantly greater among Black ( $1.28,95 \% \mathrm{CI}=1.18-1.40, P$ for sex difference $<0.001$ ) than in Hispanic $(1.00, \mathrm{CI}=0.91-1.12 ; P=0.48)$ or White (1.03, CI $=0.96-1.10 ; P=0.27$ ) participants among whom the variance ratio was not statistically significant from unity.

Second, to test the prediction that variance in reproductive success is higher in men than in women, we calculated the
male-to-female variance ratio in the total number of offspring that men and women had fathered or given birth to by age $40-$ 47 years (Figure 1 ). In the total sample, the variance in the number of children was $10 \%$ higher in men (2.25) than in women (2.04), as indicated by the variance ratio of $1.10(95 \%$ $\mathrm{CI}=1.05-1.15, P$ for sex difference $=0.002$ ). There were no ethnic differences in this variance ratio, as indicated by overlapping CIs and point estimates of different groups (Black: $1.15, \mathrm{CI}=1.06-1.25, P=0.007$; Hispanic: $1.09, \mathrm{CI}=0.98-$ $1.21, P=0.13$; and White: $1.07, \mathrm{CI}=1.00-1.14, P=0.08)$.

Third, to test the key prediction that mating success should be more strongly correlated with reproductive success in men than in women, we examined sex differences in the association between spouse number and number of offspring produced. We found evidence in support of this prediction, as male, but not female, reproductive success benefited from multiple spouses (Figure 2; Supplementary Table S1). Table 2 shows regression models testing for sex differences in this association among individuals with at least one spouse. The gradient was significantly stronger in men than in women in the total sample and in Black and Hispanic participants. The sex difference in the linear gradient was not statistically significant in White participants $(P=0.10)$.

As shown in Figure 2, there was a positive association between the number of spouses and average number of biological children in men. Compared with men with 1 spouse, men with 3 or more spouses had $19 \%$ more children in the total sample. This difference was more pronounced in Black ( $44 \%$ more children) and Hispanic (39\% more children) than in White men ( $16 \%$ more children). By contrast, women did not increase their number of children by having more than one spouse (Figure 2; Supplementary Table S1). Adjusting for parental education and participants' own adult education did not substantially alter these results (Supplementary Table S1). We also examined whether men's ethnic differences in the spouse number - offspring number gradient were accounted for by socioeconomic background. These ethnic differences were unaffected by adjustments for parental and own education (data not shown).

Finally, to investigate the relationship between serial monogamy and age- and parity-specific fertility patterns in more detail for each sex, we fitted separate discrete-time survival analysis models for the birth of the first to the sixth child (Table 3). In men, time-varying spouse number (indicating marital status separately at each year) was not associated with the odds of the birth of the first and second child but did predict odds of births beyond the second child. Men with their second and third (or later) spouse were more likely to have a third, fourth, fifth, and sixth child at a given age compared with men with their first spouse. This association followed a dose-response pattern, with the odds ratios being approximately twice as high for those with 3 spouses or more compared with those with 2 spouses. In women, there was no overall association between time-varying spouse number and age-specific fertility.

## DISCUSSION

The origins of sex differences in behavior have been long debated in biological (Kokko and Jennions 2008) and social (Wood and Eagly 2002) sciences, and the potential importance of sexual selection in contemporary human societies constitutes one of the most intriguing topics for social sciences (Aarssen 2007). Evolutionarily, males are suggested to have evolved behavioral strategies that favor the acquisition of more sexual partners than females because they gain higher fitness benefits from this reproductive strategy than do females (Bateman 1948). This leads to the predictions that

Table 1
Descriptive statistics for the sample at the end of the follow-up period

|  | Men |  |  |  | Women |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | All | Black | Hispanic | White | All | Black | Hispanic | White |
| Age (years) | 43.64 (2.26) | 43.39 (2.19) | 43.26 (2.21) | 43.29 (2.25) | 43.68 (2.24) | 43.34 (2.18) | 43.35 (2.24) | 43.52 (2.21) |
| Parental education | 11.71 (3.49) | 11.32 (2.63) | 8.92 (4.44) | 12.93 (2.85) | 11.59 (3.42) | 11.23 (2.73) | 8.92 (4.21) | 12.81 (2.78) |
| Own education | 13.25 (2.53) | 12.76 (2.05) | 12.35 (2.71) | 13.66 (2.60) | 13.39 (2.49) | 13.20 (2.17) | 12.62 (2.77) | 13.79 (2.48) |
| Age at first birth | 26.22 (5.66) | 24.63 (5.46) | 25.46 (5.56) | 27.45 (5.51) | 23.68 (5.80) | 21.71 (5.39) | 23.06 (5.61) | 25.09 (5.72) |
| Number of children | 1.89 (1.50) | 2.04 (1.66) | 2.15 (1.59) | 1.70 (1.33) | 2.07 (1.43) | 2.17 (1.55) | 2.39 (1.52) | 1.91 (1.29) |
| None ${ }^{\text {a }}$ | 22.22 | 20.21 | 19.18 | 24.29 | 15.96 | 15.86 | 11.67 | 17.08 |
| One ${ }^{\text {a }}$ | 17.54 | 20.13 | 14.49 | 17.08 | 16.23 | 17.64 | 13.62 | 16.28 |
| Two ${ }^{\text {a }}$ | 30.62 | 26.30 | 27.70 | 34.45 | 33.64 | 27.99 | 31.78 | 38.17 |
| Three ${ }^{\text {a }}$ | 16.70 | 16.10 | 19.89 | 16.10 | 20.85 | 22.33 | 23.74 | 19.11 |
| Four ${ }^{\text {a }}$ | 8.05 | 9.39 | 11.65 | 5.77 | 8.65 | 10.03 | 11.28 | 6.78 |
| Five ${ }^{\text {a }}$ | 3.00 | 4.56 | 4.97 | 1.33 | 2.82 | 3.24 | 4.67 | 1.87 |
| Six or more ${ }^{\text {a }}$ | 1.86 | 3.31 | 2.13 | 0.98 | 1.85 | 2.91 | 3.24 | 0.69 |
| Spouse number | 1.33 (0.82) | 1.33 (0.89) | 1.31 (0.79) | 1.33 (0.79) | 1.32 (0.80) | 1.08 (0.79) | 1.41 (0.79) | 1.45 (0.77) |
| None ${ }^{\text {a }}$ | 12.00 | 16.82 | 11.22 | 9.29 | 11.12 | 22.73 | 7.52 | 5.39 |
| One ${ }^{\text {a }}$ | 54.03 | 45.26 | 55.26 | 58.97 | 55.06 | 51.86 | 54.99 | 56.75 |
| Two ${ }^{\text {a }}$ | 23.38 | 25.94 | 24.57 | 21.23 | 24.04 | 20.55 | 26.33 | 25.63 |
| Three or more ${ }^{\text {a }}$ | 10.59 | 11.99 | 8.95 | 10.50 | 9.78 | 4.85 | 11.15 | 12.23 |
| $n$ | 3700 | 1118 | 704 | 1733 | 4010 | 1236 | 771 | 1873 |

Values are means (and standard deviations) unless otherwise indicated. Data for 145 men and 130 women not included in the groups of Black, Hispanic, or White participants are not presented separately in the table.
${ }^{a}$ Values are percentages of participants.
the variance in numbers of partners and offspring is greater, and the association between mating and reproductive success is stronger in males than in females. The latter prediction must be satisfied if sexual selection is to operate. Studies directly testing all the 3 key predictions of this hypothesis in men and women have been lacking (Brown et al. 2009).

The present findings from a nationally representative sample of Americans living in the late 20th century support the hypothesis that serial monogamy is positively associated with reproductive success in men. In the total sample, the variances in the number of children and lifetime number of spouses were $10 \%$ and $5 \%$ higher, respectively, in men than in women. Crucially, men who had had 3 or more consecutive spouses by the age 40-47 years had $19 \%$ more children than men with only 1 partner. This association was independent of the participants' socioeconomic background. A more detailed analysis based on age- and parity-specific survival analysis modeling demonstrated that although serial monogamy was not important in determining whether or not men reproduced at all, it did influence the probability of having children beyond the second child. In women, having more than 1 partner did not increase or decrease the overall number of children. The observed sex differences in 1) variance in mating success,
2) variance in reproductive success, and 3) the strength of the association between mating and reproductive success suggest that Bateman's predictions may apply in postindustrialized societies with social monogamy and the potential for serial monogamy.
The strength of association between mating and reproductive success is known as the Bateman gradient. Sexual selection is expected to act more strongly on traits enhancing mating success in the sex with a steeper Bateman gradient because that sex has more to gain from multiple mating (Brown et al. 2009). Given that serial monogamy increased reproductive success in men, heritable traits associated with male serial monogamy may be under positive sexual selection. Behavioral characteristics of both males and females may contribute to creating these selective advantages (Eliassen and Kokko 2008). Such characteristics may include a preference for multiple partners and higher propensity for divorce in men. Women, in turn, may prefer certain male characteristics and demand different amounts of paternal investment from men, thus creating reproductive environments that benefit specific male reproductive strategies. Future research should seek to identify the male and female traits affecting the selective advantage of male serial monogamy.


Figure 1
Male-to-female variance ratios (and 95\% CIs) of spouse number (left-hand panel) and number of offspring (right-hand panel). Values above 1.00 indicate higher variance in men than in women.


Figure 2
Average number of biological children at age $40-47$ years by spouse number and ethnic group in men and women, adjusted for birth year and subsample membership. The vertical lines are 95\% CIs.

There were some differences between ethnic groups. Men's positive association between serial monogamy and reproductive success was considerably stronger in Black and Hispanic than in White men independently of socioeconomic background. Sex differences in the variance of spouse number and in the association between spouse number and number of offspring were not statistically significant in White participants, suggesting that not all Bateman predictions may hold universally across different populations. Several factors may contribute to these differences, including variation in parental investment (Trivers 1972) and operational sex ratio (Emlen and Oring 1977; Kokko and Jennions 2008). Previous studies have shown higher rates of multipartnered and nonmarital fertility in Black and Hispanic than in White populations (Wu 2005; Guzzo and Furstenberg 2006; Manlove et al. 2008), and Black and Hispanic participants in the present sample also had higher variance in offspring number and began childbearing earlier than White participants. In addition, divorce rates are higher in Blacks than in others (Bulanda and Brown 2007). These reproductive characteristics and other sociodemographic factors may create different conditions for the success of a serially monogamous reproductive strategy and thereby explain the observed ethnic differences in Bateman's predictions. Thus, ethnic categorization is here best interpreted as a proxy measure for the socioecological conditions characterizing individuals' reproductive environments, and fur-
ther research is needed to identify the specific factors underlying these differences.

Evolutionary psychologists have examined different aspects of sexual behavior and mate choice, such as the preference for sexual variety (Schmitt 2003), extrapair sexual relations (Brand et al. 2007), emotional reactions to short-term mating (Campbell 2008), and attitudes toward monogamy (Schmookler and Bursik 2007). These studies seldom measure actual fertility outcomes because most evolutionary psychologists assume that evolved psychological mechanisms are unlikely to lead to evolutionarily adaptive outcomes in contemporary populations even if they are associated with proxy measures of reproductive success, for example, number of sexual partners (Pérusse 1993). However, there are actually very few studies directly assessing this hypothesis of adaptive lag (Laland and Brown 2006). Previous studies have demonstrated associations between reproductive success and evolutionarily relevant individual characteristics, such as personality traits, physical attractiveness, and social status in contemporary societies (Hopcroft 2006; Nettle and Pollet 2008; Jokela 2009; Jokela and Keltikangas-Järvinen 2009; Jokela et al. 2009; Jokela et al. 2010). Together with these studies, the present findings suggest that sexual selection may continue to operate, at least in some instances, in a similar manner as it is assumed to have operated in the evolutionary past.

Table 2
Sex differences in the association between spouse number and number of offspring in participants with at least one spouse

|  | All | Black | Hispanic | White |
| :--- | :--- | :---: | :---: | :---: |
| Sex $(0=$ female and $1=$ male $)$ | $-0.39(-0.56,-0.21)$ | $-0.76(-1.12,-0.41)$ | $-0.64(-1.05,-0.23)$ | $-0.30(-0.51,-0.08)$ |
| Spouse number | $-0.03(-0.10,0.04)$ | $0.02(-0.15,0.18)$ | $0.03(-0.14,0.19)$ | $-0.02(-0.11,0.06)$ |
| Sex $\times$ Spouse number | $0.18(0.07,0.29)$ | $0.45(0.21,0.68)$ | $0.33(0.08,0.58)$ | $0.10(-0.02,0.24)$ |
| $P$ value for sex difference | 0.001 | $<0.001$ | 0.009 | 0.104 |
| $n$ | 6815 | 1884 | 1338 | 3340 |

Values are coefficients (and 95\% CIs) of linear regression models. The main effect of spouse number shows the association in women whereas main effect + sex interaction effect gives the strength of the association in men. All models adjust for age, ethnicity, and subsample membership.

Table 3
Predicting childbirth by time-varying spouse number

|  | First child | Second child | Third child | Fourth child | Fifth child | Sixth child |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Men $(n=3700)$ |  |  |  |  |  |  |
| $\quad$ No spouse | $0.06(0.05,0.07)$ | $0.06(0.05,0.07)$ | $0.14(0.11,0.17)$ | $0.26(0.19,0.36)$ | $0.35(0.22,0.57)$ | $0.37(0.18,0.74)$ |
| First spouse | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) |
| Second spouse | $0.95(0.79,1.14)$ | $0.82(0.69,0.98)$ | $1.26(1.01,1.57)$ | $2.18(1.58,2.99)$ | $1.97(1.21,3.19)$ | 1.97 (0.82, 4.76) |
| Third or later spouse | $0.88(0.54,1.43)$ | $1.13(0.80,1.60)$ | $2.03(1.39,2.96)$ | $3.53(1.39,2.96)$ | $4.75(2.35,9.60)$ | $3.83(1.28,11.44)$ |
| Women $(n=4010)$ |  |  |  |  |  |  |
| No spouse | $0.09(0.08,0.10)$ | $0.11(0.10,0.12)$ | $0.22(0.18,0.25)$ | $0.36(0.29,0.45)$ | $0.51(0.34,0.76)$ | $0.70(0.38,1.30)$ |
| First spouse | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) | 1.00 (reference) |
| Second spouse | $0.84(0.71,1.01)$ | $0.90(0.77,1.06)$ | $1.15(0.95,1.41)$ | $1.45(1.07,1.96)$ | $1.30(0.74,2.27)$ | 1.06 (0.46, 2.45) |
| Third or later spouse | $0.81(0.54,1.23)$ | $0.57(0.38,0.86)$ | $1.26(0.85,1.88)$ | $1.26(0.85,1.88)$ | $1.24(0.32,4.83)$ | 0.26 (0.04, 1.93) |
| $P$ value for sex difference | 0.267 | 0.038 | 0.015 | $<0.001$ | 0.023 | 0.027 |

Values are odds ratios from discrete-time survival analyses assessing the probability of having a child at a given age in participants who have not had a child by that age. Values in parentheses are $95 \%$ CIs. All models adjust for birth year, time, time2, and ethnicity. $P$ value for sex difference tests for sex difference in the association between spouse number and odds of childbirth among participants with at least one spouse. Six separate discrete-time survival analyses in men and women.

Evolutionarily, humans are often described as mildly polygynous. Most traditional societies have allowed polygyny, although usually only a minority of men has been able to have more than 1 wife (Marlowe 2000). Morphological traits (e.g., sexual dimorphism in body size; Frayer and Wolpoff 1985), psychological dispositions (e.g., male preference for sexual variety; Schmitt 2003), and genetic evidence (Hammer et al. 2008) also imply polygyny in human evolution. From this perspective, modern serial monogamy can be seen as a mating system in which males benefit from their tendency toward multiple mating without the need for resources to support several wives concurrently. However, the observed population differences in the Bateman gradient suggest that the opportunity for serial monogamy does not necessarily lead to higher male reproductive success associated with multiple mating. Understanding the socioecological factors involved in these population differences may help us to better understand the evolution of social monogamy more recently in human history (Fortunato and Archetti 2010).
The main strengths of the present study include a nationally representative heterogenous population with detailed data on marital and fertility history collected over a long period of time. However, at least 4 limitations need to be considered in interpreting the findings. First, we examined the association between number of spouses and reproductive success, which leaves out short-term relationships and extrapair sexual relations. According to 2 literature reviews, the average rate of nonpaternity is between $2 \%$ and $4 \%$ in contemporary societies (Bellis et al. 2005; Anderson 2006). Such a low prevalence of nonpaternity is unlikely to substantially bias our conclusions. The association between extrapair copulations and serial monogamy, if any, is most likely to be positive; serial monogamy requires repeated divorces, and extramarital affairs are associated with marital dissatisfaction and increased risk of divorce (Buss and Shackelford 1997; Atkins et al. 2001; Previti and Amato 2004). Thus, the omission of unknown biological children from offspring count may have yielded underestimates of the association between serial monogamy and reproductive success in men. Future studies should use different measures of mating success to examine whether the Bateman gradient depends on the nature of indicators for mating success.

Second, we assessed offspring count but not other outcomes relevant to reproductive success, such as offspring quality or parental investment. These could be relevant especially when considering the potential reproductive advantages of multiple
mating in women who might benefit from multiple mating via male resource provision or other mechanisms increasing offspring quality (Hrdy 2000; Soltis 2002). However, in a population with low child mortality (US Census Bureau 2003), offspring count is likely to be the most important component of reproductive success.
Third, not all the participants, men in particular, had reached the end of their reproductive age. This may have led to an underestimation of the observed associations because reproductive variance among men could have further increased with age. However, according to the US population statistics (Martin et al. 2004), individuals aged 44 years or younger account for $97 \%$ and $>99 \%$ of total fertility rates in men and women, respectively, suggesting that the age restriction was not a major limitation of the study. Fourth, the division of men and women into ethnic groups is not exclusive because these groups do not represent completely separate reproductive populations: Over the time period from 1970 to 2005 , the proportion of interethnic marriages of all marriages in the United States increased from approximately $1-6 \%$ (Harris and Ono 2005). Nevertheless, the prevalence of interethnic marriages is sufficiently low for a valid subpopulation analysis based on ethnicity.

In conclusion, the present results provide direct evidence of the reproductive advantages associated with serial monogamy in a postindustrial human population. On average, men increase their reproductive success by having several consecutive spouses, whereas serial monogamy is not associated with the number of children in women. In this respect, contemporary serial monogamy bears resemblance to the sex-specific reproductive consequences of polygyny, although the present sex differences were considerably smaller in magnitude than those reported for polygyny in some preindustrial populations (Brown et al. 2009). Extrapolating from these results, it seems plausible that heritable traits precipitating male serial monogamy are under positive sexual selection in contemporary societies, which may create sexual conflicts in mating and reproductive strategies between the sexes (Käär et al. 1998). The determinants of serial monogamy and the socioecological factors modifying its reproductive consequences should be of interest to evolutionary studies of mating behavior.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco .oxfordjournals.org/.

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## REFERENCES

Aarssen LW. 2007. Some bold evolutionary predictions for the future of mating in humans. Oikos. 116:1768-1778.
Anderson KG. 2006. How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. Curr Anthropol. 47:513-520.
Arnold SJ. 1994. Bateman's principles and the measurement of sexual selection in plants and animals. Am Nat. 144:S126-S149.
Arnold SJ, Duvall D. 1994. Animal mating systems-a synthesis based on selection theory. Am Nat. 143:317-348.
Atkins D, Baucom D, Jacobson N. 2001. Understanding infidelity: correlates in a national random sample. J Fam Psychol. 15: 735-749.
Bateman AJ. 1948. Intra-sexual selection in Drosophila. Heredity. 2:349-368.
Bellis MA, Hughes K, Hughes S, Ashton JR. 2005. Measuring paternal discrepancy and its public health consequences. J Epidemiol Community Health. 59:749-754.
Borgerhoff Mulder M. 1987. On cultural and reproductive successKipsigis evidence. Am Anthropol. 89:617-634.
Borgerhoff Mulder M. 2009. Serial monogamy as polygyny or polyandry? Hum Nat. 20:130-150.
Brand RJ, Markey CM, Mills A, Hodges SD. 2007. Sex differences in self-reported infidelity and its correlates. Sex Roles. 57:101-109.
Brown GR, Laland KN, Borgerhoff Mulder M. 2009. Bateman's principles and human sex roles. Trends Ecol Evol. 24:297-304.
Bulanda JR, Brown SL. 2007. Race-ethnic differences in marital quality and divorce. Soc Sci Res. 36:945-967.
Buss DM. 1998. Sexual strategies theory: historical origins and current status. J Sex Res. 35:19-31.
Buss D, Shackelford T. 1997. Susceptibility to infidelity in the first year of marriage. J Res Pers. 31:193-221.
Buss DM, Schmitt DP. 1993. Sexual strategies theory-an evolutionary perspective on human mating. Psychol Rev. 100:204-232.
Campbell A. 2008. The morning after the night before-affective reactions to one-night stands among mated and unmated women and men. Hum Nat. 19:157-173.
Clutton-Brock TH. 1989. Mammalian mating systems. Proc R Soc B Biol Sci. 236:339-372.
Eliassen S, Kokko H. 2008. Current analyses do not resolve whether extra-pair paternity is male or female driven. Behav Ecol Sociobiol. 62:1795-1804.
Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. 197:215-223.
Forsberg AJL, Tullberg BS. 1995. The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden. Ethol Sociobiol. 16: 221-232.
Fortunato L, Archetti M. 2010. Evolution of monogamous marriage by maximization of inclusive fitness. J Evol Biol. 23:149-156.
Frayer DW, Wolpoff MH. 1985. Sexual dimorphism. Ann Rev Anthropol. 14:429-473.
Gangestad SW, Simpson JA. 2000. The evolution of human mating: trade-offs and strategic pluralism. Behav Brain Sci. 23:573-587.
Guzzo KB, Furstenberg FF. 2006. Multipartnered fertility among American men. Demography. 44:583-601.
Hammer MF, Mendez FL, Cox MP, Woerner AE, Wall JD. 2008. Sexbiased evolutionary forces shape genomic patterns of human diversity. PLoS Genet. 4:e1000202.
Harris DR, Ono H. 2005. How many interracial marriages would there be if all groups were of equal size in all places? A new look at national estimates of interracial marriage. Soc Sci Res. 34:236-251.
Hopcroft RL. 2006. Sex, status, and reproductive success in the contemporary United States. Evol Hum Behav. 27:104-120.
Hrdy SB. 2000. The optimal number of fathers-evolution, demography, and history in the shaping of female mate preferences. In: LeCroy D, Moller P, editors. Evolutionary perspectives on human reproductive behavior. Vol. 907. New York: New York Academy of Sciences. p.75-96.

Jokela M. 2009. Physical attractiveness and reproductive success in humans: evidence from the late 20th century United States. Evol Hum Behav. 30:342-350.
Jokela M, Hintsa T, Hintsanen M, Keltikangas-Järvinen L. 2010. Adult temperament and childbearing over the life course. Eur J Pers. 24:151-166.
Jokela M, Keltikangas-Järvinen L. 2009. Adolescent leadership and adulthood fertility: revisiting the "central theoretical problem of human sociobiology". J Pers. 77:213-230.
Jokela M, Kivimäki M, Elovainio M, Keltikangas-Järvinen L. 2009. Personality and having children: a two-way relationship. J Pers Soc Psychol. 96:218-230.
Käär P, Jokela J, Merilä J, Helle T, Kojola I. 1998. Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. Evol Hum Behav. 19:139-151.
Kokko H, Jennions MD. 2008. Parental investment, sexual selection and sex ratios. J Evol Biol. 21:919-948.
Kruger DJ, Schlemmer E. 2009. Male scarcity is differentially related to male marital likelihood across the life course. Evol Psychol. 7: 280-287.
Laland KN, Brown GR. 2006. Niche construction, human behavior, and the adaptive-lag hypothesis. Evol Anthropol. 15:95-104.
Manlove J, Logan C, Ikramullah E, Holcombe E. 2008. Factors associated with multiple-partner fertility among fathers. J Marriage Fam. 70:536-548.
Marlowe FW. 2000. Paternal investment and the human mating system. Behav Processes. 51:45-61.
Martin JA, Hamilton BE, Sutton PD, Ventura SJ, Menacker F, Kirmeyer S. 2004. Births: final data for 2004. Natl Vital Stat Rep. 55:1-104.

Nettle D, Pollet TV. 2008. Natural selection on male wealth in humans. Am Nat. 172:658-666.
Pérusse D. 1993. Cultural and reproductive success in the industrial societies: testing the relationship at the proximate and ultimate levels. Behav Brain Sci. 16:267-322.
Pollet TV, Nettle D. 2008. Driving a hard bargain: sex ratio and male marriage success in a historical US population. Biol Lett. 4:31-33.
Previti D, Amato P. 2004. Is infidelity a cause or a consequence of poor marital quality? J Soc Pers Relat. 21:217-230.
Reynolds JD. 1996. Animal breeding systems. Trends Ecol Evol. 11: 68-72.
Salzano FM, Neel JV, Mayburyl D. 1967. Further studies on Xavante indians.I. Demographic data on 2 additional villages-genetic structure of tribe. Am J Hum Genet. 19:463-489.
Schmitt DP. 2003. Universal sex differences in the desire for sexual variety: tests from 52 nations, 6 continents, and 13 islands. J Pers Soc Psychol. 85:85-104.
Schmitt DP. 2005. Sociosexuality from Argentina to Zimbabwe: a 48-nation study of sex, culture, and strategies of human mating. Behav Brain Sci. 28:247-275.
Schmitt DP, Shackleford TK, Duntley J, Tooke W, Buss DM. 2001. The desire for sexual variety as a key to understanding basic human mating strategies. Pers Relatsh. 8:425-455.
Schmookler T, Bursik K. 2007. The value of monogamy in emerging adulthood: a gendered perspective. J Soc Pers Relat. 24:819-835.
Sear R, Mace R. 2008. Who keeps children alive? A review of the effects of kin on child survival. Evol Hum Behav. 29:1-18.
Skirbekk V. 2008. Fertility trends by social status. Demogr Res. 18:145-180.
Snyder BF, Gowaty PA. 2007. A reappraisal of Bateman's classic study of intrasexual selection. Evolution. 61:2457-2468.
Soltis J. 2002. Do primate females gain nonprocreative benefits by mating with multiple males? Theoretical and empirical considerations. Evol Anthropol. 11:187-197.
Tang-Martinez Z, Ryder TB. 2005. The problem with paradigms: Bateman's worldview as a case study. Integr Comp Biol. 45:821-830.
Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man, 1871-1971. Chicago (IL): Aldine. p. 136-179.
US Census Bureau. 2003. Statistical abstract of the United States, minihistorical statistics (HS-13). Washington (DC): US Census Bureau.
Wood W, Eagly AH. 2002. A cross-cultural analysis of the behavior of women and men: implications for the origins of sex differences. Psychol Bull. 128:699-727.
Wu LL. 2005. Cohort estimates of nonmarital fertility for US women. Demography. 45:193-207.


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