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Original Article

The presence of a paternal grandmother lengthens interbirth interval following the birth of a granddaughter in Krummhörn (18th and 19th centuries)

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Abstract

Because only daughters inherit the paternal X-chromosome, an asymmetry in adaptive investment decisions has been suggested for certain patrilineal kin. Namely, paternal grandmothers (PGMs) may favor a granddaughter over a grandson, because (within the limits of paternity uncertainty) the former definitely carries one of their X-chromosomes, while the latter definitely does not. Here, we test the hypothesis that the PGMs' sex-specific favoritism influences reproductive scheduling. Using family-reconstitution data, we analyzed interbirth intervals (IBIs) in the historical population from the Krummhörn (Ostfriesland, Germany). In order to account for potentially timevarying effects on IBIs we applied (and combined) both the additive hazards regression of Aalen and the Cox proportional hazards model. We found that the presence of the PGM but not that of the maternal grandmother (MGM), correlates with the IBI following the birth of a grandchild as a function of the grandchild's sex. Specifically, in the presence of a PGM, the IBIs following the birth of a granddaughter are longer than in her absence. However, contrary to predictions from theoretical life history framework, model estimates for a PGM's effect on a mother's IBI did not significantly vary over time This study supports the hypothesis that PGM behavior differs according to her grandchild's sex. Further research should now explore the biological mechanism underlying this phenomenon.

Keywords: Paternal grandmothers; Interbirth intervals; Life history theory; X-chromosomal relatedness; Krummhörn

1. Introduction

Female reproductive functioning is extremely sensitive to external factors (e.g., food supply, lactation, social stress). These factors are influenced by familial environment (e.g., Reiches et al., 2009). Kin-selection and altruism based on inclusive fitness (Hamilton, 1964a, 1964b) therefore are assumed to play a key role in the evolution of human life history, especially in the case of postreproductive female longevity (see contributions in Voland, Chasiotis, & Schiefenhövel, 2005). Even under prehistoric and historic conditions, a significant portion of any female population survived after menopause and probably gave intergenerational support through alloparenting (see Hrdy, 2009 for an overview). The Grandmother Hypothesis suggests that human female longevity evolved because grandmothers can increase their inclusive fitness by provisioning grandchildren (Hawkes et al., 1998). However, for a historical European population located in Krummhörn (Ostfriesland, Germany), Voland and Beise (2002) recognized opposite effects between maternal and paternal grandmothers: While maternal grandmothers (MGMs) decrease grandchild mortality, paternal grandmothers (PGMs) increase it. This contextual difference in grandmaternal effect can be explained by the differential fitness costs of additional reproductions between men and women (e.g., Penn & Smith, 2007), resulting in an in-law conflict over the reproductive rate of a woman (e.g., Euler & Michalski, 2008, Leonetti, Nath, & Heman, 2007). Krummhörn mothers-in-law are assumed to take advantage of their

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daughter-in-law's ability to work, thereby increasing her psychological stress, which, in turn, increases her children's stillbirth and neonatal mortality rates. In other words, Krummhörn PGMs trade reproduction for economic exploitation (Voland & Beise, 2005).

For several reasons, women are assumed to benefit more from the increased reproduction of their sons than daughters (e.g., Leonetti et al., 2007): Firstly, among sons, the mortality risk of childbearing is for a daughter-in-law rather than a blood relative. This does not have a very high impact on patrilineal fitness because a possible remarriage of the man could compensate for the lost potential reproduction of a deceased wife. Also, the degree of paternity uncertainty may influence the adaptiveness of a PGM's investment in grandchildren. To counter this, X-chromosome-related traits displayed by offspring may serve as additional cues for kinship recognition mechanisms and therefore influence adaptive investment decisions (Fox et al., 2010). Considering X-chromosomal relatedness, PGMs are assumed to favor granddaughters over grandsons, because (within the limits of paternity uncertainty) granddaughters definitely carry one of their X-chromosomes, while grandsons definitely do not (Fox et al., 2010). On the one hand, this situation results in quantitative genetic differences, with PGMs sharing a larger proportion of their genes with their granddaughters than with their grandsons. On the other hand, traits which are coded on the X-chromosome could serve as trigger for kinship recognition mechanisms and therefore influence adaptive investment decisions to overcome paternity uncertainty (Fox et al., 2010). Because they share no sex chromosomes, PGMs cannot employ an X-chromosome based system of kinship recognition to identify grandsons.

Recently, Rice, Gavrilets, and Friberg (2010) offered an alternative explanation predicting also that a PGM's investment in grandchildren is biased toward females, as described by Fox et al. (2010). Rice et al. (2010) showed that so-called 'green beard' alleles leading to discriminative behavior towards their noncarriers may invade the X chromosome disproportionately and consequentially would overproportionally harm male offspring.

In contrast to the explanation offered by Fox et al. (2010) this form of intragenomic conflict is theoretically associated with fitness costs, particularly in case of the PGM (see Rice et al., 2010). For all of these reasons, it is expected that investment of a PGM is biased towards female offspring. Breastfeeding can be used to test predictions of adaptive investment decisions (Tracer, 2009; Trivers, 1972). Age at weaning, therefore, is a useful estimator of received investment from mothers (Quinlan, Quinlan, & Flinn, 2005). Because breastfeeding suppresses ovulation (*lactational amenorrhea*), in natural fertility populations breastfeeding correlates with the time span between one individual's birth date and the birth date of the next born sibling (interbirth interval, IBI) (Quinlan et al., 2005; Tracer, 2009; Vitzthum, 2008 for reviews). Thus, we expect that a significant part of the PGM's effect on a mother's IBIs should be modulated by the sex of the grandchild. It is important to note that this simple substitution of the dependent variable 'allocated investment' with a theoretical surrogate parameter for the time of breastfeeding bares a serious theoretical problem because it may be the case that after the child's optimal weaning age is reached it will no longer benefit from continued breastfeeding because of the associated opportunity costs in inclusive fitness (Trivers, 1972). Therefore a PGM's adaptive (in terms of fitness-maximizing) influences on a mother's reproduction may vary over time, e.g., a PGM may suppress maternal reproduction for two years after a mother has given birth, and then may increase the mother's likelihood to have another child. We therefore also accounted for timevarying effects in this study. To do this, recent packages for the software R 2.11.1 (R Development Core Team, 2010) have been applied to analyze IBIs provided by the family reconstitution data of the Krummhörn population (see Voland, 2000 for a methodological review). Grandchildren deceased within the time of the IBI have been excluded from our analysis, because survival status of the child influences the IBI (see Galdikas & Wood, 1990).

Here, we test for differences between IBIs following granddaughters and grandsons, in light of the absence or presence of the MGM or PGM. To illustrate possible differences in this time-to-event data we use Kaplan–Meier plots, which graph the proportion still awaiting the event (in our case the birth of the next sibling) against time using both 'real data' IBIs and model predictions. Since we detected the violation of the proportionality assumption of the standard Cox model, we fit the Cox-Aalen model and the fully-nonparametric Aalen, respectively. Finally, model runs using averaged covariates did support our hypothesis that if the PGM is present in her granddaughter's birth parish, then granddaughters (if surviving their toddler age) are confronted relatively later with the birth of a younger sibling than girls without a local PGM in the Krummhörn population. However, we were neither able to quantify any potential fitness outcomes nor to show that components of this contextual difference in grandmaternal investment do significantly vary over time.

2. Materials and methods

2.1. The Krummhörn database

Krummhörn is a coastal region characterized by fertile marsh soil in Ostfriesland (Germany). A long-term family reconstitution (see Voland, 2000 for a methodological review) offers data mainly for the 18th and 19th centuries for 27 parishes from a total of 32 parishes. Socioecologically, the Krummhörn region can be described as a 'saturated habitat', where limited access to resources leads to wide variation in reproductive success. In the case of the Krummhörn farmers, a land-based local resource

competition often demands some form of family-planning for heritable resources, characterized by discrimination against surplus male offspring (Beise & Voland, 2008; Voland & Dunbar, 1995; Willführ, 2009).

2.2. Data selection procedures

For practical demands and to avoid incompletely-documented family histories (and possible biases in the calculated IBI), the following criteria were required for inclusion in the study sample. Families providing the initial sample were presupposed to be completely known in their reproductive history from the written documents:

1. Parental marriage and death (at least of the first-dying parent) must be exactly dated in written documents.
2. Only first marriages were included in data selection.

Families who emigrated, thus leaving the study area, have been excluded due to missing death dates of the parents (see above). Migration between different parishes within the study area can be traced. This initial sample supplied data of 19,236 individuals from 4049 families. Out of theoretical and operational reasons we additionally excluded cases by following criteria:

- Due to missing values and methodological problems discussed in Willführ (2009), birth cohorts before 1720 or after 1869 were excluded (18177 remaining cases).
- Families with birth dates not exactly known from the written documents, still births and multiple births were excluded (13,084 remaining cases).
- Lastborn children have been excluded (10,201 remaining cases)
- Toddlers who died during the time of IBI were excluded (7985 remaining cases).
- Cases with unknown age of the mother have been excluded. (7380 remaining cases).
- To take the known discrimination against male offspring among farmers into consideration, wealthy families (holding more than 74 grasen of landownership) have been excluded (6832 remaining cases).
- Presence of the MGM, or the PGM respectively, only was assumed if both of the following proxies were fulfilled:
  1. Death date of the grandmother must follow the birth date of the next born grandchild (grandchildren, whose grandmother died within their IBI have been excluded).
  2. Death of grandmother and birth of grandchild must occur in the same parish. To avoid cases in which the grandmother moved to the birth place of a grandchild afterwards, we only included matrilocal or patrilocal families living exclusively with the MGM or the PGM. Thus the birth place of the child must have to be the same as the birth place of the mother (in case of MGM) or the father (in case of the PGM).

To reduce model complexity we excluded families for whom the presence of both grandmothers has been assumed (thus presence of the MGM or the PGM in this study is exclusive). In order to avoid potentially confounding influences of the spouses' other kin (siblings, aunts and uncles) 'philopatric' families (if a spouse's birth parish is the same as his child's birth parish) were excluded from the proportion of families without both grandmothers (in total: 1124 remaining cases). This was done because residence patterns in Krummhörn tend to be patrilocal and thus even in case of a PGM's death, the remaining family often lived close to other patrilineal kin.

Table 1 describes included families and Fig. 1 gives sample characteristics of IBIs we used for analysis.

2.3. Theoretical model

Our hypothesis predicts differences in IBIs between families living exclusively with the MGM or the PGM, which depend on the sex of child. We assume an interaction effect of the presence of the PGM and her grandchild's sex on the IBI: we hypothesize that a girl living in the same parish with the PGM should lead to a relatively longer IBI. Our final model therefore includes five main predictors to estimate the IBI following the birth of a grandchild:

1. $female_j$ ('$grandchild_j$ is female')
2. MGM_j ('MGM_j is present')
3. PGM_j ('PGM_j is present')
4. MGM_j:$female_j$ ('MGM_j is present and $grandchild_j$ is female')
5. PGM_j:$female_j$ ('PGM_j is present and $grandchild_j$ is female')

The theoretical model thus looks like this

$$IBI_j \sim female_j + MGM_j + PGM_j + MGM_j{:}\ female_j + PGM_j{:}\ female_j + '\ldots'$$

'…' abbreviates for predictors, which are known to influence a mother's IBI (e.g., Low, 1991) and, therefore, have been additionally included in the model:

- Grandchild $_j$'s birth order
- Age of the $mother_j$ at birth of $grandchild_j$

Table 1
Statistical parameters for Krummhörn families (1720-1870) included in analysis, whether living with the maternal grandmother (MGM) or the paternal grandmother (PGM)

	N (families)	Deceased toddlers (excluded)	Girls+boys (total=1124)	Proportion died before 15 years	Mean mother's age at birth
None	174	15.2 %	262+226	11.9 %	30.2
MGM	84	14.4 %	98+98	13.3 %	28.8
PGM	163	11.8 %	222+218	9.5 %	30.1

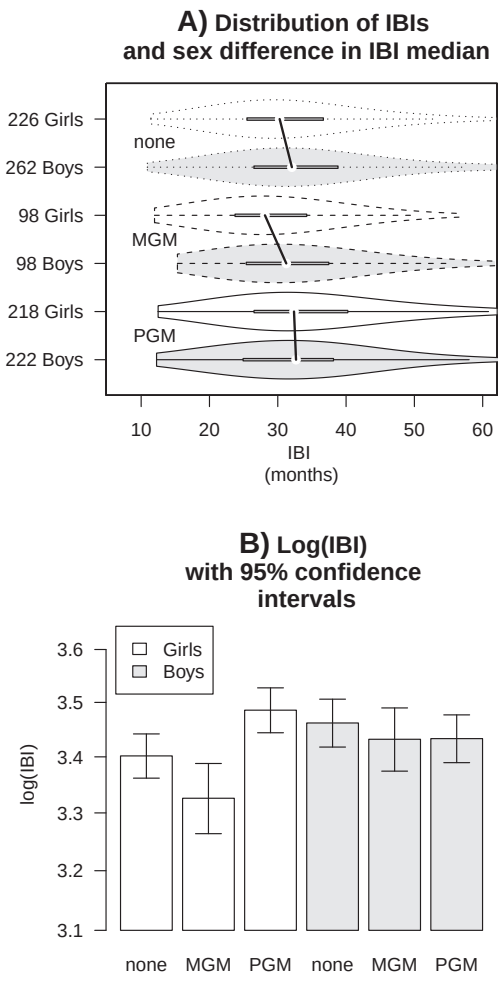

Fig. 1. Panel A gives violin plots (a combination of boxplot and kernel distribution plot) for IBIs following the birth of a girl or a boy separated for families, where the PGM is present, where both grandmothers are absent or were the MGM is present. Panel B presents asymptotic tests with 95% confidence intervals (see Coeurjolly et al., 2008) to show differences in log-transformed IBI values.

- Interaction effect between birth order and the effect of a mother's age
- Age of the mother$_j$ at her first birth
- Estimated hazard ratio for the effect the specific birth parish$_k$ (as estimated in a separate Cox model, stratified for birth order)—if nonsignificant this was set to 1 thus practically excluded.

However, the predicted correlation between the sex of a grandchild and the presence of the PGM on a mother's IBI would also remain significant without controlling for any confounding effects (but not in case of the PGM living in another parish than her grandchild). Cohort effects were found to be neglectable since we were not able to estimate any of these on a 90% confidence level (after the exclusion of deceased toddlers from analysis). Robust standard errors have been calculated according to the specific family ID of the child.

2.4. Proportional and additive hazards model

IBIs do represent time-to-event data, which can be analyzed by appropriate methods of survival analysis. In the standard Cox proportional hazards model (Cox, 1972) a risk indicator $Y_i(t)$ models the baseline hazard $\lambda_i(t)$ which is multiplied with a vector of linear predictors $X_i(t)$ and their coefficients β:

$$\lambda_i(t) = Y_i(t)\lambda_0(t)\ exp\left(X_i(t)^T\beta\right) \tag{1}$$

However, as the assumption of proportional hazards demands constant (or at least unidirectional) effects, the Cox model fails to detect nonlinear, time-varying effects of covariates. To avoid violations of the proportionality assumption, the model may be stratified to move nonproportional terms as categorical covariates in the baseline hazard. However, this method sometimes leads to problems if the reference category is not carefully chosen or if there are interaction effects between proportional terms and 'strata' variables (see Baldi et al., 2006). The approach of Aalen in contrast assumes that covariates act additively on the hazard. The model takes the form

$$\lambda_i(t) = Y_i(t)X_i(t)^T\alpha(t) \tag{2}$$

where $\alpha(t)$ is a nonparametric p-dimensional regression function that is constrained by $\lambda_i(t)\geq 0$. Direct measurement of the time-dependent coefficients $\beta_k(t)$ returned from $\alpha(t)$ in this case is practically difficult. Instead, this model estimates the *cumulative incidence function*, which is the slope of the cumulative coefficients $\beta_k(t)$, against time.

$$A(t) = \int_0^t \alpha(s)ds \tag{3}$$

In this case, the slope of $A(t)$ gives a rough estimate of $\alpha(t)$. Goodness-of-fit procedures are mainly based on martingale residuals and include test processes to count scores for the departure from the null under constant effects (see references in Baldi et al., 2006). The Cox-Aalen model (suggested by Scheike & Zhang, 2002) combines the additive and the multiplicative approach. This approach extends the traditional Cox model by allowing the baseline intensity to depend on covariates through the additive Aalen model.

$$\lambda_i(t) = Y_i(t)\left(X_i(t)^T\alpha(t)\right)\ exp\left(Z_i(t)^T\beta\right) \tag{4}$$

The Cox-Aalen model is part of the R-package 'timereg' (see Scheike, Martinussen, & Silver, 2010). We chose covariate effects that might act additively on the risk, and we allowed covariates to have multiplicative effects. Although including the main predictors in the additive Aalen model did not significantly increased goodness-of-fit (see electronic supplement), we decided to apply the full Aalen model to make predictions. This decision was based on biological

Table 2
Estimated coefficients and test for proportionality of the standard Cox proportional hazards model for IBIs in final data selection

Model 1: Cox Proportional Hazards								
n=1124; R^2= 0.129; Wald test=168.6 on 10 df (p<.001)								
	Coef.	SE	Robust SE	z	Pr(>|z|)	Test for proportionality		
						rho	Chisq (zph)	p-val H_0
Main Predictors:								
Female	0.258	0.0920	0.104	2.49	0.013	0.0129	0.243	0.622
MGM	0.189	0.122	0.133	1.43	0.154	0.00275	0.0109	0.917
PGM	0.222	0.0968	0.104	2.14	0.033	0.02576	0.935	0.334
Female: MGM	0.0745	0.170	0.176	0.42	0.672	0.01483	0.277	0.598
Female: PGM	-0.403	0.134	0.140	-2.88	0.004	-0.01044	0.140	0.709
Covariates to control for:								
Mother age at first birth	0.189	0.0273	0.0275	6.88	<0.001	-0.0908	12,0	<0.001
Mother age at specific birth	-0.213	0.0276	0.0260	-8.25	<0.001	0.116	15.8	<0.001
Birth order	0.271	0.135	0.140	1.93	0.0535	0.0177	0.448	0.503
Birth order: Mother age at specific birth	0.00332	0.00360	0.00340	0.978	0.328	-0.0504	2.88	0.0896
Parish	0.0386	0.00747	0.00885	4.37	<0.001	-0.0632	6.86	0.00882

Toddlers who deceased during the time of IBI have been excluded. Test of proportionality is based on Schoenfeld-residuals and was performed with the 'cox.zph ()' function provided by Therneau and Lumley, 2009. Toddlers who deceased during the time of IBI have been excluded.
Robust standard errors are calculated according to a child's specific family ID. N (total)=1124, see Fig. 1 for subgroups.

reasoning since we assume that the statistical correlation between the IBI and the foreborn child's fitness outcomes (survival, reproductive success) will decrease over time or even change (see introduction).

3. Results

Within the Krummhörn data of the years 1730−1870, IBIs from 406 families were suitable for inclusion in analysis. We observed a pattern in a mother's IBI based on the presence of a PGM and the child's sex. Violin plots (a combination of boxplots and density distribution plots, see Messing, 2010) (Fig. 1A) indicate that IBIs following the birth of a girl are generally several weeks shorter than IBIs following the birth of a boy – except in the case of families where the PGM is present. Parametric log-transformed confidence intervals (see Coeurjolly, Drouilhet, Lafaye De Micheaux, & Robineau, 2008) for IBIs support the assumption of a conditional effect of the PGM, dependent on the sex of the grandchild (Fig. 1B).

Table 3
Multiplicative and additive terms in the Cox-Aalen model

Model III: Cox-Aalen						
Main predictors: proportional Cox terms:						
	Coef.	S.E.	Robust S.E.	D2log(L)^−1	z (Pr>|z|)	Lin, Wei, Ying-Test for Proportionality:
Female	0.293	0.0968	0.0945	0.0939	3.03 (p=.00248)	17.0 (p=.182)
MGM	0.206	0.125	0.122	0.124	1.65 (p=.0990)	8.24 (p=.730)
PGM	0.237	0.101	0.100	0.0984	2.34 (p=.0194)	19.1 (p=.142)
Interaction: female with MGM	<0.01	0.173	0.166	0.172	0.0535 (p=.957)	5.55 (p=.816)
Interaction: female with PGM	-0.399	0.137	0.130	0.135	-2.91 (p=.0036)	11.7 (p=.349)

Controlled predictors: additive Aalen terms		
	Sup. (P) (test for nonsignificant effects)	Kolmogorov−Smirnov Test (test for constant effects)
(Intercept)	3.16 (p=.053)	1.73 (p=.636)
Mother age at first birth	6.44 (p<.001)	0.144 (p=.287)
Mother age at specific birth	7.11 (p<.001)	0.146 (p=.314)
Birth order	3.13 (p=.047)	0.822 (p=.306)
Birth order: mother age at specific birth	3.94 (p=.004)	0.0216 (p=.309)
Birth parish	4.61 (p=.001)	0.0372 (p=.617)

Estimated coefficients and test for proportionality are given for the main predictors acting proportionally on the baseline hazard. This specific baseline hazard is modeled additively and therefore can account for potentially non-proportional effects of covariates, which may vary over time. Toddlers who deceased during the time of IBI have been excluded.
Robust standard errors are calculated according to a child's specific family ID. n (total)=1124, see Fig. 1 for subgroups.

As the standard Cox model we initially fit was rejected by model diagnostics indicating nonproportional hazards (see Table 2 and Supplementary Fig. S1), we firstly moved all confounding covariates to the additive part of the Cox-Aalen model. Table 3 indicates that estimated coefficients of the Cox-Aalen are very similar to the initial standard Cox model (compare Table 2). Although the assumption of proportionality in the Cox-Aalen model was not violated (see right columns in Table 3), plotted score processes indicate that model performance decreases in case of relatively long IBIs (compared to the full Aalen model, Supplementary Fig. S2 and Fig. S3). Considering the potentially timevarying effects of our main predictors, we fit the fully nonparametric Aalen model (Table 4). Thus for all considered models both the predictor 'female' and the interaction term 'PGM:female' were estimated significantly and in accordance with our hypothesis (see Tables 3 and 4). Kaplan–Meier plots, which are separated by sex of the grandchild help illustrate this contextual difference of grandmaternal effects: only IBIs following the birth of a granddaughter exhibit opposite effects in the presence of the PGM and the MGM (Fig. 2A). Contrastingly, IBIs following the birth of a grandson exhibit no comparable contextual difference in grandmaternal effects (Fig. 2D). Model predictions using averaged covariates (for secondborns with corresponding mean age for mothers, etc.) both for the Cox-Aalen and the Aalen model reflect the same pattern: following the birth of a girl, predicted grandmaternal effects on IBIs are significantly opposite (Fig. 2B and C), while predicted IBIs following the birth of a boy are very similar in the presence of the PGM and the MGM (Fig. 2E and F). This means that when the PGM is present, IBIs following the birth of a granddaughter are predicted to be relatively lengthened (compared to IBIs following the birth of a grandson).

Cumulative coefficients plots with 95% confidence intervals in Fig. 3 indicate that the effect of 'female' and the interaction effect 'PGM:female' both are estimated significantly before the time of 30 months and beyond the time of 48 months since a mother's last birth, thus effectively compensating for each other. The Aalen model also was used to predict IBI differences dependent on the sex of the grandchild, if a family lives with no grandmother, or the MGM, or the PGM respectively. Results show that IBIs following the birth of a female are predicted to be shorter than IBIs following the birth of a male only in the absence of the PGM (Fig. 4B and C). In contrast, no correlation between a child's sex and a mother's IBI was predicted for families living in the same parish as the PGM (Fig. 4A).

Table 4
Tests for constant effects and test for non-significant effects of the Aalen additive hazard model

Model III: Aalen additive hazards			
	Cramer von Mises Test; H_0: constant effect	Kolmogorov-Smirnov; H_0: constant effect	Supremum test of significance H_0: $B(t)=0$
Main predictors:			
Female	2.05 (p=.197)	0.505 (p=.183)	3.22 (p=.045)
MGM	1.64 (p=.514)	0.372 (p=.792)	2.62 (p=.217)
PGM	1.28 (p=.409)	0.467 (p=.289)	2.35 (p=.349)
Female: MGM	1.89 (p=.845)	0.895 (p=.378)	1.82 (p=.779)
Female: PGM	3.93 (p=.216)	0.783 (p=.142)	3.41 (p=.027)
Controlled covariates:			
(Intercept)	2.1 (p=.544)	1.62 (p=.595)	3.02 (p=.078)
Mother age at first birth	0.436 (p=.008)	0.193 (p=.002)	7.30 (p<.001)
Mother age at specific birth	0.751 (p=.004)	0.238 (p=.001)	8.55 (p<.001)
Birth order	4.28 (p=.285)	0.927 (p=.081)	3.27 (p=.035)
Birth order: Mother age at specific birth	0.008 (p=.809)	0.0147 (p=.619)	4.27 (p=.002)
Parish	0.006 (p=.566)	0.0304 (p=.564)	4.75 (p<.001)

Fig. 3 gives cumulative coefficients for the main predictors 'female' and 'PGM:female'. Toddlers who deceased during the time of IBI have been excluded.

4. Discussion

It has previously been suggested that X-chromosome relatedness could have an impact on PGM investment behavior (e.g., Fox et al., 2010; Rice et al., 2010). We applied this genetic incentive for favoritism to test for sex-specific differences in IBIs. Because a well-known 'replacement' strategy (Straka-Geiersbach & Voland, 1988) produces a negative relationship between toddler mortality and IBIs, the strong effect of toddler mortality would overshadow any theoretical predictions of that kind we aimed at testing here. Therefore, deceased recently-weaned children were excluded in analysis. In all of the considered models, IBIs following the birth of a male offspring who survived early infancy are slightly longer than IBIs following the birth of a comparable female offspring. This correlation could be interpreted as a result of differences in the time of maternal physiological recovery, but could also be the result of an often-described sex-bias in lactation, at least for lower birth ranks in agricultural, patrilineal populations with limited resources (e.g., Quinlan et al., 2005). However, with PGM presence the typical difference between the IBIs following boys and girls disappears (Figs. 1 and 4). Cumulative coefficients of the Aalen model show that also within the lower range of the IBI (meaning before the 36th month since a mother's last birth) the partly compensating effects are already estimated significantly, although contrary to our initial expectation estimated effects did also increase drastically among/for very long IBIs (Fig. 3). However, the results for very long IBIs should be considered with caution as the sample size was small (Fig. 1). Results indicate a *relative* lengthening of IBIs following the birth of a granddaughter compared to IBIs following the birth of

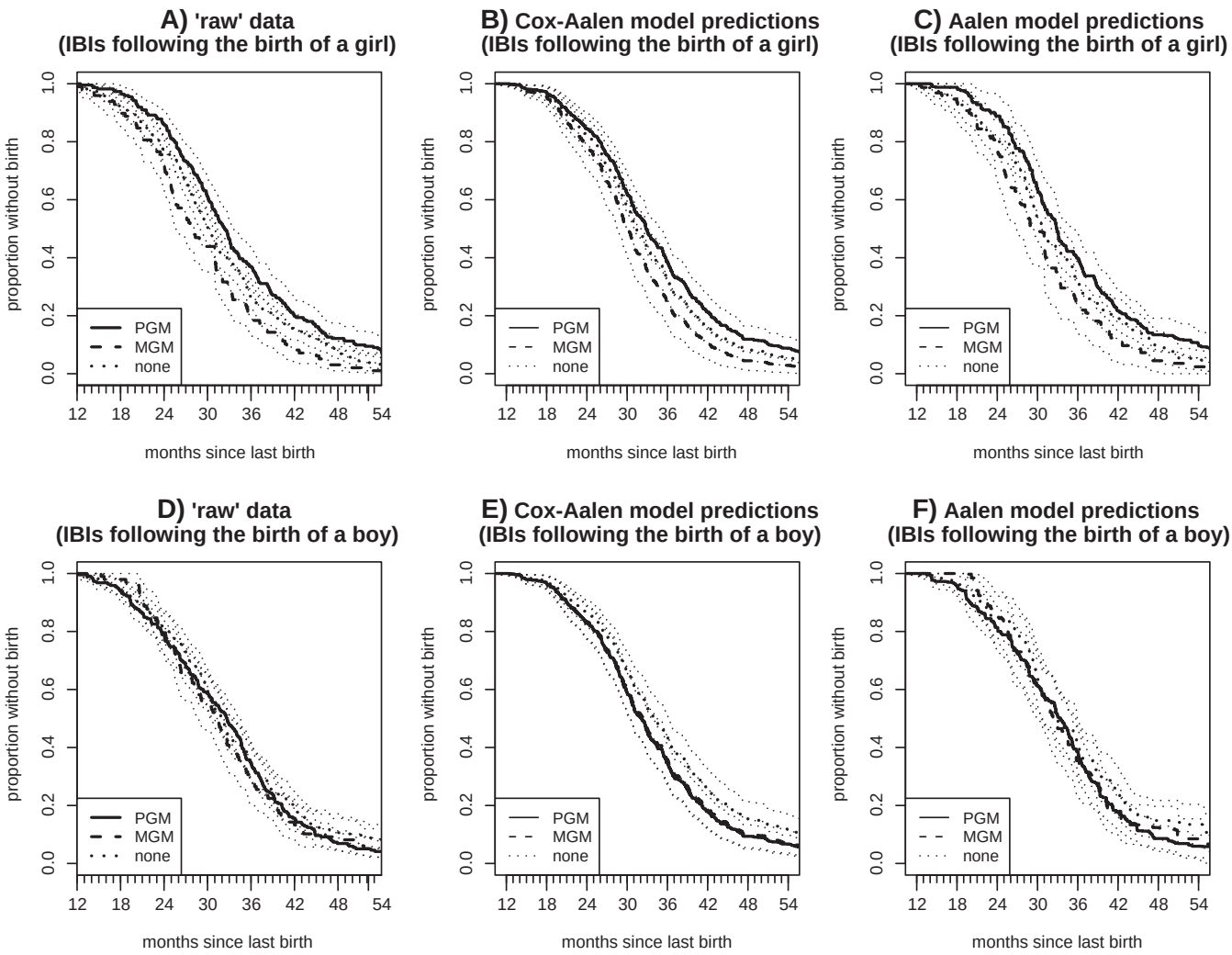

Fig. 2. Kaplan–Meier plots showing IBIs with pointwise 95% confidence intervals Top panels show IBIs following the birth of a girl. Panel A graphs IBIs in real family data, where both grandmothers were absent (dotted line), only the MGM was present (broken line), or only the PGM was present (solid line); Panel B presents analogous predictions based on the Cox-Aalen model fit (see Table 3). Panel C shows estimates from the fully-nonparametric Aalen model (see Table 4 and Fig. 3). Bottom panels show specific curves for IBIs following the birth of a boy. Deceased toddlers are excluded.

a grandson in the presence of the PGM—which could also mean a relative shortening of IBIs following the birth of a grandson. Therefore, results are in accordance both with Fox et al. (2010) and Rice et al. (2010) and provide further evidence for a conditional sex-dependent behavioral difference of a PGM towards her grandchildren.

Presented data is not sufficient yet to separate 'fitness-maximizing' differences in kin investment (e.g., adapted to paternal uncertainty, see Fox et al., 2010) from a 'negative Green-beard-effect' (Rice et al., 2010) which is assumed to decrease inclusive fitness. One possible way in which kin may try to impel their preferred tendencies for a specific reproductive investment strategy is to encourage earlier weaning (harming offspring), or to encourage delaying weaning (benefiting offspring). According to Trivers (1972), the time point of weaning is relevant in terms of fitness consequences both for mother and offspring. The lower limit of an IBI is constrained by a maternal hormonal mechanism. *Lactational amenorrhea* suppresses reproductive functioning, depending on frequency of suckling (see Vitzthum, 2008 for a review). However, a mother's opportunity to breastfeed intensely may depend on work load and/or resource demands by other family members (e.g., Panter-Brick, 1991, Piperata, 2009). Grandmothers are well suited to relieve the work load on mothers. This may not only be advantageous for the mother's health (and therefore theoretically allow for *shorter* IBIs), but also this may allow for delayed weaning and perhaps *prolonged* IBIs. Lacking any anthropometric data, we are not able to determine if the contextual effect of the PGM on a mother's IBIs we describe indicates reduced maternal investment in grandsons or increased investment in granddaughters. Therefore, future studies of sex differences in body parameters (e.g., growth, weight gain) of the affected offspring could be useful in determining if the PGM's effect on granddaughters is beneficial only when compared to their

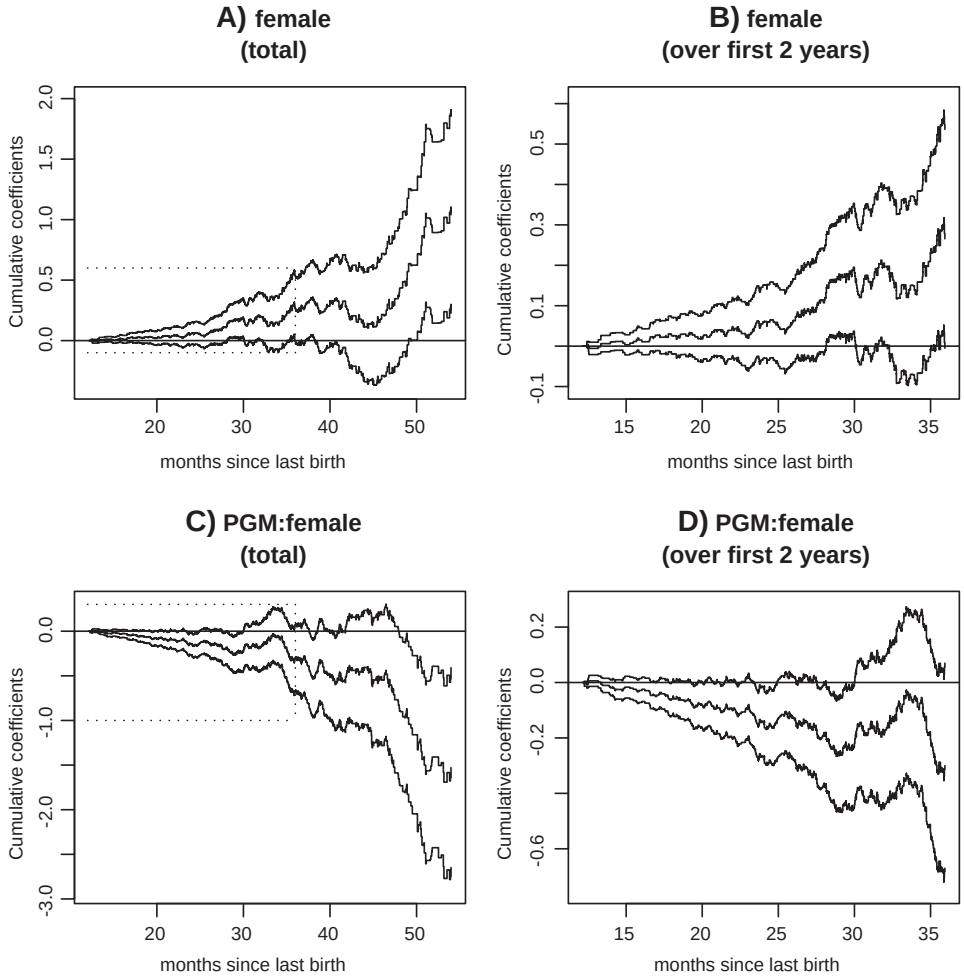

Fig. 3. Cumulative coefficients in the additive hazards Aalen model (only if estimated significant, see supplement for non-significant estimates). Left panels (A+C) present total effects and right panels (B+D) are restricted to the first two years (12th-36th months since last birth). Pointwise 95% confidence intervals are given (thus, if both confidence bands cross the zero line, effect is estimated with $p<.05$).

brothers or also compared to the MGM's effect on grandchildren. In addition to the possibility of reducing the mother's incentive to wean an infant, grandmothers have other ways in which they can influence the parental care received by their grandchildren. These include the amount and composition of nutrients provided, and social stress or violations of maternal autonomy (e.g., spatial separation from infant). The PGM's general tendency to accelerate reproduction, (e.g., Table 3, see also Sear, Mace, & McGregor, 2003; Leonetti et al., 2007) seems to hold differently for grandsons and granddaughters surviving their toddler age.

PGMs transmit one X-chromosome to granddaughters; thus, girls always carry one paternal X-chromosome, which stems from their PGM. For MGMs, however, the proportion of their X-chromosome transmitted to granddaughters is not certain due to the X-chromosome of the maternal grandfather. When the mortality of recently-weaned children is ruled out, estimated changes in the effect of sex on the length of IBIs indeed indicate a preference of PGMs towards granddaughters (Table 2). These differences in PGM behavior may not only relate to quantitatively genetic differences between the sexes (resulting in higher proportion of genetic similarity between PGMs and their granddaughters compared to their grandsons), but also may reflect several other aspects of X-chromosome-related traits. Despite the important theoretical difference between the explanations offered by Fox et al. (2010) and Rice et al. (2010), in regard to any potentially adaptive function of this phenomenon, both of these (in each case plausible) explanations predict that PGMs will channel their investment in grandchildren more selectively than MGMs. Although intragenomic conflict associated with the asymmetric transmission of the X chromosome is constrained by fitness costs, it may contribute substantially to this phenomenon (Rice et al., 2010). In addition to this, X-chromosome-related traits could also serve adaptively as markers for estimating relatedness and therefore decrease potential opportunity costs for paternal investment (Isles, Davies, & Wilikinson, 2006; Fox et al., 2010). Among men, specific cognitive mechanisms have shown to modulate their amount of paternal investment according to physical resemblance (Alvergne,

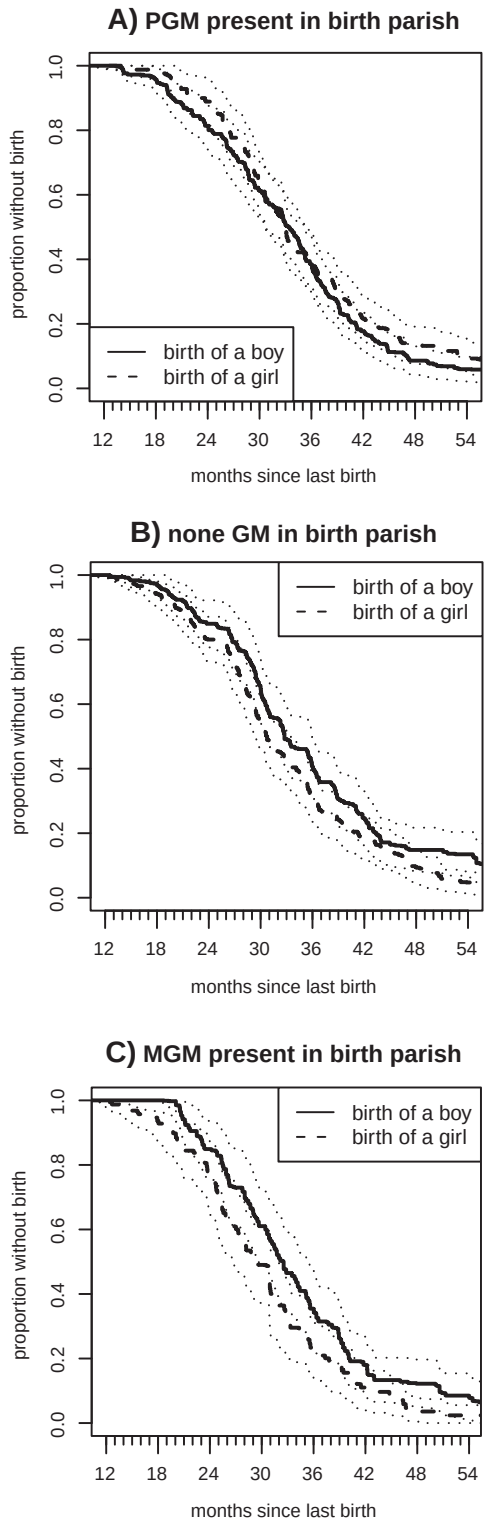

Fig. 4. Aalen model predictions (see Table 4) for IBIs with 95% pointwise confidence bands using averaged covariates. Differences in IBIs, following the birth of a grandson are shown using a solid line and a granddaughter using a broken line, between families where only the PGM (Panel A) was present in birth parish or grandmothers were absent (Panel B) or only the MGM (Panel C) was present in birth parish.

Faurie, & Raymond, 2009; Platek et al., 2004). Perhaps a similar mechanism is active in PGMs as an anti-cuckolding strategy (e.g., facial resemblance, odor, behavioral traits). Many studies emphasize the role of the X-chromosome in fertility-related traits and brain development (see references in Isles et al., 2006 and references in Fox et al., 2010). Because X-chromosomal inactivation is established early in embryogenesis (before and at the time of gastrulation, see Brockdorff & Turner, 2007 for a review) and maintained among cell-lineages throughout the lifespan, mammalian females are constituted as 'patch-like' genetic mosaics: It seems therefore possible that PGMs adjust their investment towards grandchildren, depending on whether their X chromosome is expressed in certain body parts (e.g. the face) of their granddaughters (Fox et al., 2010). This explanation of PGM's favoritism towards granddaughters differs from the contextual difference in PGM behavior described by Rice et al. (2010) because the former is adapted to parental uncertainty, while the latter only propagates the reproduction of the paternal X chromosome even in costs of it's carrier's inclusive fitness. Since paternal uncertainty and the risk of an X-chromosomal 'evolutionary dead end' are both only relevant for the patriline, both of these theories similarly predict that the PGM's investment strategy will be more variable than the MGMs. In each case, the PGM's investment is theoretically predicted either to fall below or to exceed the amount of investment that would maximize the fitness of her grandchild's mother, as it is in the PGM's interest to channel maternal resources into specific offspring even with costs to future reproduction. A drastic example of the first case (forcing low investment) is a situation in which the PGM would benefit from the replacement of an existing grandchild (whether replacing a grandson with a granddaughter or a non-carrier with a 'green-beard'). If the reproductive value of a specific child (including parental certainty) to the PGM is relatively low, death of this child could be disadvantageous for the mother but advantageous for the PGM because, in this way, the PGM speeds up another chance for her son to produce offspring with potentially higher reproductive value (or a green-beard). But this classical 'evil mother-in-law' is only one side of the story, because collision of reproductive interests is inevitable in the second case (forcing high investment): if estimated relatedness (or the probability of a 'green-beard') is high and an existing grandchild is 'desired' in terms of fitness by the PGM, then the PGM should allocate more investment toward this grandchild. This reallocation of resources could differ from the ideal proportions from a daughter-in-law's point of view. In-law conflict becomes obvious in situations in which the PGM would benefit from replacement of an existing grandchild, but conflicting reproductive interests is inevitable because any bias towards female offspring is costly in terms of a mother's different incentive to invest in sons. This is because both parental uncertainty and the inheritance of the X-chromosome do not pose any 'adaptive' problem to the mother.

In conclusion, this study suggests that grandmothers do not represent a homogenous group within the in-law-conflict scenario. PGMs indeed differ in their investment strategy from MGMs (see also Pollet, Nelissen, & Nettle, 2009). An increased infant mortality in the presence of PGMs (as opposed to MGMs) is known for the Krummhörn (Voland & Beise, 2002), where stress due to hard work could also play a role (Voland & Beise, 2005). Further studies concerning the relationship between PGMs and their granddaughters seem very promising. Of course, this research area demands further genetic investigation.

Supplementary materials related to this article can be found online at doi:10.1016/j.evolhumbehav.2010.11.004.

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References

Alvergne, A., Faurie, C., & Raymond, M. (2009). Father-offspring resemblance predicts paternal investment in humans. *Animal Behaviour*, *78*, 61–68, doi:10.1016/j.anbehav.2009.03.019.

Baldi, I., Ciccone, G., Ponti, A., Rosso, S., Zanetti, R., & Gregori, D. (2006). An Application of the Cox-Aalen Model for Breast Cancer Survival. *Austrian Journal of Statistics*, *35*(1), 77–88.

Beise, J., & Voland, E. (2008). Intrafamilial Resource Competition and Mate Competition Shaped Social-Group-Specific Natal Dispersal in the 18th and 19th Century Krummhörn Population. *American Journal of Human Biology*, *20*, 325–336, doi:10.1002/ajhb.20730.

Brockdorff, N., & Turner, B. M. (2007). Dosage Compensation in Mammals. In C. D. Allis, T. Jenuwein, & D. Reinberg (Eds.), *Epigenetics* (pp. 321–340). Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.

Coeurjolly, J. -F., Drouilhet, R., Lafaye De Micheaux, P., & Robineau, J. F. (2009). asympTest: A Simple R Package for Classical Parametric Statistical Tests and Confidence Intervals in Large Samples. *The R Journal*, *1*(2), 26–30.

Cox, D. R. (1972). Regression models and life tables (with Discussion). *Journal of the Royal Statistical Society, Series B*, *34*, 187–220.

Euler, H., & Michalski, H. A. (2008). Grandparental and extended kin relationships. In C. A. Salmon, & T. K. Shackelford (Eds.), *Family Relationships—An Evolutionary Perspective* (pp. 230–255). Oxford: Oxford University Press.

Fox, M., Sear, R., Beise, J., Ragsdale, G., Voland, E., & Knapp, L. A. (2010). Grandma plays favourites—X-chromosome relatedness and sex-specific childhood mortality. *Proceedings of the Royal Society B*, *277*, 567–573, doi:10.1098/rspb.2009.1660.

Galdikas, B. M. F., & Wood, J. W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropolog*, *83*, 185–191, doi:10.1002/ajpa.1330830207).

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, *7*, 1–16, doi:10.1016/0022-5193(64)90038-4.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, *7*, 17–52, doi:10.1016/0022-5193(64)90039-6.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academies of Sciences USA*, *95* (3), 1336–1339.

Hrdy, S. B. (2009). *Mothers and others—The evolutionary origins of mutual understanding*. Belknap/Harvard: Cambridge.

Isles, A. R., Davies, W., & Wilikinson, L. S. (2006). Genomic imprinting and the social brain. *Philosophical Transactions of the Royal Society B*, *361*, 2229–2237, doi:10.1098/rstb.2006.1942.

Kraus, D. (2009). Proptest: Tests of the proportional hazards assumption. R package version 0.1-4. http://CRAN.R-project.org/package=proptest.

Leonetti, D. L., Nath, D. C., & Heman, N. S. (2007). In-law conflict. *Current Anthropology*, *48*(6), 861–890, doi:10.1086/520976.

Low, B. S. (1991). Reproductive life in nineteenth century Sweden: An evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, *12*, 411–448.

Messing, S. (2010). Wvioplot: Weighted violin plot. R package version 0.1. http://CRAN.R-project.org/package=wvioplot.

Panter-Brick, C. (1991). Lactation, birth spacing and maternal work-loads among two castes in rural Nepal. *Journal of Biosocial Science*, *23*, 137–154, doi:10.1017/S0021932000019179.

Penn, D. J., & Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *Proceedings of the National Academies of Sciences USA*, *104*(2), 553–558, doi:10.1073/pnas.0609301103.

Piperata, B. A. (2009). Variation in maternal strategies during lactation: The role of the biosocial context. *American Journal of Human Biology*, *21*, 817–827, doi:10.1002/ajhb.20898.

Platek, S. M., Raines, D. M., Gallup, G. G., Mohamed, F. B., Thomson, J. W., Myers, T. E., et al. (2004). Reactions to children's faces: males are more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, *25*, 394–405, doi:10.1016/j.evolhumbehav.2004.08.007.

Pollet, T. V., Nelissen, M., & Nettle, D. (2009). Lineage based differences in grandparental investment: evidence from a large British cohort study. *Journal of Biosocial Science*, *41*, 355–379, doi:10.1017/S0021932009003307).

Quinlan, R. J., Quinlan, M. B., & Flinn, M. V. (2005). Local resource enhancement and sex-biased breastfeeding in a Caribbean community. *Current Anthropology*, *46*, 471–480, doi:10.1086/430017.

R Development Core Team. (2010). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reiches, M., Ellison, P. T., Lipson, S., Sharrock, K., Gardiner, E., & Duncan, L. G. (2009). Pooled energy budget and human evolution. *American Journal of Human Biology*, *21*, 421–429, doi:10.1002/ajhb.20906.

Rice, W. R., Gavrilets, S., & Friberg, U. (2010). The evolution of sex-specific grandparental harm. *Proceedings of the Royal Society B*, *277*, 2727–2735, doi:10.1098/rspb.2010.0409.

Scheike, T., Martinussen, T., & Silver, J. (2010). Timereg: Timereg package for flexible regression models for survival data. R package version 1.3-0. http://CRAN.R-project.org/package=timereg.

Scheike, T., & Zhang, M. (2002). An additive–multiplicative Cox–Aalen regression model. *Scandinavian Journal of Statistics*, *29*(1), 75–88, doi:10.1111/1467-9469.00065.

Sear, R., Mace, R., & McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, *24*, 25–42, doi:10.1016/S1090-5138(02)00105-8.

Straka-Geiersbach, S., & Voland, E. (1988). Zum Einfluβ der Säuglingssterblichkeit auf die eheliche Fruchtbarkeit am Beispiel der Krummhörn, 18. und 19. Jahrhundert ([On the influence of infant mortality on marital fecundity in historical Krummhörn, 18th and 19th centuries]). *Homo*, *39*, 171–185.

Therneau, T., & Lumley, T. (2009). Survival: Survival analysis, including penalised likelihood. R package version 2.35-4. http://CRAN.R-project.org/package=survival.

Tracer, D. P. (2009). Breastfeeding structure as a test of parental investment theory in Papua New Guinea. *American Journal of Human Biology*, *21*, 635–642, doi:10.1002/ajhb.20928.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man 1871–1971* (pp. 136–179). Chicago: Aldine.

Vitzthum, V. J. (2008). Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*, *37*(4), 1–21, doi:10.1146/annurev.anthro.37.081407.085112.

Voland, E. (2000). Contributions of family reconstitution studies to evolutionary reproductive ecology. *Evolutionary Anthropology*, *9*, 134–146, doi:10.1002/1520-6505(2000)9:3<134::AID-EVAN3>3.0.CO;2-M.

Voland, E., & Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant mortality in historical Krummhörn. *Behavioral Ecology and Sociobiology*, *52*, 435–443, doi:10.1007/s00265-002-0539-2.

Voland, E., & Beise, J. (2005). The husband's mother is the devil in the house: Data on the impact of the mother-in-law on stillbirth mortality in historical Krummhörn (1750–1874) and some thoughts on the evolution of postgenerative female life. In E. Voland, A. Chasiotis, & W. Schiefenhövel (Eds.), *(2005) Grandmotherhood—The evolutionary significance of the second half of female life* (pp. 239–255). New Brunswick & London: Rutgers University Press.

Voland E., Chasiotis A., & Schiefenhövel W. (Eds.) *Grandmotherhood—The evolutionary significance of the second half of female life*. New Brunswick & London: Rutgers University Press.

Voland, E., & Dunbar, R. I. M. (1995). Resource competition and reproduction—The relationship between economic and parental strategies in the Krummhörn population (1720–1874). *Human Nature*, *6*, 33–49, doi:10.1007/BF02734134.

Willführ, K. P. (2009). Short- and long-term consequences of early parental loss in the historical population of the Krummhörn (18th and 19th Century). *American Journal of Human Biology*, *21*, 488–500, doi:10.1002/ajhb.20909.