

Grandparental and Extended Kin Relationships

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Modern societies have undergone changes that impact grandparental and other extended kin relationships. Birth rates and conjugal stability have decreased while life expectancy and residential mobility have increased. State welfare provisions have largely replaced dependence on kin support in many modern states. Extended families have become smaller with children having fewer siblings, fewer aunts and uncles, and fewer cousins. We have patchwork and 'bean-pole' families around us. The breakdown of traditional family structures has been proclaimed repeatedly. But do these demographic changes touch deeper family structures? Scientists with an evolutionary perspective are reluctant to confirm and hesitant to consider the present time unique. Most people have or will have grandchildren, and all have or had grandparents. With rising life expectancy, more people will have living grandparents and will be grandparents for a longer portion of their lives. The plays may change, but the plots remain the same. The mother-daughter relationship will remain the center of the family. With rising divorce rates and child custody typically given to mothers, matrilineal ties are strengthened and men marginalized from the family. The role of the maternal grandmother might therefore become even more important in the future than it has been in the past.

Much family research has been done by sociologists, who traditionally bear little consideration of a human nature with sex differences. They tend to break families at generations (e.g. parents vs. grandparents) and group grandparents as a homogenous quartet (e.g., Szinovacz, 1998). When distinctions are made, grandmothers and grandfathers may be differentiated, but typically without consideration of lineage. Only in rare cases (e.g., Dench & Ogg, 2003; Fingerman, 2004; Rossi & Rossi, 1990) are grandparents categorically distinguished into the four types of grandparents, but if so, without theoretical guidance from evolutionary theory about basic sex differences. Evolutionary psychologists heed the advice of Socrates to cut hunted game (meaning nature) at its joints. In this perspective the differentiation along sex *and* lineage is crucial. There are grandmothers and grandfathers, and what is good for the goose may not be good for the gander.

In this chapter, we argue that grandparenthood may trigger psychological adaptations with relationship-specific features. Grandparental investment cannot be understood adequately without consideration of its Darwinian fitness consequences. We similarly cannot understand relationships with aunts/uncles and nieces/nephews without such a consideration. Because parents are mediators of grandparent and grandchild relationships, the evolutionary analysis of grandparenthood sheds light on the

seemingly universal plight of in-law relationships, most conspicuous in the conflict between mothers-in-law and daughters-in-law. Investment in progeny and emotional closeness of intergenerational dyads is highly and robustly structured. This structure is parsimoniously and to a considerable extent accounted for by a few basic reproductively relevant variables including sex-specific reproductive strategy and relationship uncertainty (Euler, Hoier, & Rohde, in press).

Reproductive Strategy and Relationship Uncertainty as Basic Determinants of Grandparental Investment

The reproductive strategy of the female mammal demands high maternal investment. Maximizing genetic replication generally requires maximizing maternal investment, whereas for males with their high reproductive potential the opportunity costs of paternal investments are higher. Maternal investment is thus obligatory, paternal investment more facultative, that is, depending on circumstances. This asymmetry between the sexes has far-ranging consequences, also in the area of intergenerational solidarity. The particular consequences are not always straightforward, but are mediated by socioecological circumstances, like subsistence conditions, mating and kinship system, division of labor, residence pattern, lineality, resource control, and inheritance rules (Holden, Sear, & Mace, 2003; Leonetti, Nath, Hemam, & Neill, 2005; Voland & Beise, 2005).

Juvenile humans, relative to other primates, show the highest demand for parental investment. To be able to fulfill these demands, mothers need help to raise offspring and appear to contain features that offset the investment demands of offspring (e.g., preferences for mates of high social standing, resources, ambition; Buss, 2003). The traditional view is that fathers provide help in various forms including time, provisions of food, offering protection, and socialization of children. However, even though humans belong to a rare few primate species where paternal investment occurs at all, the absolute investments made by fathers are small relative to those made by mothers. Even among Aka pygmies where fathers have been considered to be most helpful, their investment pales in comparison to the investment made by mothers (Hewlett, 1991). As to food, the caloric contribution of fathers in hunter-gatherer societies is not as impressive as once thought. Hunting successes come unpredictably, are generally shared among the tribe in order to contribute to the status of the hunter, and even the total calories from hunting are less than those from gathering. And above all, Pleistocene men were probably just not around much of the time, but roaming and ranging, fighting and philandering. Babies, however, required constant attention.

Help for mothers may therefore have come dependably from closely related females, most notably from the mother's mother, less from her sisters and some from her preadolescent daughters. Grandmaternal support can help explain the relatively short human inter-birth interval in natural fertility populations (Mace & Sear, 2005). In ancestral populations, without modern conveniences such as grocery stores, baby carriages, and baby formula, the inter-birth interval was probably around three years if circumstances were good. This appears long, but only compared to birth rates of historic times before the modern demographic transition. Compared to other primates such a birth interval is rather short (Galdikas & Wood, 1990). Help from maternal grandmothers is assumed to have enabled human mothers to attain such a short inter-birth interval. In addition to increasing the fertility of her daughter, grandmother's help may also decrease the mortality of her grandchildren (Sear & Mace, in press).

Grandmothers can help only if they have a surplus of resources, which they might have if they do not themselves have infants that demand care. A unique feature of human female life history that may have hinged on this balance between female investment in offspring and in grandchildren is menopause. The idea of menopause as a reproductive adaptation was first put forth by Williams (1957) and later referred to as the "grandmother hypothesis", not quite correctly so, because Williams was apparently considering only the older female as a mother, not as a grandmother: "... it may have become advantageous for a woman of forty-five or fifty to stop dividing her declining faculties between the care of extant offspring and the production of new ones" (p. 407-408). Hamilton (1966) expanded on this notion of "a special value of the old woman as mother or grandmother" (p. 37), but was reluctant to consider it an adaptation. We could, therefore, distinguish between a weak and a strong version of the Grandmother Hypothesis, the weak one referring merely to the menopausal cessation of reproduction, the strong one adding care of grandoffspring.

The Grandmother Hypothesis is intuitively appealing, but debate continues whether menopause is indeed an adaptation, or only a by-product or modern artifact (for a summary see Volland, Chasiotis, & Schiefenhövel, 2005). There are strong data suggesting that grandmaternal help can contribute to the fitness of the mother and to the survival of the grandoffspring (Hawkes, K., O'Connell, K. J. F., & Blurton-Jones, N. G., 1989; Hawkes et al., 2000; Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004), and thus to the inclusive fitness of the grandmother herself. Most convincing are recent data by Sear and Mace (in press) on the effect of the presence of kin on child survival rates among natural fertility populations. The presence of the maternal grandmother contributed to grandoffspring survival in the majority of studies

(10 out of 12 studies). The presence of the other three grandparents was overall less beneficial to grandoffspring. Surprisingly, Voland and Beise (2002) even showed that in a historical northern German population it was better for child survival if the paternal grandmother, that is the mother-in-law, was *not* alive.

To help the adult daughter in her maternal effort is in the inclusive fitness interest of a postmenopausal woman, and the best she can offer her daughter is her time, food acquisition in subsistence societies, and child care universally. Her husband, the maternal grandfather, may be of additional help, but his opportunity costs are higher which means that he can be assumed to be generally less inclined to help his daughter than his spouse is inclined. Grandparental resources are limited and their allocation must be maximized. How much should be invested in the adult son and his offspring? The son is not as burdened with child care as is the daughter, but he can be aided in his reproductive effort, not by time for child care, but by the transfer of status and wealth if socioecological conditions permit transformation of status and wealth into sexual access. These conditions lead to a comparably high reproductive variance of males, as seen in traditional pastoral societies with a mating system of optional polygyny. Ancestral Pleistocene environments, however, were presumably not characterized by extreme sex differences in reproductive variance. Under conditions of relative pervasive monogamy, be it ecologically imposed like in the Stone Ages or culturally imposed like in modern societies, time investment in the adult daughter and her children rather than in the adult son and his offspring should be the more desirable option for postmenopausal women. Whether daughter-biased investment is subsumed under matrilineal bias, allomothering, or cooperative breeding, the ultimate cause derives from the sex-specific reproductive strategy of humans.

The role of paternity uncertainty, or more precisely, grandmaternity and grandpaternity uncertainty, was first mentioned by Dawkins (1976). Grandparents throughout human evolutionary history had varying degrees of certainty in their relatedness to grandchildren. Maternal grandmothers could have been more certain about their relatedness to grandchildren than other grandparents. The maternal grandfather and the paternal grandmother each have one link of paternity uncertainty, the paternal grandfather has two links. The discrepancy between assumed and actual paternity in current Western societies is less than three percent, rather than the ominous 10% which appears to be more a modern myth than a fact (Euler, 2004), but it may have well been around 10% or even more in earlier times. Relationship certainty is, therefore, a feature to be considered when evaluating preferential grandpaternal investment,

although it has in our judgment weaker effects than have sex-specific reproductive strategies. For many researchers in evolutionary accounts of grandparenthood, however (e. g. Smith, 1991), paternity uncertainty is the only factor considered. The problem with such a monocausal explanation is the observation that generally the maternal grandfather invests more in grandoffspring than the paternal grandmother invests. This problem has been specifically addressed by Laham, Gonsalkorale, and von Hippel (2005) with an account called 'Preferential Investment in More Certain Kin' (see also Beise, 2005, p. 232-233), whose charm is parsimoniousness. Laham et al.'s 'outlet theory' will be discussed in more detail below. We take the position that sex-specific reproductive strategy and paternity uncertainty are ultimate causes which both contribute to the obvious matrilineal bias in human family structures in general and to discriminative grandparental investment in particular (Euler, Hoier, & Rohde, 2001).

The Solicitude Rank Order of Grandparents

Grandparent-grandoffspring relationships may be approached from different perspectives. The informant may be the grandoffspring, the linking parent, or the grandparent. The three information sources appear to be mostly consistent, although grandparents themselves tend to ascribe the greatest importance to and express the highest satisfaction with the grandparental role, feel most closeness to kin, and claim the highest rate of contact (Dench & Ogg, 2003). The informant may be questioned about a plethora of proxies for investment, including ratings of grandparental solicitude, naming favorite grandparents/grandoffspring, and contact frequencies. The determinants of grandparental investments, finally, are not restricted to sex-specific reproductive strategy and paternity uncertainty. These two variables are important, but nevertheless account for only a fraction of the total variance. We shall present empirical results which cover some aspect of each of the three avenues.

The first study conducted to investigate preferential grandparental investment from an evolutionary perspective was, to our knowledge, Smith (1988, 1991). Differential investment among grandparents was predicted on the basis of relationship uncertainty, which yielded equal investment for the paternal grandmother and the maternal grandfather. In a sizeable sample of $N = 587$, however, Smith (1991) found not only maternal grandparents to spend more time with grandchildren than paternal grandparents, and grandmothers more than grandfathers, but also maternal grandfathers more than paternal grandmothers. This pattern was seen in so-called unilineal grandparents (those who have grandchildren only through daughters or through sons) as well as in bilineal grandparents (grandchildren through daughters and sons).

Moreover, the difference between the investment of grandmothers and grandfathers should have been the same as the difference between maternal and paternal grandparents, but the latter was larger. The two deviations from the predictions were explained post hoc by resorting to other factors.

Euler and Weitzel (1996) deduced an ordered prediction about grandparental solicitude from the combined effects of both sex-specific reproductive strategy and paternity uncertainty. The former, as the stronger determinant, predicts a higher solicitude for children of daughters than children of sons. The latter, as the weaker factor, predicts a higher solicitude by grandmothers than by grandfathers. The amount of solicitude was assessed by asking adult participants about the amount of grandparental care received in childhood, under the assumption that ratings by recipients of care are a good, maybe even better indicator of grandparental solicitude than ratings given by grandparents themselves, because norms of impartiality prevent grandparents from making self-descriptive statements about favored grandchildren. A convenience sample of both student and community participants (720 male, 1,125 female, 12 unspecified; ages 16 to 80 years) were asked how much each grandparent had cared for them ("*gekümmert*") up to the age of seven years. The German verb *kümmern* has both a behavioral and a cognitive-emotional meaning, namely (1) to care for, to look after, and (2) to be emotionally and/or cognitively concerned about. From the total sample of 1,857 respondents a subset of 603 cases were selected for analysis whose four grandparents were all still alive when the participant was seven years old.

The results confirmed predictions about the discriminativeness of grandparental solicitude. The maternal grandmother was rated as having been the most caring, followed by the maternal grandfather, the paternal grandmother, and the paternal grandfather. Maternal grandparents were significantly more caring than paternal grandparents, and grandmothers significantly more than grandfathers. The effect sizes, given as the partial η^2 , which denotes the variance attributable to the effect of interest divided by this variance plus error variance, were .11 for the lineage effect (maternal vs. paternal) and .17 for the effect of sex of grandparent. Both effects together account for a sizable proportion of the variance.

Of special interest, apart from the insufficiency of paternity uncertainty as the only basic determinant, is the finding that the maternal grandfather cared more than the paternal grandmother. If grandparental care giving were solely determined by a social role which ascribes child care predominantly to women, then both types of grandmothers should provide more care than both grandfathers. Accordingly, this argument should apply particularly to the older grandchildren in the sample, whose grandparents

presumably subscribe more to traditional gender roles than grandparents of younger participants. However, the difference was statistically significant in the opposite direction and even more pronounced for the older (40 years or more) than for the younger participants.

This same pattern of discriminative grandparental solicitude has been found in comparable studies in various countries, including the U.S. (DeKay, 1995), France (Steinbach & Henke, 1998), Belgium (van Ranst, Verschueren, & Marcoen, 1995), and Greece (Pashos, 2000). Pashos (2000), who studied within-culture variation in grandparental investment, found that among urban Greeks the pattern of grandparental solicitude was similar to other studies, but among rural Greeks it differed, especially for male respondents, who rated the care given by paternal grandparents higher than by maternal grandparents. A similar deviation from the standard pattern of modern Western societies has been reported by King and Elder (1995) who found that paternal grandparents appeared more salient in American farm families. Grandchildren in farm families, as compared to rural non-farm families, lived closer to their paternal grandparents, visited them more frequently, and rated the quality of their relationship higher. In pastoral societies with patrilocality, patrilinearity, and corresponding inheritance rules, the investment in offspring of sons pays the grandparents reproductively more than investment in offspring of daughters. These findings point to the need to appreciate socioecological conditions which moderate, or even reverse, patterns of grandparental solicitude that might otherwise be missed by predicting effects based only on lineage and sex-specific reproductive strategies.

Various studies of aspects of grandparental investment other than grandchild-rated solicitude were investigated have confirmed the general pattern of discriminative grandparental investment, including perception of closeness to (Fischer, 1983), time spent with grandchildren (Smith, 1988, 1991), interaction frequencies (Eisenberg, 1988; Hartshorne & Manaster, 1982; Hoffman, 1978/1979; Pollet, Nettle, & Nelissen, 2006; Salmon, 1999), emotional closeness to grandparents (Eisenberg, 1988; Hoffman, 1978/1979; Kennedy, 1990; Matthews & Sprey, 1985; McBurney, Pashos, & Gaulin, 2006; Robins & Tomanec, 1962; Rossi & Rossi, 1990; Russell & Wells, 1987), naming favorite (Kahana & Kahana, 1970; Steinbach & Henke, 1998) or emotionally closest grandparents (Hodgson, 1992), gifts received from grandparents (DeKay, 1995), grandparental mourning after a grandchild's death (Littlefield & Rushton, 1986), and adoption of grandchildren (Daly & Wilson, 1980; Schiefenhövel & Grabolle, 2005). Missing from this listing are grandparental bequests, about which no data are known to the authors.

Even the informal terms of address of grandparents are telling in various languages. The maternal grandmother is most often of all grandparents addressed with an endearing or diminutive name. For example, in Germany the maternal grandmother might be called "my dear granny" (German: "die liebe Oma", or "Omilein"), whereas the paternal grandmother is just called "the other grandmother" (Euler, Hoier, & Pölitz, 1998).

Moderating Variables

Sex-specific strategy and paternity uncertainty are not the only determinants of grandparental investment. There are three interacting generations involved, which—together with the socioecological context—open gateways for a variety of variables relevant for an evolutionary analysis, about which data are available. A treatment of constructivistic variables may be found elsewhere (e.g. Szinovacz, 1998).

Residential Proximity

The rule "Out of sight, out of mind" applies to the grandparent-grandoffspring relationship. The greater the distance between grandparent and grandchild, the less time spent together (Smith, 1991), the less contact (Hodgson, 1992), the lower the solicitude rating by the grandoffspring (Euler & Weitzel, 1996), and the less closeness (Robins & Tomanec, 1962). Salmon (1999), however, found no negative correlation between distance and frequency of visits and phone calls. In many reports, the means of residential distance do not differ between the types of grandparent in modern neolocal societies (e.g. Euler & Weitzel, 1996; Pashos, 2000; Smith, 1991; Thomas, 1989), but there are also exceptions of closer proximity to paternal (e. g. King & Elder, 1995; Salmon, 1999) or to maternal grandparents (Michalski & Shackelford, 2005). Considering the role of the maternal grandmother as a source of support and investment in grandoffspring, greater residential distance from maternal than from paternal grandparents is somewhat surprising, and is at odds with the strong version of the grandmother hypothesis (Hawkes et al. 2000) and the role we ascribe to invest directly in the daughter's offspring. The problem may be explained by other dispersal determinants in non-natural fertility populations (Koenig, 1989), as a mismatch phenomenon, as is the finding that grandmothers are emotionally closest to daughters even if they are childless (Nosaka & Chasiotis, 2005). In any case, the possible confounding influence of residential distance is a necessary control in research on grandparent-grandchild relationships.

The negative correlations between residential distance and ratings of grandparental investments seem to vary systematically over the four types of grandparents, that is, inverse with the general

grandparent ranking. For maternal grandmothers the correlation tends to the smallest, for the paternal grandfather the largest (Euler & Weitzel, 1996). This may be an indication that the investments of the maternal grandmother are the least facultative and investments of the paternal grandfather the most facultative.

Marital Status of Grandparent

Grandparents typically come in pairs and show, due to shared obligations towards kin, a high degree of similarity in care (Euler & Weitzel, 1996). This acts as a confound when assessing the independent solicitude of each grandparent type. Therefore, grandparents living alone show a different pattern of solicitude, depending on the reason for singlehood. Widowed grandparents did not differ from those who were married, but separated or divorced grandparents did differ. The investment of maternal grandmothers was not affected by the presence (or absence) of her mate. The presence of a mate putatively related to the grandchild was a factor for the other grandparent types—for the paternal grandmother it matters a bit, for the maternal grandfather a lot, but most for the paternal grandfather (see also Dench & Ogg, 2003). The family ties of grandfathers, particularly of paternal grandfathers, are seriously weakened upon separation from the wife. What is true for fathers is equally and still true for grandfathers: Putative (grand)paternal effort is actually to a large portion mating effort (Anderson, Kaplan, & Lancaster, 1999).

Number of Living Grandparents, Number of Grandchildren

Although one might expect that a grandparent's solicitude decreases with the number of other grandparents, such a dilution effect was not found by Euler and Weitzel (1996). Participants did not rate a grandparent's investment differently if the participant had two, three, or four grandparents alive during childhood.

We would assume diminishing returns for investment in a particular grandchild as the number of grandchildren a grandparent has increases. This can be predicted based on the increased attractiveness of alternative investments. A share of investment in all grandchildren pays more than investment in only a subset of grandchildren. We would, therefore, predict that the total investment of grandparents is correlated positively, but the share for each single grandchild negatively, with the number of grandchildren. This was indeed found by Smith (1991). The dilution effect has also been reported repeatedly from grandoffspring ratings: Grandparental investment is rated lower, the more cousins (Laham et al., 2005) or the more aunts or uncles (Euler et al., in press) the grandoffspring reports.

Age of Grandparent, Parent, and Grandchild

As expected, grandparental investment correlates negatively with age of grandchild (e. g. Dench & Ogg, 2003), and it also correlates negatively with age of parent (Smith, 1991). The findings are unclear as to the effect of grandparent age. Smith (1991, p. 163) reports a small but significantly negative correlation with all grandparents, but this measure appears to be confounded with type of grandparent, because the maternal grandmother is, on average, the youngest and the paternal grandfather is, on average, the oldest. Euler and Weitzel (1996; see also Pashos, 2000) found only small but not significant negative correlations, separate for each grandparent type, between grandparent age and rated grandparental solicitude. However, the age ranges were not large in these between-subject comparisons and possible cohort confounds were not controlled. We expect changes in overall investment and specific types of investment as a function of the increasing ages of grandparents and grandchildren.

Sibling Constellation of Parent

A puzzling deviation from the dilution effect was found by Euler et al. (in press) and is shown in Fig. 1. Contrary to intuition and dilution effect, paternal grandparents care less for the child (that is, the participant giving the rating) of a single son than if the son has a sibling. The data in Fig. 1 are from a total sample of 1696 participants, mostly college students, collected over several years, with the same effect shown in every yearly subsample. The sample sizes for the data points in Fig. 1 vary between $N = 136$ (maternal grandfather, daughter no sibling) and $N = 770$, maternal grandmother, daughter more than two siblings). All cases were included where either the father or the mother, but not both, have the number of siblings along the horizontal axis

(Fig 1 about here)

We tested various hypotheses to account for this single son deviation from the dilution effect. For paternal grandparents with two adult offspring, the caregiving for the grandchild did not depend on the sex of the son's sibling. This finding excluded an explanation of the basis of some sort of sibling fairness, like if the son has a sister, her kids get so much attention, so for fairness his kids should get an equal amount. Several possible hypotheses remain to account for these data, for example (1) the mother-in-law/daughter-in-law conflict hypothesis, (2) the son-as-heir hypothesis, and (3) the sibling competition hypothesis.

The relationship between the mother-in-law (MiL) and the daughter-in-law (DiL) is burdened with conflict (see next section for more detail). If parents have a son as the single offspring, there is only one

female in the next generation, the son's spouse, and she is an in-law. The conflict cannot be attenuated or made less salient by other offspring or other in-laws. Whatever the dynamic details of this conflict problem, the hypothesis would predict that the MiL/DiL relationship, but not the father-in-law(FiL)/daughter-in-law(DiL) relationship, should be poorer if the son is an only child than if the son has one or more siblings. This prediction was indeed supported. The Mil/DiL relationship in case of a son as only child was numerically lower than the relationship in cases where the son has a brother, a sister, only brother, and only sisters. It was significantly poorer than if the son had at least a brother and at least a sister. No comparable differences were found for the FiL/DiL relationships.

The son-as-heir hypothesis relies on data selection artifact and originates from the following observation. The sex ratio at birth (boys to 100 girls), according to the 1989 census in Germany, was for families within the lower half of income (< 4000 German marks) 105.2 for families with one child, 104.6 for those with two children, and 104.1 for those with three or more children. For the upper half of income (>4000 marks) it was, respectively, 118.8, 110.1, and 112.9 (Müller, 1992). The difference between the poorer and the richer families demonstrates the Trivers-Willard effect. Notable is the extremely high male-biased sex ratio in families with only one child (son). This high ratio of 118.8 may be due to the desire for a male heir. Many couples want a male child. If the first child is a boy, the desire is satisfied. If the first child is a girl, they try again. This means that among families with a boy as the single offspring there is a larger proportion of couples with an interest less in children per se than among families with other offspring combinations, including families with a daughter as a single child. Couples who have only one male child may on average be less inclined towards parental investment. Extending this argument, they may be less inclined for later grandparental investment. This latter extension, however, may be debatable if one argues that there are relationship-specific adaptations and that parental investment cannot be generalized sweepingly into grandparental investment. The son-as-heir hypothesis of the lowered grandparental investment in offspring of a male singleton has not been tested empirically so far.

An alternative explanation of lowered grandparental investment in grandoffspring by single sons may be based on sex-specific sibling competition of parents over their parent's investments in their children. If (a) siblings compete with each other over grandparental investments and (b) sons compete more intensely for parental resources than daughters do, then the pattern may be interpretable based on this conjecture. Grandchildren through sons without siblings may receive less investment than grandchildren

through sons with siblings because psychological mechanisms are not activated in the mind of the only child, here the adult son that triggers his motivation to secure resources from his parents for his children. This effect might be predicted not to hold for women because sisters may not compete as intensely with siblings for access to parental resources. Although speculative, the impact of parental competitiveness for grandparental resources deserves a closer look in future research. Parents may not be explicitly competitive with siblings about grandparental resources but they may emphasize to their children the importance of spending time with grandparents as a means of extracting more grandparental resources for their children than for their sibling's children.

The sex constellation of the extended family is the central aspect of the outlet theory of Laham et al. (2005). To explain why maternal grandfathers are emotionally closer to grandchildren than paternal grandmothers, the authors point to differences in paternity-certain outlets between these grandparents. The maternal grandfather has the more certain outlet in the children of his daughter rather than in the children of his son for whom he would be the paternal grandfather. The paternal grandmother, however, who might also be a maternal grandmother, may prefer to invest as the maternal grandmother in the children of her daughter rather than as a paternal grandmother in the children of her son. This outlet bias adds to the investment of the maternal grandfather and detracts from the investment of the paternal grandmother. Laham et al. (2005) present empirical support for this hypothesis. If the maternal grandfather has other grandchildren through daughters but the paternal grandmother does not, the preference for the maternal grandfather over the paternal grandmother should be most evident. If, in contrast, the paternal grandmother has other grandchildren through daughters but the maternal grandfather does not, the outlet theory would predict a preference for the paternal grandmother over the maternal grandfather. Laham et al. did indeed find a preference for the maternal grandfather only in the first case but not in the second one. However, a preference reversal in the second case was not observed.

Laham et al. (2005) concede that their outlet considerations amount to small effect sizes. They certainly need to be considered as moderating variables, but they cannot account by themselves alone for the generally found higher solicitude of the maternal grandfather over the paternal grandmother and thus discount the effect of sex-specific reproductive strategy. Our data base does not contain information about the existence of other grandchildren but rather about parents' siblings. If the father has only a sister and the

mother only a brother, the solicitude of the paternal grandmother is not rated higher than that of the maternal grandfather, nor is it if the father has as siblings only sisters and the mother only brothers.

The higher solicitude of the maternal grandfather over the paternal grandmother is only to a minor extent determined by availability of paternity-certain outlets. A larger determinant is laterality (matrilateral vs patrilateral) and thus sex-specific reproductive strategy. The largest determinant, however, is simply the sex-specificity of the particular care behavior. To identify features of grandparental investment, the authors have developed an inventory including various acts that grandparents may do for their grandchildren. In an initial examination of these acts, two-hundred and thirty German students (59 male, 171 female) were asked to rate 55 specific activities on a 10-point scale as to how much each of the four grandparents had done with or for them. To quantify the grandparental sex-specificity of each activity, we calculated the difference between the mean for both grandmothers and the mean for both grandfathers. For the item-specific laterality difference we calculated the difference between maternal and paternal grandparents. Across items, the maternal grandfather/paternal grandmother difference correlated $r = .31$ ($p = .02$) with the laterality difference and $r = .89$ with the sex-specificity of the behavior. Only for extreme female-gendered behaviors, like cooking for the grandchild or making clothes for him or her, does the paternal grandmother overtake the paternal grandfather.

Birth Rank

Salmon (1999) reported a marked birth order effect of the linking parent. According to reports of adult grandoffspring, grandparents had significantly less contact with grandchildren of their middleborn daughters or sons than with grandchildren of firstborn and lastborn offspring, a finding explained by the fact that middleborns show less attachment to their parents and less kinship ties than do firstborns or lastborns (see Sulloway, this volume). With respect to the global grandparental solicitude rating by adult grandoffspring, we could not replicate the clear V-shaped pattern (firstborn high, middleborn low, lastborn high) in a sample of 1689 student participants (507 males, 1182 females, 7 undeclared), collected over three consecutive years. The sample sizes for the 12 cells (four grandparent types, three birth rank types) ranged from $N = 114$ (paternal grandparent, lastborn father) to $N = 302$ (paternal grandmother, middleborn father). No effect of parental rank on grandparental caregiving could be observed except that parents of lastborn parents were rated as numerically more solicitous than parents of middleborn parents, statistically

significant for maternal grandparents (maternal grandmother $t = 2.86$, $df = 430$, $p < .01$, $d = .29$; maternal grandfather $t = 2.39$, $df = 391$, $p < .05$, $d = .25$).

With respect to grandchild birth rank, we are aware of no published data except that Leonetti et al. (2005) found among the Bengali in India the presence of the paternal grandmother to be positively related to grandchild weight, but with no child birth rank differences.

Sex of Grandchild

If grandparents are asked about their overall investment or their emotional closeness to a grandchild, the sex of the grandchild generally does not matter (e.g. Robins & Tomanec, 1962; Thomas, 1989), owing perhaps to a reluctance to express favoritism. Evolutionary theories would not predict a general preference by grandchild sex (Daly & Wilson, 1990) except in interaction with other factors, like parental resource capacity (Trivers & Willard, 1973). Euler and Weitzel (1996) reported support for a Trivers-Willard effect only for the maternal grandparents, and also Leek and Smith (1991) found no clear support. However, overall investment does not tell us whether specific acts are done preferentially for female or for male grandchildren.

If adult grandoffspring are reporting grandparental investment, females give somewhat higher ratings in some studies (e. g. Euler & Weitzel, 1996; Salmon, 1999), but not in others (e. g. Laham et al., 2005; Pashos, 2000; Robins & Tomanec, 1962; Spitze & Ward, 1998). A sex difference could be due to a grandparental preference for females, or to the higher family sentiment of females compared to males (Salmon & Daly, 1996) which would result in a positive rating bias in female grandoffspring. A general rating bias would be expected to affect all grandparents equally. This, however, is not the case, as the analysis of the first authors cumulative data file ($N = 3545$) showed. Females rate only the care of the maternal grandparents and of the paternal grandmother higher than male participants, all significant but with very small effect sizes ranging from $d = 0.08$ (maternal grandfather) to $d = 0.19$ (maternal grandmother). Paternal grandfathers, in contrast, were not rated differently by male and female grandoffspring.

The preferential treatment of a certain grandchild sex is activity-specific. From the data sample mentioned above about 55 specific grandparental activities, we calculated the mean ratings over all four grandparents for each item. On 14 out of the 55 items female participants gave a significantly higher rating, male participants on none of them. The collection of the 14 items revealed that there seems not to be a

primary positive bias for the female grandchild, but rather a secondary one. Girls are socially/emotionally more responsive than boys (item example: Grandparent "smooched or cuddled with me"), are considered in more need of surveillance ("... picked me up from school"), and ask more often for help than boys do ("... taught me skills, e.g. bicycling, swimming"). What is true for parents seems also true for grandparents: Girls get more (grand)parental attention, because they accept care easier and reward the caregiver more than boys do. This explanation solves the finding that paternal grandfathers are the only grandparent not to get higher ratings from female than from male grandoffsprings: Paternal grandfathers do not invest enough to produce a difference.

A theoretical possibility for a particular statistical interaction between grandparent and grandoffspring sex was suggested by Chrastil, Getz, Euler, and Starks (2006). Ignoring paternity uncertainty, grandparents are equally related to male and female grandchildren only with respect to autosomal genes, not genes on the sex chromosomes. Because males are heterozygous for sex chromosomes, paternal grandparents are not symmetrically related to male and female grandoffspring. The Y chromosome is directly passed from the paternal grandfather to his grandson, and only along this route. This allows for the prediction that paternal grandfathers favor grandsons over granddaughters. The prediction was tested with two different data sets and found no clear support. Sex chromosome selection, if it produces differential effects at all, is not strong enough to override paternity uncertainty effects.

Across generations, same-sex dyads tend to show higher investments than cross-sex dyads (Thomas, 1994; Godoy et al., 2006). The principle "Like father, like son; like mother, like daughter" applies to grandparent-parent dyads (Euler et al., 2001) and grandparent-grandoffspring dyads (Salmon, 1999). We calculated the ratings given on the 55 activity items to both grandmothers combined and both grandfathers combined, and found a numerical same-sex preference on 51 items, 17 of which were significant.

Phenotypical Similarity

Unlike some of the moderating variables discussed so far, the phenotypical similarity between investment provider and investment receiver is a variable of unique importance to adaptationist thinking, because resemblance is a cue of genetic relatedness. Grandparents should use such cues and be influenced by resemblance to the grandchild. It has been shown that males are more affected by resemblance to children than females are (e. g. Platek, Burch, Panyavin, Wasserman, & Gallup, 2002). Likewise, we should expect that the more links of paternity uncertainty, the higher should be the correlation between

grandparental investment and perceived resemblance, either in looks, or in behavior, or both. Thus, maternal grandmothers should be least affected, paternal grandfathers most, with the other two grandparents in between. Also the resemblance to adult offspring could be a factor guiding investment decisions. Grandparents should make their investment in grandoffspring more dependent on similarity to sons than to daughters.

There is meager empirical support for these predictions and more evidence would be desirable. Leek and Smith (1991) found positive correlations between help given and personality similarity to adult offspring as well as to grandchildren. However, without differentiation as to sex this finding is too vague to bear on the influence of paternity uncertainty. Euler (1994) reported that the correlation between resemblance in behavior and/or appearance and grandoffspring-rated solicitude were—over the four grandparent types—inversely related to solicitude. The correlations were $r = .37$ for the maternal grandmother, $r = .39$ for the maternal grandfather, $r = .42$ for the paternal grandmother, and $r = .47$ for the paternal grandfather. The differences between the coefficients, however, were not statistically significant.

Type of Investment Activity

The type of grandparental investment activity, like parental effort, is strongly determined by the gender of the investor. Grandmothers tend to do the time-consuming, empathic, caring, and consoling activities, whereas grandfathers tend to do the repairs, teach skills (except for cooking), and spend money. Whether the difference in caregiving ratings between maternal grandfathers and paternal grandmothers is large, small, or even reversed is solely determined by the general grandparental gender difference in behavior.

To assess the activities that serve as best predictors of grandparental solicitude, we correlated the overall solicitude rating with the 55 activity ratings and obtained the highest correlations (mostly $r > .60$) for activities which consume time (e. g. "Spent time with me", "Played games with me") and for activities indicating empathy and emotional closeness (e. g. "Was proud of me", "Complimented me", "Encouraged me"). Devoted time and emotional closeness are the best behavioral and subjective proxies of kin investment.

Quality of Grandparent/Parent Relationship

Parents, particularly the mother, act as gatekeepers who regulate grandparental access to grandchildren. Grandparental solicitude should therefore depend on the quality of the grandparent-parent

relationship. We correlated the ratings given retrospectively by our adult participants to the quality of relationship to each of the eight grandparent-parent dyads with the solicitude ratings for each grandparent. The coefficients were between $r = .35$ (maternal grandmother/father) and $r = .54$ (maternal grandfather/mother; sample sizes between $N = 1107$ and $N = 1557$). For each grandparent type, the correlation with the relationship to the mother was significantly larger than with the relationship to the father. The size of the difference (z values) was ordered along the rank of grandparents (highest for the maternal grandmother and lowest for the paternal grandfather). This might mean that the relationship of the grandparent with the mother of the grandchild is most important for the maternal grandmother, because her grandmaternal investment is the strongest, in decreasing order for the other three grandparent types. Comparable findings have been reported by Michalski and Shackelford (2005) and McBurney et al. (2006).

The grandparent-parent relationships are not solely determined by personal idiosyncrasies or biographic happenstances, but are themselves shaped by reproductive determinants and their adaptive consequences. Euler et al. (2001; in press) took three basic reproductive factors to predict the relationship quality of each of the eight possible grandparent-parent dyads: (1) Consanguinity: The ties to own adult offspring is closer than to their in-law spouses; (2) Sex-specific reproductive strategy: The relationship to the adult daughter, and to her husband as her reproductive assistant, should be better than the relationship to the adult son, because the daughter is more restricted to a strategy of maximizing parental care whereas the son has better options for a strategy of maximizing mates. These filial options are not aided by a good relationship to the son's spouse, but by rejecting or exploiting the daughter-in-law. The loss of the DiL, who would care for her kids with *her* mother's help after an eventual separation, is—from the grandparental reproductive viewpoint—less detrimental than the loss of the SiL. (3) Paternity uncertainty: A better relationship is expected between grandmothers and adult offspring than between grandfathers and offspring. As to the spouses of the offspring, paternity uncertainty diminishes the (positive or negative) value of the spouse. It makes the relationship with the welcomed spouse, the SiL, less positive and the relationship with the 'rejected' spouse, the DiL, less negative. As to in-law offspring, the relationship between MiL and SiL would be predicted to be comparatively good, the one between MiL and DiL relatively poor.

The eight grandparent-parent dyads in our current cumulative data file received the following mean ratings (1 = very bad relationship, 7 = very good relationship) from the participants of all adolescent and adult ages: Mother/Daughter (that is, maternal grandmother and mother) 5.69, Father/Daughter 5.41, Mother/Son 5.35, Father/Son 5.11, MiL/SiL 4.70, FiL/SiL 4.62, FiL/DiL 4.41, MiL/DiL 4.24 (sample sizes between $N = 1276$ and $N = 1798$). Comparable results for several of these dyads or combinations thereof are found in Fingerman (2004), Rossi and Rossi (1990), Szydlik (1995), and Young and Willmott (1957). The MiL/SiL relationship is thus comparatively good, contrary to deprecative of male jokes about the mother-in-law. The MiL/DiL relationship, however, in agreement with cross-cultural stereotypes about the mother-in-law nagging the daughter-in-law, is the most contentious of all grandparent-parent relationships.

Because women are the reproductively limiting sex, control of female reproduction was in the inclusive fitness interest of family members in ancestral populations and still is in current natural fertility populations. Conflicts of interest emerge between the maternal and paternal family lines. The maternal grandmother has invested massively in her daughter, whereas the paternal grandmother is not as heavily invested in the same woman, her daughter-in-law. The fitness interests of mother and daughter overlap considerably whereas those of mother and daughter-in-law are restricted to the time of marriage (Voland & Beise, 2005). A daughter-in-law is replaceable, a daughter is not. The fitness interest of the maternal grandmother is thus conservation of her daughter's maternal resources, whereas the fitness interest of the paternal grandmother is exploitation of her DiL's maternal resources. Maternal grandparents, especially maternal grandmothers, thus add to grandchild survival, whereas paternal grandparents facilitate birth rate (Mace & Sear, 2005). The intrafamilial conflict between matriline and patriline can even be traced down to the genetic level, where maternally imprinted genes may inhibit and paternally imprinted genes stimulate fetal growth (Burt & Trivers, 2006).

Aunts, Uncles and Cousins

Not only grandparents, but other relatives as well, act in benefit of their own inclusive fitness interests when they care for relatives. The analysis of investment of aunts and uncles has the advantage of avoiding coresidence as a confound. Brothers and sisters of a parent, unlike grandmothers and grandfathers, typically do not live together and thus act relatively independently of each other. Several studies have investigated the investment of consanguineal aunts and uncles by having college students rate whether maternal aunt or uncle or paternal aunt or uncle show more concern (Gaulin, McBurney, &

Brakeman-Wartell, 1997; Hoier, Euler, & Hänze, 2000; McBurney, Simon, Gaulin, & Geliebter, 2001; see also Rossi & Rossi, 1990). More investment was reported in the offspring of sisters than in the offspring of brothers and more by aunts than by uncles, supporting the predictions from evolutionary theory.

Social scientists of the past have not regarded genetic relatedness as a breaking point of human social nature. Robins and Tomanec (1962), for example, in the tradition of Talcott Parsons, considered grandparents and aunts/uncles in the same category of relatives just outside the circle of the nuclear family, and were surprised to find that their subjects felt closer to grandparents than to aunts/uncles. That there are consanguineal and affinal aunts/uncles, but no affinal grandparents except for stepgrandparents, did not occur to them. The role of genetic relatedness as a harbinger of feelings of closeness to nieces and nephews has been nicely demonstrated in a recent study by Segal, Seghers, Mechanic, and Castillo (in press). Monozygotic twins expressed greater closeness toward the children of their co-twin than did dizygotic twins. In accordance with previous studies, female twins from same-sex pairs expressed greater closeness toward their nieces/nephews than male twins from same-sex pairs. Again, correlations between perceived similarity to niece/nephew and closeness ratings were slightly higher for twins with male co-twins than for twins with female co-twins.

The relationship with cousins, finally, differs due paternity certainty. Comparative, the relationship is genetically most certain with children of mother's sister and least certain with children of father's brother. Closeness of relationship, as measured by willingness to help, emphatic concern, and contact frequency co-varied accordingly (Jeon & Buss, 2007).

Concluding Remarks

The reproductive asymmetry between the sexes is evident in various asymmetries of intergenerational family relationships. The matrilineal bias bestows the maternal grandmother with a unique and prominent role in grandparental relationships, as evident in many different forms of investment in grandoffspring and particularly in feelings of emotional closeness, which can be considered the proximate process mediating the various forms of investment.

The data are consistent with the hypothesis of grandparent-specific adaptations (Daly, Salmon, & Wilson, 1997). Mothers in ancestral environments often lived long enough to become grandmothers and make relationship-specific contributions to their inclusive fitness. For example, whereas parental investment is largely insensitive to sex of offspring (Daly & Wilson, 1990), grandparental investment is

clearly sensitive to the parental sex and at the same time insensitive to grandoffspring sex. Likewise, we would not be surprised if future studies reveal that fondness of grandoffspring is not congruent with parental fondness of offspring. Grandparents frequently seem to take a particular grandparental pride in the sheer number of their grandoffspring which appears not to be equalled by parental pride in number of own offspring. If lineage is one of the joints at which nature is to be carved, grandparental pride in number of grandoffspring might be more pronounced for paternal than for maternal grandparents.

As organisms are equipped with reward mechanisms to motivate execution of problem-specific adaptations in the appropriate situations, most grandparents appear happy to be able to invest in grandchildren. Indeed, almost all grandparents find grandchildren and investment in them rewarding (Dench & Ogg, 2003), even at an age when otherwise acedia takes its toll.

The approach to intergenerational relations guided by evolutionary theory and adaptationist hypotheses has already furthered our understanding of kin structures and promises to yield more. Such an approach can help researchers clear blurs, to integrate contributions from separate disciplines, to ask meaningful questions, to guide research, to inform public policies, and to provide personal insights into our own family lives. Nearly a century ago William McDougall (1908/1960) admonished the "philosophers" for their lack of interest in kin matters like parental instincts. The topic of grandparental investment still does not have a place in standard textbooks of motivational or social psychology, but having a close grandparent as well as having grandchildren adds to life quality. Grandchildren are, after all, tangible tokens of genetic posterity.

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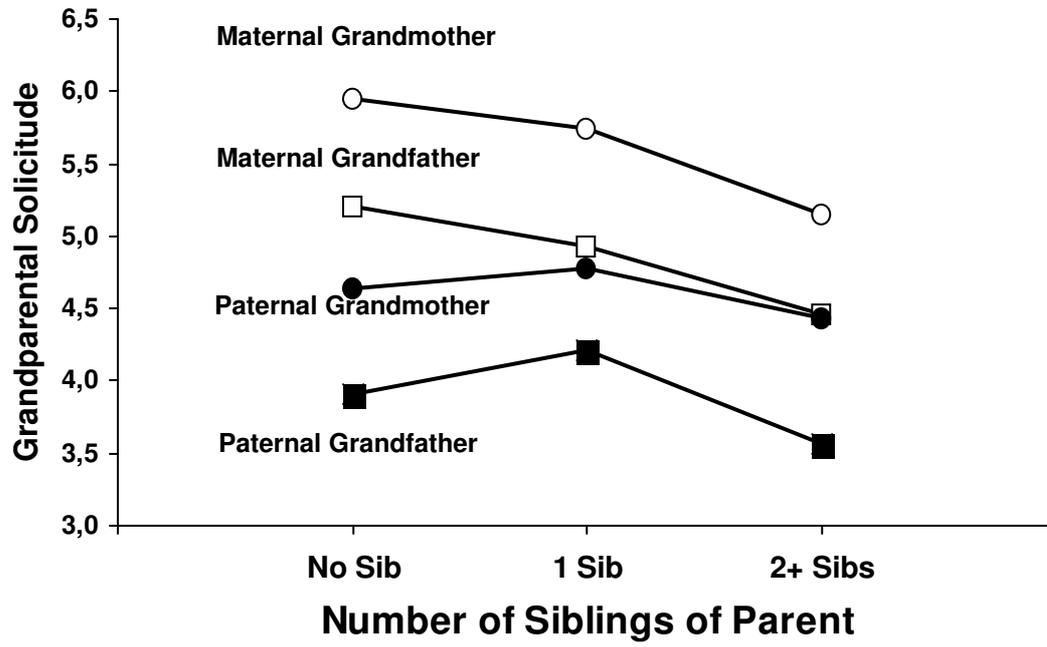


Figure captions

Fig. 1. Rated grandparental solicitude as a function of number of siblings of parent.

