Justus-Liebig-Universität Gießen
Fachbereich Biologie und Chemie

Kumulativ-Dissertation

Die „Großmutter-Hypothese“ und genomische Konflikte

Konditionale Einflüsse von Großmüttern auf reproduktives Verhalten in Familien der ostfriesischen Krummhörn (1720–1874)

Dipl.-Biol. Johannes Johow

Juli 2012

betreut durch Prof. Dr. Eckart Voland

Abstract und Zusammenfassung

Abstract. According to the "Grandmother Hypothesis", human reproduction can be described as a three-generation enterprise with postmenopausal mothers assisting their offspring in reproduction. However, previous studies have shown a high variability in the influences of postmenopausal mothers on offspring mortality and fertility of their daughters and daughters-in-law which is still not well understood. In order to investigate of what causes this variation in grandmaternal effects, reconstituted family data from a historical population in the East Frisian Krummhörn region has been analyzed. The results indicate that effects of grandmothers depend on differences in genetic relatedness and have to be differentiated according to socioeconomic constraints. While from a grandmother's perspective, intergenomic in-law conflict results from relatedness asymmetries between descendents of the parental lineages, sexually-antagonistic, intragenomic conflicts are due to the asymmetrical inheritance of the paternal sex chromosomes, which differs from the rest of the genome. In the case of the Krummhörn family reconstitution, merging of models of kinship ecology with data on socio-economic constraints of families offers new perspectives for the study of conditional grandmother's effects. This review summarizes the accumulated findings and theoretical improvements that have occurred within different branches of research being recently developed from the intitial grandmother hypothesis.

Zusammenfassung. Der „Großmutter-Hypothese“ zufolge lässt sich menschliche Fortpflanzung als ein Drei-Generationen-Unternehmen beschreiben, in dem postmenopausale Mütter ihren Nachwuchs bei der Reproduktion unterstützen. Bisherige Studien zeigen allerdings eine hohe Variabilität in den Einflüssen postmenopausaler Mütter auf Fruchtbarkeit und Nachwuchssterblichkeit ihrer Töchter und Schwiegertöchter, die noch nicht gut verstanden ist. Um die Ursachen für diese Variabilität zu untersuchen, wurden rekonstituierte Familiendaten einer historischen Population in der ostfriesischen Krummhörn-Region analysiert. Den Ergebnissen zufolge müssen die Effekte von Großmüttern sowohl für unterschiedliche genetische Abstammungslinien als auch für unterschiedliche sozioökonomische Beschränkungen differenziert werden. Während aus großmütterlicher Sicht intergenomische Schwiegerkonflikte aus der asymmetrischen Verwandtschaft zwischen Angehörigen beider elterlicher Abstammungslinien resultieren, sind sexuell-antagonistische, intragenomische Konflikte eine Folge der vom restlichen Genom abweichenden, asymmetrischen Vererbung der väterlichen Geschlechtschromosomen. Im Falle der Krummhörn-Familienrekonstitutionsstudie eröffnet das Zusammenführen von Daten zu individuellen, sozioökonomischen Beschränkungen mit Modellen zur Verwandtenökologie neue Perspektiven zur Untersuchung von konditionalen großmütterlichen Effekten. Dieser Überblicksartikel fasst kumulierte Ergebnisse und theoretische Entwicklungen zusammen, die sich in letzter Zeit innerhalb verschiedener Forschungszweige aus der ursprünglichen Großmutter-Hypothese entwickelt haben.

Danksagung

Diese Arbeit wurde ermöglicht durch die Unterstützung und den Rückhalt vieler Menschen, bei denen ich mich an dieser Stelle gerne herzlich bedanke.

Bei Prof. Dr. Eckart Voland möchte ich mich für die exzellente Betreuung und das entgegengebrachte Vertrauen bedanken. Weil wissenschaftliche Arbeit teilweise auch Leistungsdruck und Frustration mit sich bringen kann, bin ich ihm besonders dankbar dafür, mich immer daran zu erinnern, dass derartige Belastungen nicht den ultimaten Zweck von Forschung ausmachen.

Meinen Eltern, Christiane (geb. Gerlach) und Joachim, bin ich nicht nur für ihre großzügige materielle Förderung während meines gesamten Studiums dankbar, sondern besonders auch für den Zuspruch und ihren Beistand während zwischenzeitlich recht ungewissen Zeiten des Studienwechsels und Umzugs nach Gießen.

Meiner Freundin, Isabelle Cobres, danke ich besonders für ihre große Rücksichtnahme und das Verständnis für Einschränkungen, die sich während einigen Phasen der Arbeit ergeben haben. Sie hat viele Texte Korrektur gelesen und mir außerdem, genau wie viele andere Freunde und Bekannte erleichtert, trotz allen Fristen und Gutachtern jederzeit „auf dem Teppich“ zu bleiben und niemals zu verzweifeln.

Überaus dankbar bin ich außerdem dem Fachbereich für Biologie und Chemie für das gewährte „Darwin-Stipendium“ und das mir entgegengebrachte Vertrauen. Der auf diese Weise entstandene Freiraum hat mir während den letzten beiden Jahren sehr dabei geholfen, mich voll auf die wissenschaftliche Arbeit konzentrieren zu können.

Auch dem gesamten Kollegium am Zentrum für Philosophie, vor allem Kai-Uwe Dworschak, Dr. Ulrich Frey, Anke Gaussmann, Rebbeca Rehm, Hannes Rusch, Charlotte Störmer, Ingrid Weil und Dr. Kai Willführ gilt hier mein Dank für die gute Zusammenarbeit und Unterstützung.

Die vorgestellten Untersuchungen profitieren nicht nur von der Qualität und Breite der bereitgestellten Datengrundlage sondern auch von den frei verfügbaren Programmpaketen, die von mir (völlig unentgeltlich) zur statistischen Analyse genutzt werden konnten. Daher danke ich auch allen Entwicklern und Unterstützern der freien Software *R* für die Bereitstellung ihrer investierten Arbeit.

Und, *last but not least*, auch an meine Großmutter Helga (geb. Schmiga): Herzlichen Dank für Unterstützung und Verköstigung!

Für Isa und Jonathan
♡

Inhalt

1 Erweiterte Zusammenfassung

1.1 Einleitung

Die so genannte „Großmutter-Hypothese“ beschreibt die postmenopausale Lebensspanne von Frauen als evolutionäre Angepasstheit an kooperative Fortpflanzungsstrategien (Hamilton, 1966; Hawkes et al., 1998). Demnach ähnelt die Kinderaufzucht in Familien funktional den kooperativen Brutgemeinschaften bestimmter Vogelarten, bei denen generative „Brüter“ von anderen (meist genetisch-verwandten) „Helfern“ in ihrem Reproduktionsaufwand unterstützt werden können (Turke, 1988; Emlen, 1995; Hrdy, 2008). Postmenopausale Frauen erscheinen für die Helferrolle prädestiniert weil sie zwar in der Regel sehr erfahren sind aber gleichzeitig erzwungenermaßen selber keine Kinder mehr bekommen können (Hrdy, 2009, 2005). Der Großmutter-Hypothese zufolge lässt sich menschliche Reproduktion als ein Drei-Generationen-Unternehmen beschreiben, in dem Ressourcentransfers über mehrere Generationen hinweg eine bedeutende Rolle spielen (Sear & Coall, 2011; Hawkes et al., 1998; Leonetti et al., 2007).

Auch wenn durch diese Theorie großmütterliche Unterstützung prinzipiell vorausgesagt wird, bleiben die genauen Verhaltensmechanismen und spezifischen Investmentkanäle noch weitgehend unklar (Überblick in Johow et al. im Erscheinen). Was die in bisherigen Studien festgestellte hohe Variabilität von großmütterlichen Effekten auf mütterliche Fruchtbarkeit und Nachwuchssterblichkeit betrifft, zeigt sich, dass diese offenbar kontextabhängig differenziert werden müssen (Überblick in Coall & Hertwig, 2010; Sear & Mace, 2008).

Einerseits ist eine Unterscheidung von Großmüttern hinsichtlich ihrer Abstammungslinie erforderlich weil mütterliche und väterliche Großmütter in unterschiedlicher Weise mit der Mutter verwandt sind (z. B. Voland & Beise, 2002). Aus dieser unterschiedlichen Verwandtschaft resultieren jeweils spezifische Probleme infolge von mütterlichen Risiken oder der Vaterschaftsunsicherheit (z. B. Euler & Michalski, 2008; Leonetti et al., 2007). Andererseits könnte für die Effekte der väterlichen Großmutter – aufgrund der asymmetrischen X-chromosomalen Verwandtschaft zu ihren Enkeln – auch das Geschlecht der Enkelkinder eine Rolle spielen (Fox et al., 2010; Rice et al., 2010). Welche Fitnesskomponenten (z. B. Fruchtbarkeit oder Nachwuchssterblichkeit) durch Großmütter beeinflusst werden können d. h. ob und wie mütterliche oder väterliche Großmütter ihre reproduktiven Interessen mittels spezifischer Helferstrategien durchsetzen können, hängt vermutlich stark von den ökologischen bzw. sozioökonomischen Bedingungen einer Familie ab (z. B. Kushnick, 2012; Low, 2005). Angebot und Nachfrage an großmütterlicher Unterstützung orientieren sich an Opportunitätsräumen, welche z. B. von der Ressourcenverteilung innerhalb der Familie oder auch von Arbeitsmöglichkeiten bestimmter Familienmitglieder abhängen können (Überblick in Coall & Hertwig, 2010). Zur Untersuchung dieser Zusammenhänge sollen großmütterliche Einflüsse auf reproduktives Verhalten anhand von rekonstituierten Familiendaten einer historischen Population für unterschiedliche Verwandtschaftbeziehungen und Sozialgruppen differenziert werden.

Im folgenden wird zunächst die Theorie zur Großmutter-Hypothese zusammengefasst und der aktuelle Stand der Forschung auf diesem Gebiet umrissen. Dabei werden Hypothesen zu konditionalen Einflüssen von Großmüttern auf reproduktives Verhalten in Krummhörner Familien formuliert. Zur Überprüfung der Hypothesen werden eigene Untersuchungen an Daten der historischen Population der Krummhörn-Region in Ostfriesland (18.-19. Jhd.) vorgestellt. Schließlich wird diskutiert, inwieweit die vorgestellten Studien dabei helfen können, die Vielfalt reproduktiver Strategien – auch in unterschiedlichen sozioökonomischen Bedingungen – besser zu verstehen.

1.1.1 Die Großmutter-Hypothese

Alterungsprozesse wurden bereits von Williams (1957) als Schattenseite früher Reproduktionsvorteile beschrieben. Im Zuge einer antagonistischen Pleiotropie können Merkmale selektiert werden, die zu frühen Stadien der Entwicklung den Reproduktionserfolg steigern auch wenn dies gleichzeitig die Überlebenswahrscheinlichkeit zu späteren Stadien senkt (Williams, 1957). Wenn solche „schädlichen“ Auswirkungen nach Beendigung der Reproduktion auftreten (d. h. sich nicht nachteilig auf den Reproduktionserfolg auswirken), würde diese Form der Alterung keinen reproduktiven Nachteil darstellen (Williams, 1957). Tatsächlich scheinen nur wenige Organismen eine dem Menschen vergleichbare Langlebigkeit über das generative Alter hinaus aufzuweisen (Überblick in Austad, 1997, s. auch Foote 2008). Die Langlebigkeit von Frauen mehrere Dekaden über ihre Fekundität hinaus bildet eine im Vergleich zu andereren Primaten erklärungsbedürftige Ausnahme (Hawkes, 2011).

Williams (1957) merkt zu der außergewöhnlichen Langlebigkeit von Frauen an, dass Reproduktion bei Menschen (wie im übrigen generell bei jeglicher Form von Brutpflege) eben mehr umfasse als die Produktion von Gameten – schließlich ist menschlicher Nachwuchs nach der Geburt noch längere Zeit auf die Mutter angewiesen. Die postreproduktive Phase einer Mutter begänne deshalb frühestens zu dem Zeitpunkt, an dem ihr jüngstes Kind von ihr unabhängig sei (Williams, 1957). Eine begrenzte Gebärfähigkeit könne somit laut Williams (1957) verhindern, dass Mütter an einer Folgegeburt sterben und so das Überleben von bereits vorhandenem Nachwuchs gefährden (später als *„stopping early“ Hypothesis* bezeichnet, s. Hawkes et al. 1998).

Hamilton (1966) beschäftigte sich ebenfalls mit der Evolution organismischer Lebensspannen und speziell mit der Bedeutung der kooperativen Fortpflanzung für die menschliche Langlebigkeit. In seinem Aufsatz „*the moulding of senescence by natural selection*“ erklärt er weniger die scheinbar frühe Aufgabe der Gebärfähigkeit bei Frauen als vielmehr das relativ lange Überleben über die Menopause hinaus (Hamilton, 1966). Hamilton (1966, S. 12) schlussfolgert: „[...] *postreproductive life-spans may evolve when the old animal still benefits its younger relatives.*“. Die Unterstützung jüngerer Verwandte – wie z. B. der eigenen Kinder – in deren Reproduktion, böte älteren Frauen die Gelegenheit, ihren Reproduktionserfolg auch nach dem Verlust ihrer Fruchtbarkeit *indirekt* zu steigern (Hamilton, 1966).

Diese Vermutung stützt sich wesentlich auf das von Hamilton (1964a,b) zuvor formalisierte Konzept der Inklusivfitness wonach darwinische Fitness mehr umfasst als die Produktion von eigenen Nachkommen. Weil der relative Anteil einer bestimmten Genvariante innerhalb der Folgegeneration durch die Fortpflanzung aller ihrer Träger in gleicher Weise beeinflusst wird, ist Nachwuchs von genetisch-ähnlichen Individuen zu einem gewissen Teil mit eigenem Nachwuchs äquivalent (Fisher, 1958). Aus diesem Grund kann die Unterstützung von anderen Trägern einer Genvariante – oder auch die Diskriminierung von Nichtträgern – unter Umständen die Fitness des betreffenden Allels steigern (Überblick in West & Gardner, 2010). Für die Evolution sozialen Verhaltens sind daher laut Hamilton (1964a,b) sowohl die Bilanz aus den spezifischen Kosten (K) und Nutzen (N) des individuellen Verhaltens als auch die genetische Korrelation zwischen den Beteiligten (r) von entscheidender Bedeutung. Als Invasionskriterium für die populationsgenetische Etablierung von Allelen welche ein Helferverhalten bewirken, gilt laut Hamilton (1964a,b) die formale Bedingung:

$$K < r \cdot N \tag{1.1}$$

Die resultierenden Kosten des Verhaltens für den Helfer müssen demnach kleiner sein als das Produkt aus dem produzierten Nutzen für den Empfänger der Hilfe und der genetischen Verwandtschaft zwischen Helfer und Empfänger. Hieraus folgt die auch für großmütterliche Effekte wichtige Einsicht, dass mit steigender genetischer Verwandtschaft – unter ansonsten gleichen Bedingungen – die Bereitschaft zur Hilfe zunehmen sollte.

Die Idee, dass Großmütter indirekt ihren Reproduktionserfolg steigern können wurde später vor allem durch Soziobiologinnen aufgegriffen (z. B. Hrdy, 1981; Hawkes, 1989; Lancaster & King, 1985; Pavelka & Fedigan, 1991). Allerdings wurde die Großmutter-Hypothese aufgrund von theoretischen Überlegungen hinterfragt und infolge empirischer Befunde in ihrem Erklärungswert bezweifelt (z. B. Driscoll, 2009; Strassmann & Garrard, 2011; Peccei, 2001). Zum einen können die reproduktiven Vorteile welche durch eine indirekte Reproduktion entstehen offenbar nur schwer die Nachteile aufwiegen, welche aus einer Aufgabe der direkten Reproduktion resultieren (Hill & Hurtado, 1991).

Dieser Einwand richtet sich nicht direkt gegen die Großmutter-Hypothese (d. h. die Annahme einer angepassten postgenerativen Lebensspanne) sondern vielmehr gegen die von Williams (1957) formulierte *„stopping early“ Hypothesis*. Die Frage nach den evolutionären Ursachen der Menopause ist bei Erklärungen zu der außergewöhnlichen Langlebigkeit von Frauen durchaus berechtigt. Ihm wird üblicherweise begegnet, indem auf stammesgeschichtliche Beschränkungen in der Anzahl befruchtungsfähiger Follikel im Leben einer Frau verwiesen wird (Peccei, 1995). Allerdings scheinen neuere Untersuchungen zumindest die theoretische Möglichkeit einer fortgesetzten Follikelproduktion einzuräumen (White et al., 2012). Unabhängig vom Mechanismus der Menopause gilt allerdings, dass Frauen und Schimpansinnen ungefähr im selben Alter schlichtweg keine weiteren Kinder mehr bekommen (Hawkes, 2011). Bei der Angepasstheit welche durch die Großmutterhypothese erklärt wird, handelt es sich demnach weniger um die vermeintlich „frühe“ Aufgabe der (direkten) Reproduktionsfähigkeit von Frauen sondern vielmehr um die im Vergleich zu Schimpansinnen anschließend verlängerte Lebensspanne über das generative Alter hinaus (Hawkes et al., 1998).

Kritiker der Großmutter-Hypothese verweisen außerdem darauf, dass positive Effekte von Großmüttern auf Fitnesskorrelate wie Kinderzahl und Nachwuchssterblichkeit in empirischen Studien vor allem in patrilokalen Gesellschaften oft nicht feststellbar sind (vgl. Strassman & Kurapati, 2010). Wie allerdings in den folgenden Abschnitten beschrieben, resultieren bedeutende genomische Konflikte über den Aufwand von großmütterlichen Ressourcen aus den zwangsläufig asymmetrischen Verwandtschaftsverhätnissen innerhalb von Familien. Neuere Untersuchungen zeigen dabei, dass neben intergenomischen Konflikten zwischen den Angehörigen beider elterlicher Abstammungslinien im Falle der väterlichen Großmutter auch intragenomische Konflikte über die Frequenz des väterlichen X-Chromosoms in der Folgegeneration eine Rolle spielen könnten (Rice et al., 2010; Seki, 2012).

1.1.2 Stand der Forschung

Seit Hawkes et al. (1998) gezeigt haben, dass Großmütter vermutlich auch in historischen und prähistorischen Zeiten signifikante Beiträge zur Nahrungsmittelversorgung einer Familie leisten konnten, ist diese Argumentation vielfach ausdifferenziert worden. Zum Beispiel argumentiert auch Hrdy (2005), dass Müttern erst durch die intergenerationale Hilfe älterer Frauen ermöglicht wurde, innerhalb relativ kurzer Zeit oft zu gebären und mehrere Kinder gleichzeitig aufzuziehen. So wird vermutet, dass großmütterliche Unterstützung als Schlüsselanpassung eng mit anderen spezifisch menschlichen Merkmalen in Verbindung steht, wie einer langsamen, sexuellen Reifung und kurzen Zwischengeburtenabständen (z. B. Robson et al., 2006).

Hinweise auf eine adaptive Funktion der postmenopausalen Lebensspanne wurden z. B. anhand historischer Daten aus Finnland geliefert, welche zeigen, dass die Anwesenheit einer Großmutter (ohne dabei zwischen mütterlicher oder väterlicher Großmutter zu differenzieren) mit einer um ca. 12% erhöhten Überlebenswahrscheinlichkeit der Enkelkinder einhergeht (Lahdenperä et al., 2004). Außerdem zeigen Lahdenperä et al. (2004) dass Großmütter für jedes Jahrzehnt, welches sie über das Alter von 50 Jahren hinaus überlebt haben im Durchschnitt jeweils 2 Enkelkinder mehr zu erwarten hatten. In einer Untersuchung an einer indischen Population wurde festgestellt, dass Großmutteranwesenheit mit kürzeren Zwischengeburtenabständen einhergeht (Nath et al., 2000). Tymicki (2004) zeigt für historische Daten aus Polen, dass die Anwesenheit von Großeltern wie auch Onkeln und Tanten mit einer erhöhten, abgeschlossenen Fruchtbarkeit (d. h. Gesamtzahl mütterlicher Geburten) einhergeht. Allerdings führt dort lediglich die mütterliche Grotßmutter aber nicht die väterliche Großmutter zu einer signifikanten Erhöhung der Anzahl an überlebenden Nachkommen (Tymicki, 2008). Auch in einer ländlichen Population aus Gambia wird die mütterliche Fruchtbarkeit vor allem durch die väterliche Großmutter gesteigert während die Überlebenswahrscheinlichkeit der Enkel vor allem durch die mütterliche Großmutter erhöht wird (Sear et al., 2002, 2003). Hier zeigt sich auch, dass der Ernährungszustand des Kindes besser ist, falls es von der mütterlichen Großmutter Unterstützung erhält (Sear et al., 2000).

In einer Auswertung vorangehender Studien zu Verwandteneffekten auf die Nachwuchssterblichkeit haben Sear & Mace (2008) festgestellt, dass mütterliche Großmütter im Vergleich zu väterlichen Großmüttern häufiger und effizienter das überleben der Nachkommen sicherstellen. Demnach ist für potentielle Effekte die genetische Abstammungslinie einer Großmutter von entscheidender Bedeutung, d. h. Großmütter haben andere Einflüsse auf die Reproduktion ihrer Töchter als auf die Reproduktion ihrer Schwiegertöchter. Auch in der historischen Population der Krummhörn in Norddeutschland senkt z. B. lediglich die Anwesenheit der mütterlichen Großmutter die Säuglingssterblichkeit während die Anwesenheit der väterlichen Großmutter diese sogar leicht erhöht (Voland & Beise, 2002). Vergleichbare Befunde sind auch für eine historische Population aus Japan berichtet worden (Jamison et al., 2002). Voland & Beise (2005) zeigen anhand der Krummhörner Population zudem ähnliche Unterschiede auch im Falle der mütterlichen Totgeburtlichkeit und interpretieren diese ebenfalls mit einem ambivalenten Verhältnis zwischen Schwiegermutter und Schwiegertochter, das aus der im Vergleich zur leiblichen Mutter geringeren genetischen Verwandtschaft resultiert.

Genomische Konflikte

Nach Hamilton (1964a,b) ist auch zu erwarten, dass hinsichtlich Ressourcen und Risiken der Mutter deutliche Interessensunterschiede zwischen mütterlichen und väterlichen Verwandten bestehen – schließlich sind nur erstere mit der Mutter verwandt (Leonetti et al., 2007; Voland & Beise, 2005). Je nachdem ob es sich um Verwandte des Mannes oder um Verwandte der Frau handelt, resultieren aus diesem Unterschied unterschiedliche Kostenfunktionen was die Schonung bzw. Ausnutzung von mütterlichen Ressourcen betrifft (Voland & Beise, 2005).

Zwischen den Geschlechtern herrscht ein Konflikt hinsichtlich der reproduktiven Strategie, z. B. leiden Frauen stärker als Männer unter dem Aufwand und den Risiken einer gesteigerten Fruchtbarkeit (Penn & Smith, 2007). Genetische Verwandte der Mutter müssen die mit der Reproduktion einhergehenden gesundheitlichen Risiken generell höher gewichten als Schwiegerverwandte. Im Vergleich zu Schwiegerverwandschaft ist genetische Verwandtschaft exklusiv und nicht ersetzbar (Leonetti et al., 2007). Außerdem haben nur matrilineare Verwandte absolute Gewissheit, dass sie mit dem Nachwuchs der Mutter auch tatsächlich verwandt sind weil sie nicht von Vaterschaftsunsicherheit betroffen sind (Voland & Beise, 2002, s. auch Kap. 4). Bei mütterlichen Risiken und Vaterschaftsunsicherheit handelt es sich um Probleme welche beide Abstammungslinien unterschiedlich betreffen und die zudem auch stark durch ökologische bzw. sozioökonomische Bedingungen beeinflusst werden können (z. B. Low, 2005, bzw. Kap. 4).

Leonetti et al. (2007) gehen dem Schwiegerkonflikt zwischen mütterlichen und väterlichen Verwandten anhand von Daten für die Population der nordindischen *Khasi* nach und zeigen, dass die mütterliche Großmutter hier das Interesse ihrer Tochter zugunsten einer moderaten Familienplanung durchzusetzen hilft. Dieser Befund deutet auf ein Schonungsmotiv seitens mütterlicher Verwandter hin, welches die Mutter vor tendenziell ausbeuterischen patrilinearen Fertilitätsansprüchen schützt (Leonetti et al., 2007). Auch Borgerhoff-Mulder (2009) zeigt für eine ländliche Bevölkerung aus Tansania, dass sich die Interessen eines Paares hinsichtlich der angestrebten Familiengröße (und dem effizienten Einsatz von Verhütungsmitteln) zwischen Mann und Frau unterscheiden sowie und dass für mütterliche Verwandte Möglichkeiten bestehen, die Mutter in diesem Konflikt zu unterstützen.

Für das zeitgenössische Großbritannien wurde gezeigt, dass mütterliche Großeltern häufigeren Kontakt zu ihren Enkeln haben und diese zudem finanziell stärker unterstützen als väterliche Großeltern (Pollet et al., 2009). Eine andere Studie an multinationalen europäischen Daten bestätigt dieses Phänomen und weist dabei auch auf die Bedeutung vorhandener Investmentoptionen hin (Danielsbacka et al., 2011). Dabei betonen die Autoren die Bedeutung der Vaterschaftsunsicherheit für die Evolution von adaptiven Investmententscheidungen (Danielsbacka et al., 2011; Pollet et al., 2009).

Neuerdings hat eine Metastudie anhand von sieben unterschiedlichen Datensätzen festgestellt, dass geschlechtsspezifische Unterschiede in den Effekten von Großmüttern auf die frühe Sterblichkeit ihrer Enkel mit Unterschieden in der X-chromosomalen Verwandtschaft korrelieren (Fox et al., 2010). Dies deutet auf eine Rolle X-chromosomaler Genkomplexe in der Evolution von Langlebigkeit und großmütterlichen Reproduktionsstrategien hin (s. Kap. 3 bzw. Kap. 4). Die so genannte *„X-linked Grandmother Hypothesis“* sieht die postgenerative Langlebigkeit weniger als für den Organismus vorteilhafte Angepasstheit, sondern eher als Folge intragenomischer Konflikte über die relative Frequenz der Geschlechtschromosomen in der Folgegeneration (Rice et al., 2008, s. auch Kap. 4).

Die Vermutung, dass Verwandteninvestment durch die asymmetrische Vererbung der Geschlechtschromosomen unterschiedlich beeinflusst werden könnte, wurde bereits zuvor geäußert (Chrastil et al., 2006). Vor allem die reproduktive Separierung der Geschlechtschromosomen im Zuge der sexuellen Evolution bietet Anlass zu der Vermutung, dass unter den Geschlechtschromosomen ein evolutionäres Wettrüsten mittels so genannter antagonistischer Adaptationen stattfindet (Rice, 1984, 1992; Dawkins & Krebs, 1979). Weil die sexuelle Rekombination im Falle der Geschlechtschromosomen fast vollständig unterdrückt ist, kommt es hier in besonderem Maße zu intragenomischen Konflikten über die relative Frequenz des jeweiligen Chromosoms in der Folgegeneration (Rice et al., 2008).

Dabei könnten so genannte *Green-Beard*-Effekte eine besondere Rolle spielen (Rice et al., 2008). Ein *Green-Beard*-Effekt resultiert aus dem Zusammenwirken der folgenden drei Merkmalskomponenenten, welche entweder durch ein pleiotropes Gen oder durch mehrere, zusammenhängende Gene codiert werden können (Hamilton, 1964a,b; Dawkins, 1976; Rice et al., 2008):

1. Ein wahrnehmbares Merkmal unterscheidet Träger von Nichtträgern.
2. Durch einen Erkennungsmechanismus für dieses Merkmal lassen sich Träger und Nichtträger identifizieren.
3. Die Diskriminierung von identifizierten Nichtträgern wird gewährleistet, z. B. mittels eines konditionalen Verhaltens durch dem Nichtträgern Ressourcen vorenthalten werden.

Diese drei Komponenten würden eine Form des kooperativen Verhaltens bewirken, welches auch abweichend vom genealogischen Verwandtschaftsgrad zu einer gegenseitigen Bevorzugung zwischen Merkmalsträgern führt (Hamilton, 1964a,b). Rice et al. (2008, 2010) haben kürzlich gezeigt, dass aufgrund der sehr speziellen Vererbung der Geschlechtschromosomen die Invasion von *Green-Beard*-Allelen auf dem im Vergleich zum Y-Chromosom sehr viel größeren X-Chromosom theoretisch begünstigt wird. Weil das väterliche X-Chromosom lediglich an Töchter weitergegeben wird und in jedem Falle von der Mutter des Vaters, also der väterlichen Großmutter stammt, könnte ein *Green-Beard*-Effekt X-chromosomaler Genkomplexe zu einer Bevorzugung von Enkelinnen gegenüber Enkeln durch die väterliche Großmutter führen (Rice et al., 2010). Intragenomische Konflikte resultieren aus dem Umstand, dass der *Green-Beard*-Effekt zu einer Diskriminierung der Nichtträger auch unter jenen Verwandten führt, welche ansonsten einen hohen Anteil an Allelen mit der väterlichen Großmutter teilen (Rice et al., 2008). Ein „negativer *Green-Beard*-Effekt“ d. h. die Schädigung von männlichen Enkeln durch die väterliche Großmutter kann deshalb theoretisch bis zu einem gewissen Grad nachteilig für die Reproduktion ihres restlichen (d. h. autosomalen) Genoms sein (Rice et al., 2008).

Das würde bedeuten, weibliche Langlebigkeit ist lediglich für die Reproduktion des X-Chromosoms vorteilhaft, wohingegen für das Genom insgesamt keine Reproduktionsvorteile zu erwarten sind (s. Kap. 4). Einige Autoren vertreten in der Tat die Ansicht, die postgenerative Lebensspanne von Frauen lasse sich nur sehr schwer durch eine Steigerung der Inklusivfitness (wohlgemerkt für das gesamte Genom) erklären (z. B. Strassman & Kurapati, 2010). Der von Rice et al. (2008) beschriebene Mechanismus des *sexually-antagonistic zygotic Drive* für das X-Chromosom böte hierfür eine Erklärung. Zum Beispiel wird in Kap. 3 der Hypothese nachgegangen, dass auch großmütterliche Einflüsse auf die Länge der Zwischengeburtenabstände von Unterschieden in der X-chromosomalen Verwandtschaft – möglicherweise mittels eines *Green-Beard*-Effektes – beeinflusst werden könnten. In Kap. 4 wird anhand des von Rice et al. (2010) entwickelten mathematischen Modells gezeigt, dass sogar im Falle einer hohen Vaterschaftsunsicherheit X-chromosomale Genkomplexe bestimmte Merkmale in der menschlichen *Life History* opportunistisch zugunsten ihrer eigenen Reproduktion beeinflussen könnten.

Sozioökonomische Beschränkungen

Insgesamt kommen auch Sear & Mace (2008) in ihrem Übersichtsartikel zur Nachwuchssterblichkeit zu dem Schluss, dass ein beträchtlicher Teil an Variabilität in den festgestellten Verwandteneffekten nach wie vor nicht erklärt werden kann. Strassman & Kurapati (2010) gehen sogar so weit, kooperative Fortpflanzung in so genannten *natural fertility*-Populationen (d. h. ohne effektive Geburtenkontrolle) als ein generell eher seltenes Phänomen zu betrachten. Vermutlich lassen sich auch die Effekte von Großmüttern auf Fertilität und Nachwuchssterblichkeit aufgrund der beschriebenen Abhängigkeiten von ökologischen Opportunitätsräumen und Eigenschaften des Nachwuchs nur schlecht generalisieren, selbst wenn die genetische Abstammungslinie berücksichtigt wird (Sear & Mace, 2008). All dies deutet darauf hin, dass Kooperation in Verwandtennetzwerken keinesfalls bedingungslos erfolgt und dass sich Verwandteneffekte kontextabhängig voneinander unterscheiden. Richtung und Außmaß von Verwandteneffekten orientieren sich an Opportunitätskosten der in Frage kommenden Helfer und an der Machtverteilung zwischen reproduktiven Individuen und Helfern sowie zwischen den Helfern untereinander (vgl. Beekman et al., 2003).

Unter sozioökonomischen Beschränkungen – wie im Falle der landlosen Bevölkerung der historischen Krummhörn – wird erwartet, dass die Reproduktion budgetiert erfolgt wobei genetisch verwandte Frauen gegenüber nicht-verwandten Frauen bevorzugt werden könnten. Großmütter könnten beispielsweise versuchen, ihre leibliche Töchter vor schwerer Arbeitsbelastung zu schonen und stattdessen eher die Schwiegertochter ökonomisch ausbeuten. Anders dürfte die Situation im Falle von wohlhabenden Großbauerfamilien sein: Hier kann oft Personal eingestellt werden dass den Arbeitsausfall einer schwangeren Frau kompensiert, so dass Schwiegertöchter in Großbauerfamilien eher unter dem Risiko der reproduktiven Ausnutzung stehen. Für Mütter in wohlhabenden Großbauerfamilien fallen dann vermutlich jene Risiken ins Gewicht, welche aus den exzessiven Fertilitätsansprüchen der väterlichen Abstammungslinie resultieren können (Leonetti et al., 2007; Borgerhoff-Mulder, 2009) – falls Reproduktion eben nicht durch ökonomische Ressourcen limitiert ist.

1.1.3 Zielstellung der Arbeit

Aus der von Hamilton (1964a,b) entwickelten und eingangs geschilderten Theorie zur Verwandtenselektion lassen sich Hypothesen zur Funktionslogik von menschlichen Verwandtennetzwerken entwickeln (z. B. Euler & Michalski, 2008). Einerseits sollte die Bereitschaft zur Unterstützung zwischen Individuen mit derem genetischen Verwandtschaftsgrad zunehmen. Das heißt, es wird erwartet, dass bei asymmetrischen Verwandtschaftsverhältnissen unterschiedliche Effekte von Verwandten ausgehen (vgl. Leonetti et al., 2007). Aus diesem Umstand lässt sich u. a. direkt ableiten, dass das reproduktive Verhalten einer Mutter durch ihre leibliche Mutter (d. h. die mütterliche Großmutter) vermutlich anders beeinflusst wird als durch ihre Schwiegermutter (d. h. die väterliche Großmutter) weil zu letzterer nur eine relativ geringe Verwandtschaft besteht (Leonetti et al., 2007; Voland & Beise, 2005). Inwieweit sich die Effekte mütterlicher und väterlicher Großmütter auf mütterliche Investmententscheidungen im Einzelfall äußern, könnte jeweils von ökologischen Opportunitätsräumen abhängen (Beekman et al., 2003). Weil sich männliche und weibliche Interessen hinsichtlich Fruchtbarkeit und Elternverhalten je nach Verfügbarkeit von Ressourcen unterschiedlich realisieren lassen, könnten auch Verwandte je nach Ressourcenlage unterschiedliche Investmentstrategien verfolgen, z. B. indem sie der Mutter entweder mittels einer Verringerung der Nachwuchssterblichkeit eine niedrigere Fruchtbarkeit ermöglichen oder indem sie Ressourcen bereitstellen, welche eine höhere Fruchtbarkeit ermöglichen (s. auch Diskussion hierzu in Kap. 2).

Um diese Zusammenhänge besser zu verstehen, sollen anhand von Daten einer historischen Population in Ostfriesland (s. Abschnitt 1.2) funktionale Beziehungen zwischen der Anwesenheit der mütterlichen bzw. väterlichen Großmutter und dem reproduktivem Verhalten in Familien aufgedeckt werden. Um mögliche konditionale Investmententscheidungen zu erkennen, werden zusätzlich Wechselwirkungen mit weiteren Faktoren berücksichtigt. Neben der genetischen Abstammungslinie von potenziellen

Helfern gehören hierzu auch Variablen des sozioökonomischen Kontext (hier: landlose Arbeiterfamilien vs. landbesitzende Großbauern) sowie das Geschlecht des Nachwuchs.

Die in Kap. 2 vorgestellten Untersuchungen sollen dabei helfen, die beschriebene Kontextabhängigkeit von großmütterlichen Effekten in verschiedenen sozioökonomischen Bedingungen besser zu verstehen. Hierzu wurden Einflüsse von Großmüttern auf das Heiratsalter, das Alter zur ersten Geburt und auf die abgeschlossene Fruchtbarkeit von Müttern in landlosen Arbeiter- sowie in wohlhabenden Großbauerfamilien untersucht.

Die Länge der Zwischengeburtenabstände bietet sich als Indikator für mütterliche Investmententscheidungen an, weil die Konzeptionswahrscheinlichkeit während der Stillperiode deutlich reduziert ist (Howie & McNeilly 1982; Überblick in Vitzthum 2008). Somit deutet ein verkürzter Abstand zur nachfolgenden Geburt darauf hin, dass das Kind durch die Mutter entweder relativ früh abgestillt wurde oder bereits früh verstorben ist (s. auch Tracer 2009). Für die in Kap. 3 beschriebene Untersuchung von Großmuttereffekten auf die Länge der Zwischengeburtenabstände mussten deshalb jene Kinder, welche innerhalb des Zwischengeburtenabstands verstorben sind, ausgeschlossen werden. Von Interesse sind hier Unterschiede in den Einflüssen zwischen der mütterlichen und der väterlichen Großmutter. Vermutet wurde zunächst ein matrilineares Schonungsmotiv gegenüber tendenziell exzessiven patrilinearen Fertilitätsansprüchen, wie sie für einige Populationen beschrieben sind (Leonetti et al., 2007). Demzufolge würden väterliche Großmütter im Vergleich zu mütterlichen Großmüttern – im Durchschnitt – zu einer Verkürzung der Zwischengeburtenabstände führen.

Im Falle der väterlichen Großmutter könnten Effekte auf die Länge der Zwischengeburtenabstände zudem auch durch deren asymmetrische X-chromosomale Verwandtschaft zu ihren Enkeln und Enkeltöchtern beeinflusst werden (Fox et al., 2010; Rice et al., 2010). Es wäre zu erwarten, dass in Anwesenheit der väterlichen Großmutter Zwischengeburtenabstände nach der Geburt eines Mädchens vergleichsweise länger ausfallen als nach der Geburt eines Jungen (s. Abschnitt 1.1.2). Die Einflüsse von Großmüttern auf die Länge der Zwischengeburtenabstände sind Thema der in Kap. 3 vorgestellten Untersuchungen. Hierbei wurden die Effekte welche von der mütterlichen bzw. väterlichen Großmutter ausgehen, wie beschrieben, je nach Geschlecht des vorgeborenen Kindes differenziert.

Die Untersuchung dient dabei der Beantwortung folgender Fragen:

- Wie unterscheiden sich die Einflüsse zwischen mütterlicher und väterlicher Großmutter auf das mütterliche Alter zur ersten Geburt und die folgenden Zwischengeburtenabstände sowie die totale Geburtenzahl in unterschiedlichen sozioökonomischen Bedingungen?
- Könnten Unterschiede in der X-chromosomalen Verwandtschaft – wie sie bei Großmüttern in Abhängigkeit des Geschlechts des Enkels auftreten – adaptive Investmententscheidungen beeinflussen (vgl. Fox et al., 2010; Rice et al., 2010)?

1.2 Datengrundlage und statistische Modellierung

Das seit 1985 betriebene Langzeitprojekt „Die Familien der Krummhörn“ widmet sich der Rekonstitution von ostfriesischen Familien in der Krummhörn-Region, vornehmlich während des 18. und 19. Jahrhunders (Überblick in Voland, 2000). In ökologischer Terminologie, bevölkerte die Population der Krummhörn gewissermaßen ein „gesättigtes Habitat“, in dem die Reproduktionsmöglichkeiten durch die verfügbaren reproduktiven Ressourcen (Wohn- und Arbeitsplätze) bereits seit dem ausgehenden Mittelalter sehr stark limitiert wurden (z. B. Shenk et al., 2010). Aus vorangehenden Untersuchungen sind sozialgruppenspezifische Reproduktionsstrategien bekannt die dem unter Großbauern auftretenden Verdrängungswettbewerb (*local resource competition*) bzw. der besonders unter Töchtern aus landlosen Familien verbreiteten Konkurrenz um Partner (*local mate competition*) in unterschiedlicher Weise Rechnung tragen (Beise & Voland, 2008).

Insgesamt liegen für die Untersuchung Einträge zu Geburt, Ehe und Tod von insgesamt über 64 000 Personen vor, welche aus über 24 000 Familien stammen. Diese Informationen stammen überwiegend aus Kirchenbüchern bzw. Ortssippenbüchern, in denen u. a. Geburts-, Heirats- und Sterbedaten von Einwohnern dokumentiert sind. Die genealogische Verknüpfung von Parental- und Filialgenerationen erfolgte mittels Methoden der Familienrekonstitution, wie sie in Voland (2000) beschrieben sind. Eine Besonderheit der Krummhörn-Population bieten z. B. aus Steuerlisten stammende, detaillierte Informationen zu den Besitzverhältnissen und ausgeübten Berufen der Bewohner, so dass insgesamt ein umfassendes Bild von individuellen Lebensläufen innerhalb verschiedener Familien nachverfolgt werden kann (Voland, 2000).

Diese Datenbank muss allerdings – in Abhängigkeit von der spezifischen Fragestellung – nach bestimmten Kriterien (z. B. exakte Datumsangaben sowie Vollständigkeit der Einträge) eingeengt werden, um Artefakte bzw. Fehler in der Dokumentation nach Möglichkeit auszuschließen. Für die Untersuchungen zu großmütterlichen Einflüssen auf das Heiratsalters der Mutter bzw. ihr Alter zur ersten Geburt in Kap. 2 mussten u. a. jene Mütter ausgeschlossen werden, bei deren Hochzeit bzw. erster Geburt bereits beide Großmütter des Kindes tot waren, da diese Wahrscheinlichkeit stark mit dem Alter der Mutter korreliert. Insgesamt gingen so lediglich die Daten von 946 Müttern aus 793 Natalfamilien in die Untersuchung ein, welche alle Kriterien zu Vollständigkeit der Angaben und den spezifischen Untersuchungsgruppen erfüllen (s. Abschnitt 2.2.1). Für die Untersuchung der abgeschlossenen Fruchtbarkeit dieser Mütter ist es erforderlich, dass für keinen der Ehepartner ein Sterbealter unter 45 Jahren verzeichnet ist, was die Anzahl der Fälle noch weiter (auf 465 Mütter aus 401 Natalfamilien) reduziert. Die in Kap. 3 beschriebene Untersuchung zu großmütterlichen Einflüssen auf die Länge der Zwischengeburtenabstände schließt neben allen innerhalb des Zwischengeburtenabstandes verstorbenen Kindern auch die (vergleichsweise zahlenschwache)

Gruppe der Großbauerfamilien aus, so dass hier die Zwischengeburtenabstände von 1124 (vorgeborenen) Kindern aus 421 Natalfamilien berücksichtigt werden konnten.

Die zu untersuchenden Zusammenhänge zwischen der Anwesenheit von Verwandten und zumindest nachträglich „messbaren“ Merkmalen reproduktiven Verhaltens (z. B. dem Alter der Mutter oder dem Abstand zwischen den Geburten) lassen sich approximativ mittels mathematischer Formeln darstellen. Beziehungen zwischen Variablen werden in statistischen Modellen nicht deterministisch sondern stochastisch repräsentiert, d. h. es wird angenommen dass mögliche Beobachtungen jeweils spezifische Wahrscheinlichkeiten aufweisen. Vor allem in biologischen Daten ist es wichtig, Heterogenität aufgrund von unterschiedlichen Varianten angemessen zu berücksichtigen (vgl. Bolker et al., 2008). Ein derartiges Problem entsteht z. B. im Fall verschiedener Mütter aus derselben Herkunftfamilie innerhalb einer Stichprobe: Schwestern sind sich aufgrund ihrer gemeinsamen Abstammung wahrscheinlich auch in phänotypischer Hinsicht überdurchschnittlich ähnlich, was der statistischen Grundannahme widerspricht, dass verschiedene Fälle voneinander unabhängig sein müssen. Um diesem Umstand Rechnung zu tragen, erfolgte die Modellkalibrierung und Schätzung der Unsicherheit robust gegenüber miteinander korrelierten Schwester-Fällen (die ID der mütterlichen Natalfamilie diente als entsprechende *Cluster*-Variable).

Für die Untersuchungen wurden historische Vitaldaten und deren genealogische Verhältnisse mittels verschiedener, jeweils frei-erhältlicher Programmbibliotheken innerhalb der Softwareumgebung *R* analysiert (R Development Core Team 2011; Angaben zu den in den Untersuchungen verwendeten Paketens finden sich in den entsprechenden Kapiteln).

Die in den Untersuchungen verwendeten proportionalen und additiven Modelle zur Analyse von Überlebenszeiten wurden ursprünglich entwickelt im Zusammenhang mit epidemiologischen oder ingenieurwissenschaftliche Fragestellungen (vgl. Mills, 2011). Diese Verfahren haben gegenüber anderen generalisierten linearen Modellen mehrere Vorteile. Einerseits können zensierte Daten (d. h. unvollständig beobachtete Fälle) wie sie in Überlebensanalysen häufig aufgrund von Migration oder konkurrierender Ereignisse (d. h. unterschiedlicher Arten des Untersuchungsaustritts) auftreten in vielen Fällen dennoch in die Analyse einfließen. Andererseits verzichtet das semi-parametrische Cox *proportional hazards* Modell darauf, den sogenannten *baseline hazard* d. h. die grundsätzliche Wahrscheinlichkeit für ein Ereignis während eines bestimmten Zeitraums, näher zu spezifizieren. So lassen sich innerhalb des Cox Modells Einflüsse auf die Wahrscheinlichkeit für das Eintreten eines Ereignisses sogar dann identifizieren, wenn die Verteilung dieser Wahrscheinlichkeiten über die Zeit für den Grundzustand unbekannt ist (Cox, 1972). Eine bedeutende Grundannahme des so genannten Cox-Modells besteht aber darin, dass für die spezifizierten Einflussfaktoren (im Gegensatz zur nonparametrischen *baseline*), Proportionaliät angenommen wird. Weil deshalb Änderungen der Effekte über die Zeit innerhalb des Cox-Modells nur eingeschränkt repräsentiert werden können, wird in Kap. 3 und Kap. 2 das vollständig nonparametrische, addititve Aalen-Modell zu Untersuchungen herangezogen (Martinussen & Scheike, 2006).

Bei der Untersuchung von großmütterlichen Effekten auf die mütterliche Gesamtzahl an Geburten (Kap. 2) gilt es, so genannte Zähldaten zu analysieren. Hierfür eignet sich prinzipiell das Poisson-Modell (auch weil in diesem Fall die Stichprobe lediglich aus Müttern besteht und somit keine Inflation an Nullwerten besteht). Dieses generalisierte, lineare Modell nimmt an, dass die logarithmierte Geburtenzahl von Müttern (d. h. von Frauen mit mindestens einer Geburt) innerhalb der Stichprobe einer Poisson-Verteilung unterliegt wobei hier die Varianz der Schätzungen deren Mittelwert übersteigt (*overdispersion*). Eine Ursache hierfür könnte sein, dass sich Frauen aus unterschiedlichen Natalfamilien – vermutlich auch aufgrund genetischer Einflüsse – überdurchschnittlich voneinander unterscheiden. Deshalb wird diesem Umstand Rechnung getragen, indem das Modell unterschiedliche Achsenabschnitte für unterschiedliche mütterliche Natalfamilien annimmt (*mixed intercept model*).

1.3 Zusammenfassung der Ergebnisse

Dieser Abschnitt gibt einen Überblick über die Ergebnisse jener Arbeiten, welche als Fachartikel Teil der vorliegenden Dissertation sind. Zu detaillierten Angaben der verwendeten Methoden sei auf den Methodenteil des entsprechenden Kapitels verwiesen.

1.3.1 Mütterliches Heiratsalter und das Alter zur ersten Geburt

In der in Kap. 2 beschriebenen Studie wird untersucht, wie in unterschiedlichen sozioökonomischen Bedingungen das Heiratsalter der Mutter sowie das Alter zur ersten Geburt durch die Anwesenheit einer mütterlichen oder väterlichen Großmutter beeinflusst werden. Hierbei wird deutlich, dass das Heiratsalter einer Mutter und ihr Alter zur ersten Geburt in landlosen Arbeiterfamilien anders mit der Anwesenheit der mütterlichen Großmutter zusammenhängt als in Großbauerfamilien (s. Abb. 2.1). Modellberechnungen zeigen im Falle von Arbeiterfamilien, dass Mütter wenn sie ihre erste Geburt im Wohnort der mütterlichen Großmutter (d. h. ihrer leiblichen Mutter) haben zum Zeitpunkt ihrer Hochzeit bzw. ihrer ersten Geburt durchschnittlich über ein Jahr jünger sind als Mütter die zu dieser Zeit bei der väterlichen Großmutter (d. h. ihrer Schwiegermutter) leben. Für Mütter in sozioökonomisch privilegierten Großbauerfamilien, welche generell zur Hochzeit bzw. zum Zeitpunkt der Geburt des ersten Kindes um 1-2 Jahre jünger sind als Mütter in Arbeiterfamilien, haben die Schätzungen der Großmuttereffekte jedoch entgegengesetzte Richtungen. In Großbauerfamilien sind Mütter, wenn sie ihre erste Geburt nahe der mütterlichen Großmutter haben, demnach tendenziell älter als jene Mütter, welche ihre erste Geburt nahe der väterlichen Großmutter haben.

1.3.2 Abgeschlossene Fruchtbarkeit von Müttern

Außerdem kann in Kap. 2 gezeigt werden, dass der beschriebene konditionale Einfluss, welcher von der mütterlichen Großmutter auf das Alter einer Mutter zum Zeitpunkt ihrer ersten Geburt ausgeht, nicht ohne Folgen bleibt, was deren Gesamtzahl an Geburten betrifft. Jene Mütter welche nahe der mütterlichen Großmutter leben, haben in der Gruppe der Arbeiterfamilien die höchste Fruchtbarkeit, wohingegen sie in der Gruppe der Großbauerfamilien die niedrigste Fruchtbarkeit aufweisen. Diese Unterschiede können modelliert und in Simulationsläufen dargestellt werden (s. Abb. 2.4). Während in dem finalen Modell die Erhöhung der Geburtenzahl aufgrund der Anwesenheit der mütterliche Großmutter in der Gruppe der Arbeiterfamilien lediglich als schwach signifikant angezeigt wird ($P = 0.059$), zeigt sich eine deutliche Umkehrung dieses Effekts in der Gruppe der Großbauerfamilien, wonach die mütterliche Großmutter unter dieses Bedingungen zu einer niederigeren Fruchtbarkeit führt ($P = 0.018$).

1.3.3 Die Länge der Zwischengeburtenabstände

In Kap. 3 werden mögliche Einflüsse von Großmüttern auf die Länge der Zwischengeburtenabstände untersucht. Ein Vergleich der Zwischengeburtenabstände (innerhalb der Gruppe der die Säuglingszeit überlebenden Kinder) zeigt, dass die Anwesenheit der väterlichen Großmutter im Geburtsort, im Gegensatz zur mütterlichen Großmutter, je nach Geschlecht des Kindes unterschiedlich mit der Länge des Zwischengeburtenabstandes korreliert. Nur die Anwesenheit der väterlichen Großmutter (aber nicht der mütterlichen Großmutter) führt zu einer Verlängerung des Zwischengeburtenabstandes nach geborenen Mädchen (aber nicht nach geborenen Jungen). Die Zwischengeburtenabstände nach der Geburt eines Mädchens sind zwar generell im Durchschnitt mehrere Wochen kürzer als nach der Geburt eines Jungen, allerdings verschwindet dieser Unterschied falls die väterliche Großmutter im Wohnort der Familie anwesend ist (s. Abb. 3.1). Dieser konditionale Effekt, welcher in Abhängigkeit vom Geschlecht des Kindes auftritt, zeigt sich auch wenn mittels statistischer Modelle die Einflüsse anderer Kovariaten (z. B. Geburtenrang, Alter der Mutter und Geburtskohorte) kontrolliert werden.

1.4 Diskussion

Die Einflüsse von mütterlichen bzw. väterlichen Großmüttern auf das reproduktive Verhalten in Familien der historischen Krummhörn verdeutlichen exemplarisch die strategische Vielfalt an Verwandtschaftsbeziehungen in unterschiedlichen sozioökonomischen Bedingungen. Dabei bilden asymmetrische genetische Verwandtschaftsverhältnisse die Ausgangslage für genomische Konflikte in Familien (vgl. Kamel et al., 2010, für Meeresorganismen) wobei hier je nach sozioökonomischen Bedingungen entweder (wie im Falle der Großbauern) die weibliche Fekundität oder (wie im Falle der landlosen Bevölkerung) die ökonomische Arbeitskraft der Frau im Mittelpunkt des Konflikts steht. Es kann sich dabei um Schwiegerkonflikte handeln, bei denen unterschiedliche genetische Interessen zwischen Mutter und Vater gewissermaßen auf deren Natalfamilien so auch auf Großeltern ausstrahlen (Leonetti et al., 2007; Scelza, 2011; Voland & Beise, 2002). Aber aber die differenzielle X-chromosomale Verwandtschaft zwischen der väterlichen Großmutter und ihren Enkeln unterschiedlichen Geschlechts kann bewirken, dass sich die reproduktiven Interessen hinsichtlich des Geschlechterverhältnis unter dem Nachwuchs zwischen der Mutter und der väterlichen Großmutter unterscheiden (z. B. Fox et al., 2010; Rice et al., 2010, vgl. Diskussion in Kap. 3).

1.4.1 Schwiegerkonflikte und sozioökonomischer Kontext

Die in Kap. 2 beschriebenen Unterschiede in den Einflüssen mütterlicher und väterlicher Großmütter auf das mütterliche Alter zur ersten Geburt und deren totale Geburtenzahl scheinen die Annahme von konditionalen Verhaltensstrategien zu bekräftigen. Mütter in landlosen Arbeiterfamilien, welche ihre erste Geburt im Wohnort der mütterlichen Großmutter (d. h. im Wohnort ihrer Natalfamilie) haben, bekommen deutlich früher ihr erstes Kind und erreichen aufgrund ihres verlängerten reproduktiven Intervalls auch eine höhere Gesamtgeburtenzahl d. h. abgeschlossene Fruchtbarkeit. In Großbauernfamilien dagegen, welche insgesamt eine höhere Fruchtbarkeit aufweisen, geht ein tendenziell gegensätzlicher Effekt von der mütterlichen Großmutter aus, d. h. hier haben Frauen – wenn sie ihre erste Geburt im Wohnort ihrer Mutter hatten – eine vergleichsweise niedrige Fruchtbarkeit.

Diese Zusammenhänge zeigen, dass Mütter in ressourcenarmen Bedingungen offenbar beschleunigend auf die (in dieser Gruppe relativ späte) Aufnahme der Reproduktion ihrer Töchter einwirken während die (ansonsten meist relativ frühe) erste Geburt von Frauen in Großbauerfamilien durch die Anwesenheit von deren Mutter verzögert wird. Auch wenn nicht als signifikant angezeigt, zeigten sich für die Effekte der Schwiegermutter in beiden Fällen gegensätzliche Tendenzen. Das heißt, in landlosen Familien könnten Schwiegermütter die erste Geburt ihrer Schwiegertochter noch weiter verzögern bzw. in Großbauerfamilien darüber hinaus beschleunigen. So zeigt sich insgesamt ein Muster, in welchem Großmütter die mit der Mutter verwandt sind, Unterschiede aufgrund von sozioökonomischen Bedingungen abmildern während Großmütter die mit dem Vater verwandt sind, diese Unterschiede im Vergleich zwischen unterschiedlichen Sozialgruppen sogar tendenziell verstärken.

Es ist plausibel, dass reproduktiver Erfolg in sehr unterschiedlichem Maße durch weibliche Fruchtbarkeit oder verfügbare Helfer beschränkt wird weil jeweils unterschiedliche reproduktive Ressourcen als limitierender Faktor wirken können (vgl. Beekman et al., 2003). Je nachdem, welche Art von reproduktiven Ressourcen auf die genetische Fitness limitierend wirkt (z. B. ökonomische Ressourcen oder weibliche Fekundität), ergeben sich aus diesen Einschränkungen auch unterschiedliche reproduktive Interessen (z. B. Low, 2005). Dies hat auch Auswirkungen auf das Mächteverhältnis der Beteiligten innerhalb von Partnermarkt und Familiennetzwerken und führt so zu konditionalen Investmentstrategien. Unter Bedingungen der Ressourcenknappheit könnten die elterlichen Opportunitätskosten, welche bei der Schwangerschaft einer Schwiegertochter anfallen (Verlust von Arbeitskraft für den elterlichen Haushalt) evtl. reproduktive Vorteile einer erhöhten Fruchtbarkeit gänzlich aufwiegen (Voland & Beise, 2002, 2005). Die in Kap. 2 vorgestellten Daten zeigen, dass Schwiegertöchter in landlosen Arbeiterfamilien wahrscheinlich eher im Hinblick auf ihre Arbeitskraft ausgebeutet wurden, während das schwiegermütterliche Interesse in wohlhabenden Großbauerfamilien vermutlich eher eine teilweise riskanten Steigerung der mütterlichen Fruchtbarkeit betraf.

Als mögliche Erklärung für diesen kontextuellen Unterschied in den Effekten der mütterlichen Großmutter und der väterlichen Großmutter auf die mütterliche Fruchtbarkeit bietet sich an, dass adaptives Investment ein dynamisches System – ähnlich einer so genannten *source-and-sink*-Dynamik – darstellt. Hier werden Ressourcen spezifisch in die Reproduktion bestimmter Verwandte alloziert, wobei die ökologischen Bedingungen dafür ausschlaggebend sind, inwieweit individuelle Interessen zwischen mehreren potenziellen Helfern und Brütern durchgesetzt werden können. So wird deutlich, dass die Effekte aufgrund einer unterschiedlichen Verwandtschaft (d. h. mütterliche vs. väterliche Großmutter) offenbar in Wechselwirkung mit Unterschieden in den sozioökonomischen Bedingungen (d. h. Landlose bzw. Großbauern) stehen. Demnach müssen die Effekte welche von der mütterlichen und väterlichen Großmutter auf das Heiratsalter und die Fruchtbarkeit von Müttern ausgehen zusätzlich entsprechend der Sozialgruppenzugehörigkeit der Familie differenziert werden (s. Kap. 2).

Beise (2005) zeigt ebenfalls kontextuelle Unterschiede in den Einflüssen der paternalen Großmutter auf die Kindersterblichkeit anhand eines Vergleichs von Familien aus der historischen Gründer-Population Québecs im kanadischen St. Lawrence Valley mit der Situation in der historischen Krummhörn. Nur innerhalb der Québec-Population, welche in demographischer Hinsicht sehr stark von der Krummhörn abweicht, zeigen sowohl mütterliche wie auch väterliche Großmütter einen positiven Effekt auf die kindliche Überlebenswahrscheinlichkeit, während im Falle der Krummhörn-Population lediglich die maternale Großmutter das kindliche Überleben verbesserte (Beise, 2005). Beise (2005) interpretiert diese Diskrepanz als Folge von unterschiedlichen reproduktionsökologischen Rahmenbedingungen und Verfügbarkeit von Ressourcen, weil es sich zumindest bei der frühen Population Québecs im Gegensatz zur Krummhörn um eine typische so genannte *frontier*-Population mit anfangs nahezu unbegrenzten Expansionsmöglichkeiten handelt. Hier treten Schwiegertöchter und Töchter sehr viel seltener in Konkurrenz zueinander, ganz im Gegenteil, handelt es sich doch bei dem limitierenden Faktor von Reproduktionserfolg in dieser Population eher um weibliche Fekundität anstatt um (reichlich vorhandene) Grundlagen der ökonomischen Subsistenz.

Rodrigues & Gardner (2012) haben kürzlich gezeigt, wie stark sich Verwandtschaft und intrafamiliäre Konkurrenz wechselseitig beeinflussen können und dass deshalb gerade innerhalb von Populationen mit heterogen verteilten Ressourcen fakultatives Hilfe- bzw. Konkurrenzverhalten selektiv begünstigt wird. Auch Barclay & Reeve (2012) argumentieren, dass Individuen, je nachdem ob sie sich in einer eher guten oder eher schlechten individuellen Verfassung befinden, unterschiedliche Formen der Hilfe anbieten können. Um die Dynamik in einem solchen System aus potentiellen *Sinks* (d. h. Müttern) bzw. potentiellen *Sources* (d. h. Helfern) zu untersuchen, ist es nötig, auch Einflüsse von Geschwistern beider Eltern mit zu berücksichtigen, schließlich können Geschwister sowohl Ressourcen beisteuern als auch um Ressourcen konkurrieren. Theoretisch sollten insbesondere Schwägerinnen als potentielle Konkurrentinnen der Mutter besonders einflussreich sein weil sie für väterliche Verwandte (wie z. B. die väterliche Großmutter) eine bedeutende Investmentalternative darstellen.

1.4.2 Unterschiede in der X-chromosomalen Verwandtschaft

Kap. 3 zeigt, dass auch die Unterschiede in der X-chromosomalen Verwandtschaft zwischen den geborenen Enkeln und der väterlichen Großmutter für deren Investmententscheidungen von Bedeutung sein könnten. Dabei wurden Unterschiede in den Einflüssen von Großmüttern auf die Länge der Zwischengeburtenabstände innerhalb der Gruppe der die Säuglingszeit überlebenden Kinder deutlich, welche mit der differenziellen, X-chromosomalen Verwandtschaft zu Enkelinnen oder Enkeln korrelieren. Dabei zeigt sich, dass in Anwesenheit der väterlichen Großmutter Zwischengeburtenabstände nach der Geburt eines Mädchens vergleichsweise länger ausfallen als Zwischengeburtenabstände nach der Geburt eines Jungen. Dieser Unterschied deutet auf eine Diskriminierung männlicher Enkel durch die väterliche Großmutter hin weil infolge der verkürzten Zwischengeburtenabstände männliche Enkel im Vergleich zu ihren Schwestern relativ früh mit der Geburt eines Geschwisters konfrontiert werden.

Die spezielle Form der heterogametischen Reproduktion zeichnet sich bei Menschen dadurch aus, dass lediglich Töchter das väterliche X-Chromosom erben, welches ausnahmslos von der väterlichen Großmutter stammt (vgl. Fox et al., 2010). Es wurde vermutet, dass X-chromosomale Allele deshalb eine Rolle für die Bevorzugung weiblicher Enkel durch die väterliche Großmutter spielen könnten indem sie Mechanismen der Verwandtschaftserkennung beeinflussen und z. B. aufgrund spezifischer Merkmale Unsicherheiten der Vaterschaft seitens patrilinearer Verwandte reduzieren (Fox et al., 2010).

Rice et al. (2010) haben außerdem gezeigt, dass die spezielle Situation der Geschlechtschromosomen zu intragenomischen Konflikten und zur Evolution von „*grandparental harm*“ führen kann. Hierbei handelt es sich um eine Form der Schädigung von phänotypisch identifizierten Nichtträgern des großelterlichen Geschlechtchromosoms aufgrund der in Abschnitt 1.1.2 beschriebenen „*Green-Beard*“-Effekte. Die phänotypische Erscheinung könnte auch deshalb von besonderer Bedeutung sein weil bei weiblichen Säugern im Zuge der Dosiskompensation jeweils eines der X-Chromosomen epigenetisch inaktiviert wird (Überblick in Brockdorff & Turner, 2007). Weil diese (tatsächlich oder scheinbar wahllose) Inaktivierung eines der X-Chromosomen in einem relativ frühen embryonalen Stadium (bis zur Gastrulationsphase) erfolgt und über die Zelllinien hinweg stabil ist, sind weibliche Säuger als genetisches Mosaik ihrer beiden X-Chromosomen konstituiert, welche in jeweils unterschiedlichen, diskreten Bereichen exprimiert werden. Es könnte sein, dass auch die großmütterliche Verhaltensstrategie (d. h. die Bevorzugung oder Schädigung) gegenüber Enkeltöchtern daran ausgerichtet wird, inwieweit bestimmte Merkmale (z. B. Körperform, Geruch, Verhalten) durch das betreffende X-Chromosom der Großmutter geprägt sind (s. Diskussion in Kap. 3).

Die in Kap. 4 präsentierten Modelle zeigen, dass X-chromosomale *Green-Beard*- Allele für die väterliche Großmutter selbst noch im Falle einer extrem hohen Vaterschaftsunsicherheit selektiv begünstigt würden (Abb. 4.3). Dies liegt daran, dass männliche Enkel niemals das X-Chromosom ihrer väterlichen Großmutter tragen können und deshalb für deren X-Chromosom immer einen geringeren Reproduktionswert (nämlich 0) aufweisen als Enkeltöchter. Männliche Enkel stellen allerdings für die Reproduktion des X-Chromosoms potentielle Konkurrenten zu Enkeltöchtern, so dass die Schädigung männlicher Enkel durch die väterliche Großmutter auch bei einer hohen Vaterschaftsunsicherheit für die Reproduktion des X-Chromosoms unter vielen Umständen vorteilhaft sein kann.

Eine solche Schädigung männlicher Enkel durch die väterliche Großmutter ist allerdings prinzipiell nachteilhaft für das autosomale Genom (Rice et al., 2008). Seki (2012) hat kürzlich den Konflikt zwischen autosomalen und X-chromosomalen Genen über das relative Investment in Enkelkinder anhand eines einfachen (haploiden) Modells mit jeweils zwei Allelen für zwei Loci untersucht. Seki (2012) interpretiert seine Modellergebnisse als Hinweis darauf, dass sich in dem intragenomischen Konflikt zwischen Autosomen und X-Chromosomen erstere unter den meisten Bedingungen durchsetzen würden. Allerdings berichtet Seki (2012) auch, dass die Frequenz von autosomalen bzw. X-chromosomalen Angepasstheiten innerhalb der Population unter bestimmten Bedingungen oszillieren kann so dass für unterschiedliche Populationen eine Vielzahl von Lösungen für den Ausgang dieses Konflikts existieren könnte. Andererseits stellt Seki (2012) selbst fest, dass durch sein Modell wichtige Einflüsse ignoriert werden wie z. B. die unterschiedliche Rekombinationsrate zwischen beiden Kontrahenten (vgl. Rice et al., 2010)).

1.4.3 Fazit und Ausblick

Die Vermutung, dass für die festgestellte Variabilität in großmütterlichen Effekte auf das Reproduktionsverhalten sowohl die asymmetrische Verwandtschaft zur Mutter als auch unterschiedliche ökologische Bedingungen (z. B. aufgrund einer unterschiedliche Ressourcenverfügbarkeit) von Bedeutung sein können, wird durch die hier vorgestellten Untersuchungen erhärtet. Die Ergebnisse zeigen, dass Helfereffekte hochgradig konditional sind und sich sogar innerhalb einer bestimmten Helfergruppe wie bei mütterlichen oder väterlichen Großmüttern kontextabhängig unterscheiden können. Wie sich gezeigt hat, äußern sich genomische Konflikte in menschlichen Familien daher offenbar in Abhängigkeit von sozioökonomischen Bedingungen, so dass Untersuchungen zu Verwandteneffekten immer auch den jeweiligen sozioökonomischen Kontext mit berücksichtigen müssen.

Mace & Alvergne (2012) haben anhand historischer Daten aus Gambia gezeigt, dass sich der Konflikt zwischen Matri- und Patrilinie auch in der reproduktiven Konkurrenz zwischen jüngeren und älteren Frauen widerspiegelt. Diese Konkurrenzsituation wird zwischen Müttern und Töchtern offenbar anders gelöst als zwischen Schwiegermüttern und Schwiegertöchtern (Mace & Alvergne, 2012). Wie Mace & Alvergne (2012) zeigen, wird die Reproduktion der Mutter durch die erste Geburt der eigenen Tochter deutlich gedrosselt (d. h. verlängerte Zwischengeburtenabstände und eine geringere Wahrscheinlichkeit weiterer Geburten) während schwiegertöchterliche Geburten keine vergleichbaren Effekte bewirken. Offenbar schränken Mütter ihre eigene Reproduktion ein, um stattdessen ihre Töchter in deren Reproduktion zu unterstützen während sie ihren Schwiegertöchtern diese Hilfe nicht oder nur teilweise zukommen lassen (Mace & Alvergne, 2012).

Diese von Mace & Alvergne (2012) beschriebene reproduktive Konkurrenz zwischen jüngeren und älteren Frauen könnte auch für die in Kap. 2 vorgestellten Befunde eine Rolle spielen. Gerade für junge Frauen dürften die Einflüsse von Mutter bzw. Schwiegermutter auf Eheschließung und Familiengründung nicht unerheblich gewesen sein (Apostolou, 2010). Auch wenn sich die reproduktiven Phasen zwischen Mutter und Tochter (im Sinne von Phasen des Kinderkriegens) in der Krummhörn aufgrund des relativ späten Heiratsalters kaum überlappen, könnte das zur Aufzucht der Kinder benötigte Investment auch mehrere Jahre nach der letzten Geburt der Mutter noch zu Konkurrenzsituationen mit frühgeborenen Töchtern führen. Es wäre denkbar, dass wie von Mace & Alvergne (2012) beschrieben, Mütter ihre eigene Reproduktion drosseln um stattdessen verstärkt ihre eigene Tochter in deren Reproduktion zu unterstützen bzw. ihr diese zu ermöglichen. Der Befund, dass Töchter früher ihre erste Geburt haben wenn sie zu diesem Zeitpunkt bei ihrer Mutter leben ist dahingehend zu überprüfen, ob deren Mütter (d. h. die mütterliche Großmutter) ihre Fertilität, ähnlich wie in der Studie von Mace & Alvergne (2012) abbremsen.

Besonders interessant wäre auch in diesem Zusammenhang der Einfluss der sozioökonomischen Bedingungen, weil – wie ebenfalls bereits von Mace & Alvergne (2012) vermutet – eine hohe Ressourcenverfügbarkeit (etwa im Falle von Großbauer-Familien) diese Form der Konkurrenz zwischen Müttern und Töchtern abmildern könnte, so dass in Großbauernfamilien durchaus beide Generationen simultan Kinder bekommen könnten. Diese Zusammenhänge sind zurzeit Gegenstand von weiterführenden Untersuchungen.

Literatur

☞[zitiert auf Seite(n)]

Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior*, 31, 39–47. [☞19]

Austad, S. N. (1997). Postreproductive survival. In K. W. Wachter & C. E. Finch (Eds.), *Between Zeus and the salmon. The biodemography of longevity* (pp. 161–174). National Academy Press, Washington, DC. [☞2]

Barclay, P. & Reeve, H. K. (2012). The varying relationship between helping and individual quality. *Behavioral Ecology*, 23(4), 693–698. [☞17]

Beekman, M., Komdeur, J., & Ratnieks, F. L. (2003). Reproductive conflicts in social animals: who has power? *Trends in Ecology and Evolution*, 18(6), 277–282. [☞8, 9, 16]

Beise, J. (2005). The helping and the helpful grandmother – The role of maternal and paternal grandmothers in child mortality in the seventeenth- and eighteenth century population of French settlers in Québec and Canada. In E. Voland, A. C. A., & W. Schiefenhövel (Eds.), *Grandmotherhood – The Evolutionary Significance of the Second Half of Female Life* (pp. 215–238). New Brunswick & London: Rutgers University Press. [☞16]

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. [☞11]

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2008). Gerneralized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24(3), 127–135. [☞12]

Borgerhoff-Mulder, M. (2009). Tradeoffs and sexual conflict over women's fertility preferences in Mpimbwe. *American Journal of Human Biology*, 21, 478–487. [☞6, 9]

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. [☞18]

Chrastil, E. R., Getz, W. M., Euler, H. A., & Starks, P. T. (2006). Paternity uncertainty overrides sex chromosome selection for preferential grandparenting. *Evolution and Human Behavior*, 27, 206–223. [☞7]

Coall, D. A. & Hertwig, R. (2010). Grandparental investment: Past, present, and future. *Behavioral and Brain Sciences*, 33, 1–59. [☞1, 2]

Cox, D. R. (1972). Regression models and life tables (with discussion). *Journal of the Royal Statistical Society Series B (Statistical Methodology)*, 34, 187–220. [☞12]

Danielsbacka, M., Tanskanen, A. O., Jokela, M., & Rotkirch, A. (2011). Grandparental child care in Europe: Evidence for preferential investment in more certain kin. *Evolutionary Psychology*, 9, 3–24. [☞6]

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press. [☞7]

Dawkins, R. & Krebs, J. R. (1979). Arms races between and within species. *Proceeding of the Royal Society London Series B: Biological Sciences*, 205, 489–511. [☞7]

Driscoll, C. (2009). Grandmothers, hunters and human life history. *Biology and Philosophy*, 24(5), 665–686. [☞3]

Emlen, S. T. (1995). An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, 92, 8092–8099. [☞1]

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. [☞1, 9]

Fisher, R. A. (1958). *The Genetical Theory of Natural Selection*. Dover Publications. [☞3]

Foote, A. D. (2008). Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biology Letters*, 4(2), 189–191. [☞2]

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. [☞1, 6, 10, 15, 17]

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7, 1–16. [☞3, 5, 7, 9]

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, 7, 17–52. [☞3, 5, 7, 9]

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12(1), 12–45. [☞1, 2, 3]

Hawkes, K. (1989). Hardworking Hadza grandmothers. In V. Standen & R. A. Foley (Eds.), *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals* (pp. 341–366). Oxford: Blackwell Scientific Publications. [☞3]

Hawkes, K. (2011). How grandmother effects plus individual variation in frailty shape fertility and mortality: guidance from human-chimpanzee comparisons. *Proceedings of the National Academy of Sciences of the United States of America*, 107(Suppl 2), 8977—-8984. [☞2, 4]

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academies of Sciences USA*, 95, 1336–1339. [☞1, 2, 4]

Hill, K. & Hurtado, A. M. (1991). The evolution of premature reproductive senescence and menopause in human females: An evaluation of the 'Grandmother Hypothesis'. *Human Nature*, 2(4), 313–350. [☞4]

Howie, P. W. & McNeilly, A. S. (1982). Effect of breast-feeding patterns on human birth intervals. *Journal of Reproduction and Fertility*, 65(2), 545–557. [☞10]

Hrdy, S. B. (1981). „Nepotists" and „altruists": The behavior of old females among macaques and langur monkeys. In P. T. Amoss & S. Harrell (Eds.), *Other Ways of Growing Old: Anthropolgical Perspectives* (pp. 59–96). Stanford: Stanford University Press. [☞3]

Hrdy, S. B. (2005). Cooperative breeders with an ace in the hole. In E. Voland, A. Chasiotis, & W. Schiefenhövel (Eds.), *Grandmotherhood: The evolutionary significance of the second half of female life* (pp. 295–317). Rutgers University Press. [☞1, 4]

Hrdy, S. B. (2008). Evolutionary context of human development: The cooperative breeding model. In C. A. Salmon & T. K. Shackelford (Eds.), *Family Relationships - An Evolutionary Perspective* (pp. 39–68). Oxford University Press. [☞1]

Hrdy, S. B. (2009). *Mothers and others – The evolutionary origins of mutual understanding*. Belknap/Harvard: Cambridge. [☞1]

Jamison, C. S., Cornell, L. L., Jamison, P. L., & Nakazato, H. (2002). Are all grandmothers equal? A review and a preliminary test of the "Grandmother Hypothesis" in Tokugawa Japan. *American Journal of Physical Anthropology*, 119, 67–76. [☞5]

Johow, J., Wilführ, K., & Voland, E. (Im Erscheinen). Reproductive strategies in female post-generative life. In M. L. Fisher, J. R. Garcia, & R. S. Chang (Eds.), *Evolution's Empress: Darwinian Perspectives on the Nature of Women* (pp. XXX–XXX). Oxford University Press, New York. (Alle Autoren haben gleich zu dieser Arbeit beigetragen.). [☞1]

Kamel, S. J., Grosberg, R. K., & Marshall, D. J. (2010). Family conflicts in the sea. *Trends in Ecology and Evolution*, 25, 442–449. [☞15]

Kushnick, G. (2012). Helper effects on breeder allocations to direct care. *American Journal of Human Biology*, 24, 545–550. doi:10.1002/ajhb.22268. [☞2]

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., & Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, 428, 178–181. [☞5]

Lancaster, J. B. & King, B. J. (1985). An evolutionary perspective on menopause. In J. K. Brown & V. Kerns (Eds.), *Her Prime: A New View of Middle-Aged Women* (pp. 13–20). South Hadley, Mass. (USA): Bergin and Garvey. [☞3]

Leonetti, D. L., Nath, D. C., & Hemam, N. S. (2007). In-law conflict – women's reproductive lives and the roles of their mothers and husbands among the matrilineal Khasi. *Current Anthropology*, 48, 861–890. [☞1, 6, 9, 10, 15]

Low, B. S. (2005). Women's lives there, here, then, now: a review of women's ecological and demographic constraints cross-culturally. *Evolution and Human Behavior*, 26, 64–87. [☞2, 6, 16]

Mace, R. & Alvergne, A. (2012). Female reproductive competition within families in rural Gambia. *Proceedings of the Royal Society: Biological Sciences*, X, XXX–XXX. in press, doi: 10.1098/rspb.2011.2424. [☞19, 20]

Martinussen, T. & Scheike, T. H. (2006). *Dynamic regression models for survival data*. New York: Springer. [☞13]

Mills, M. (2011). *Introducing Event History and Survival Analysis*. Sage: London. [☞12]

Nath, D. C., Leonetti, D. L., & Steele, M. S. (2000). Analysis of birth intervals in a non-contracepting Indian population: An evolutionary ecological approach. *Journal of Biosocial Science*, 32, 343–354. [☞5]

Pavelka, M. S. M. & Fedigan, L. M. (1991). Menopause: a comparative life history perspective. *Yearbook of Physical Anthropology*, 34, 13–38. [☞3]

Peccei, J. S. (1995). A hypothesis for the origin and evolution of menopause. *Maturitas*, 21, 83–89. [☞4]

Peccei, J. S. (2001). Menopause: Adaptation or epiphenomenon? *Evolutionary Anthropology*, 10, 43–57. [☞3]

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. [☞6]

Pollet, T. V., Nelissen, M., & Nettle, D. (2009). Lineage based differences in grandparental investment: evidence froma large British cohort study. *Journal of Biosocial Science*, 41, 355–379. doi:10.1017/S0021932009003307. [☞6]

R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna and Austria, 2.12 edition. ISBN 3-900051-07-0. URL: http://www.R-project.org. [☞12]

Rice, W. R. (1984). Sex chromosomes and the evolution of sexual dimorphism. *Evolution*, 38, 735–742. [☞7]

Rice, W. R. (1992). Sexually antagonistic genes – experimental evidence. *Science*, 256, 1436–1439. [☞7]

Rice, W. R., Gavrilets, S., & Friberg, U. (2008). Sexually antagonistic 'zygotic drive' of the sex chromosomes. *PLoS Genetics*, 4(12), e1000313 (12 pages). doi:10.1371/journal.pgen.1000313. [☞7, 8, 18]

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. [☞1, 4, 7, 8, 10, 15, 17, 18]

Robson, S. L., van Schaik, C. P., & Hawkes, K. (2006). The derived features of human life history. In K. Hawkes & R. R. Paine (Eds.), *The Evolution of Human Life History* (pp. 17–44). Santa Fe and New Mexico: School of American Research Press and Oxford: James Currey Ltd. [☞4]

Rodrigues, A. M. M. & Gardner, A. (2012). Evolution of helping and harming in heterogenous populations. *Evolution*, XXX, XXX–XXX. doi:10.1111/j.1558-5646.2012.01594.x. [☞17]

Scelza, B. A. (2011). Female mobility and postmarital kin access in a patrilocal society. *Human Nature*, 22(4), 377–393. DOI: 10.1007/s12110-011-9125-5. [☞15]

Sear, R. & Coall, D. (2011). How much does family matter? cooperative breeding and the demographic transition. *Population and Development Review*, 37(suppl.), 81–112. [☞ 1]

Sear, R. & Mace, R. (2008). Who keeps children alive? a review of the effects of kin on child survival. *Evolution and Human Behavior*, 29, 1–18. [☞ 1, 5, 8]

Sear, R., Mace, R., & McGregor, I. A. (2000). Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society of London, Series B*, 267, 1641–1647. [☞ 5]

Sear, R., Mace, R., & McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, 24(1), 25–42. doi:10.1016/S1090-5138(02)00105-8. [☞ 5]

Sear, R., Steele, F., McGregor, I. A., & Mace, R. (2002). The effects of kin on child mortality in rural Gambia. *Demography*, 39, 43–63. [☞ 5]

Seki, M. (2012). Intra-individual conflicts between autosomal and X-linked altruistic genes: Evolutionary perspectives of sex-specific grandmothering. *Journal of Theoretical Biology*, 304, 273–285. [☞ 4, 18]

Shenk, M. K., Mulder, M. B., Beise, J., Clark, G., Irons, W., Leonetti, D., Low, B. S., Bowles, S., Hertz, T., Bell, A., & Piraino, P. (2010). Intergenerational wealth transmission among agriculturalists. *Current Anthropology*, 51, 65–77. [☞ 11]

Strassman, B. I. & Kurapati, N. T. (2010). Are humans cooperative breeders? most studies of natural fertility populations do not support the grandmother hypothesis. *Behavioral and Brain Sciences*, 33, 35—-38. [☞ 4, 8]

Strassmann, B. I. & Garrard, W. M. (2011). Alternatives to the grandmother hypothesis. a meta-analysis of the association between grandparental and grandchild survival in patrilineal populations. *Human Nature*, 22, 201–222. [☞ 3]

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. [☞ 10]

Turke, P. (1988). Helpers at the nest: childcare networks on ifaluk. In L. Betzig, M. B. Mulder, & P. Turke (Eds.), *Human Reproductive Behavior: A Darwinian Perspective* (pp. 173–188). Cambridge, UK: Cambridge University Press. [☞ 1]

Tymicki, K. (2004). Kin influence on female reproductive behavior: The evidence from reconstitution of the Bejsce parish registers, 18th to 20th centuries, Poland. *American Journal of Human Biology*, 16, 508–522. [☞ 5]

Tymicki, K. (2008). When do kinsmen really help? Examination of cohort and parity-specifickin effects on fertility behavior. The case of the Bejsce parish register reconsitution study, 17th-20th centuries, Poland. In T. Bengtsson & G. P. Mineau (Eds.), *Kinship and Demographic Behavior in the Past* (pp. 135–154). Springer Science + Business Media B.V. [☞5]

Vitzthum, V. J. (2008). Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*, 37(4), 1–21. [☞10]

Voland, E. (2000). Contributions of family reconstitution studies to evolutionary reproductive ecology. *Evolutionary Anthropology*, 10(1), 134–146. [☞11]

Voland, E. & Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioral Ecology and Sociobiology*, 52, 435–443. [☞1, 5, 6, 15, 16]

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. C. . W. Schievenhövel (Eds.), *Grandmotherhood—The evolutionary significance of the second half of female life* (pp. 239–255). New Brunswick & London: Rutgers University Press. [☞5, 6, 9, 16]

West, S. A. & Gardner, A. (2010). Altruism, spite, and greenbeards. *Science*, 327, 1341–1344. DOI: 10.1126/science.1178332. [☞3]

White, Y. A. R., Woods, D. C., Takai, Y., Ishihara, O., Seki, H., & Tilly, J. L. (2012). Oocyte formation by mitotically active germ cells purified from ovaries of reproductive-age women. *Nature Medicine*, 18, 413–442. [☞4]

Williams, G. C. (1957). Pleiotropy and natural selection and the evolution of senescence. *Evolution*, 11, 398–411. [☞2, 4]

2 Conditional grandmother effects on age at marriage, age at first birth, and completed fertility of daughters and daughters-in-law in historical Krummhörn

Der folgende Text wurde als Artikel in der Zeitschrift *Human Nature* im Jahre 2011 zur Veröffentlichung angenommen und befindet sich im Erscheinen. Das Copyright liegt bei Springer Science+Business Media. Der Nachdruck erfolgt mit freundlicher Genehmigung von Springer Science+Business Media. Die Autoren sind:

Johannes Johow, Zentrum für Philosophie und Grundlagen der Wissenschaft Universität Giessen, Germany
Eckart Voland, Zentrum für Philosophie und Grundlagen der Wissenschaft Universität Giessen, Germany (corresponding author, Fon: + (49)-641-99-15550, Fax: + (49)-641-99-15509, Email: eckart.voland@phil.uni-giessen.de)

Abstract. Based on historic data pertaining to the Krummhörn population (18th - 19th centuries, Germany), we compared reproductive histories of mothers according to whether the maternal grandmother (MGM) or the paternal grandmother (PGM) or neither of these was resident in the parents' parish at the time of the first birth of the mother. In contrast to effects of PGMs, we discovered conditional differences in the MGM's effects between landless people and wealthier commercial farmers. Our data indicates that the presence of the MGM only lowers the woman's age at marriage (AAM) and her age at the birth of her first child (AFB) in the case of landless families. However, among commercial farmers, who can generally be characterized by a lower AAM and AFB, we found opposite tendencies for the MGM's effect leading to a relative small delay in AAM and AFB. Moreover, we also analyzed differences in the completed fertility (i. e. children ever born, CEB). Results indicate that landless families in general do have fewer CEB compared to commercial farmers except for those families where the MGM has been present. Emphasizing that the adaptiveness of investment decisions should depend on the interaction of genetic, lineage-specific ("intrinsic") and ecologically imposed ("extrinsic") constraints, we conclude that kin strategies consequently address different fitness components under different conditions.

2.1 Introduction

2.1.1 Mothers and mothers-in-law

The current emphasis on cooperative breeding in the field of human behavioral ecology and evolutionary psychology has not only led to new empirical insights but also to new theoretical problems (see Hrdy, 2009; Reiches et al., 2009). There is a need for research into the adaptiveness of conditional investment strategies of maternal and paternal kin in particular (cf. Johow et al., 2011). Reviewing studies on the effects of kin on child survival, Sear and Mace (2008, p. 15) came to the conclusion that an "analysis of what causes this variation in kin support should be the next step in furthering our understanding of the human family". Their conclusion is based on the considerable variation in the impact of kin that was detected in past research, even if potential helpers are divided into groups according to sex, age and lineage. This variation may be a consequence of the fact that adaptive investment can address different aspects of fitness such as fertility, child mortality and the reproductive value of existing offspring (Voland, 1998). Generally speaking, sex-related differences in the opportunity cost incurred by reproduction (mainly by reason of pregnancy, birth and lactation being solely female tasks) not only lead to differences in men and women's reproductive strategies but also inevitably result in diverging adaptive investment strategies between their kin (Leonetti et al., 2007; Penn and Smith, 2007). Therefore, the presence of genetic relatives – either of the mother (i.e. matrilineal) or of her husband (i.e. patrilineal) – is expected to correlate differently with levels of maternal fertility.

The assumption of fundamental differences between matrilinear and patrilinear investment strategies is supported by several empirical studies, showing that maternal grandmothers (MGMs) are more inclined to invest in grandchildren than paternal grandmothers (PGMs) (Euler and Michalski, 2008; Pollet et al., 2009; Voland and Beise, 2002). One hypothesis, for example, is a matrilinear motive to protect maternal health and counteract the patrilinear tendency towards exploitative fertility demands (Leonetti et al., 2007). This protective motive is consistent with indications of disparate preferences between mothers-in-law and daughters-in-law in planning the size of the family (Kadir et al., 2003) and it is possible, under certain circumstances, that the MGM may increase the likelihood of using contraceptives (Borgerhoff-Mulder 2009 for a village population in Tanzania). In addition, studies investigating a "natural fertility" population from the Gambia also suggest that female fertility tends to be enhanced more by patrilinear relatives than matrilinear ones (Allal et al., 2004; Sear et al., 2003).

2.1.2 Female age at marriage, age at first birth and the average number of offspring (completed fertility)

The first dependent variable, whose susceptibility to the influence of grandmothers is the topic of this study, is a woman's age at marriage (AAM). We know from historic, European communities that the onset of reproduction was often governed by marriage, strictly in accordance with the cultural norms (see Gehrmann 2003; Devos and Kennedy 1999). For several historical populations, differences in the AAM related to hypergamic behavior have been shown to produce a positive correlation between social status and fertility (see Voland, 1990; Clarke and Low, 2001; Skjaervoe et al., 2011). In many populations, marriage usually precedes the birth of the first child, and the female AAM and age at first birth (AFB) are highly correlated (cf. Udry and Cliquet, 1982). Even in bygone Krummhörn communities, which were the source of the data employed in the present study, so-called "illegitimate" births among unmarried women only accounted for a minority (less than 5 percent of all mothers in sample).

Whereas AAM tends to represent an arbitrary institutionalized event rather than a life-history transition, seen from an evolutionary perspective, the AFB is a typical life-history variable (cf. Robson et al., 2006). Differences in the AFB are thought to reflect reproductive strategies and cannot be influenced by differences in the survival status of any existing offspring. As the first full-term pregnancy, the AFB marks a fundamental life-history transition from somatic investment (or indirect reproductive effort such as pre-reproductive supportive behavior) to direct reproductive effort. The high demands and exigencies posed by pregnancy, birth and lactation are hardly compatible with continued growth, the search for a partner, or hard physical labour (Kaplan et al., 2002). These cost of reproduction (including opportunity cost), which form part of the trade-off regarding the optimum AFB, creates a bottom age limit for the birth of the first child. This limit is considerably less pronounced for men, even in the event of fatal complications in the case of their wife. For this reason, we assume, other things being equal, a stronger patrilinear interest in an early onset of generative behaviour and high fertility than the matrilinear one (Leonetti et al., 2007). Investigating a Caribbean village population, (Flinn, 1988) discovered that parents (and fathers in particular) strive to protect their daughters from commencing reproduction early in order to avoid a precipitated mating of their daughter with an unwanted son-in-law. On the other hand, Sear and Mace (2009) describe a (relatively weak) opposite effect in the case of women from the Gambia, namely that the presence of the father tends to lower the AFB.

These disparate findings could be due to fluctuations in the opportunity cost of reproduction under different socio-economic conditions. In that case, grandmother effects on the AFB should not only vary substantially between daughters and daughters-in-law but also between social groups living in different socio-economic conditions. Sear

(2008) also points out that cooperative relations can easily switch to competitive rivalry, depending on how social and ecological contexts vary. Reproductive conflicts arise because of differences that emerge in the opportunity cost of reproduction, and the relevant “power” of those involved always depends on ecological constraints, too (Beekman et al., 2003). Similarly, Apostolou (2010) argues that control over wealth in agropastoral societies provides men with more power over their offspring’s mating decisions compared to hunter-gatherer societies. Whilst socially accepted opportunities for gainful employment outside the family household enables working-class (landless) families to earn an income that is independent of the parents’ trade, on the one hand, it simultaneously determines the opportunity cost in the event of the onset of reproduction. Adaptive matrilinear and patrilinear investment needs to take this opportunity cost into account, in just the same way as adaptive parental investment, under various socio-economic conditions (cf. Houston et al., 2005). If, for example, circumstances allow the family sufficient scope to manage without a young women’s labour input at least for the time being, this might substantially reduce the economic opportunity cost of an early pregnancy on the patrilinear side, whereas other significant risks would still remain on the matrilinear side (such as the mother’s health risks and her effective ineligibility for marriage). The maternal fitness cost of an early pregnancy is therefore another decisive factor in determining a grandmother’s tendency to influence a daughter’s or daughter-in-law’s AFB. Due to the genetic relationship, these risks play a much greater role on the matrilinear side (since the man can always look for a new female partner “if the worst comes to the worst”).

2.1.3 Testing conditionality in grandmother effects

To test whether this hypothetical influence exerted by the MGM and the PGM on the AFB is reflected in the data pertaining to Krummhörn’s landless and commercial farming families, we investigated some data recorded in the family reconstitution study for Krummhörn in Ostfriesland (East Frisia) going back to the 18th and 19th centuries (methodological review: Voland 2000). During the period under review, the social make-up of this community was highly stratified, with different selective regimes in force between the landless and commercial farming families inducing social group specific reproductive strategies (cf. Beise and Voland 2008). Both matrilocal and patrilocal residence patterns can be found within the portion of philopatric families, i.e. those staying in the same parish where one or both of the spouses were born. We compared the AAM and AFB of mothers in landless families and wealthy commercial farming families, according to whether the MGM or the PGM lived in the same parish as the family at the time of the first birth. Families who lived in a parish without either grandmother were used as a control group in both cases while presupposing that at least one grandmother was still alive at the time of a mother’s first birth. Socially highly heterogeneous groups with smallholdings or medium-sized areas of land (containing civil servants as well as skippers, for example) were excluded from the study for the sake of simplification.

Because adequate resources for reproduction are only available at an early stage among commercial farming families in the case of the Krummhörn population, their fertility preferences should prove to be higher on the patrilinear side, i.e. in terms of the sons' marriages, than on the matrilinear side or the daughters' marriages. We can therefore expect the AFB to be comparatively higher in MGM families than in PGM opposite, non-significant tendencies families. The PGM might have the effect of overcoming the delaying tendencies of the daughter-in-law more easily by exerting social pressure, for example (Rotkirch and Janhunen, 2009). Circumstances in low-income. landless families are likely to be rather different: Reproduction is subject to budgeting because the loss of a grown woman's labour input is accompanied by substantial economic costs for the family. In view of uncertain paternity and economic exploitability of the daughter-in-law, grandmothers are likely to give priority to supporting their daughter's reproductive intentions by investing their own labour input and resources. It can accordingly be predicted that a relatively high availability of resources, as in the case of the Krummhörn commercial farming families, permits a relatively low AAM and AFB. As a consequence, women who marry younger and start reproducing earlier (as in wealthy farmer families) can have an increased completed fertility simply due to the comparably longer time span until the menopause. It is a known fact that young women exchange reproductive opportunities for patrilinear resources, so to speak, (particularly in the form of land ownership) in the Krummhörn community (Voland and Engel, 1990).

It could be that some women are able to compensate for their later start with shorter intervals between births and/or a later final birth. Besides the differences in the AAM and the AFB, we consequently analyzed differences in the total number of children ever born (CEB) as well, taking only live births of mothers with completed fertility into account, in this case. We not only applied various poisson mixed models but also a heckman 2-step model, which accounts for the possibility of a selection bias between the total sample and the mothers with completed fertility.

2.2 Methods

2.2.1 The Krummhörn database

Krummhörn is a coastal region in Ostfriesland (East Frisia), bounded by the North Sea and moorland, which has been used for farming since the Middle Ages and consequently became a popular location for settlements at a fairly early stage (Ohling, 1963). The family reconstitution study for the historic population that lived in this region is primarily based on church records and tax documents (cf. Voland, 2000). The socio-ecological situation in the bygone days of Krummhörn had already been compared with a "saturated habitat", as local competition for resources and mates called for specific reproductive strategies (cf. Beise and Voland 2008, for example). Data from 27 parishes (from a total of 32 parishes) are available for the study, predominantly for the 18th-19th century era. Incorporating the parishes in the database makes it possible to trace the migration of individuals within the Krummhörn area (which occurred quite frequently) to a satisfactory degree. Only those mothers whose reproductive history can be regarded as "documented in full" were investigated, i.e. it is imperative to know the exact marriage date (or wedding announcement) and date of death of the spouse who died first . In addition, the following criteria were applied in an attempt to exclude any possible artefacts or anomalies caused by gaps in the documentation and, wherever possible, to reduce the complexity of the statistic model. Only first and single marriages were analysed. In the case of the hazard models used to model AAM and AFB, we included all mothers of children who were born between the years 1720 and 1874. However, for the analysis of the number of a mother's children ever born (CEB), all mothers born after 1829 must have been excluded to make sure that we only deal with cases of completed reproductive histories, since data registration ends in 1874. The sequence in which the children were born had to be clearly identifiable from the known dates of birth (families with missing birth dates were excluded). It was imperative to know the AFB. Mothers with an AFB lower than 15 years (less than 1 permille) or higher than approx. 35 years (the 95 percent quantile) were excluded as fairly implausible, so these cases were deemed to be invalid.

This sample provided data from 17,455 individuals who were born to 3158 mothers. For the specific purposes of this study, it was also necessary to fulfill the following criteria:

Socio-economic situation of the family (created by a woman's marriage) was estimated on the basis of the amount of land this family cultivated. Families who operated little land or a medium-sized acreage (i.e. smallholdings and middle-sized farms) were excluded, as there can be quite substantial variations in the socio-economic conditions of this group. Families who did not administer any land were finally compared with commercial farming families with an acreage of more than 74 grasen (one gras being the equivalent of approximately 0.92 acres). In the case of the landless families, it was also presumed that maternal and paternal grandparents did not work on land of more than 74 grasen, as this would also increase heterogeneity within the sample. Mothers who were still unmarried more than one year following the birth of their first child were excluded. Mothers with a protogenetic interval above the 95 percent quantile (˜ 3.1 years) were excluded due to the relatively high probability of an unregistered still birth. The MGM or the PGM was assumed to have been present if the following criteria were met:

1. The relevant grandmother's date of death must be after the birth of the first child.
2. The relevant grandmother's place of death must also be the place of birth of the first child. To avoid cases in which the grandmother subsequently moved to her grandchild's birth place, we also presumed earlier entries for her place of proclamation or marriage.

Finally we only included families where at least one grandmother was alive at the time of the first birth – regardless of whether she was present or absent. Families where both grandmothers were present in their grandchild's birth parish are also excluded.

In total, the final data sample includes 946 mothers who are descended from 793 families of origin. In order to investigate mothers' completed fertility, we also applied the following criterion for inclusion in this specific analysis: Families where the age at death of one of the spouses is recorded as being below 45 years have been excluded. Of all 946 mothers included in the final sample, we found 465 mothers from 401 families-of-origin whose fertility was completed (see tab. 2.1 for Ns of specific subgroups). The decision to include only mothers with completed fertility was taken in order to avoid the possibility of bias in the case of different mortality between certain groups. However, these differences in hazard may also cause a selection bias owing to a comparably higher selection for maternal robustness within groups of increased maternal mortality. For this reason, the results of such restricted analyses may show phenotypic correlations rather than effects on female fertility due to kin support. To check for this possible shortcoming, we additionally applied the Heckman 2-step model, which accounts for the probability of a mother not being included in the second sample of the outcome model for CEB (Toomet and Henningsen, 2008).

2.2.2 Regression models

The theoretical model for estimating the AFB of a mother$_j$ depending on the presence of the MGM$_j$ or the PGM$_j$ and taking the socio-economic status ("farm$_j$") into account is expressed as follows:

$AFB_j \sim MGM_j + PGM_j + MGM_j : farm_j + PGM_j : farm_j + strata(season_j) + strata(cohort_j) + cluster(ID_j)$
AFB: age at first birth
MGM: maternal grandmother (0: absent, 1: present)
PGM: paternal grandmother (0: absent, 1: present)
farm: socio-economic status (0: no land, 1: more than 74 grasen)
MGM:farm/ PGM:farm: interactive effects
cohort: cohort factor (quartile of birth year)

season: season of birth of the mother (quantile of birt month
) ID: ID of the mother's family-of-origin

All analyses were performed using recent versions of the software environment R 2.12.1 (R Development Core Team, 2011). Cox and Aalen models are implemented in the "timereg" package (Martinussen and Scheike, 2006). The special ´strata' function was included on the right-hand side of the model formula to divide the data into subgroups with different baseline hazard functions. "Cluster" is used to specify mothers from the same family of origin as non-independent observations and is accordingly used to compute robust standard errors. As soon as any violation of the proportionality assumption was diagnosed within the original Cox model using the test provided by (Therneau and Lumley, 2009), we transferred all the terms from these models to the additive Aalen model. The Aalen model is able to account for time-varying effects of covariates. Plotted cumulative coefficients show corresponding changes in the effects over time. Plotted cumulative coefficients of the Aalen estimates were finally used to test for time-varying effects of the main predictors on the AAM and the AAM. These plots indicate significant effects on the AAM and AFB on a 95 percent significance level whenever the confidence bands cross the zero line.

The poisson mixed model was applied in order to test if possible effects of grandmothers on a mother's AAM and AFB have an impact on the completed fertility of a generative career. Numbers of children ever born (CEB) were modeled using a mixed intercept poisson model (Bailey and Alimadhi, 2007) on a subsample consisting only of mothers with completed fertility (selection criteria see above). Basically, we used the same formula as in the AAM and AFB models except that we moved the strata and cluster variables (i.e. the cohort variable, the season variable and the ID of the mother's family of origin) into random intercept terms of the model. The poisson mixed model thus takes the following form:

$CEB_j \sim farm_j + MGM_j + PGM_j + MGM_j : farm_j + PGM_j : farm_j + (1|season_j) + (1|cohort_j) + (1|ID_j)$

Goodness-of-fit was evaluated by gradually removing non-significant estimates and testing candidate models against each other in terms of ANOVA. To check for the effects of grandmothers living elsewhere at the date of birth of the first child, a subsample of the data was finally used which excluded every locally present grandmother while replacing the variables MGM and PGM with the predictors "MGM alive elsewhere" and "PGM alive elsewhere". This model simply compares the group where only the MGM is alive elsewhere at the date of birth of the first child with the group where the PGM is alive elsewhere.

In order to test for a possible selection bias resulting from the exclusion of mothers who died during their generative phase, we also applied the Heckman 2-step model. However, the outcome model accounting for a possible selection bias estimated the

Table 2.1: Observed median values for maternal age at marriage (AAM), age at first birth (AFB), and the number of children ever born (CEB) for landless and farmer families within data sample.

	Grandmothers absent	MGM present	PGM present
(Landless)	(N = 269)	(N = 266)	(N = 335)
Median AAM (years)	25.30	24.49	25.53
Median AFB (years)	26.03	25.09	26.33
(Farmers)	(N = 36)	(N = 17)	(N = 23)
Median AAM (years)	22.42	23.03	21.96
Median AFB (years)	23.19	24.18	22.87
(Landless)	(N = 120)	(N = 137)	(N = 164)
Median CEB	5	6	6
(Farmers)	(N = 22)	(N = 8)	(N = 14)
Median CEB	7	5	7

effects in accordance with the Poisson mixed model, and therefore only is provided in the supplement.

2.3 Results

Grandmothers, age at marriage and the birth of the first child (AFB). As illustrated in Fig. 2.1 panel A and panel B, the MGM's effect on the maternal age at marriage (AAM) and the age at first birth (AFB) differs between the families of landless and those of commercial farming families: with landless families, the presence of the MGM leads on average to a relatively low AAM and AFB, while among commercial farmers the MGM tends to lead to a relatively high AAM and AFB (see also Table. 2.1). Kaplan-Meier plots for the AFB in Fig. 2.2 not only show the clear distinction between the grandmother effects in landless families but also considerable uncertainty in the case of the commercial farming families, which could be due to the relatively small number of cases studied in this group.

The fit of initial, multivariate Cox models, allowing for strata effects due to different cohorts and seasons of the mother's birth shows violations of the proportionality assumption (see right column in supplementary Table S1). Therefore all the terms from these models were moved to the additive Aalen models.

Results of the additive Aalen models given in Table 2.2 and Fig. 2.3 should be interpreted as follows: In case of constant effects of a covariate the plotted cumulative coefficients against time in Fig. 2.3 should approximate a straight line. The left-hand columns in Table 2.2 and presented p-values refer to tests which are based on this rational thus signifcant p-values would indicate varying estimates over time. The right-hand colums give a test for non-significance of the total effect, that is when the cumulative effect is 0 at the endpoint. Since the PGM effects could not be estimated significantly at any time in the full model (see blue graphs in supplementary Fig. S1) we excluded these terms from the best fit model (Table 2.2). Plots of the estimated cumulative regression coefficient (with pointwise 95 percent confidence bands) demonstrate the effect of belonging to the group of commercial farmers instead of the landless people (´farm') significantly increases the hazard of marriage and first birth (left-hand panels in Fig. 2.3). There is an increase approx. between the age of 20 and approx. 25 for the effect of the MGM in landless families. Taking into consideration the main effects of "farm" and the MGM, there is also an interaction effect showing opposite estimates in case of farmer families where the MGM is present (right-hand panels in Fig. 2.3). Thus, taken by itself, "being farmer" and "presence of the MGM" both are associated with earlier marriage and earlier first birth of a woman but not in case of a combination of these.

However, any significant differences in the grandmother effects between landless and commercial farming families disappear when applying our models to families whose grandmothers lived in a parish other than of the parents (see supplementary Table S3).

Fertility outcomes: Differences in the numbers of children ever born (CEB). Considering total number of children ever born (CEB) between mothers who belong to a farmer family and mothers who belong to a landless family, it is apparent that mothers in landowning (farmer) families have on the average about 1.3 more children than mothers in landless families (Means: 7.0 in commercial farmer families and 5.7 in landless families; Paired t-Test on random sample: t = 2.1059, df = 43, p-value = 0.041). Table 2.1 and Panel C and D in Fig. 2.1 show observed CEB for mothers of different case groups within each of the socioeconomic groups (landless and farmers). While Panel C in Fig. 2.1 indicates that among landless people the presence of the MGM may correlate positively with maternal CEB, opposite tendencies are found in case of farmers (Panel D in Fig. 2.1) for which the presence of the MGM may correlate negatively with CEB.

To model CEB, we applied a mixed intercept poisson regression accounting for overdis-

Table 2.2: Aalen additive hazards models on the influence exerted by the maternal and paternal grandmother (MGM and PGM respectively) on a mother's age at marriage (AAM) depending on a family's socio-economic status ("farm"). The left hand columns give tests for the null of constant effects (thus significant P-values indicate effects varying over time). The Supremum Test given in the right hand columns tests for the null that overall effect is 0 (at the observed maximum of time). See cumulative coefficients plots given in fig. 2.3 to consider the direction and strength of these effects at specific time-points. Strata estimates are not shown.

	Test for time invariant effects				Test for non-significant effects	
	Kolmogorov-Smirnov test	*P* (const.)	Cramer von Mises test	*P* (const.)	Supremum-test	*P* (B(t)=0)
			AAM, Best Fit Model			
(Intercept)	1.420	0.001	36.200	0.000	9.14	<0.001
Farm	1.590	0.003	7.350	0.156	4.31	<0.001
MGM	0.434	0.330	2.040	0.205	4.32	0.002
MGM:farm	1.470	0.076	13.300	0.182	3.25	0.032
			AAM, Full Model			
(Intercept)	0.659	0.001	7.8400	0.000	7.15	0.000
farm	0.456	0.424	3.2600	0.144	3.51	0.009
MGM	0.139	0.586	0.0777	0.594	3.75	0.010
PGM	0.137	0.396	0.2080	0.160	1.77	0.707
MGM:farm	0.404	0.878	1.2400	0.615	2.89	0.075
PGM:farm	1.240	0.045	18.7000	0.012	2.38	0.252

Table 2.3: Aalen additive hazards models on the influence exerted by the maternal and paternal grandmother (MGM and PGM respectively) on a mother's age at first birth (AFB) depending on a family's socio-economic status ("farm"). The left hand columns give tests for the null of constant effects (thus significant P-values indicate effects varying over time). The Supremum Test given in the right hand columns tests for the null that overall effect is 0 (at the observed maximum of time). See cumulative coefficients plots given in fig. 3 to consider the direction and strength of these effects at specific time-points. Strata estimates are not shown.

	Test for time invariant effects				Test for non-significant effects	
	Kolmogorov-Smirnov test	*P* (const.)	Cramer von Mises test	*P* (const.)	Supremum-test	*P* (B(t)=0)
			AFB, Best Fit Model			
(Intercept)	1.590	0.001	48.9000	0.000	9.33	<0.001
farm	1.320	0.017	5.8000	0.228	4.17	0.002
MGM	0.613	0.099	6.3900	0.034	4.16	0.002
MGM:farm	1.420	0.117	15.2000	0.168	3.46	0.019
			AFB, Full Model			
(Intercept)	0.6870	0.001	8.6700	0.000	7.23	0.000
farm	0.3630	0.548	1.7900	0.238	3.51	0.004
MGM	0.1350	0.631	0.3100	0.204	4.03	0.002
PGM	0.0977	0.754	0.0989	0.377	2.04	0.500
MGM:farm	0.3900	0.890	0.8820	0.760	2.75	0.106
PGM:farm	1.3900	0.016	24.8000	0.008	2.68	0.127

Table 2.4: Poisson mixed models on the influence exerted by the maternal and paternal grandmother (MGM and PGM respectively) on a mother's age at marriage (AAM) and a mother's age at first birth (AFB) depending on a family's socio-economic status ("farm"). Panel A gives the full model finally used to calculate the predictions shown in Fig. 2.4. Panel B reports the best fit model excluding non-significant estimates of the full model. Panel C presents an unconditional model without interaction effects.

	Estimate	Std. Error	z value (P-val.)
A) CEB, Final Model			
AIC=505; BIC=542; LogLIK=-243; deviance=487			
(Intercept)	1.6766	0.0403	41.6 (<0.001)
farm	0.3706	0.0881	4.2 (<0.001)
MGM	0.1017	0.0538	1.9 (0.059)
PGM	0.0648	0.0528	1.2 (0.22)
farm:MGM	-0.4224	0.1787	-2.4 (0.018)
farm:PGM	-0.2173	0.1415	-1.5 (0.125)
B) CEB, Best Fit Model			
AIC=503.9; BIC=532.8; LogLIK=-244.9; deviance=489.9			
(Intercept)	1.71354	0.02640	64.91 (<0.001)
farm	0.27714	0.06794	4.08 (<0.001)
MGM	0.06504	0.04435	1.47 (0.1425)
Farm:MGM	-0.32948	0.16951	-1.94 (0.0519)
C) CEB, Unconditional Model			
AIC=507.4; BIC=536.4; LogLIK=-246.7; deviance=493.4			
(Intercept)	1.70504	0.03801	44.85 (<0.001)
farm	0.22151	0.06311	3.51 (<0.001)
MGM	0.05586	0.05083	1.10 (0.27)
PGM	0.03078	0.04911	0.63 (0.53)
AIC	BIC	LogLik	deviance

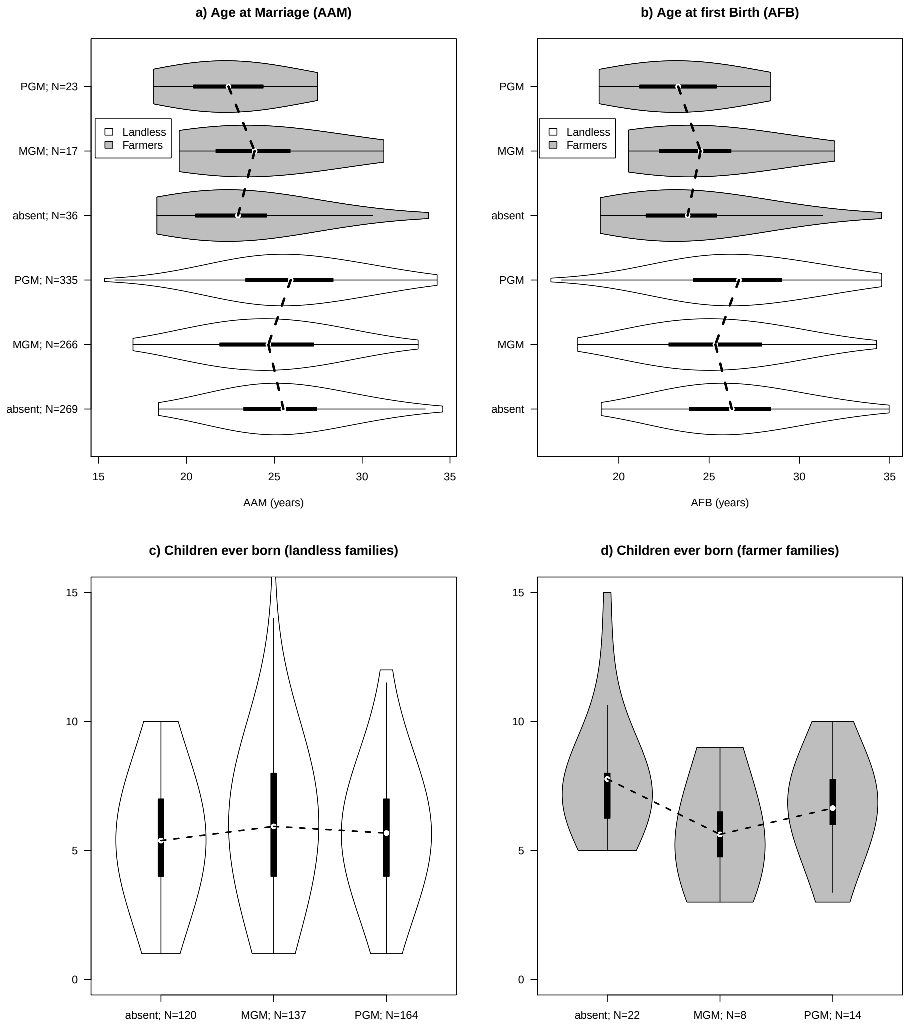

Figure 2.1: The violin plots depicted here give an estimate of the relative likelihood of obtaining values (kernel density distribution) and the position of the actual quartiles (the 'boxes') and mean (connected with dashed lines for illustrative purposes). a) Woman's age at marriage (AAM) plus the number of cases in the groups under investigation for landless (white) and farmers (gray). b) Age of the mothers at the birth of their first child (AFB). Bottom panels show the numbers of children ever born (CEB) among landless people (c) and commercial farmers (d), respectively.

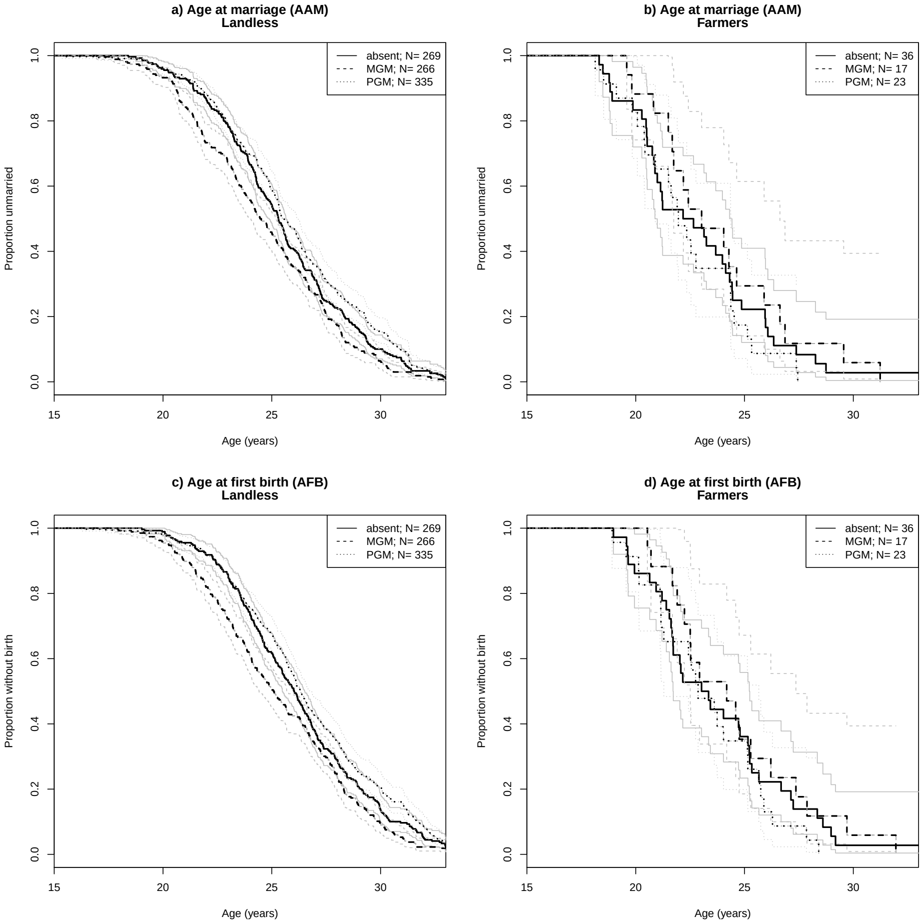

Figure 2.2: Kaplan-Meier plots for the proportion of mothers awaiting their marriage (panels a + b) and the birth of their first child (panels c + d) against their age with 95% confidence intervals (without controlling the cohort effects). These statistics include mothers from families who either live without either of the grandmothers (continuous line) or with the MGM (dashed line) or with the PGM (dotted line) in the same parish. Landless families are depicted on the left-hand side (panels a + c), and commercial farming families on the right-hand side (panels b + d).

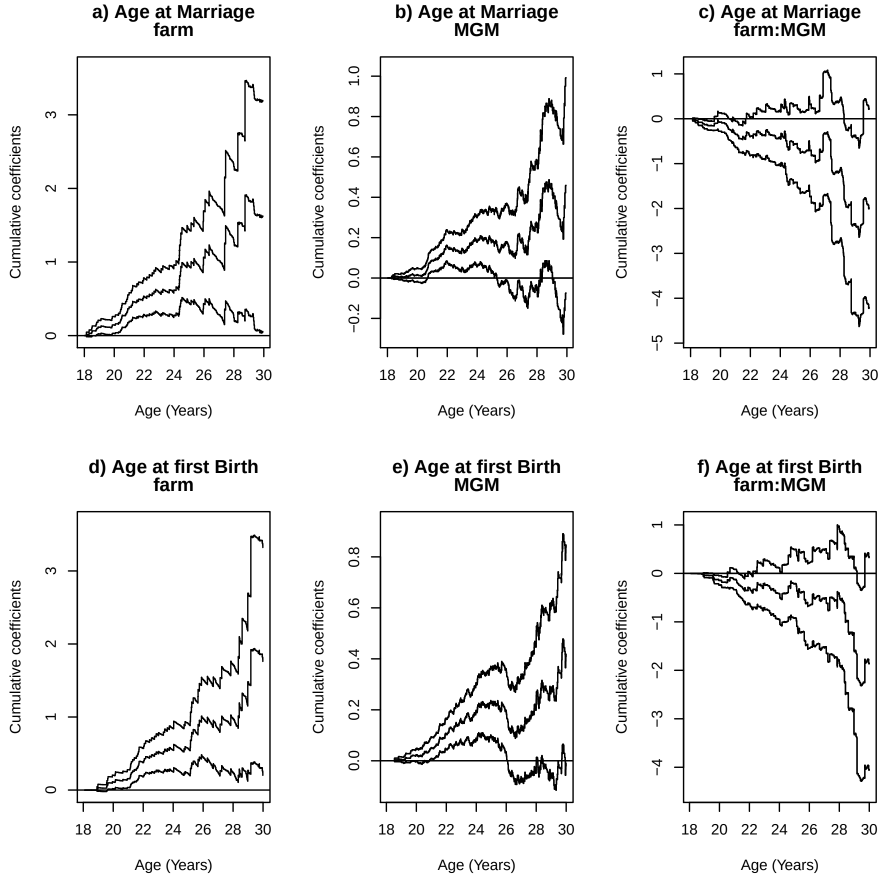

Figure 2.3: Cumulative regression coefficients in the Aalen best fit models (see Table 2.2). Given are pointwise 95% confidence bands for estimated effects exerted by farmer status ("farm"), the maternal grandmother (MGM) and the interaction with farmer status ("MGM:farm") on the age at marriage (AAM, panels a-c) and the age at first birth (AFB, panels d-f) of the mothers under investigation. Thus whenever the confidence band crosses the 0 line the specific effect is estimated significantly ($P < 0.05$). Non-significant estimates of the paternal grandmother (see Table 2.2 and blue lines in supplementary Fig. S1) are excluded from this "best fit" model.

Table 2.5: Estimates in case of grandmothers being absent from the parent's parish at time of birth of the first child. Strata estimates are not shown.

CEB, Absent grandmothers only (separate sample)			
	Estimate	Std. Error	z value (P-val.)
(Intercept)	1.65880	0.05701	29.098 (<0.001)
farm	0.41712	0.19092	2.185 (0.0289)
MGM	0.06664	0.07051	0.945 (0.3446)
Farm:MGM	-0.16778	0.21180	-0.792 (0.4283)

Table 2.6: ANOVA estimates indicating if there are significant differences in the goodness-of-fit between specific models.

Tested models (df: degrees of freedom)	Chi^2 (P-value)
Model B (7 df) and model A (9 df)	2.88 (0.23)
Model C (7 df) and model A (9 df)	6.4789 (0.039)
Model B (7 df) and model C (9 df)	3.59 (<0.001)

persion between mothers from different families. Model selection criteria indicate that including an interaction terms between the grandmother variables and the "farm" variable significantly increases the goodness-of-fit compared to the unconditional model (see Table 2.3). Neither the PGM alone nor the interaction effect between farmer status and the PGM were estimated significantly (all p>0.1) so these terms have been removed in a best fit model which shows a similar goodness-of-fit (Table 2.3). Whereas estimates of the best fit model indicate that landownership correlates positively with the mother's CEB (p<0.001), it was not possible to obtain a significant estimate for the effect of the MGM alone (p=0.14). However, the interaction between MGM and farmer status gives a negative estimate at a borderline significance level (p=0.0519). To make model predictions, we nevertheless decided to include the predictors "farm", "MGM" and "PGM" and both interaction effects of these in our final model (Table 2.3) in order to compare all groups specifically. By comparing the estimates between the final model and the best fit model in Table 2.3 it was possible to verify that the two models are similar. Fig. 2.4 shows the model predictions based on our final model presented in Table 2.3. It is apparent that the estimated differences in the CEB between landless families and farmer families disappear in the case of families where the MGM has been present at the time of the first birth. This is because the presence of the MGM correlates positively with CEB among landless families but negatively among commercial farmers. In order to account for any selection bias due to the restriction for mothers who died before the age of 45, we also fit the heckman 2-step model. The results of this model are in accordance with the results of the poisson mixed models

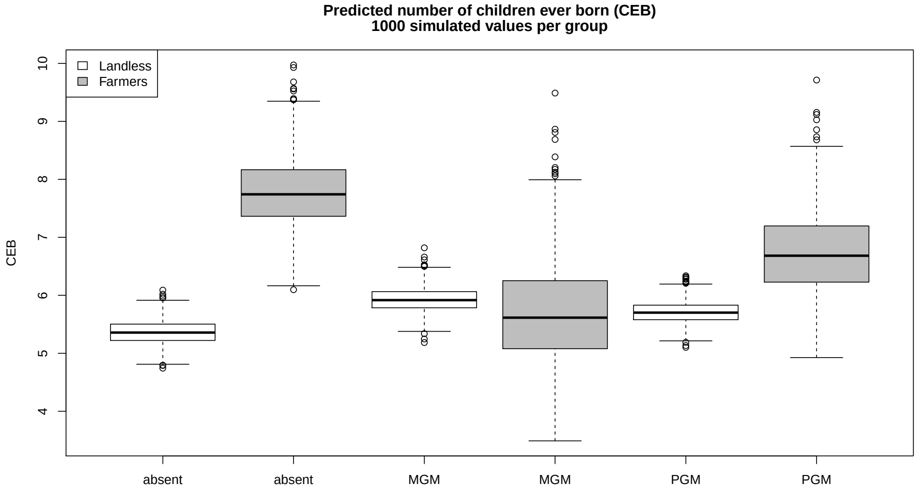

Figure 2.4: Model predictions of the number of children ever born (CEB) to mothers living in the same parish either with the maternal or the paternal grandmother (MGM and PGM respectively) at the date of the first birth, depending on the family's socio-economic status ("farm"). Each prediction is based on 1000 simulated values of the Poisson mixed model described in Table 2.4A.

presented in Table 2.3 and therefore are provided in the supplement. As in case of the AAM/AFB-analyses, also in case of the CEB, no signifcant estimate for any grandmother effect could be obtained if considering grandmothers living elsewhere than at the parent's parish at the time of first birth of the mother (see Table 2.3).

2.4 Discussion

We have presented data from the historical population of the Krummhörn showing how the presence of the maternal grandmother (MGM) or the paternal grandmother (PGM) is associated with a woman's age at marriage (AAM), age at first birth (AFB) and the number of children ever born (CEB). It is important to mention that women who marry a commercial farmer are usually younger than those marrying a landless labourer – regardless of the presence of grandmothers (Voland and Dunbar, 1997). With regard to the AAM in other historical societies, we also know that local elite men married the youngest brides which can partly be accounted for by socioeconomic constraints and preferences (Schlumbohm, 1991; Røskaft et al., 1992). The difference in the

AAM between women marrying a landless husband and women marrying a commercial farmer also extends to their AFB (Fig. 2.1) and CEB (Fig. 2.4, see also Voland 1990; Klindworth and Voland 1995). These social differences in the average AAM, AFB and CEB are subject to variation, however, with regard to the grandmother's presence. To begin with, we took a look at the connections between the presence of the MGM/PGM and the AAM, AFB and CEB for each of these groups. As regards the presence of the MGM at time of the mother's first childbirth, we found significant correlations with the AAM, AFB and CEB in every case. There is, however, a clear distinction, depending on the socio-economic conditions: it is only in the case of the landless that the MGM is associated with lower AAM (Diff.: approx. 0.8 years), lower AFB (Diff.: approx. 0.9 year) and higher CEB (Diff.: approx. 1 child) compared to the control group, while we found no effect for the paternal grandmother (PGM). A different situation emerges in the case of the commercial farmer families: here, the MGM is associated with higher AAM (Diff.: 0.6 years), higher AFB (Diff.: approx. 1 years) and lower CEB (Diff.: 2 children,) compared to the control group.

Model estimates support the assumption that the MGM's presence causes different effects between these social groups living under such dissimilar socio-economic conditions. The PGM's effects were found statistically non-significant. However, estimates show opposite tendencies compared to the MGM's effects both among landless people and among commercial farmers (see Table 2.1 and blue lines in Fig. S1 in electronic supplement). Due to the partially time-varying effects of our covariates, we applied the additive hazards model of Aalen. It is plausible that the effect of the MGM on her daughter's likelihood of marriage and first birth varies over time (see Fig. 2.3) because a mother may discourage (or prevent) her daughter from marrying early for a certain period but subsequently change her attitude. This is because a woman's maternal quality and value on the marriage market will alter over time, and these changes affect matrilineal and patrilineal opportunity cost due to marriage and first birth in a different manner. We interpret the marginal estimate in the case of the commercial farmers in some of these models as a consequence of the small sample size. Unbalanced case numbers between landless people and farmers also affect goodness-of-fit tests and conventional model selection criteria. So, in spite of the suggested best fit model (Table 2.3B), we decided to apply the full model presented in Table 2.3A in order to make predictions about a mother's completed fertility (Fig. 2.4). Significant estimates of these effects are also maintained in the Heckman 2-step model (see supplementary Table S2), which accounts for a possible selection bias, for instance, as a result of certain differences in maternal mortality between the different groups. The fact that the geographical proximity between grandmother and mother plays a role is demonstrated by the disappearance of this conditional effect when we take a look at families where the grandmothers lived outside the parental parish: In this case, no significant effect can be detected (see Table 2.5).

From a life history theory point of view, the AFB is a determinant factor in assessing the potential number of subsequent children she gives birth to and is consequently of considerable relevance in terms of her fitness, especially in the case of historical populations (Balakrishnan et al., 1988). For any female population, the AFB is restricted by the fitness cost of an early pregnancy. This fitness cost might be caused by the mother's effective ineligibility for the partner market or by a delicate maternal constitution and correspondingly poor opportunities for investment, for instance. Compensation for the deficiency in investment opportunities on the part of the mother in the case of a relatively early pregnancy might ideally be found in the form of a substitute mother, particularly a grandmother. This is because she can provide for and take good care of the child without suffering any real drawbacks in terms of her own reproductive success herself (Voland et al., 2005). It is for this reason that Coall and Hertwig (2010) propose that young mothers, in particular, benefit most from the support of a grandmother, partly because they are relatively dependent and partly because they can take advantage of the grandmother's assistance for a comparatively long time. The decline in investment opportunities for grandmothers during the course of their lifetime would accordingly be a motivation for encouraging the early production of grandchildren. Basing his research on an 18th and 19th century Japanese population with a patrilineal inheritance system, Skinner (2004) has demonstrated that the impact the PGM has on reproductive behavior depends on the age structure of those involved. It is plausible that the respective compromises revealed in the in-law conflict not only differ over the course of a lifetime but are also dependent on the room for maneuver accorded to any helpers, which in turn depends on their age (cf. Houston et al. 2005 for parental investment).

At least within agropastoral societies, the onset of reproduction is determined to a large degree by parental control over marriage (Apostolou, 2010). The parents of both the man and/or the woman may either permit or prohibit their offspring to marry and breed at their site by means of social pressure and/or economic dependencies. Under harsh conditions, it would appear that PGMs abandon attempts to support their daughters-in-law in producing grandchildren at an early stage. The earlier onset of reproduction being supported solely by the presence of the MGM could suggest that this opportunity cost arising from the loss of labor input on the part of the young mother is more likely to be offset by genetic relatives (kin) than by in-laws. According to data relating to smallholders in 19th century France, as analyzed in a socio-historical study, women going to live in the extended family of their husband (patrilocal marriage arrangement) married several years later than women marrying under matrilocal conditions (Margadant, 1998).

The situation is different in the case of commercial farmers, where the economic cost of marrying tends to hinge on the couple's inherited estate. Parents' "concerns about unscheduled marriage" (Lorenzen-Schmidt, 2003) were not unfounded, particularly in the case of families who owned land: the dowry required for couples embarking on family life was one of the main causes, not only of economic fluctuations and financial crises, but also of bankruptcy among the commercial farming community in these areas. By contrast, the economic cost incurred by pregnancy, birth and lactation was of hardly any consequence. As a rule, the family heir normally waited until taking over the parents' farm before marrying, and a married couple was usually able to delegate the bulk of the manual work to servants and farm hands (or possibly to unmarried siblings); so an early pregnancy in the case of married heirs of commercial farms is relatively "cheap".

One possible explanation for the contextual difference in the impact the MGM and PGM have on their daughter's or daughter-in-law's AFB may be that adaptive investment represents some kind of source-sink dynamics. Source-sink systems can be characterized by multiple patches of varying quality influencing each other through the flow of a certain good. In our case, genetic relatives represent patches interchanging reproductively relevant resources as a good, i.e. kin support. In this situation each individual inevitably faces a trade-off between the opportunities to breed or to 'help' (by releasing familial resources, for instance). So, the decision as to whether a woman represents either a contributor (a source) or a recipient (sink) of kin support is mainly determined through her transition to motherhood. Helper effects on breeder allocations to direct care vary due to the different opportunity cost between individuals determined by socio-ecological constraints.

It would appear that the reproductive interests of female kin are more regularly supported by family networks than those of female in-laws (Sear and Mace, 2008). It would be adaptive to make sure that genetically related females can achieve a fertility level near the maternal optimum while in case of in-laws however, exploitation of maternal resources (either reproducitvely or economically) might conflict with maternal interests (cf. Leonetti et al., 2007). Presented data is consistent with the assumption of a matrilineal motive to buffer environmental "disturbances" on maternal fertility. Past research has already revealed differences in infant mortality and stillborn babies with different grandmother situations (Voland and Beise, 2002, 2005), which also need to be taken into account here. The question whether the daughter-in-law's fertility was exploited by the female population of Krummhörn over and beyond the maternal optimum in the case of commercial farming families calls for further investigation into the fitness consequences resulting from the head start farmers' wives had because of their lower AFB.

In conclusion, our results may support the assumption of lineage-specific differences in grandmothering while simultaneously underlining the need for a differentiated approach to the specific opportunity cost that affects both matrilinear and patrilinear helpers. This study indicates that the interaction between lineage-specific relations and socio-economical conditions helps to explain the behavioral diversity evident in human kin effects.

Acknowledgements

We would like to thank Isabelle Cobres for inspiring discussion. Besides, we are thankful to two anonymous reviewers for providing valuable help during earlier stages of the manuscript. Financial support came from Deutsche Forschungsgemeinschaft (DFG) and from a personal grant to JJ from the University of Giessen.

References

☞[cited on page(s)]

Allal, N., Sear, R., Prentice, A. M., and Mace, R. (2004). An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proceedings of the Royal Society B: Biological Sciences*, 271:465–470. [☞28]

Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior*, 31:39–47. [☞30, 46]

Bailey, D. and Alimadhi, F. (2007). Poisson.mixed: Mixed effects poisson model. In Imai, K., King, G., and Lau, O., editors, *Zelig: Everyone's Statistical Software*. http://gking.harvard.edu/zelig. [☞34]

Balakrishnan, T. R., Rao, K. V., Krotki, K. J., and Lapierre-Adamcyk, E. (1988). Age at first birth and lifetime fertility. *Journal of Biosocial Science*, 20:167–174. [☞46]

Beekman, M., Komdeur, J., and Ratnieks, F. L. (2003). Reproductive conflicts in social animals: who has power? *Trends in Ecology and Evolution*, 38(6):277–282. [☞30]

Beise, J. and 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. [☞30, 32]

Borgerhoff-Mulder, M. (2009). Tradeoffs and sexual conflict over women's fertility preferences in Mpimbwe. *American Journal of Human Biology*, 21:478–487. [☞28]

Clarke, A. L. and Low, B. S. (2001). Testing evolutionary hypotheses with demographic data. *Population and Development Review*, 27:633–660. [☞29]

Coall, D. A. and Hertwig, R. (2010). Grandparental investment: Past, present, and future. *Behavioral and Brain Sciences*, 33:1–59. [☞46]

Devos, I. and Kennedy, L., editors (1999). *Marriage and rural economy: Western Europe since 1400.* Turnhout: Brepols. [☞29]

Euler, H. and Michalski, H. A. (2008). Grandparental and extended kin relationships. In Salmon, C. A. and Shackelford, T. K., editors, *Family Relationships – An Evolutionary Perspective*, pages 230–255. Oxford: Oxford University Press. [☞28]

Flinn, M. V. (1988). Parent-offspring interactions in a Caribbean village: daughter guarding. In Betzig, L., Mulder, M. B., and Turke, P. W., editors, *Human reproductive behaviour*, pages 189–200. Cambridge: Cambridge University Press. [☞29]

Gehrmann, R. (2003). Heiratsverhalten als historisches Problem. *Historical Social Research,*, 28:8–28. [☞29]

Houston, A. I., Szekely, T., and McNamara, J. M. (2005). Conflict between parents over care. *Trends in Ecology and Evolution*, 20:33–38. [☞30, 46]

Hrdy, S. B. (2009). *Mothers and others – The evolutionary origins of mutual understanding*. Belknap/Harvard: Cambridge. [☞28]

Johow, J., Fox, M., Knapp, L., and Voland, E. (2011). The presence of a paternal grandmother lengthens interbirth interval following the birth of a granddaughter in Krummhörn (18th and 19th centuries). *Evolution and Human Behavior*, 32(5):315–325. [☞28]

Kadir, M. M., Khan, F. F. F. A., and Sajan, F. (2003). Do mothers-in-law matter? family dynamics and fertility decision-making in urban squatter settlements of Karachi, Pakistan. *Journal of Biosocial Science*, 35:545–558. [☞28]

Kaplan, H., Lancaster, J. B., Tucker, W. T., and Anderson, K. (2002). Evolutionary approach to below replacement fertility. *American Journal of Human Biology*, 34:233–256. [☞29]

Klindworth, E. and Voland, E. (1995). How did the Krummhörn elite males achieve above-average reproductive success? *Human Nature*, 6:221–240. [☞45]

Leonetti, D. L., Nath, D. C., and Hemam, N. S. (2007). In-law conflict – women's reproductive lives and the roles of their mothers and husbands among the matrilineal Khasi. *Current Anthropology*, 48:861–890. [☞28, 29, 47]

Lorenzen-Schmidt, K. J. (2003). Bäuerliches Heiratsverhalten und Stellenübertragung in den holsteinischen Elbmarschen (1650-1950). *Historical Social Research*, 28:76–91. [☞46]

Margadant, T. W. (1998). Marriage contracts and stem-family households in the Lot-et-Garonne 1812–1872. In Brunet, G., Fauve-Chamoux, A., and Oris, M., editors, *Le choix du conjoint*, pages 283–294. Lyon. [☞46]

Martinussen, T. and Scheike, T. H. (2006). *Dynamic regression models for survival data.* New York: Springer. [☞34]

Ohling, G. D. (1963). Kulturgeschichte der Krummhörn. In Ohling, J., editor, *Die Acht und ihre sieben Siele. Kulturelle, wasser- und landwirtschaftliche Entwicklung einer ostfriesischen Küstenlandschaft*, pages 38–288. Pewsum: 1. Entwässerungsverband Emden. [☞31]

Penn, D. J. and Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *Proceedings of the National Academies of Sciences USA*, 304(2):553–558. doi:10.1073/pnas.0609301103. [☞28]

Pollet, T. V., Nelissen, M., and 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. [☞28]

R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna and Austria, 2.12 edition. ISBN 3-900051-07-0. URL: http://www.R-project.org. [☞34]

Reiches, M., Ellison, P. T., Lipson, S., Sharrock, K., Gardiner, E., and Duncan, L. G. (2009). Pooled energy budget and human evolution. *American Journal of Human Biology*, 21:421–429. [☞28]

Robson, S. L., van Schaik, C. P., and Hawkes, K. (2006). The derived features of human life history. In Hawkes, K. and Paine, R. R., editors, *The Evolution of Human Life History*, pages 37–44. Santa Fe and New Mexico: School of American Research Press and Oxford: James Currey Ltd. [☞29]

Røskaft, E., Wara, A., and Viken, A. (1992). Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700-1900. *Ethology and Sociobiology*, 313:443–461. [☞44]

Rotkirch, A. and Janhunen, K. (2009). Maternal guilt. *Evolutionary Psychology*, 8:90–106. [☞31]

Schlumbohm, J. (1991). Social differences in age at marriage: examples during the xviiith and xixth centuries. In Helin, E., editor, *Historiens and Populations*, pages 593–607. Louvain-la-Neuve: Academia. [☞44]

Sear, R. (2008). Kin and child survival in rural Malawi. *Human Nature*, 39:277–293. [☞29]

Sear, R. and Mace, R. (2008). Who keeps children alive? a review of the effects of kin on child survival. *Evolution and Human Behavior*, 29:3–18. [☞28, 47]

Sear, R. and Mace, R. (2009). Family matters: kin, demography and child health in a rural Gambian population. In Bentley, G. R. and Mace, R., editors, *Alloparenting in Human Societies*, pages 50–76. Cambridge: Cambridge University Press. [☞29]

Sear, R., Mace, R., and McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, 24(3):25–42. doi:10.1016/S1090-5138(02)00105-8. [☞28]

Skinner, G. W. (2004). Grandparental effects on reproductive strategizing: Nobi villagers in early modern Japan. *Demographic Research*, 31:111–147. [☞46]

Skjaervoe, G. R., Bongard, T., Vikenc, A., Stokke, B. G. D., and Roskaft, E. (2011). Wealth, status, and fitness: a historical study of Norwegians in variable environments. *Evolution and Human Behavior*, 32(5):305–314. [☞29]

Therneau, T. and Lumley, T. (2009). *Survival: Survival analysis and including penalised likelihood. R package version 2.35-4.* http://CRAN.R-project.org/package=survival. [☞34]

Toomet, O. and Henningsen, A. (2008). Sample selection models in r: Package sampleSelection. *Journal of Statistical Software*, 27(7):1–23. URL: http://www.jstatsoft.org/v27/i07/. [☞33]

Udry, J. R. and Cliquet, R. L. (1982). A cross-cultural examination of the relationship between ages at menarche, marriage, and first birth. *Demography*, 39:53–63. [☞29]

Voland, E. (1990). Differential reproductive success within the Krummhörn population (Germany and 18th and 19th centuries). *Behavioral Ecology and Sociobiology*, 26:65–72. [☞29, 45]

Voland, E. (1998). Evolutionary ecology of human reproduction. *Annual Review of Anthropology*, 27:347–374. [☞28]

Voland, E. (2000). Contributions of family reconstitution studies to evolutionary reproductive ecology. *Evolutionary Anthropology*, 30(3):134–146. [☞30, 32]

Voland, E. and Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioral Ecology and Sociobiology*, 52:435–443. [☞28, 47]

Voland, E. and Beise, J. (2005). The husband's mother is the devil in the house: Data on the impactof the mother-in-law on stillbirth mortality in historical Krummhörn (1750–1874) and some thoughts on the evolution of postgenerative female life. In Voland, E. and Schievenhövel, A. C. . W., editors, *Grandmotherhood—The evolutionary significance of the second half of female life*, pages 239–255. New Brunswick & London: Rutgers University Press. [☞47]

Voland, E., Chasiotis, A., and Schiefenhövel, W., editors (2005). *Grandmotherhood – The Evolutionary Significance of the Second Half of Female Life*. New Brunswick & London: Rutgers University Press. [☞46]

Voland, E. and Dunbar, R. I. M. (1997). The impact of migration and social status on female age at marriage in a historical population. *Journal of Biosocial Science*, 29:355–360. [☞44]

Voland, E. and Engel, C. (1990). Female choice in humans: A conditional mate selection strategy of the Krummhörn women (Germany 1720-1874). *Ethology*, 84:144. [☞31]

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

Der folgende Text wurde als Artikel in der Zeitschrift *Evolution and Human Behavior* im Jahre 2011 publiziert. Das Copyright liegt bei www.elsevier.com. Der Nachdruck erfolgt mit freundlicher Genehmigung von www.elsevier.com. Die Autoren sind:

Johannes Johow, Zentrum für Philosophie und Grundlagen der Wissenschaft Universität Giessen, Germany
Molly Fox, Department of Biological Anthropology, University of Cambridge, UK
Leslie A. Knapp, Department of Biological Anthropology, University of Cambridge, UK
Eckart Voland, Zentrum für Philosophie und Grundlagen der Wissenschaft Universität Giessen, Germany (corresponding author, Fon: + (49)-641-99-15550, Fax: + (49)-641-99-15509, Email: eckart.voland@phil.uni-giessen.de)

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.

3.1 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,b) 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 2007). Even under prehistoric and historic conditions, a significant portion of any female population survived after menopause and probably gave intergenerational support through alloparenting (Hrdy, 2009). 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 and Smith, 2007), resulting in an in-law conflict over the reproductive rate of a woman (e.g., Euler and Michalski 2008, Leonetti et al. 2007). Krummhörn mothers-in-law are assumed to take advantage of their 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 and 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 et al. (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 (e.g. 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 et al., 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, 2011) 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 (e.g. Galdikas and 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 ox 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.

3.2 Materials and methods

3.2.1 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 and Voland, 2008; Voland and Dunbar, 1995; Willführ, 2009).

3.2.2 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.
3. 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 (18,177 remaining cases).
- Families with birth dates not exactly known from the written documents, still births and multiple births were excluded (13084 remaining cases).
- Lastborn children have been excluded (10,201 remaining cases)
- Toddlers who died during the time of IBI were excluded (7,985 remaining cases).
- Cases with unknown age of the mother have been excluded. (7,380 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 (6,832 remaining cases).
- Presence of the MGM, or the PGM respectively, only was assumed if both of the following proxies were fulfilled:
    - 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).
    - 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 1,124 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 3.1 describes included families and Fig. 3.1 give sample characteristics of IBIs we used for analysis.

3.2.3 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$_j$ ˜ female$_j$+MGM$_j$+PGM$_j$+MGM$_j$:female$_j$+PGM$_j$:female$_j$+...

...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 motherj at birth of grandchild$_j$
- 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.

3.2.4 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:

$$\lambda_i(t) = Y_i(t)\lambda_0(t)exp(X_i(t)^T\beta)$$

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

$$\lambda_i(t) = Y_i(t)X_i(t)^T\alpha(t)$$

where α(t) is a nonparametric p-dimensional regression function that is constrained by $Xi(t) = 0$. 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 $\beta(t)$, against time.

$$A(t) = \int \alpha()(s)ds_0^t$$

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 and 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.

$$\lambda_i(t) = Y_i(t)(X_i(t)^T\alpha(t))exp(Z_i(t)^T\beta)$$

The Cox-Aalen model is part of the R-package "timereg" (see Scheike et al. 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 reasoning since we assume that the statistical correlation between the IBI

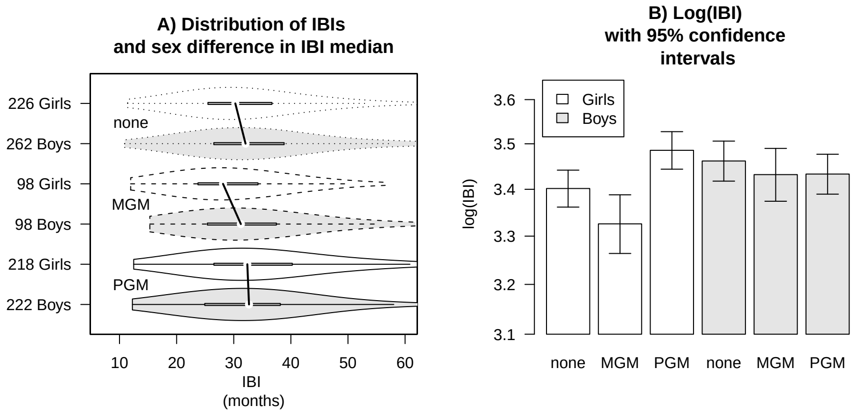

Figure 3.1: Panel A gives violin plots (a combination of boxplot and kernel distribution plot) for interbirth intervals (IBIs) following the birth of a girl or a boy separated for families, where the PGM is present, where both grandmothers are absent or were the MGM is present. Panel B shows asymptotic tests with 95% confidence intervals (see Coeurjolly et al., 2009) to show differences in logarhythmized values of IBIs.

and the foreborn child's fitness outcomes (survival, reproductive success) will decrease over time or even change (see introduction).

3.3 Results

Table 3.1: 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

Table 3.2: Estimated coefficients and test for proportionality of the standard Cox proportional hazards model for IBIs in final data selection. 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.

	Cox Model Estimates					Test for Proportionality		
	Coef.	SE	Robust SE	z	Pr(>lzl)	rho	χ^2	*P*
			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:					
Age at 1st birth	0.189	0.0273	0.0275	6.88	<0.001	-0.0908	12.0	<0.001
Age at birth (a)	-0.213	0.0276	0.0260	-8.25	<0.001	0.116	15.8	<0.001
Birth Order (b)	0.271	0.135	0.140	1.93	0.0535.	0.0177	0.448	0.503
Interaction (a):(b)	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

N = 1124; R^2= 0.129; Wald test = 168.6 on 10 df ($P < 0.001$).Robust standard errors are calculated according to a child's specific family ID. N (total) = 1124, see fig. 3.1 for subgroups.

Table 3.3: Multiplicative and additive terms in the Cox-Aalen model. Estimated coefficients and test for proportionality are given for the main predictors acting propotionally 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.

Main Predictors

Proportional Cox Terms

	Coef.	SE	Robust SE	1/D2log(L)	z (P)	Lin, Wei, Ying-Test for Proportionality
female	0.293	0.0968	0.0945	0.0939	3.03 (P=0.00248)	17.0 (P=0.182)
MGM	0.206	0.125	0.122	0.124	1.65 (P=0.0990)	8.24 (P=0.730)
PGM	0.237	0.101	0.100	0.0984	2.34 (P=0.0194)	19.1 (P=0.142)
Female:MGM	<0.01	0.173	0.166	0.172	0.0535 (P=0.957)	5.55 (P=0.816)
Female:PGM	-0.399	0.137	0.130	0.135	-2.91 (P=0.0036)	11.7 (P=0.349)

Controlled Predictors

Additive Aalen Terms

	Supremum-Test (P)	Kolmogorov-Smirnov-Test (P)
(Intercept)	3.16 (P=0.053)	1.73 (P=0.636)
Mother age at first birth	6.44 (P<0.001)	0.144 (P=0.287)
Mother age at specific birth (a)	7.11 (P<0.001)	0.146 (P=0.314)
Birth Order (b)	3.13 (P=0.047)	0.822 (P=0.306)
Interaction (a):(b)	3.94 (P=0.004)	0.0216 (P=0.309)
Birth parish	4.61 (P=0.001)	0.0372 (P=0.617)

Robust standard errors are calculated according to a child's specific family ID. N (total) = 1124, see fig. 3.1 for subgroups.

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. 3.1 panel A) 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 et al., 2009) for IBIs support the assumption of a conditional effect of the PGM, dependent on the sex of the grandchild (Fig. 3.1 panel B).

As the standard Cox model we initially fit was rejected by model diagnostics indicating nonproportional hazards (see Table 3.2 and Supplementary Fig. S1), we firstly moved all confounding covariates to the additive part of the Cox-Aalen model. Table 3.3 indicates that estimated coefficients of the Cox-Aalen are very similar to the initial standard Cox model (compare Table 3.2). Although the assumption of proportionality in the Cox-Aalen model was not violated (see right columns in Table 3.3), 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 3.4). 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 3.3 and 3.4). 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. 3.2 panel A). Contrastingly, IBIs following the birth of a grandson exhibit no comparable contextual difference in grandmaternal effects (Fig. 3.2 panel D). 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. 3.2 panel B and C), while predicted IBIs following the birth of a boy are very similar in the presence of the PGM and the MGM (Fig. 3.2 panel E 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. 3.3 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. 3.4 panel B and

Table 3.4: Test for constant effects and test for non-significant effects of the Aalen additive hazards model

Model III: Aalen additive hazard			
	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)	0.782 (p=.142)	3.41 (p=.027)
Controlled covariates:			
(Intercept)	2.1 (p=.544)	1.62 (p=.595)	3.02 (p=0.078)
Mother age at first birth	0.436 (p=.0008)	0.193 (p=.0002)	7.30 (p<.001)
Mother age at specific birth	0.751 (p=.0004)	0.238 (p=.0001)	8.55 (p<.001)
Birth order	4.38 (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)

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. 3.4 panel A).

3.4 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 and 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-weanedchildren 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. 3.1 and 3.4). 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. 3.3). However, the results for very long IBIs should be considered with caution as the sample size was small (Fig. 3.1). Results indicate a relative lengthening of IBIs following the birth of a granddaughter compared to IBIs following the birth of 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 oppor-

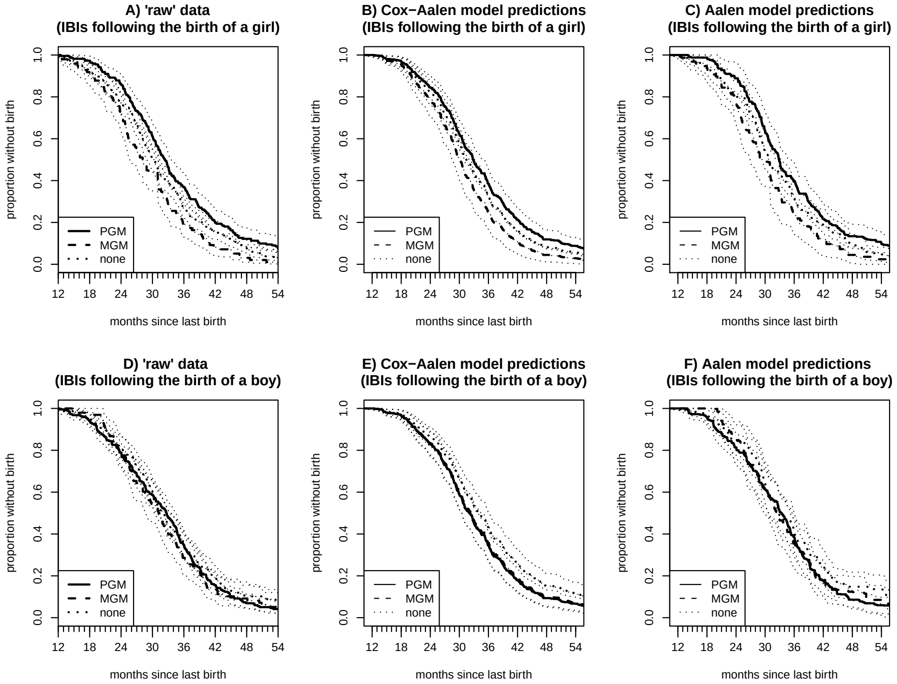

Figure 3.2: Kaplan-Meier plots showing IBIs with pointwise 95% confidence intervals Top panels show IBIs following the birth of a girl. Panel A graphs IBIs in real data for families, where either both grandmothers were absent (dotted line), or only the MGM was present (broken line), or only the PGM was present (solid line); panel B gives analogously predictions based on the Cox-Aalen model fit (see table 3.3); panel C gives estimates from the fully-nonparametric Aalen model (see table 3.4 and fig. 3.3). Analogously, bottom panels show specific curves in case of IBIs following the birth of a boy. Deceased toddlers have been excluded.

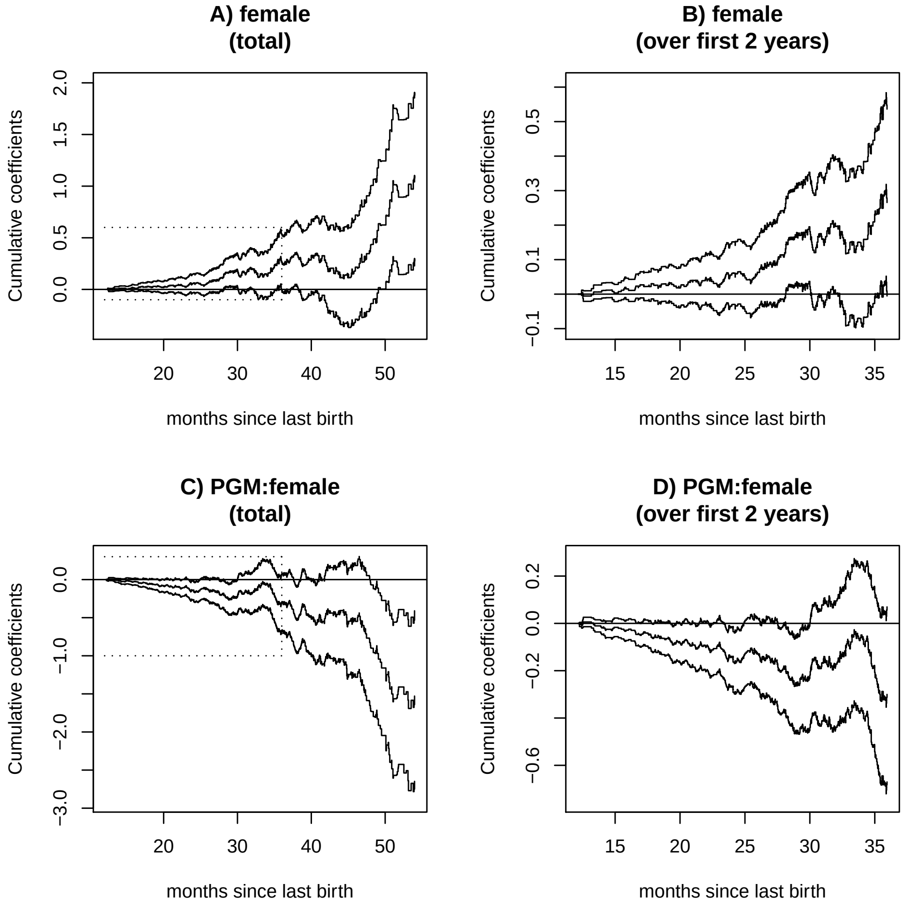

Figure 3.3: Cumulative coefficients in the additive hazards model of Aalen (only if estimated significantly, see supplement for non-significant estimates). Left panels (A + C) give effects in total and right panels (B + D) have been restricted to the time over the first three years of IBI. Pointwise 95% confidence intervals are given (thus if both confidence bands cross the zero line, effect is estimated with $P < 0.05$).

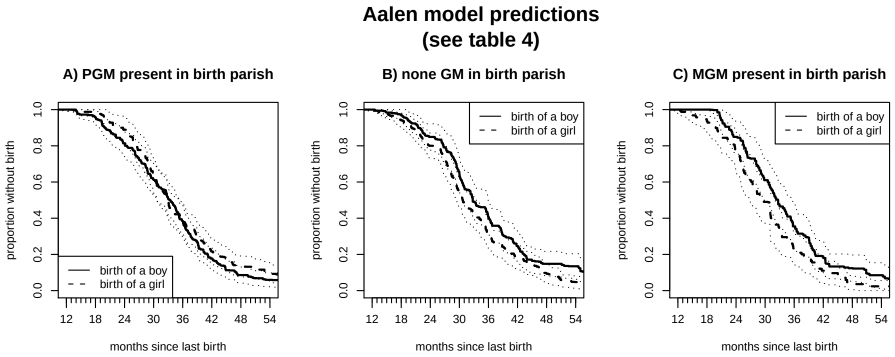

Figure 3.4: Aalen model predictions (see 3.4) for IBIs with 95% pointwise confidence bands using averaged covariates. Given are differences in IBIs following the birth of a grandson (solid line) and a granddaughter (broken line) between those families where either both grandmothers were absent (panel A) or exclusively the MGM (panel B) or the PGM (panel C) was present in birth parish.

tunity 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 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 et al. 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 3.2). 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 et al., 2006; Fox et al., 2010). Among men, specific cognitive mechanisms have shown to modulate their amount of paternal investment according to physical resemblance (Alvergne et al., 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 and 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 PGMshould 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 et al. 2009). An increased infant mortality in the presence of PGMs (as opposed to MGMs) is known for the Krummhörn (Voland and Beise, 2002), where stress due to hard work could also play a role (Voland and 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.

References

☞[cited on page(s)]

Alvergne, A. C., Faurie, and Raymond, M. (2009). Father-offspring resemblance predicts paternal investment in humans. *Animal Behaviour*, 78:61–68. doi:10.1016/j.anbehav.2009.03.019. [☞70]

Baldi, I., Ciccone, G., Ponti, A., Rosso, S., Zanetti, R., and Gregori, D. (2006). An application of the Cox-Aalen model for breast cancer survival. *Austrian Journal of Statistics*, 35:77–88. [☞59]

Beise, J. and 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. [☞56]

Brockdorff, N. and Turner, B. M. (2007). Dosage compensation in mammals. In Allis, C. D., Jenuwein, T., and Reinberg, D., editors, *Epigenetics*, pages 321–340. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press. [☞70]

Coeurjolly, J. F., Drouilhet, R., Micheaux, P. L. D., and Robineau, J. F. (2009). asympTest: A simple R package for classical parametric statistical tests and confidence intervals in large samples. *The R Journal*, 2(2):26–30. [☞60, 64, 98]

Cox, D. R. (1972). Regression models and life tables (with discussion). *Journal of the Royal Statistical Society and Series B*, 34:187–220. [☞58]

Euler, H. and Michalski, H. A. (2008). Grandparental and extended kin relationships. In Salmon, C. A. and Shackelford, T. K., editors, *Family Relationships – An Evolutionary Perspective*, pages 230–255. Oxford: Oxford University Press. [☞54]

Fox, M., Sear, R., Beise, J., Ragsdale, G., Voland, E., and 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. [☞54, 55, 66, 70]

Galdikas, B. M. F. and Wood, J. W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology*, 83:185–191. [☞55]

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7::1–16. [☞54]

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, 7::17–52. [☞54]

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., and Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academies of Sciences USA*, 95:1336–1339. [☞54]

Hrdy, S. B. (2009). *Mothers and others – The evolutionary origins of mutual understanding*. Belknap/Harvard: Cambridge. [☞54]

Isles, A. R., Davies, W., and 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. [☞70]

Leonetti, D. L., Nath, D. C., and Hemam, N. S. (2007). In-law conflict – women's reproductive lives and the roles of their mothers and husbands among the matrilineal Khasi. *Current Anthropology*, 48:861–890. [☞54, 69]

Low, B. S. (1991). Reproductive life in nineteenth century sweden: An evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, 12:411–448. [☞58]

Messing, S. (2010). *Wvioplot: Weighted violin plot. R package version 0.1.* http://CRAN.R-project.org/package=wvioplot. [☞64]

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. [☞69]

Penn, D. J. and Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *Proceedings of the National Academies of Sciences USA*, 204(2):553–558. doi:10.1073/pnas.0609301103. [☞54]

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. [☞69]

Platek, S. M., Raines, D. M., Gallup, J., Gordon, G., Mohamed, F. B., Thomson, J. W., Thomas, E., Panyavin, I. S., Levin, S. L., Davis, J. A., Fonteyn, L. C. M., and Arigo, D. R. (2004). Reactions to children's faces: Males are more affected by resemblance than females are and and so are their brains. *Evolution and Human Behavior*, 25:394–405. [☞70]

Pollet, T. V., Nelissen, M., and Nettle, D. (2009). Lineage based differences in grandparental investment: evidence froma large British cohort study. *Journal of Biosocial Science*, 41:355–379. doi:10.1017/S0021932009003307. [☞71]

Quinlan, R. J., Quinlan, M. B., and Flinn, M. V. (2005). Local resource enhancement and sex-biased breastfeeding in a Caribbean community. *Current Anthropology*, 46:471–480. [☞55, 66]

R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna and Austria, 2.12 edition. ISBN 3-900051-07-0. URL: http://www.R-project.org. [☞55]

Reiches, M., Ellison, P. T., Lipson, S., Sharrock, K., Gardiner, E., and Duncan, L. G. (2009). Pooled energy budget and human evolution. *American Journal of Human Biology*, 21:421–429. [☞54]

Rice, W. R., Gavrilets, S., and 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. [☞55, 66, 70]

Scheike, T., Martinussen, T., and 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. [☞59]

Scheike, T. and Zhang, M. (2002). An additive–multiplicative Cox–Aalen regression model. *Scandinavian Journal of Statistics*, 29:75–88. doi:10.1111/1467-9469.00065. [☞59]

Sear, R., Mace, R., and McGregor, I. A. (2003). The effects of kin on female fertility in rural Gambia. *Evolution and Human Behavior*, 24(2):25–42. doi:10.1016/S1090-5138(02)00105-8. [☞69]

Straka-Geiersbach, S. and Voland, E. (1988). Zum Einfluss der Säuglingssterblichkeit auf die eheliche Fruchtbarkeit am Beispiel der Krummhörn and 18. und 19. jahrhundert [on the influence of infant mortality on marital fecundity in historical Krummhörn, 18th and 19th centuries]. *Homo*, 39:171–185. [☞66]

Therneau, T. and Lumley, T. (2009). *Survival: Survival analysis and including penalised likelihood. R package version 2.35-4.* http://CRAN.R-project.org/package=survival. [☞62, 102]

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. [☞55]

Trivers, R. (1972). Parental investment and sexual selection. In Campbell, B., editor, *Sexual Selection and the Descent of Man 1871–1971*, pages 136–179. Chicago: Aldine. [☞55, 66]

Vitzthum, V. J. (2008). Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*, 37(4):1–21. [☞55, 66]

Voland, E. (2000). Contributions of family reconstitution studies to evolutionary reproductive ecology. *Evolutionary Anthropology*, 20(1):134–146. [☞55, 56]

Voland, E. (2007). Evolutionary psychology meets history: Insights into human nature through family reconstitution studies. In Dunbar, R. I. M. and Barrett, L., editors, *Oxford handbook of evolutionary psychology*, page 415–432. Oxford: Oxford University Press. [☞54]

Voland, E. and Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioral Ecology and Sociobiology*, 52:435–443. [☞54, 71]

Voland, E. and 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 Voland, E. and Schievenhövel, A. C. . W., editors, *Grandmotherhood—The evolutionary significance of the second half of female life*, pages 239–255. New Brunswick & London: Rutgers University Press. [☞54, 71]

Voland, E. and Dunbar, R. (1995). Resource competition and reproduction - the relationship between economic and parental strategies in the Krummhörn population (1720-1874). *Human Nature*, 6:33–49. [☞56]

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(4):488–500. [☞56, 57]

4 The Selfish Grandma Gene – The Roles of the X-Chromosome and Paternity Uncertainty in the Evolution of Grandmothering Behavior and Longevity

Der folgende Text wurde als Artikel in der Zeitschrift *International Journal of Evolutionary Biology* im Jahre 2011 publiziert. Verbreitung und Vervielfältigung sind gemäß Lizenz unter Nennung der Originalarbeit (doi:10.4061/2011/165919) zulässig. Die Autoren der Arbeit sind:

Molly Fox, Department of Biological Anthropology, University of Cambridge, UK
Johannes Johow, Zentrum für Philosophie und Grundlagen der Wissenschaft Universität Giessen, Germany
Leslie A. Knapp, Department of Biological Anthropology, University of Cambridge, UK (corresponding author, Email: lak26@cam.ac.uk)

Abstract. When considering inclusive fitness, it is expected that individuals will provide more care towards those with whom they are more closely related. Thus, if a selfish X-linked genetic element influenced care giving, we would expect care giving to vary with Xrelatedness. Recent studies have shown that X-chromosome inheritance patterns may influence selection of traits affecting behavior and life-history. Sexually antagonistic (SA) zygotic drive could encourage individuals to help those with whom they aremore likely to share genetic material at the expense of other relatives. We reanalyze previously reported data in light of this new idea. We also evaluate the effects of paternity uncertainty on SA-zygotic drive. Our evidence suggests that human paternal discrepancy is relatively low. Using published models, we find the effects of paternal discrepancy do not override opportunity for selection based on X-relatedness. Based on these results, longevity and grandmothering behaviors, including favoritism, may be more heavily influenced by selection on the X-chromosome than by paternity uncertainty.

4.1 Introduction

Care giving between family members may be influenced by genes in ways that encourage people to treat relatives differently according to their degrees of relatedness (Hamilton, 1964a,b). The importance of genetics in care giving behaviors within families is somewhat intuitive: one would expect a woman to care more for her son than for her nephew, and more for her sister than for her cousin. In other words, it is expected that people vary the amount of care they provide proportionally to their genetic relatedness with family members. It follows that a gene which encourages such a care giving pattern may also be adaptive, as those who carry it help others who are most likely to carry it. The idea that differential relatedness encourages preferential behaviors is not new.Many publications have reported evidence supporting kin selection and several recent studies have explored the ways in which adopted children may be treated differently than biological children, how step-parents may invest less in step children than in biological children, and how the extent of paternal care may vary based on likelihood of paternity (Anderson et al., 1999; Anderson, 2000; Santrock et al., 1982; Borders et al., 1998; Barber, 2000). Along these same lines, grandmothering behavior has been implicated in our species' unique post-menopausal longevity. The advantages that grandmothers bestow upon certain grandchildren may create opportunity for the selection of selfish genetic elements that increase longevity. Beyond this, it has been suggested that sexually antagonistic zygotic drive (SA-zygotic drive) may contribute to the behavioral pattern of some grandmothers helping granddaughters at the expense of grandsons (Rice et al., 2010). Recent research has shown how inheritance patterns of the X-chromosome may create opportunity for selection of traits affecting human behavior and life history. Here, we reanalyze previously published data in light of the SA-zygotic drive argument. We also re-evaluate data related to prehistoric rates of paternal discrepancy and consider how discrepancy would affect SA-zygotic drive. We present models that examine how paternity uncertainty and X-linked selfish mutations may influence selection. We find that even the highest estimated rates of paternity uncertainty do not override models for selection on grandmothers based on X-chromosome relatedness. Therefore, the differential genetic relatedness between family members may explain the ways in which women treat their grandchildren, as well as the longevity of our species.

4.2 Grandmothering Behavior

4.2.1 X-Linked Grandmother Hypothesis

The grandmother hypothesis, originally formulated to account for menopause itself, has since often been utilized in discussions of postmenopausal longevity (Hawkes et al.,

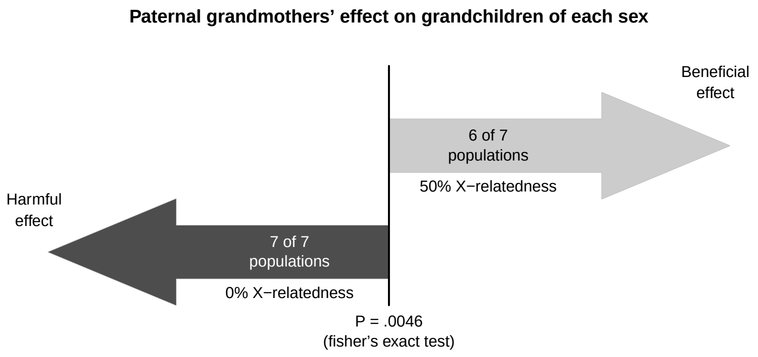

Figure 4.1: Analysis of the PGMs effect on grandchildren using data from Fox et al. (2010). Light grey (top) represents granddaughters, and dark grey (bottom) represents grandsons.

1997, 2000; Hawkes, 2003). This view holds that postmenopausal longevity evolved in our species because women with genetic elements coding for increased lifespan experienced increased inclusive fitness, as they were able to increase their daughters' fertility and the survivorship of their grandchildren (Hawkes et al., 1997, 2000; Hawkes, 2003). Fox et al. (2010) proposed an X-linked grandmother hypothesis, based on the fact that there is variation in X-chromosome sharing between grandmothers and grandchildren depending on the sex of the grandchild and whether the grandmother is from the matriline or patriline. This differential genetic relatedness creates differential incentives for grandmothers to invest in grandchildren. In Fox et al.'s (2010) analysis of seven populations, the variation in grandmothers' effect on grandchild likelihood of mortality correlated with their X-relatedness.

4.2.2 X-Linked Granddaughter Favoritism Hypothesis

The differential X-relatedness between grandmothers and grandchildren creates opportunity for genes that affect behaviors associated with grandparenting to cluster on the X-chromosome. When paternal grandmothers (PGMs) invest in granddaughters, there is a better return on that investment for the X-chromosome than for the autosomes, so X-linked alleles for grandparenting will be more strongly selected than autosomal alleles (Wilder, 2010; Chrastil et al., 2006).

Table 4.1: The circumstances under which an X-linked gene coding for favoritism of granddaughters would persist in a population (based on Rice et al.'s 2010 mathematical model).

When X-linked mutation helping granddaughters at expense of grandsons is expressed in:	It would increase in frequency provided the expense to grandsons is no more than (values below) times the benefit to granddaughters
All grandparents (dominant expression)	2
All grandparents (additive expression)	1.5
Grandmothers only (dom or add expression)	3
Paternal grandmothers only (dom or add expression)	no limit

Table 4.2: Data from Fox et al. (2010) analyzed according to predictions based on SA-zygotic drive model (Rice et al., 2010). PGM: paternal grandmother; MGM: maternal grandmother; SA: sexually antagonistic; GD: granddaughter; GS: grandson. Check mark indicates that the population data in Fox et al. does conform to the Rice et al. prediction, and a dash indicates that it does not.

Population	PGM helps GD and harms GS	MGM helps GD and harms GS
Germany	✓	-
England	✓	-
Ethiopia	✓	-
Canada	✓	-
Japan	✓	-
Gambia	-	-
Malawi	✓	-

One pattern of grandparenting behavior observed in Fox et al.'s (2010) meta-analysis is that of PGMs decreasing survivorship of grandsons. This phenomenon can be viewed in light of selfish genetic elements on the X-chromosome. SA-zygotic drive refers to selfish genetic material on the X or Y chromosomes that helps offspring who carry it and harms offspring who do not carry it (Rice et al., 2008). Rice et al.'s (2010) mathematical model reveals the circumstances under which natural selection would cause X-linked mutations that affect grandparenting behavior to persist. This can be thought of as an "X-Linked Granddaughter Favoritism Hypothesis". For a selfish X-linked mutation, the only relatedness that affects selection is X-chromosome relatedness. X-relatedness varies by line of descent and sex of grandchild, so an X-linked mutation in a woman has a 50% chance of being transmitted to her son's daughter, 0% chance of being transmitted to her son's son, and a 25% chance of being transmitted to her daughter's child of either sex. Using these values in Rice et al.'s (2010) mathematical model shows that a dominant X-linked mutation causing all grandparents to help granddaughters at the expense of grandsons would increase in frequency as long as the magnitude of the cost to grandsons is no more than twice the benefit to granddaughters. What if the X-linked mutation were only expressed in certain grandparents (Table 4.1)? An X-linked mutation that causes only females (i.e., grandmothers and not grandfathers) to help granddaughters at the expense of grandsons would increase in frequency as long as the expense to grandsons is no more than three times the benefit to granddaughters. An

X-linked mutation that is only expressed in PGMs would increase in frequency as long as there was a benefit to granddaughters, no matter what the effect on grandsons. This means that if an X-linked mutation arose which only affected how women treat their sons' children (in other words, the way paternal grandmothers treat their grandchildren) in terms of helping granddaughters at the expense of grandsons, there would be no hindrance to that mutation reaching fixation in the population. Overall, there are many opportunities for mutations to accumulate on the X-chromosome that cause granddaughters to be favored at the expense of grandsons. Although selection for this phenotype occurs only in PGMs, Rice et al.'s (2010) model indicates that it can evolve in other grandparents as a correlated effect. Table 4.1) shows the predictions of the X-Linked Granddaughter Favoritism Hypothesis and the circumstances under which this phenotype would accumulate.

The present study analyzes the data from Fox et al.'s (2010) meta-analysis of seven geographically and temporally varied populations, in light of Rice et al.'s (2010) discussion of SA-zygotic drive. Rice et al.'s (2010) model suggests that granddaughters should be favored at the expense of grandsons. The predictions (Table 4.1)) in order of increasing effect strength are that granddaughters are helped at the expense of grandsons by (1) and (2) All grandparents, (3) Grandmothers, and (4) Paternal grandmothers. The third prediction, that all grandmothers might favor granddaughters at the expense of grandsons, is not supported by the data, as the maternal grandmother (MGM) never exhibits this trend. However, in six of the seven populations PGMs have the predicted effect of helping granddaughters and harming grandsons, providing some support for the fourth prediction (Table 4.2)).

Considering Fox et al.'s (2010) results, the PGM had a harmful effect on grandsons in all seven populations, and a helping effect on granddaughters in six of the seven populations (Figure 4.1). This trend was statistically significant: Fisher's exact test $P = .0046$. These results are consistent with the X-Linked Granddaughter Favoritism Hypothesis, which suggests that selfish genetic material on the X-chromosome coding for helping granddaughters at the expense of grandsons should be most strongly favored as it is only expressed in PGMs. This PGM-grandson harming behavior, first noticed by Jamison et al. (2002) who described the effect in their own data as "startling to say the least", is consistent with the presence of X-linked mutations encoding sexually antagonistic phenotypes.

The aforementioned studies found evidence of PGMs favoring granddaughters, consistent with the fourth prediction of the X-Linked Granddaughter Favoritism Hypothesis (Table 4.1). But based on the limitations of the statistics and the number of study populations, this may not be the most sensitive method that could be employed to test the hypothesis. When each of the 28 effects measured in Fox et al.'s (2010) meta-analysis are considered individually, only five were statistically significant, although the directionalities of the effects were highly significant (Figure 4.1). The conclusions of

Jamison et al. (2002) and Fox et al. (2010), therefore, provide a limited amount of evidence for the fourth prediction of the X-Linked Granddaughter Favoritism Hypothesis. Further research is needed to verify a PGM-specific trend. Also, it is important to note that these studies only examine grandchild mortality rates, not behavior, health, or any other measure of favoritism. These studies were conducted not to analyze behaviors, but rather, as an opportunity to evaluate evidence related to the grandmother hypothesis. Therefore, if the specific predictions of Rice et al. (2010) are to be tested rigorously, perhaps we should look at behavior, rather than mortality rates.

Evidence supporting favoritism of granddaughters via SA-zygotic drive comes from questionnaire studies in which grandparents and grandchildren are asked to evaluate their relationships with each other. Euler and Weitzel (1996) found that grandparents provided more care to granddaughters than to grandsons. Participants were asked to rank amount of care on a scale from 1 to 7, and mean granddaughter care was 4.45 and grandson care was 4.23. These results support the first rediction of the X-Linked Granddaughter Favoritism Hypothesis (Table 4.1). Adding their own data to that of Euler and Weitzel, Chrastil et al. (2006) found that granddaughters were favored over grandsons by both MGMs ($P < .0001$) and PGMs ($P = .003$). This favoritism of granddaughters over grandsons provides further support for the third prediction of the hypothesis (Table 4.1).

4.3 Longevity

4.3.1 Sexually Antagonistic Zygotic Drive and Grandmother Longevity

The X-Linked Granddaughter Favoritism Hypothesis can account for SA-zygotic drive causing some, or even all, grandparents (via side-effect of selection on PGM) to carry X-linked traits that induce favoritism of granddaughters at the expense of grandsons. By the same logic, SA-zygotic drive may cause perpetuation of an X-linked longevity gene.

If, as suggested by the evidence presented above, some grandmothers favor granddaughters, then those girls with grandmothers who live longer would have the greatest advantage, as they would experience the benefits of that favoritism longer. This effect may be tempered by costs associated with having a grandmother, which may increase as she ages. Additionally, the benefits of a grandmother may only benefit young grandchildren. Further research should explore these and other limits of grandmother benefits. Nonetheless, if a grandmother has X-linked genetic elements causing her to live longer to at least a certain extent, her granddaughters may disproportionately survive. The result might be that the X-linked genetic elements will increase in frequency in the population.

There may be natural selection for selfish X-linked alleles that help one sex of grandchild at the expense of the other. If presence of a PGM (i.e., surviving) for more years helps girls and harms boys, then there is opportunity for natural selection of X-linked alleles that increase longevity. Using Rice et al.'s (2010) formula, in which relatedness (R) refers to X-relatedness because this hypothesis considers only X-linked traits, a selfish genetic element will be favored as long as the following condition is true:

$$R_{Helped} \times B_{Helped} > R_{Harmed} \times C_{Harmed}$$

As described in Rice et al. (2010), R_{Helped} is the relatedness to the individual helped, B_{Helped} is the benefit to the individual helped, R_{Harmed} is the relatedness to the individual harmed, and C_{Harmed} is the cost to the individual harmed. Therefore, if an allele encoding greater longevity is X-linked, it will increase in frequency as long as one of the conditions listed in Table 4.1 is met.

1. The magnitude of grandparent longevity's harming effect on grandsons is no more than twice the magnitude of the helping effect on granddaughters.
2. If an X-linked longevity allele is only expressed in females (i.e., grandmothers), it will increase in frequency as long as the magnitude of grandmother longevity's harming effect on grandsons is no more than three times its helping effect on granddaughters.
3. If an X-linked longevity allele is only expressed in PGMs (in other words, only affects the way a woman treats her sons' children), then it will be favored without constraint.

In sum, SA-zygotic drive could contribute to our species' unique phenomenon of postmenopausal longevity, as a consequence of X-linked selfish genetic elements being favored in certain grandparents.

4.3.2 Grandmother Alloparenting and Longevity

Many proponents of the grandmother hypothesis have suggested that postmenopausal longevity has evolved in our species because grandmothers can bolster their inclusive fitness by reducing the weaning age of their grandchildren and thereby diminish the interbirth interval of their daughters and/or daughters-in-law and enhance the survivorship of their grandchildren especially as toddlers. Grandmothers may be in a unique position to increase their number of descendants and the likelihood of those descendants' survival without compromising their own fertility.

A recent study by Kachel et al. (2011) set out to quantify whether grandmothering could actually be a strong enough selective force to account for the perpetuation of longevity. The authors ran three mathematical simulations to test if grandmothering could increase inclusive fitness enough to influence the evolution of human longevity and/or age at weaning and survival of grandchildren. While their results claimed to prove that grandmothering cannot account for longevity, in fact their results do not conflict with the new X-Linked Grandmother Hypothesis (Rice et al., 2010; Fox et al., 2010). This is because Kachel et al.'s (2011) study only included maternal grandchildren. Their model did not consider the effects of the paternal line and assumed that grandmothers did not provide care for their sons' children. Their results contradict studies which suggest that maternal grandmothering accounts for our species' longevity (Voland and Beise, 2002; Hawkes et al., 1998), and they cite paternal discrepancy as the reason that only maternal grandmothers are relevant to the adaptive circumstances leading to postmenopausal longevity.

If, however, SA-zygotic drive is responsible for the evolution of grandmothering and longevity alleles, the asymmetry in genetic relatedness along the paternal line is an important consideration, despite potential problems of paternity uncertainty. The previous section of this article suggests that longevity could be a result of selection purely on the PGM, and recent work by Fox et al. (2010) and Rice et al. (2010). Rice et al. (2010) suggest that PGMs' care for granddaughters could be the key to selection for grandmother care (Tables 4.1 and 4.2). Thus, Kachel et al.'s (2011) conclusion that maternal grandmothering cannot account for the selection of genetic factors affecting longevity is not in conflict with the possibility that the PGMs behavior drives selection for longevity. Further research should investigate the specific behaviors of grandmothers, and the particular ways in which granddaughters are helped and grandsons are harmed. Nevertheless, paternal relatives play an important role in the X-Linked Granddaughter Favoritism Hypothesis.

4.4 Paternity Uncertainty

Paternal discrepancy refers to cases in which a man raises a child as his own when unbeknownst to him, he is not the biological father. If this were often the case, there would be little incentive not only for men to invest in paternal care, but also for patrilineal kin to invest in caring for his children at all. With respect to the X-Linked Granddaughter Favoritism Hypothesis, high rates of paternal discrepancy would result in little selective pressure for women to engage in caretaking behaviors towards their sons' children.

Many previous studies of the grandmother hypothesis do not distinguish between MGMs and PGMs (Hill and Hurtado, 1991; Lahdenperä et al., 2004), and those that do distinguish between matrilineal and patrilineal relatedness tend to frame their analysis around paternity uncertainty (Voland and Beise, 2002; Ragsdale, 2004; Hawkes et al., 1998). Prominent researchers have claimed that selection for grandmothering behaviors and postmenopausal longevity is a result of selection exclusively on the MGM. Some studies, such as the aforementioned paper by Kachel et al. (2011), have even left PGMs out of their analysis entirely under the assumption that paternity uncertainty renders PGMs role immaterial in the evolution of human longevity. As described above, PGMs are integral to the bases of all X-linked grandmother hypotheses (Rice et al., 2010; Fox et al., 2010; Chrastil et al., 2006). Therefore, two questions cannot be ignored: how prevalent has paternal discrepancy been throughout our species existence, and how prevalent would it have to be to refute X-linked theories of longevity selection?

We suggest that paternal discrepancy may not have been much different during prehistory than it is today, based on studies of the Y-chromosome as well as anthropological information from modern hunter-gatherers (see Supplementary Material I available online at doi:10.4061/2011/165919). Based on an extensive literature review (see below), we suggest that this rate is 1.3–3.7%. We can reanalyze the likelihood of selfish X-linked genes accumulating using Rice et al.'s (2010) inequality equations by taking into account paternal discrepancy. We find that the thresholds for the accumulation of X-linked mutations causing certain grandparents to favor granddaughters at the expense of grandsons are altered only slightly. The thresholds are reported below.

4.4.1 Prevalence of Paternal Discrepancy

Paternal discrepancy is often cited in academic literature as an unsubstantiated 10% in the modern human populations (e.g., Johnson et al. 2001; Platek and Shackelford 2006; Macintyre and Sooman 1991), but there is evidence that the actual rates are far lower. Bellis et al. (2005) and Simmons et al. (2004) performed meta-analyses on geographically varied samples of 20,871 people from 17 populations, and 16,523 people from 12 populations, respectively. All of these people underwent biological tests for purposes other than discovering paternity; therefore, the studies avoided bias towards discrepancy. Bellis et al. (2005) found that median paternal discrepancy was 3.7%, and Simmons et al. (2004) reported the rate was 1.3%.

Two other studies analyzed the Y-chromosome to measure paternal discrepancy in ancient populations. Sykes and Irven (2000) found a highly significant association between British men based on surnames and Y-chromosome haplotype, tracing back to a common paternal ancestor 700 years ago. Based on their data, Sykes and Irven (2000) calculated a paternal discrepancy rate of 1.3%. A similar study analyzed the Y-chromosome similarities among modern "Cohanim" Jews, the supposed descendants of the biblical Moses (Sykes and Irven, 2000) . Skorecki et al. (1997) found that within this population, whose lineage dates back to 3,300 years ago, there is no evidence of paternal discrepancy from non-Cohanim Jews to complicate patterns of Y-chromosome

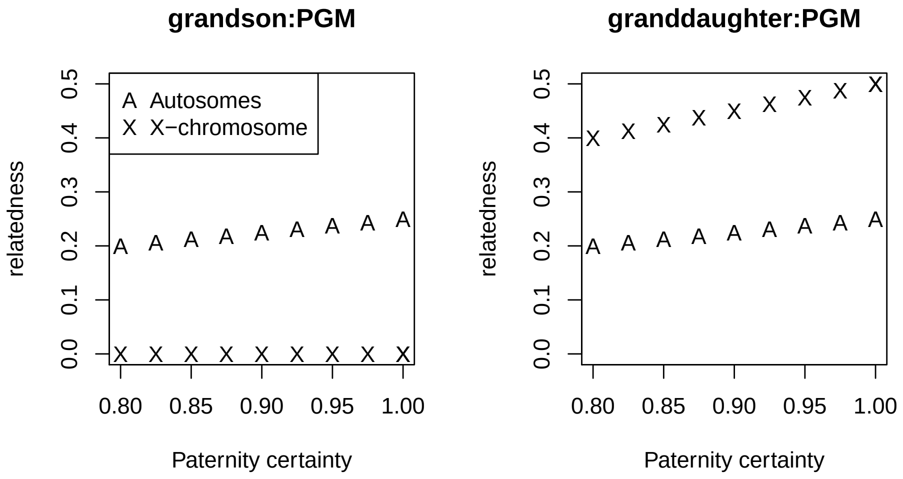

Figure 4.2: Hamiltonian r value for autosomal and X-relatedness between paternal grandmothers (PGM) and grandchildren; that is, the likelihood that any given autosomal or X-linked gene in the PGM will be present in her grandchild. These values are expressed in terms of a range of paternity certainty. (a) Shows the relatedness between a PGM and her granddaughter, and (b) shows the relatedness between a PGM and her grandson. For example, when paternal certainty is 100%, a granddaughter has a 50% chance of carrying any given X-linked allele of her PGMs, and a 25% chance of carrying any given autosomal allele of her PGMs. See Supplementary Material Table S7 for mathematical methods available online at doi:10.4061/2011/165919.

inheritance. The authors show that paternity certainty is close to 100% with high probability. Although it is possible that extramarital paternity may have occurred with a man sharing the same surname, and thus discrepancy would not be detected, these estimates of paternal discrepancy are not only low but are also consistent with results published by Simmons et al. (2004).

4.4.2 The Effect of Paternity Uncertainty on Selection for X-Linked Longevity Trait

Paternity uncertainty would surely change the likelihood of a PGM sharing an allele with her grandchild. Therefore, we have added paternal discrepancy into previously published calculations regarding the accumulation of X-linked mutations for grand-

Table 4.3: The circumstances under which an X-linked gene coding for favoritism of granddaughters would accumulate in a population using the model from Rice et al. (2010), given five rates of paternal discrepancy: 0% (as reported in Rice et al. 2010, and consistent with Skorecki et al. 1997); 1.3% (estimate based on Simmons et al. 2004 and Sykes and Irven 2000); 3.7% (estimate based on Bellis et al. 2005); 10% (popular unfounded figure included here to show range of possibility).

Rate of paternal discrepancy	0%	1.30%	3.70%	10%
When X-linked mutation helping granddaughters at expense of grandsons is expressed in:	Its frequency would increase provided the expense to grandsons is no more than (values below) times the benefit to granddaughters			
All grandparents (dominant expression)	2	1.993457	1.98167	1.947368
All grandparents (additive expression)	1.5	1.331876	1.329235	1.321429
Grandmothers only (dom or add expression)	3	2.97400	2.9280	2.8000
Paternal grandmothers only (dom or add expression)	No limit	No limit	No limit	No limit

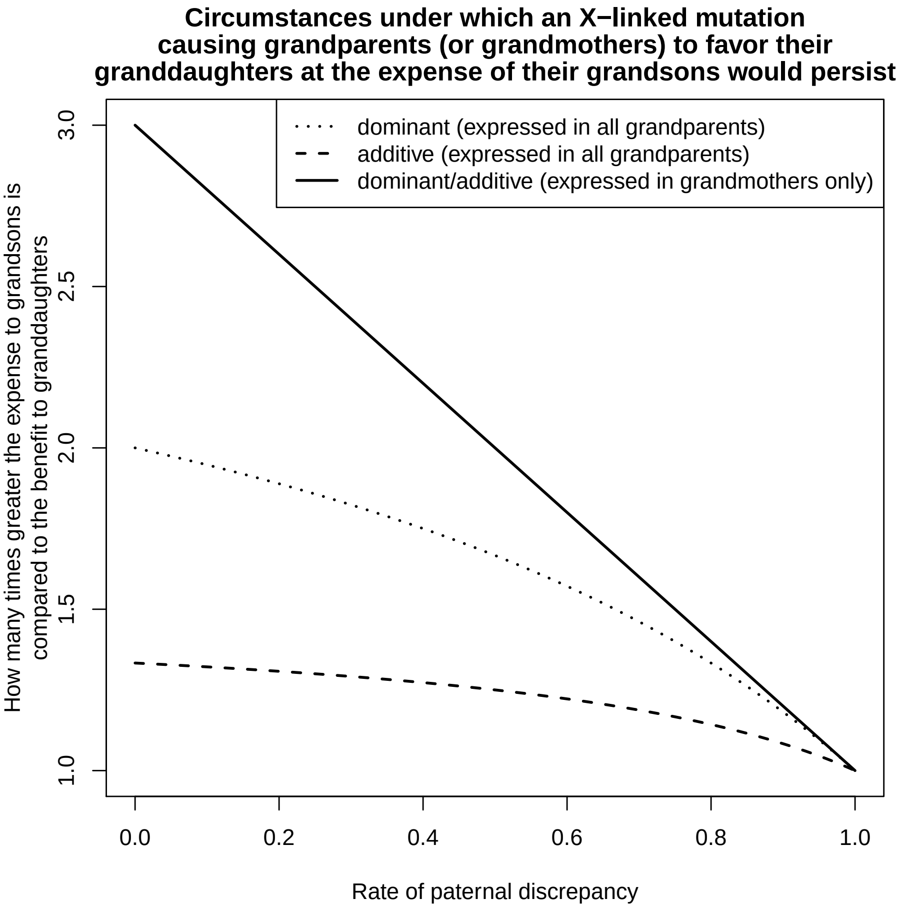

Figure 4.3: The threshold for an X-linked mutation causing grandparents (or grandmothers) to favor their granddaughters at the expense of their grandsons to accumulate. These curves represent the thresholds for which such a mutation would increase in frequency. The threshold can be described as themaximum number of times greater the expense of thismutation would be to grandsons, compared to the benefit of the mutation to granddaughters. These values were calculated using the mathematical model from Rice et al. (2010). We suggest that paternal discrepancy among our species would be approximately 1.3-3.7%. However, this graph shows a range of paternal discrepancy from 0% (all paternity is identified correctly) to 100% (all paternity is identified inaccurately).

mothering behavior and longevity. With this, we can show a range of PGM-grandchild relatedness given a generous variety of paternal discrepancy conditions. We use Rice et al.'s (2010) equations to calculate the effect magnitudes for which an X-linked granddaughter favoritism trait would increase in frequency.

While the varying relatedness between maternal and paternal grandmothers with granddaughters and grandsons has been reported before (e.g. Chrastil et al. 2006; Fox et al. 2010), these predicted relatedness values can be re-evaluated by considering rates of paternal discrepancy. Paternal discrepancy changes some aspects of the X-chromosome and autosomal genetic relatedness between (a) PGMs and granddaughters, and (b) PGM and grandsons (Figure 4.2; see Supplementary Material Table S7 for mathematical methods available online at doi:10.4061/2011/165919). Previous authors have suggested that paternity uncertainty may result in PGMs being statistically unlikely to share genes with their grandchildren and, as a consequence, selection for grandmothering traits act only on MGMs. The best estimates of both current and ancient paternal discrepancy (see above and Skorecki et al. 1997; Simmons et al. 2004; Sykes and Irven 2000; Bellis et al. 2005) range from 1.3–3.7%, although literature and textbooks often claim an unfounded 10%. To consider the widest range of possible values, we have modeled PGM-grandchild relatedness with paternal discrepancy ranging from 0% to 20% (Figure 4.2). These graphs show that although paternal discrepancy has some impact upon genetic relatedness, the comparisons between grandmother-grandchild pairs remain largely the same. The X-relatedness between a PGM and grandson is always 0%, and so hypotheses related to behaviors associated with this relationship, based on sharing no X-linked genes, still hold no matter what the amount of paternity uncertainty. The X-relatedness between a PGM and granddaughter is 50% given total paternity certainty. Even when paternity uncertainty is as high as 20% (i.e., there is a 20% chance that the PGM's son is not the biological father of the granddaughter), the X-relatedness between the PGM and granddaughter is 40%. This is because Hamiltonian relatedness refers to the statistical likelihood that two individuals share a given gene, rather than the percent of genetic material two individuals share (Hamilton, 1964a,b). Compared to the PGM-grandson relatedness of 0% and MGM-grandchild X-relatedness of 25% (which are all relationships unaffected by paternity uncertainty), PGM-granddaughter X-relatedness of 40% is still significantly higher than all other grandmother-grandchild X-relatedness. Even given an unlikely 20% rate of paternal discrepancy, the 40% chance of sharing X-linked genetic material between a PGM and granddaughter is still much higher than with a son's son (0%) and between a MGM and granddaughter (25%). Thus, there remains the same expected favoritism as Fox et al. (2010) suggested (see Table 1 in Fox et al. 2010).

Rice et al. (2010) calculated the circumstances under which an X-linked allele causing favoritism of granddaughters over grandsons would accumulate (Table 4.1). Using their inequality equations (see Table 2 of Rice et al. 2010), we have calculated new values to describe the circumstances under which the hypothetical X-linked granddaughter favoritism allele would increase in frequency, given varying degrees of paternal discrepancy (Table 4.3). Following Rice et al. (2010), we calculate the likelihood that an X-linked mutation, which causes grandparents to help their granddaughters at the expense of their grandsons, would accumulate as long as the detriment to grandsons is not more than a calculable magnitude greater than the benefit to granddaughters. Given dominant allele expression and complete paternity certainty, the threshold for selection is grandson harm at twice the expense of granddaughter help. Using the three rates of paternal discrepancy from the literature review above (0%; 1.3%; 3.7% see Skorecki et al. 1997; Simmons et al. 2004; Sykes and Irven 2000; Bellis et al. 2005) and also the popular figure of 10%, this threshold remains above 1.9. In other words, even given the highest estimated rate of prehistoric paternal discrepancy (10%), a dominant X-linked mutation that causes grandparents to help granddaughters at the expense of grandsons would accumulate as long as the expense to grandsons were no more than 1.95 times the benefit to granddaughters. The figures for additive expression, sex-specific, and lineage-specific expression are given in Table 4.3. The paternity uncertainty induced changes in threshold appear to be minor enough that the possibility of SA-zygotic drive towards granddaughter favoritism and longevity is not compromised.

The most comprehensive analysis possible measures the circumstances under which an X-linked mutation would increase in frequency, given a rate of paternal discrepancy ranging from 0 (total certainty; all fathers identify their children accurately) to 1 (total discrepancy; all fathers identify their children inaccurately) (Figure 4.3). Although total discrepancy is implausible, it is useful to visualize a curve that depicts the threshold for accumulation changes for the hypothetical X-linked mutation. A more specific analysis focuses on the curve where the threshold changes for allele frequency increase with rates of paternal discrepancy ranging from 0% to 10% (Figure 4.4). This segment of the larger threshold curve (Figure 4.3) displays the rate at which paternal discrepancy affects the threshold of the proportion benefit to granddaughters versus detriment to grandsons. This is the segment we consider to be the most likely range of paternal discrepancy rates among modern and ancient human populations. While increasing paternal discrepancy creates a stricter criterion for allele frequency increase (less detriment to grandsons compared to benefit to granddaughters), this effect is not strong (Table 4.3; Figure 4.4).

4.5 Conclusion

The asymmetrical inheritance pattern of the X-chromosome may influence selection among traits related to behavior and life history. The variation in X-relatedness between grandmothers and grandchildren, based on sex and lineage, may create opportunity for selection of genes that affect grandmothering strategy and longevity. Here, we

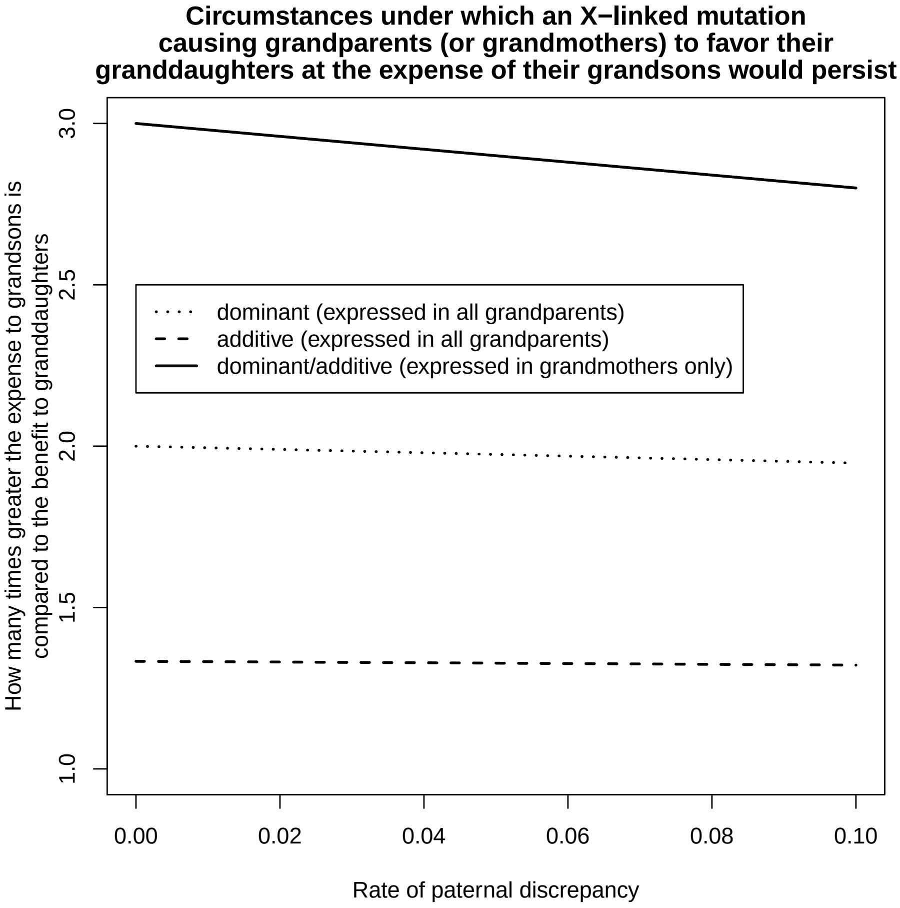

Figure 4.4: The threshold for an X-linked mutation causing grandparents (or grandmothers) to favor their granddaughters at the expense of their grandsons to accumulate. The threshold can be described as the maximum number of times greater the expense of this mutation would be to grandsons, compared to the benefit of the mutation to granddaughters. These values were calculated using the mathematical model from Rice et al. (2010). The range of paternal discrepancy is 0% (all paternity is identified accurately) and 10% (1 in 10 instances paternity is identified inaccurately). This range was chosen because previous studies suggest that our species' normal rates of paternal discrepancy may range from 1.3% to 3.7%, although many sources claim an unsubstantiated rate of 10%. Therefore, the range in this graph is meant to be inclusive and show a more sensitive scale of invasion threshold than Figure 4.3.

have reanalyzed data from seven previously-studied populations, in light of Rice et al.'s (2010) suggestion of SA-zygotic drive. The analysis explores the circumstances under which an X-linked mutation would persist, causing grandmothers to behave preferentially towards granddaughters at the expense of grandsons. The results show that six of the seven populations conform to a prediction of this hypothesis: that PGMs have a beneficial effect on granddaughters and a harmful effect on grandsons. Further research should explore how consistent this trend is between populations, and should see if this trend exists in modern industrialized populations. Additionally, future research should explore the behavioral mechanisms involved in this pattern.

Preferential grandmothering behavior may be present in other species as well. Johnstone and Cant (2010) recently reported that whales represent another clade in which postmenopausal longevity is consistently observed. Among certain whales, as a female gets older, her genetic relatedness to the members of her local group increases. This suggests that it is increasingly advantageous for her to care for individuals in her social group because she is increasingly likely to be closely related to them. The benefits of this strategy may contribute to longevity in whales. Also, some whale species are known to favor sons over their daughters, and this may directly affect fitness of individuals. Further research into preferential behaviors within families should extend to other species, for the purposes of understanding our species in the context of others.

The extent of care giving behaviors among the paternal line in our own species is often analyzed in terms of degree of paternity certainty.Many assumptions are made regarding the prevalence and importance of paternity uncertainty in the evolution of grandmothering behaviors and longevity. A review of the relevant literature ranging from cultural anthropology to genetics suggests that paternal discrepancy may be 1.3–3.7%, and there is evidence that rates today are similar to rates in prehistoric times, although more research needs to be done to confirm this. By evaluating a wide range of rates of paternal discrepancy, our models (adapted from Rice et al. 2010) suggest that the thresholds for selection of X-linked grandmothering traits are not dramatically influenced by paternal discrepancy, even when the rates are extremely high. Thus, there is opportunity for selection based on asymmetrical genetic relatedness, such as differential inheritance of sex chromosomes.

SA-zygotic drive may contribute to the evolution of human longevity. If the benefits of having a living grandmother are sufficiently advantageous for certain individuals, then this could lead to selection for longevity on a larger scale. Further research should probe the mechanisms by which paternal grandmothers have a beneficial effect on granddaughters and a detrimental effect on grandsons, in light of incentives for longevity. Additionally, as our understanding of functional genetics increases, finding X-linked traits influencing longevity and care giving would provide support for the hypotheses described herein.

Researchers should also further investigate the magnitude of the effects grandmothers have on different grandchildren. Finally, although attention has primarily focused on grandmothers and the X-chromosome, we think the roles of grandfathers and the Y-chromosome should also be explored in light of SA-zygotic drive.

Acknowledgments

The authors thank Philipp Braun for his assistance with statistical analyses, and they also thank The Gates Cambridge Trust.

References

☞[cited on page(s)]

Anderson, K. G. (2000). The life histories of american stepfathers in evolutionary perspective. *Human Nature*, 41(4):307–333. [☞78]

Anderson, K. G., Kaplan, H., and Lancaster, J. (1999). Paternal care by genetic fathers and stepfathers—I: reports from Albuquerque men. *Evolution and Human Behavior*, 20(6):105–431. [☞78]

Barber, N. (2000). *Why Parents Matter: Parental Investment and Child Outcomes*. Bergin & Garvey, London, UK. [☞78]

Bellis, M. A., Hughes, K., Hughes, S., and Ashton, J. R. (2005). Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology and Community Health*, 59:749–754. [☞86, 88, 90, 91, 102]

Borders, L. D., Black, L. K., and Pasley, B. K. (1998). Are adopted children and their parents at greater risk for negative outcomes? *Family Relations*, 47(3):237–241. [☞78]

Chrastil, E. R., Getz, W. M., Euler, H. A., and Starks, P. T. (2006). Paternity uncertainty overrides sex chromosome selection for preferential grandparenting. *Evolution and Human Behavior*, 27:206–223. [☞79, 83, 86, 90]

Euler, H. A. and Weitzel, B. (1996). Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, 7:39–59. [☞83]

Fox, M., Sear, R., Beise, J., Ragsdale, G., Voland, E., and 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. [☞79, 81, 82, 83, 85, 86, 90, 98, 102]

Hamilton, W. D. (1964a). The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7::1–16. [☞78, 90]

Hamilton, W. D. (1964b). The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, 7::17–52. [☞78, 90]

Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, 45(3):380–400. [☞79]

Hawkes, K., O'Connell, J. F., and Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans. *Current Anthropology*, 38(4):551–577. [☞78, 79]

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., and Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academies of Sciences USA*, 95:1336–1339. [☞85]

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., and Charnov, E. L. (2000). The grandmother hypothesis and human evolution. In Cronk, L., Chagnon, N., and Irons, W., editors, *Adaptation and Human Behavior: An Anthropological Perspective*, page 231–252. Aldine Transaction. [☞79]

Hill, K. and Hurtado, A. M. (1991). The evolution of premature reproductive senescence and menopause in human females: An evaluation of the "grandmother hypothesis". *Human Nature*, 2(4):313–350. [☞85]

Jamison, C. S., Cornell, L. L., Jamison, P. L., and Nakazato, H. (2002). Are all grandmothers equal? a review and a preliminary test of the "Grandmother Hypothesis" in Tokugawa Japan. *American Journal of Physical Anthropology*, 419:67–76. [☞82, 83]

Johnson, A. M., Mercer, C. H., Erens, B., Copas, A. J., McManus, S., Wellings, K., Fenton, K. A., Korovessis, C., Macdowall, W., Nanchahal, K., Purdon, S., and Field, J. (2001). Sexual behaviour in Britain: partnerships, practices, and hiv risk behaviours. *Lancet*, 358(9296):1835–1842. [☞86]

Johnstone, R. A. and Cant, M. A. (2010). The evolution of menopause in cetaceans and humans: the role of demography. *Proceedings of the Royal Society B: Biological Sciences*, 277(1701):3765–3771. [☞93]

Kachel, A. F., Premo, L. S., and Hublin, J. (2011). Grandmothering and natural selection. *Proceedings of the Royal Society B*, 278:384–391. (doi:10.1098/rspb.2010.1247). [☞84, 85, 86]

Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M., and Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, 428:178–181. [☞85]

Macintyre, S. and Sooman, A. (1991). Non-paternity and prenatal genetic screening. *Lancet*, 338(8771):869–871. [☞86]

Platek, S. and Shackelford, T. K. (2006). *Female infidelity and paternal uncertainty: Evolutionary perspectives on male anti-cuckoldry tactics*. Cambridge University Press. [☞86]

Ragsdale, G. (2004). Grandmothering in Cambridgeshire, 1770–1861. *Human Nature*, 45(3):301–317. [☞85]

Rice, W. R., Gavrilets, S., and Friberg, U. (2008). Sexually antagonistic "zygotic drive" of the sex chromosomes. *PLoS Genetics*, 4(42):e1000313 (12 pages). doi:10.1371/journal.pgen.1000313. [☞81]

Rice, W. R., Gavrilets, S., and 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. [☞78, 80, 81, 82, 83, 84, 85, 86, 88, 89, 90, 91, 92, 93, 99, 102]

Santrock, J., Warshak, R., Lindbergh, C., and Meadows, L. (1982). Children's and parents' observed social behavior in stepfather families. *Child Development*, 53:172–480. [☞78]

Simmons, L. W., Firman, R. C., Rhodes, G., and Peters, M. (2004). Human sperm-competition: testis size, sperm production and rates of extrapair copulations. *Animal Behaviour*, 68(2):297–302. [☞86, 87, 88, 90, 91, 102]

Skorecki, K., Selig, S., Blazer, S., Rappaport, B., Bradman, R., Bradman, N., Waburton, P., Ismajlowicz, M., and Hammer, M. F. (1997). Y-chromosomes of Jewish priests. *Nature*, 385(6611):32. [☞86, 88, 90, 91, 102]

Sykes, B. and Irven, C. (2000). Surnames and the Y chromosome. *American Journal of Human Genetics*, 66(4):1417–1419. [☞86, 88, 90, 91, 102]

Voland, E. and Beise, J. (2002). Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhörn. *Behavioral Ecology and Sociobiology*, 52:135–443. [☞85]

Wilder, J. A. (2010). Do grandmothers who play favorites sow seeds of genomic conflict? *BioEssays*, 32(6):157–460. [☞79]

Abbildungsverzeichnis

Tabellenverzeichnis