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Pair-Bonding Modifies the Age-Specific Intensities of Natural Selection on Human Female Fecundity

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abstract: In many animals, including humans, the ability of females to reproduce depends not only on their survival to each age but also on being pair-bonded to a mate. Exposure of the genetic variation underlying fecundity to natural selection should therefore depend on the proportion of females both alive and pair-bonded. In spite of this, female "marital" status is seldom considered to impact the strength of selection on age-specific fecundity. We used marriage-history data of preindustrial Finns who experienced conditions of natural mortality and fertility to investigate how assortative mating by age and socioeconomic status affected female fitness and underlay age-specific female marriage patterns. The probability that a female was married peaked at age 30–40 years; females who married in their early 20s to high-socioeconomic-status husbands had the highest levels of lifetime reproductive success. Greater age difference between the pair, which is typical for females who are married to high-socioeconomic-status husbands, increased the likelihood of widowhood occurring premenopause, adding to declines in the proportion of genetic variation exposed to selection with age. Using the age schedule of female marriage, we present an indicator of selection intensity on within-pair-bond fecundity. Our results suggest that the decline in selection intensity after age 30 years is a factor in the evolutionary maintenance of female reproductive senescence and menopause.

Keywords: biparental, marriage, monogamy, senescence, sensitivity, widowhood.

Introduction

Evolutionary studies of senescence—that is, physiological deterioration with age—have tended to focus on how natural selection shapes differences between age-specific mortality rates (Monaghan et al. 2008). Currently, increasing attention is being given to age-specific selection on female fecundity (Nussey et al. 2009), a major component of individual fitness. The intensity of selection on age-specific female fecundity is given by Hamilton's indicator (Hamilton 1966), which uses the probability that a female will survive to each age to estimate the expressed proportion of underlying genetic variation for fecundity (the "visible fraction" of genetic variation; Grafen 1988). If a higher proportion of genetic variation is expressed, selection against deleterious (or for beneficial) genetic variants is stronger because those variants are more likely to influence fitness and, hence, population growth. After any genetic effects on fitness are discounted by the rate of population growth (because early-age effects have a greater influence on fitness in a growing population), the resulting indicator should be inversely proportional to the age-specific frequencies of genetic variants that are deleterious to female fecundity under mutation-selection balance (assuming a stable, density-independent population in a constant environment; Charlesworth 1994). Declining probabilities of female survival to later ages are thus the reason for expecting senescent deterioration in female reproductive performance with age (Packer et al. 1998). Against this background, evidence for female reproductive senescence is found to be widespread in wild populations (Jones et al. 2008).

Many iteroparous species reproduce primarily within pair-bonds, including the majority of birds (Cockburn 2006) and some mammals, including humans (Clutton-Brock 1991; Reichard and Boesch 2003). As a consequence, it is the probability that a female is both alive and pair-bonded at each age that should determine the expressed fractions of genetic variation underlying female fecundity. Despite this, "marital" status is seldom considered to impact the strength of natural selection on age-specific fecundity. Among birds, long-term pair-bonding is generally found in long-lived species whose ecology (e.g., returning to the same breeding grounds) makes it practical to retain the same partner between years and results in limited num-

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bers of unpaired potential mates to switch to following divorce (Jeschke and Kokko 2008). Bewick's swans *Cygnus columbianus bewickii* are such a species, with the added benefit that pairing throughout the winter can help maintain dominance rank, ensuring resource access and reproductive success the following year (Scott 1980).

The prevalence of pair-bonding in human societies is likely not a consequence of modern social developments but rather an integral part of human evolution. This is highlighted by comparisons of estrus signaling between humans and chimpanzees *Pan troglodytes* (for wider contexts, see Goody 1971; Strassmann 1981; Diamond 1992; Quinlan 2008). Chimpanzee females openly display their sexual receptivity, whereas human female ovulation is a more subtle occurrence (Gangestad and Thornhill 2008). Reduced human estrus signaling and increased pair-bonding are thought to benefit fitness by lowering competition for both mates and resources within the social group (Flinn et al. 2005; Bowles 2006). Even so, within a group, females paired with higher-socioeconomic-status males and males paired with higher-reproductive-value females (e.g., younger, wealthier, and more experienced) tend to have the highest fitness (Gurven and von Rueden 2006; Pettay et al. 2007). Thus, the initial formation of pair-bonds is extremely important to both female and male fitness, and there is evidence of fine-scale mate choice on socioeconomic, phenotypic, and genetic grounds (Gangestad and Thornhill 2008; Alvergne and Lummaa 2010) and/or careful organization of offspring marriages involving payments between families (Borgerhoff Mulder 1988; Gaulin and Boster 1990). We would expect that these patterns of pair-bond formation in relation to age and socioeconomic status are reflected in the population-level probabilities that a female is both alive and pair-bonded at each age. Relating the selection-intensity indicator to mating-system variation and female fitness is therefore crucial to understanding both past and present selection intensities on the age-specific female fecundity of all pair-bonding species, including humans.

To investigate how pair-bonding modifies the intensities of natural selection on age-specific human female fecundity, we used a demographic data set that included full marriage histories from four geographically isolated populations of preindustrial Finns living in conditions of natural fertility and mortality (without advanced healthcare or contraception; Lummaa 2001; Pettay et al. 2007). During our study period (1732–1893), Finland had a high level of marital monogamy and divorce was forbidden. Remarriage for young widows was almost essential to ensure the survival of dependent offspring and to avoid destitution for the landless (Moring 2002). Older widows with supportive adult offspring had less necessity for remarriage, and these offspring might have also prevented their mother's remarriage if it delayed their inheritance (Moring 2002). First, we described the age-specific probabilities that a living female was married. We then asked how the ages at the formation and dissolution (due to either the female's or the husband's death) of a female's first marriage related to her first husband's socioeconomic status. Given this knowledge, we asked how the female's and the first husband's ages at marriage and socioeconomic statuses related to a female's lifetime reproductive success (LRS). We also investigated the likelihood of remarriage for widows according to age at widowhood, as well as the LRS associated with remarriage. Finally, we used age-specific marriage probabilities to adapt Hamilton's (1966) indicator of age-specific selection intensity to apply to within-pair-bond female fecundity. Modal ages of a human female's first marriage in the last 150 years have ranged from the late teens to the late 20s (Coale 1971), with the development of modern society increasing marital delays (Kaplan 1996). At older ages, the presence of offspring from a previous marriage could reduce the marriageability of widows (Knodel and Lynch 1985), causing the proportion of married females to decline. Age patterns of remarriage should, therefore, be the final factor shaping the probabilities that females are both alive and married at each age.

Methods

Study Population

In preindustrial Finland, law obliged local clergymen to make accurate records of the birth, death, movements, and marital status of all individuals in their parish areas (Moring 1996). These records provide exact information on a wife's and a husband's ages at marriage (i.e., pair-bond formation) and death. They also allow for the collection of information on the number of offspring produced and reared to age 15 years (the age at which they could potentially marry; Moring 1996), which we use to measure female LRS. Migration rates between parishes were low, and in most cases parish migration registers allowed for the marriage age, reproductive success, and survival of dispersers to be determined. The mating system was patrilocal and thought to be sexually monogamous within marriage to an unusually high degree (Moring 1996). The predominant constraint on marriage age was economic and highly dependent on the inheritance of family-owned land rights (Moring 1996). Female marriage was often delayed until a woman's mid to late 20s, which is consistent with the general European trend since the eighteenth century (Hajnal 1965; Coale 1971). Divorce was virtually impossible, and remarriage could occur only after the death of the previous spouse. A widow tended to remain on the farm of her late husband, either with a new husband or with the family of her son or daughter. However, the widows of landless men were without such social security in their old age, and they relied on the help of relatives, remarried, or faced destitution (Moring 2002).

From the church registers, we sampled 1,591 female offspring with known ages at death who were born to 511 mothers. Of these offspring, 40%–50% had no reproductive success of their own (Lummaa 2001; Gillespie et al. 2008). The females in our sample were born between 1732 and 1859, and the last gave birth in 1893. Our study period thus coincided with periods of natural fertility and mortality and ended before healthcare and more liberal economics began to improve standards of living in Finland (Soininen 1974).

Our data come from four geographically isolated parishes in Finland: Hiittinen, Ikaalinen, Kustavi, and Rymättylä. The socioeconomic status of each married female was assigned according to the profession of her husband as recorded in the church registers (Lahdenperä et al. 2004). This was simplified into two groups, which are hereafter referred to as landowning and landless according to those owning land versus those either renting or having no access to land (Gillespie et al. 2008). Landownership in preindustrial populations has been shown to lower age at marriage (Voland and Dunbar 1995; Moring 1996); increase the chance of remarriage, which generally occurred within 1–3 years of bereavement (Moring 2002); and increase female lifetime fecundity and reproductive success (Easterlin 1976; Gillespie et al. 2008). Although there are likely to be high levels of variation within landownership groups, this broad categorization allowed us to observe the major effects of socioeconomic differences between individuals. The multigenerational nature of our data set also gave information on the socioeconomic status of each female's father, which allowed us to control for the influence of parental socioeconomic status on female marriage patterns and reproductive success.

Statistical Analyses

We performed all analyses in the R environment (ver. 2.9.0; R Development Core Team 2009), using an information-theoretic approach based on model ranking by Akaike Information Criterion (Burnham and Anderson 2002; Bolker et al. 2009). We fitted random intercepts in mixed models to account for unobserved similarities (i.e., statistical nonindependence) between females from the same family and between data points from the same female. All models were fitted by maximum likelihood (or the Laplace approximation to maximum likelihood for non-Gaussian response variables) in the mixed-model R package lme4 (Bates and Maechler 2010). We tested our set of response variables (see below) for differences according to husband's socioeconomic status (a two-level factor: landowning vs. landless). We also controlled for differences due to parish population (a four-level factor), female's birth year (continuous), and father's socioeconomic status (a two-level factor: landowning vs. landless) as fixed effects in all analyses. All Gaussian continuous variables were standardized by zero-centering at their mean and dividing by their standard deviation (see table A1 in the online edition of the *American Naturalist* for the values used; Gelman and Hill 2007).

Each analysis entailed constructing a set of nested models (not including models with interactions or quadratic functions without their associated main terms, lower-order interactions, or linear forms) from the maximal model and fitting these to the data sample (Burnham and Anderson 2002). Akaike weights were calculated for each model and used to calculate weighted averages and standard errors for each model parameter estimate. For models where a particular variable was absent, we took its parameter estimates and their standard errors to be 0. To quantify the relative importance of each explanatory variable, we summed Akaike weights across the set of models containing each explanatory variable (we term these sums I values). To aid in I-value interpretation, we compared each one to the I value achieved by a randomly generated continuous variable with a mean of 0 and a standard deviation of 1. We expanded the nested model set to include this random variable and ran the analysis 100 times with 100 different random variables. This created a null distribution of I values, from which we used the 95% interval to interpret the significance of variation explained by each explanatory variable (Whittingham et al. 2005).

Marriage Patterns

Probability That a Living Female Was Married at Each Age. We described the population-level probability that a living female was married at each age from birth to 95 years, separately for each parish population, and also the probability of female survival to each age. From our sample of 1,591 females, 149 were excluded because of uncertainty of their exact ages at marriage, widowhood, or death. Of the remaining 1,442 females, 607 married at least once. To calculate age-specific marriage probabilities, each female was coded with a 0 if she was not married (i.e., she was alive and not yet married or she was widowed and not yet remarried) or a 1 if she was alive and married at the start of each 1-year age class. We took the mean of these binary codes for each age class as the probability that a living female was married at each age.

Age at Beginning and End of Marriage by Husband's Socioeconomic Status. We conducted three analyses linking female marriage patterns to the socioeconomic status of a female's first husband. These were (1) the difference between female age and the age of her husband at marriage and (2) the difference between the age at which a female's first marriage ended and her age at death. We used linear mixed models in which the response variable was subject to a Box-Cox power transformation to normality (the appropriate power identified using the function box.cox.powers in the R package car; Fox 2009). For each of these first two analyses, we restricted our sample to include only the 607 females who ever married. We also analyzed (3) the probability of female remarriage according to age at widowhood. For this analysis, we used only females who outlived their first husbands, which gave a reduced sample size of 364 females. We analyzed this sample set with a binomial generalized linear mixed model fitted to a probit-transformed binary response variable (1 = remarried, 0 = not remarried).

Female LRS by Female's and Husband's Marriage Ages and Socioeconomic Status. We analyzed (1) the relationship of female lifetime reproductive success (LRS; the number of offspring produced that survived to age 15 years) to the female's and her husband's ages at the female's first marriage. Using our sample of 607 females, female LRS was analyzed with a Poisson generalized linear mixed model and a log-link function. Both linear and quadratic functions of the female's and the husband's ages were included as explanatory variables, but interactions were included between linear terms only (Draper and John 1988). We also investigated (2) the association between a female's LRS and whether she married again after widowhood. For this analysis we used the sample of 364 females who outlived their first husbands. We controlled for differences in first-marriage duration between females with linear and quadratic functions of female age at first marriage and age at widowhood, with an interaction between the linear functions of age only. To investigate whether the LRS associated with female remarriage depended on age at widowhood, we added an interaction between remarriage and widowhood age.

Age-Specific Selection Intensities on Within-Pair-Bond Female Fecundity

We took as a base Hamilton's (1966) indicator (eq. [1]) of the intensity of selection on female fecundity (estimated as the ratio of female offspring born to living females) at a particular age a across the range of ages x from birth to 95 years. This was a one-sex model, considering female demography only:

$$\frac{dr}{dm_a} = \frac{e^{-ra} l_a}{\sum_{x=0}^{\infty} x e^{-rx} l_x m_x}. \tag{1}$$

Hamilton's indicator gives the sensitivity of the intrinsic rate of population growth r to changes in female fecundity m occurring at each age. l_a is the probability of female survival to each age. The effect of a change in female fecundity m at each age on the intrinsic rate of population growth r is adjusted by the value of r in the term e^{-ra}. This is because in an expanding population, changes in early-age fecundity have a greater influence on the rate of population growth. The denominator represents the population generation time, including the average age x at which female offspring are born, which again is discounted by the intrinsic rate of population growth. It is important to emphasize that this formulation assumes that age-specific fecundity is not under strong selection, that is, that the population is close to its optimal life history; that reproduction and survival schedules are constant over time, leading to a stable age distribution; and that the population is density independent and living in a constant environment (Charlesworth 1994). Although each assumption is unlikely to be wholly met by humans in preindustrial Finland, here we focus on how the conclusions from Hamilton's indicator can change when the age schedule of female pair-bonding is considered.

Our indicator (eq. [3]) is based on the principle, described by Coale (1971), that age-specific female fecundity m is a product of the probability p that a living female was married at each age and the corresponding age-specific within-pair-bond female fecundity b, $m = pb$, so that

$$\sum_{x=0}^{\infty} e^{-rx} l_x p_x b_x = 1, \tag{2}$$

and differentiating with respect to b at age a gives

$$\frac{dr}{db_a} = \frac{e^{-ra} l_a p_a}{\sum_{x=0}^{\infty} x e^{-rx} l_x p_x b_x}. \tag{3}$$

We used this indicator (eq. [3]) to calculate age-specific selection intensities on female fecundity separately for each parish population. For comparison in each case, we calculated Hamilton's (1966) indicator (eq. [1]), which does not consider the age schedule of female pair-bonding. We calculated the denominator using age-specific rates of female offspring production in each 1-year age class m_x. In calculating this value, we used our full sample of 1,591 females, who gave birth to a total of 1,761 female offspring. These data were also used to calculate the intrinsic rates of population growth r in each parish using the R package demogR (Jones 2007).

Results

Marriage Patterns

Probability That a Living Female Was Married at Each Age. Across each of the four parish populations, the percentage of females who were alive at age 15 years ranged from 44% to 64%; at age 50 years, this value ranged from 32% to 47% (fig. 1). Females married for the first time at a mean age of 27 years (range = 16–54 years); 23% of all widows remarried, and the last recorded age at which a female was still married was 90 years. In all parish populations, the probability that a living female was married, even if this was to a second husband, increased steeply from before age 20 years to her 30s, eventually peaking at around 80% in each parish in the age range 38–45 years (fig. 1). Following this peak, the probability of being married began to decline, dropping below 70% around the maximum age of reproduction (range = 46–54 years) in each parish.

Age at Beginning and End of Marriage by Husband's Socioeconomic Status. Females marrying landowning husbands married for the first time at a mean age of 24.4 years (range = 16–54 years), which is 2.9 years younger than females with landless husbands (fig. 2*A*; table A2 in the online edition of the *American Naturalist*). On average, females were 1.9 years younger (range = 34 years younger to 21 years older) than their husbands. The average age difference between females and landless husbands was 1.0 year, which increased to 2.7 years for females with landowning husbands. Thus, females who were married to high-socioeconomic-status husbands married at younger ages, but they married relatively older men.

The mean life span of married females was around 62 years (range = 22–95 years), and this was not significantly influenced by the husband's socioeconomic status (fig. 2*B*; table A2). However, the first marriages of females with landowning (vs. landless) husbands ended 3.9 years earlier, at a mean age of 47.7 years (range = 22–90 years). Thus, females who were married to high-socioeconomic-status

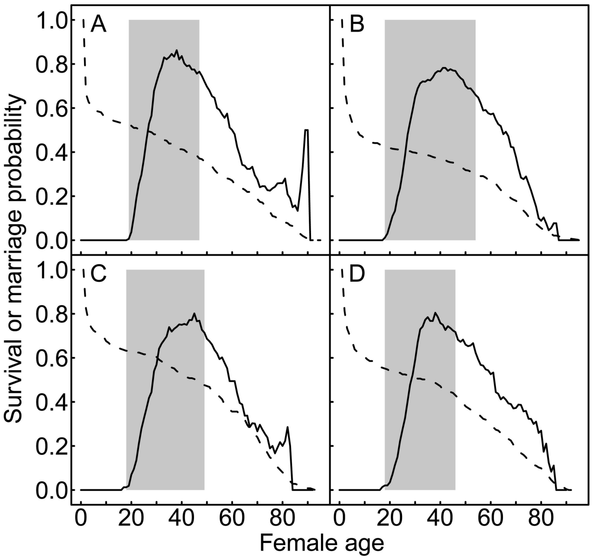

Figure 1: In each parish (*A*, Hiittinen; *B*, Ikaalinen; *C*, Kustavi; *D*, Rymättylä), the probability that a living female was married at each age (measured in years) increased steeply until her 30s, eventually peaking in the age range 38–45 years at around 80% before declining (*solid lines*). In comparison, the probability of female survival to each age (*dashed lines*) declined continuously throughout the female reproductive age range (*gray shading*).

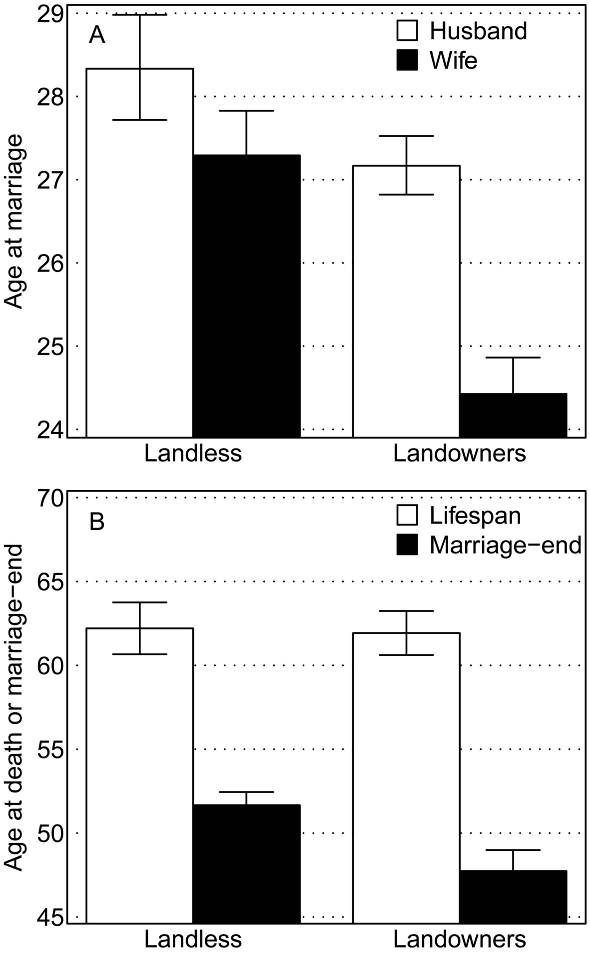

Figure 2: Husband's socioeconomic status modified the age at which a female's first marriage began and ended. *A*, Females married younger if marrying a landowning (i.e., high-socioeconomic-status) husband. *B*, Female marriages ended at younger ages if they were married to a landowning first husband. Means and error bars are back-transformed model-averaged estimates, from a linear mixed model of each response variable.

Table 1: Remarriage probability according to age when widowed and first husband's socioeconomic status

Parameter	Estimate	SE	*I*
Husband's socioeconomic status (landless)	−1.50	.21	
Versus landowning	−.25	.37	.74[a]
Age at widowhood	−1.50	.27	1.00[a]
Age at widowhood × husband's socioeconomic status (landowning)	−.54	.53	.61

Note: Females who were older when widowed were less likely to remarry, and the chance of remarriage was higher for young widows of landowning husbands. The analysis used a generalized linear mixed-effects model with a binomial error structure fitted to a probit-transformed binary response of remarried (1) or not remarried (0) following widowhood. See table A1 in the online edition of the *American Naturalist* for values used to standardize age at widowhood. Parameter estimates and standard errors were model-averaged over an Akaike Information Criterion–ranked model set. On the basis of *I* values (summed Akaike weights ranging from 0 to 1), we measured the relative explanatory power of each variable. The significance of variation explained was assessed by comparison to 50% and 95% intervals of the *I* values achieved by 100 different randomly generated continuous variables when each was added to the analysis. The 95% critical *I* value for this analysis is 0.62. We show (and plot in fig. A1 in the online edition of the *American Naturalist*) only parameter estimates of variables that exceed the 50% critical *I* value (0.31).

[a] Variable exceeds the 95% critical *I* value (i.e., strong statistical support).

husbands were less likely to be in active first marriages at older ages.

The chance of remarriage was almost 100% for the youngest widowed females, falling to 50% for females who were widowed in their late 30s (table 1; fig. A1 in the online edition of the *American Naturalist*). Females widowed at young ages who had previously been married to landowning husbands had a slightly higher probability of remarriage. Thus, young widows, particularly those of landowning husbands, had a high chance of regaining their married status after their first husbands died. However, females who were widowed after their late 30s had less than a 50% likelihood of remarriage, leading to an inevitable decline in the probability of being both alive and married with age.

Female LRS by Wife's and Husband's Marriage Ages and Socioeconomic Status. Mean female LRS was 3.1 surviving offspring (range = 0–10). Females who had married at older ages had lower LRS than did those who married youngest (fig. 3; table A3 in the online edition of the *American Naturalist*). For the youngest-married females in particular, marriage to a landowning husband increased female LRS (fig. 3). However, for females with landowning husbands, there was around a one-offspring (or 20%) reduction in LRS between a female marrying at age 20 years to a husband in his 30s and one marrying a husband in his 40s (fig. 3). Remarried widows who were widowed at older ages had lower LRS values than did those who remarried but were widowed younger (fig. 4; table A4 in the online edition of the *American Naturalist*). This decline equated to a 7.9% drop in LRS between females who were widowed at age 30 years and those widowed at age 40 years. The majority of widows who did not remarry were widowed after age 35, when not remarrying was increasingly associated with higher LRS than was remarrying (fig. 4). Such an LRS increase beyond the age of menopause could be because the married couple survived long enough to care for all offspring until age 15 years, or because these were the subset of couples who were inherently more able to produce surviving offspring and then themselves survive to old age.

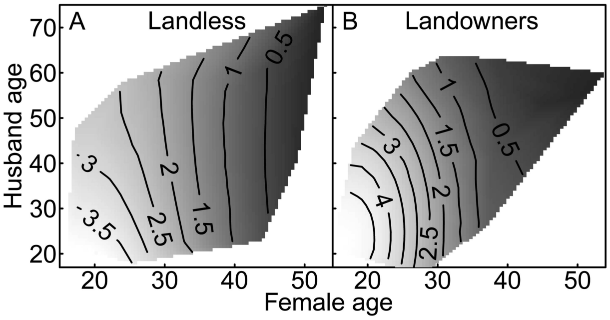

Figure 3: Contour lines show the female LRS (*Z*-axis) associated with each wife-husband marriage-age combination. Females married at later ages had lower lifetime reproductive success (LRS; the number of offspring surviving to age 15 years) than did those married at the youngest ages. The LRS of females married at young ages to husbands who were relatively older than themselves appeared to be increasingly constrained. The figure shows interpolated back-transformed predicted values that were generated using model-averaged parameter estimates from a Poisson generalized linear mixed model. The gray shaded area shows the data range of female and husband marriage-age combinations in each parish.

Figure 4: Lifetime reproductive success (LRS; the number of offspring surviving to age 15 years) declined with increasing age at widowhood for widows who subsequently remarried. Remarriage increased the LRS of females who were widowed at the youngest ages. However, for females who were widowed around the age of natural menopause, not remarrying was associated with the highest LRS. The case for widows of landless first husbands is shown in black, and for the widows of landowners it is shown in gray. The figure shows back-transformed predicted values that were generated using model-averaged parameter estimates from a Poisson generalized linear mixed model.

Age-Specific Selection Intensities on Within-Pair-Bond Female Fecundity

In all parish populations, selection intensities (the sensitivity of the intrinsic rate of population growth to age-specific changes in within-pair-bond female fecundity; eq. [3]) rose from 0 before the age of 20 years and peaked around age 30 years, declined slowly for up to the following 15 years, and then declined steeply thereafter (fig. 5). The ages at which the steep decline in selection intensity began occurred shortly after age 30 years in the parish of Hiittinen, after age 45 years in Ikaalinen, after age 45 years in Kustavi, and shortly before age 40 years in Rymättylä. At the latest recorded age of a female experiencing a live birth in each parish (range, 46–54 years), selection intensity had fallen by 73% of its maximum in Hiittinen and Rymättylä and by 77% in Ikaalinen and Kustavi. In comparison to this highly curvilinear indicator of selection intensity on age-specific female fecundity (fig. 5) that arose from considering pair-bonding at each age, Hamilton's (1966) indicator (eq. [1]; also shown for comparison in fig. 5), which uses only the probability of female survival to each age, declined continuously throughout the female reproductive years and was much less curvilinear. Thus, consideration of both survival and marriage at each age dramatically modified the expected intensities of selection on age-specific female fecundity.

Discussion

On the basis of the age-specific probabilities that a living female was pair-bonded (i.e., married) to a mate, we have presented an indicator of the intensities of in-progress natural selection on age-specific within-pair-bond fecundity. Compared with Hamilton's (1966) indicator of selection intensity, which does not consider the probabilities of being pair-bonded, our indicator is highly curvilinear with respect to female age. We can make two predictions from our observed rises and subsequent falls in age-specific selection intensities. First, increases in selection intensity with age, which occur as a greater proportion of individuals marry or form a pair-bond, is an evolutionary factor shaping the genetic basis of physiological improvements in young-age reproductive performance in birds and mam-

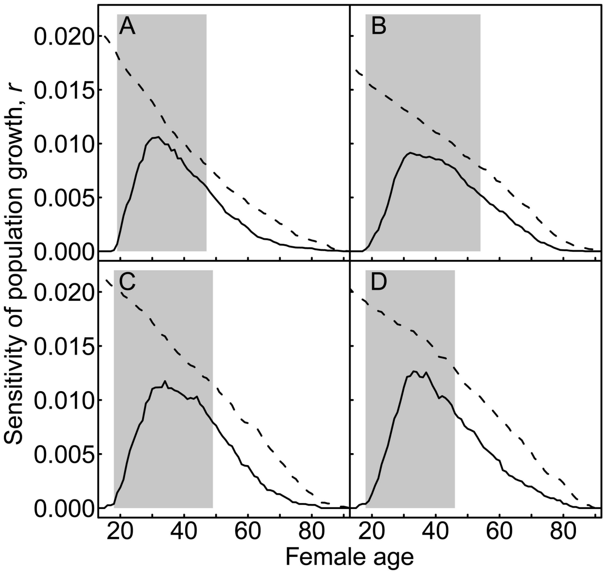

Figure 5: In each parish (*A*, Hiittinen; *B*, Ikaalinen; *C*, Kustavi; *D*, Rymättylä), selection intensities (the sensitivity of the intrinsic rate of population growth to age-specific changes in within-pair-bond female fecundity; eq. [3]; *solid lines*) rose to a peak around age 30 years, plateaued with a slow rate of decline for up to 15 years, and then declined steeply. In comparison, Hamilton's (1966) indicator of selection intensities (using survival probabilities only; eq. [1]; *dashed lines*) declined continuously throughout the age ranges of female reproduction in each parish (*gray shading*). The *Y*-axis shows the sensitivity of intrinsic population growth rate to age-specific changes in female fecundity. The intrinsic rate of population growth was 0.017 in Hiittinen, 0.0097 in Ikaalinen, 0.0091 in Kustavi, and 0.0045 in Rymättylä. Thus, all parish populations were growing. Generation times adjusted by *r* (i.e., the denominator in eq. [3]) were 20.6 years in Hiittinen, 22.4 years in Ikaalinen, 26.2 years in Kustavi, and 26.4 years in Rymättylä.

mals, including humans (Wood 1994; Bowen et al. 2006; Angelier et al. 2007). Second, the onset of a decline in selection intensity that occurs between the ages of 30 and 45 years, as the proportion of females in an active pair-bond falls, contributes to the evolutionary maintenance of two major components of human female reproductive senescence: (1) within-individual aging increases in the occurrence of fetal genetic defects, which leads to the loss of otherwise successful conceptions (Holman and Wood 2001); (2) loss of the ability to conceive, culminating in menopause, due to ovarian depletion below a certain threshold. This infertility threshold occurs just once for each individual, but it has a population-level age distribution that centers around age 41 years (Broekmans et al. 2007; Djahanbakhch et al. 2007).

Because of the relationships between age-specific female pair-bonding, a husband's socioeconomic status, and a female's lifetime reproductive success, we expect that our predictions could apply generally to human societies with marriage systems other than strict monogamy. We found that females who married high-socioeconomic-status husbands married younger than did those marrying low-socioeconomic-status husbands (fig. 2*A*). Across cultures, female age at marriage can be delayed by late sexual maturation (Borgerhoff Mulder 1989), the need to care for siblings (Sear et al. 2002), low family wealth (Gaulin and Boster 1990), or the time needed to accumulate wealth or experience (Low et al. 2002). Each factor could reduce the probability that a new genetic variant affecting young-age female fecundity is expressed. Male age at marriage can be similarly delayed by wealth, status, or experience (Gurven et al. 2006), and we found that in preindustrial Finland, high-socioeconomic-status males tended to marry the youngest females. This is a common finding, especially in polygynous societies, because female marriage to relatively older husbands, despite the potential low fertility of these men, generally brings the LRS benefits of high socioeconomic status (Josephson 2002; Helle et al. 2008). However, marrying relatively older men can increase the risk of female widowhood while she is still fertile, because mortality increases with age (Gurven et al. 2007). Widowhood before natural menopause could be a particular risk in polygynous societies for females marrying as second wives to older husbands. However, second wives have often already delayed marriage to a late age (Gibson and Mace 2007), thereby decreasing the otherwise large husband-to-second-wife age difference and the limitation to female LRS imposed by widowhood.

We found that remarriage probability declined with increasing age at widowhood, in line with other preindustrial populations (Knodel and Lynch 1985; Käär et al. 1998; Dribe et al. 2007). There are two likely reasons for this. First, older widows might have actively avoided remarriage, either because this jeopardized the survival of existing offspring or because yielding control of family wealth to adult offspring provided benefits (Moring 2002; Dribe et al. 2007). This could both increase the reproductive success of adult offspring and help to avoid the potential negative effects of remarriage on survival of younger offspring (Sear et al. 2002), therefore selecting against remarriage (Käär et al. 1998). Second, the ability to remarry after widowhood or divorce could be lower among older females because they are not favored by men because of their lower remaining reproductive value and because they may have dependent offspring who were fathered by other men (Knodel and Lynch 1985). These problems faced by older widows would be common in both monogamous and polygynous societies, as humans are unusual among animals in that females carry dependent offspring between marriages. Given that resources are never limitless, irrespective of mating system there should be selection against men marrying old females who have many dependent children fathered by other men. A possible exception to this in some human societies is when a widow marries her deceased husband's brother, who is not only related to her offspring but who benefits from preventing the loss of resources such as land or livestock to men outside the family (Mandelbaum 1938).

We propose that, at ages where many females are alive but few are pair-bonded, the selection intensity on new genetic variants influencing age-specific fecundity should be relatively weak. This would allow the accumulation of genetic variants that are deleterious to fecundity under mutation-selection balance. However, the relationship of our indicator of age-specific selection intensities to the evolutionary maintenance or change of age schedules of fecundity depends on three considerations. The first is the rate of occurrence of new genetic variants affecting fecundity. In every generation, some nonsynonymous new mutations are retained in the human genome by natural selection (Eyre-Walker and Keightley 1999). However, there is still uncertainty regarding estimates of mutation rate, particularly if new mutations occur often enough or their effects on fecundity are large enough for ongoing changes in marriage patterns to cause immediate evolutionary change. In light of this, there is recent evidence from contemporary humans that evolutionary change in a number of reproductively important traits is ongoing (Byars et al. 2010).

The second consideration is whether new genetic variants affect age-specific fecundity additively or as a proportion of the existing fecundity of each age class. Baudisch (2005) highlighted the consequences of a new genetic variant influencing age-specific fecundity acting proportionally rather than additively, as we have assumed in this study, to the existing level of age-specific fecundity. Human population studies generally agree on a fecundity schedule that declines from a peak in the early 20s and that has an increased rate of decline after the late 30s (Larsen and Vaupel 1993; Wood 1994). Thus, if new genetic variants do act in proportion to existing fecundity levels, our estimated selection intensities would be relatively stronger at already more fecund female ages. This could move our estimates of age-specific selection intensities, which incorporate the age schedule of pair-bonding and peak in the 30s, closer to Hamilton's (1966) finding of a continuous and less curvilinear decline with increasing female age.

The third consideration is of the lifetime fitness of individuals carrying each new genetic variant and the exclusivity with which one new genetic variant influences one age class only. This emphasizes the importance of reproductive costs in shaping age schedules of fecundity. For example, selection for a new genetic variant that increased fecundity in one age class would be weakened if it also caused reduced fecundity in subsequent age classes, for example, by depleting maternal energy reserves, leading to a net reduction in individual fitness (Gadgil and Bossert 1970; Charlesworth 1993).

In conclusion, we have presented an indicator of age-specific selection intensities on female fecundity that applies to species in which being alive at a reproductively capable age does not guarantee the ability to reproduce. For example, breeding rights within meerkat *Suricata suricatta* groups are highly age dependent, and they can end either by death or by displacement by other females (Hodge et al. 2008). In the wandering albatross *Diomedea exulans*, repairing does occur after partner death, but at a cost to reproductive success, suggesting that the active choice of similarly aged mates in this species acts to minimize the risk of early widowhood (Jouventin et al. 1999). We found that for preindustrial humans, incorporating the need to be alive and have a mate with whom to breed dramatically modified the age schedule of selection intensities on female fecundity, creating a selection-intensity peak in the 30s. Thus, increasing delays to family building in modern societies are likely lowering the intensity of selection on young-age female fecundity. Our results show that late-age declines in selection intensity were caused by either female death or widowhood and a reduced remarriage probability for older widows. The risk of widowhood was exacerbated by the fitness advantages of pairing with relatively older males. Therefore, in addition to other evolutionary explanations for menopause (Voland et al. 2005; Cant and Johnstone 2008), the restriction on old-age female fecundity that was imposed by widowhood could contribute to the evolutionary maintenance of steep senescent declines and the eventual curtailment of reproductive potential.

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Literature Cited

Alvergne, A., and V. Lummaa. 2010. Does the contraceptive pill alter mate choice in humans? Trends in Ecology & Evolution 25:171–179.

Angelier, F., H. Weimerskirch, S. Dano, and O. Chastel. 2007. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. Behavioral Ecology and Sociobiology 61: 611–621.

Bates, D., and M. Maechler. 2010. lme4: linear mixed-effects models using S4 classes. R package version 0.999375-33. http://cran.r-project.org/package=lme4.

Baudisch, A. 2005. Hamilton's indicators of the force of selection. Proceedings of the National Academy of Sciences of the USA 102: 8263–8268.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulson, M. H. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Borgerhoff Mulder, M. 1988. Kipsigis bridewealth payments. Pages 65–82 *in* L. Betzig, M. Borgerhoff Mulder, and P. Turke, eds. Human reproductive behaviour: a Darwinian perspective. Cambridge University Press, Cambridge.

———. 1989. Early maturing Kipsigis women have higher reproductive success than late maturing women and cost more to marry. Behavioral Ecology and Sociobiology 24:145–153.

Bowen, W. D., S. J. Iverson, J. I. McMillan, and D. J. Boness. 2006. Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. Journal of Animal Ecology 75: 1340–1351.

Bowles, S. 2006. Group competition, reproductive levelling, and the evolution of human altruism. Science 314:1569–1572.

Broekmans, F. J., E. A. H. Knauff, E. R. T. Velde, N. S. Macklon, and B. C. Fauser. 2007. Female reproductive ageing: current knowledge and future trends. Trends in Endocrinology and Metabolism 18: 58–65.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Springer, New York.

Byars, S. G., D. Ewbank, D. R. Govindaraju, and S. C. Stearns. 2010. Natural selection in a contemporary human population. Proceedings of the National Academy of Sciences of the USA 107:1787–1792.

Cant, M. A., and R. A. Johnstone. 2008. Reproductive conflict and the separation of reproductive generations in humans. Proceedings of the National Academy of Sciences of the USA 105:5332–5336.

Charlesworth, B. 1993. Natural selection on multivariate traits in age-structured populations. Proceedings of the Royal Society B: Biological Sciences 251:47–52.

———. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, NJ.

Coale, A. J. 1971. Age patterns of marriage. Population Studies 25: 193–214.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B: Biological Sciences 273:1375–1383.

Diamond, J. 1992. The third chimpanzee. Harper Collins, New York.

Djahanbakhch, O., M. Ezzati, and A. Zosmer. 2007. Reproductive ageing in women. Journal of Pathology 211:219–231.

Draper, N. R., and J. A. John. 1988. Response-surface designs for quantitative and qualitative variables. Technometrics 30:423–428.

Dribe, M., C. Lundh, and P. Nystedt. 2007. Widowhood strategies in preindustrial society. Journal of Interdisciplinary History 38: 207–232.

Easterlin, R. A. 1976. Population change and farm settlement in the northern United States. Journal of Economic History 36:45–75.

Eyre-Walker, A., and P. D. Keightley. 1999. High genomic deleterious mutation rates in hominids. Nature 397:344–347.

Flinn, M. V., D. C. Geary, and C. V. Ward. 2005. Ecological dominance, social competition, and coalitionary arms races: why humans evolved extraordinary intelligence. Evolution and Human Behavior 26:10–46.

Fox, J. 2009. car: companion to applied regression. R package versions 1.2–16. http://cran.r-project.org/package = car.

Gadgil, M., and W. H. Bossert. 1970. Life-historical consequences of natural selection. American Naturalist 104:1–24.

Gangestad, S. W., and R. Thornhill. 2008. Human oestrus. Proceedings of the Royal Society B: Biological Sciences 275:991–1000.

Gaulin, S. J. C., and J. S. Boster. 1990. Dowry as female competition. American Anthropologist 92:994–1005.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge.

Gibson, M. A., and R. Mace. 2007. Polygyny, reproductive success and child health in rural Ethiopia: why marry a married man? Journal of Biosocial Science 39:287–300.

Gillespie, D. O. S., A. F. Russell, and V. Lummaa. 2008. When fecundity does not equal fitness: evidence of an offspring quantity versus quality trade-off in pre-industrial humans. Proceedings of the Royal Society B: Biological Sciences 275:713–722.

Goody, J., ed. 1971. Kinship. Penguin Modern Sociology Readings. Penguin, Harmondsworth.

Grafen, A. 1988. On the uses of data on lifetime reproductive success, Pages 454–471 *in* T. H. Clutton-Brock, ed. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago.

Gurven, M., and C. von Rueden. 2006. Hunting, social status and biological fitness. Social Biology 53:81–99.

Gurven, M., H. Kaplan, and M. Gutierrez. 2006. How long does it take to become a proficient hunter? implications for the evolution of extended development and long life span. Journal of Human Evolution 51:454–470.

Gurven, M., H. Kaplan, and A. Z. Supa. 2007. Mortality experience of Tsimane Amerindians of Bolivia: regional variation and temporal trends. American Journal of Human Biology 19:376–398.

Hajnal, J. 1965. European marriage patterns in perspective. Pages 101–143 *in* D. V. Glass, and D. E. C. Eversley, eds. Population history: essays in historical demography. E. Arnold, London.

Hamilton, W. D. 1966. Moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Helle, S., V. Lummaa, and J. Jokela. 2008. Marrying women 15 years younger maximized men's evolutionary fitness in historical Sami. Biology Letters 4:75–77.

Hodge, S. J., A. Manica, T. P. Flower, and T. H. Clutton-Brock. 2008. Determinants of reproductive success in dominant female meerkats. Journal of Animal Ecology 77:92–102.

Holman, D. J., and J. W. Wood. 2001. Pregnancy loss and fecundability in women. Pages 15–38 *in* P. T. Ellison, ed. Reproductive ecology and human evolution. Aldine de Gruyter, New York.

Jeschke, J. M., and H. Kokko. 2008. Mortality and other determinants of bird divorce rate. Behavioral Ecology and Sociobiology 63:1–9.

Jones, J. H. 2007. demogR: analysis of age-structured demographic models. R package version 0.4.2. http://cran.r-project.org/package = demogR.

Jones, O. R., J. M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, et al. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. Ecology Letters 11:664–673.

Josephson, S. C. 2002. Does polygyny reduce fertility? American Journal of Human Biology 14:222–232.

Jouventin, P., B. Lequette, and F. S. Dobson. 1999. Age-related mate choice in the wandering albatross. Animal Behaviour 57:1099–1106.

Käär, P., J. Jokela, J. Merila, T. Helle, and I. Kojola. 1998. Sexual conflict and remarriage in preindustrial human populations: causes and fitness consequences. Evolution and Human Behavior 19:139–151.

Kaplan, H. 1996. A theory of fertility and parental investment in traditional and modern human societies. Yearbook of Physical Anthropology 101:91–135.

Knodel, J., and K. A. Lynch. 1985. The decline of remarriage: evidence from German village populations in the 18th and 19th centuries. Journal of Family History 10:34–59.

Lahdenperä, M., V. Lummaa, S. Helle, M. Tremblay, and A. F. Russell. 2004. Fitness benefits of prolonged post-reproductive life span in women. Nature 428:178–181.

Larsen, U., and J. W. Vaupel. 1993. Hutterite fecundability by age and parity: strategies for frailty modelling of event histories. Demography 30:81–102.

Low, B. S., C. P. Simon, and K. G. Anderson. 2002. An evolutionary ecological perspective on demographic transitions: modelling multiple currencies. American Journal of Human Biology 14:149–167.

Lummaa, V. 2001. Reproductive investment in pre-industrial humans: the consequences of offspring number, gender and survival. Proceedings of the Royal Society B: Biological Sciences 268:1977–1983.

Mandelbaum, D. G. 1938. Polyandry in Kota society. American Anthropologist 40:574–583.

Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. Functional Ecology 22:371–378.

Moring, B. 1996. Marriage and social change in south-western Finland 1700–1870. Continuity and Change 11:91–113.

———. 2002. Widowhood options and strategies in preindustrial northern Europe: socioeconomic differences in household position of the widowed in 18th and 19th century Finland. History of the Family 7:79–99.

Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H. Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. American Naturalist 174:342–357.

Packer, C., M. Tatar, and A. Collins. 1998. Reproductive cessation in female mammals. Nature 392:807–811.

Pettay, J. E., S. Helle, J. Jokela, and V. Lummaa. 2007. Natural selection on female life-history traits in relation to socio-economic class in pre-industrial human populations. PLoS ONE 2:e606.

Quinlan, R. J. 2008. Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. Evolutionary Anthropology 17:227–238.

R Development Core Team. 2009. R: a language and environment for statistical computing. Version 2.10.1. R Foundation for Statistical Computing, Vienna. http://r-project.org.

Reichard, U. H., and C. Boesch. 2003. Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge.

Scott, D. K. 1980. Functional aspects of the pair bond in winter in Bewick's swans (*Cygnus columbianus bewickii*). Behavioral Ecology and Sociobiology 7:323–327.

Sear, R., F. Steele, A. A. McGregor, and R. Mace. 2002. The effects of kin on child mortality in rural Gambia. Demography 39:43–63.

Soininen, A. M. 1974. Old traditional agriculture in Finland in the 18th and 19th centuries. Forssan Kirjapaino Oy, Forssa.

Strassmann, B. I. 1981. Sexual selection, paternal care, and concealed ovulation in humans. Ethology and Sociobiology 2:31–40.

Voland, E., and R. I. M. Dunbar. 1995. Resource competition and reproduction: the relationship between economic and parental strategies in the Krummhörn population (1720–1874). Human Nature 6:33–49.

Voland, E., A. Chasiotis, and W. Schiefhovel, eds. 2005. Grandmotherhood: the evolutionary significance of the second half of female life. Rutgers University Press, New Brunswick, NJ.

Whittingham, M. J., R. D. Swetnam, J. D. Wilson, D. E. Chamberlain, and R. P. Freckleton. 2005. Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: implications for conservation management. Journal of Applied Ecology 42:270–280.

Wood, J. W. 1994. Dynamics of human reproduction: biology, biometry, demography: foundations of human behaviour. Aldine de Gruyter, New York.

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Marrying a relatively older man—typical for wives with high-status husbands—increased the likelihood of widowhood, which decreased the opportunity for childbearing at older ages. (Photograph courtesy of Virpi Lummaa.)