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Lineage-based differences in grandparental investment according to adverse early life experiences of grandchildren

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Abstract

Evolutionary theory predicts a downward flow of investments from older to younger generations that represents individuals' efforts to maximize their inclusive fitness. Maternal grandparents and maternal grandmothers in particular have been consistently found to show the highest investment (e.g., time, care and resources) in their grandchildren. However, grandparental investment may depend on varying social and environmental conditions affecting the development of children, modifying the benefits and costs of grandparental investment. Using population-based survey data of English and Welsh adolescents, the present study investigates whether grandparental investment responds to adverse early life experiences (AELEs) of grandchildren. In contrast to current literature that considers grandparental investment in response to AELEs from the perspective of increased investment to meet the increased need, we predict that higher number of AELEs are associated with reduced grandparental investment as increased AELEs tend to reduce the reproductive value of grandchildren. Moreover, we predict that those grandparents who already invest less (i.e., paternal grandparents) react more strongly to elevated AELEs compared to those grandparents who invest the most (i.e., maternal grandparents and maternal grandmothers in particular). We found support for our predictions that maternal grandparents (maternal grandmothers in particular) showed investment in grandchildren that was unrelated to their grandchildren's AELEs. In contrast, paternal grandparents reduced their investment in grandchildren in cases of increased AELEs. These findings were largely robust to measurement error in the of AELEs and confounding due to omitted shared causes.

Introduction

From an evolutionary point of view, grandparental investment (i.e., costs-bearing actions of grandparents that improve the fitness of grandchildren) on descending generations results from individuals' efforts to maximize their inclusive fitness (Hamilton 1964). Compared to parental investment, the costs of grandparental investment tend to be lower, particularly for those older adults who are post-reproductive, and thus the benefits of grandparental investment in terms of inclusive fitness are predicted to out-weight the costs (Hawkes et al. 1998; Euler 2011; Kim et al. 2014; Pang 2020). Recent decades have witnessed increased opportunities for grandparental investment via improved health and increased life expectancy, also resulting in longer shared lifespan between grandparents and grandchildren (Margolis 2016; Chapman et al. 2018). Moreover, because of declining fertility rates in several Western countries, grandparents currently have fewer grandchildren, meaning that grandparents can potentially invest more in a specific grandchild as a result of lower number of alternative investment options (Coall & Hertwig 2010; Danielsbacka et al. 2011). In contrast to preindustrial farming and hunter-gatherer societies where grandparental presence has found to increase early-life survival rates of grandchildren (e.g. Lahdenperä et al. 2004; Sear & Mace 2008; Sear & Coall 2011; Strassmann & Garrard 2011; Chapman et al. 2021; Havlíček et al. 2021), we expect grandparental investment today to be directed more towards skills (e.g., cognitive functioning) and well-being in grandchildren that determine their success in modern-day societies (Kaplan 1996; Coall & Hertwig 2010; Lawson & Mace 2011). Here, we investigate grandparental investment from evolutionary perspective and consider whether the reproductive value of grandchildren influence grandparental behavior.

An essential part of understanding evolutionary processes is that adaptive evolution is ultimately a response to changing external abiotic and biotic conditions that affect optimal life history strategies (Roff 2002). For example, cooperative breeding in mammals and birds is regarded as a fitness-enhancing strategy to cope with harsh and unpredictable environments (Cornwallis et al. 2017; Lukas & Clutton-Brock 2017) and many species show behavioral plasticity to changing environmental conditions (Wong & Candolin 2015). Therefore, within a cooperative breeding context, grandparental investments in subsequent generations are likely to have evolved to track external cues that influence the fitness benefits and costs of such investments.

Previous social scientific literature on grandparental investment has identified several factors, commonly related to the socio-economic position of the grandchild's family that may influence grandparental investment (see Tanskanen & Danielsbacka 2019 for a recent review). Mostly, in this literature it is predicted that the investment of grandparents would increase in response to adverse life events in a grandchild's family and when recipient need for help is higher (Szydlik 2016; Coall et al. 2018). For example, grandparents have been found to allocate help to kin with greater need (Snopkowski & Sear 2015) and grandparents have been found to be particular important for grandchildren in the case of severe illness or death of a family member (particularly of the mother), parental divorce or financial hardship of the family (Hagestad 2006; Attar-Schwartz et al. 2009; Dunifron 2013; Perry 2021). Ultimately, in the case of the greatest need when parents are not available, where grandparents become the primary caretakers of their grandchildren, the investment is largest (Hayslip et al. 2017).

As discussed above, prior studies have approached grandparental investment as a response to increased need of support by grandchildren. Here, we propose an alternative scenario based on evolutionary theory that focuses on the balance between costs and benefits of grandparental investment, resulting from the changes in the environment where grandchildren grow up. It is suggested that increased family instability leads to increased psychological and even physical (i.e., via increased risk of experiencing violence) costs of grandparental investment (Herzberger 2019), which may decrease grandparental investment. In addition, the fitness-benefits gained from investing in grandchildren may be reduced since growing up in adverse environments may reduce grandchildren's reproductive value, i.e., their future prospects for successful survival and reproduction, and hence their fitness may be lower (Fisher 1930). This may also decrease grandparental investment. In support of this idea, reduced parental investment and earlier weaning age of children have been observed in societies living in poor environments suffering from famine, wars and high disease burden (Quinlan 2007). Moreover, within societies socioeconomic deprivation has been associated with lower offspring birth weight (Dubois & Girard 2006; Nettle 2010), shorter breastfeeding duration (Nettle 2010; Brown & Sear 2017) and reduced height in adulthood (Sheppard et al. 2015). It has been also reported that children living in deprived neighborhoods had lower contact rates with their maternal grandmothers compared to children from more wealthy areas (Nettle 2010). Such reduced parental investment in children is likely to bear long-term consequences on children's own future parenting behavior, reproduction, physical and mental health and survival (e.g. Barker 2007; Ellis et al. 2009; Brumbach et al. 2009; Nettle et al. 2013; Szepsenwol et al. 2015; Maner et al. 2017; Herzog & Schmahl 2018). This likely reduces the reproductive value of grandchildren and, consequently, the inclusive fitness-benefits grandparents receive from investing heavily in such children (Leek & Smith 1991). Furthermore, recent theoretical modeling on the evolution of early life effects on later performance has suggested that the social environment experienced by the individuals in childhood may be more important for their later performance than the abiotic environment (Kuijper & Johnstone 2019), validating the importance of measuring the social aspects of the developmental environment while considering the context-specificity of grandparental investment.

Well-established variations in grandparental lineage and gender mean that not all grandparents invest equally in their grandchildren (Tanskanen & Danielsbacka 2019). Several hypotheses have been suggested to explain the biased pattern of grandparental investment (Coall & Hertwig 2010). Paternity uncertainty favoring the investment by maternal grandmothers, following maternal grandfathers, paternal grandmothers and finally paternal grandfathers (Smith 1991). Also, there is a more general bias in investment towards matrilateral kin due to differential fitness-returns through maternal and paternal relatives (Daly & Perry 2017a). Sex-specific reproductive strategies suggest maternal kin invest more in existing grandchildren whereas paternal kin favor grandchild quantity over quality (Euler & Weitzel 1996), and sex-chromosomal selection hypothesis based on the differential inheritance of sex chromosomes between genders (Fox et al. 2010) are all put forward as potential evolutionary reasons for why some grandparents invest more than others. Currently, there seems to be no consensus on the relative importance of these hypotheses in explaining differences in grandparental investment but the common finding across a wide-range of societies and from interdisciplinary research is that maternal grandmothers invest the most in their grandchildren and paternal grandfathers invest the least (Hawkes et al. 1998; Euler 2011; Daly & Perry 2017b; Coall et al. 2018; Tanskanen & Danielsbacka 2019) or that maternal grandparents in general invest more than paternal grandparents (Daly & Perry 2017a).

The aim of the current research was to examine how grandparental investment among different grandparent types responds to adverse early life experiences (AELEs) faced by their grandchildren. Specifically, our goal was to contrast the expectations from the social scientific literature suggesting that grandparents should increase their investment on grandchildren owing to increases in need with the expectation from evolutionary theory suggesting that when the expected fitness-returns decrease (and/or the costs increase) also the grandparental investment should diminish. Moreover, we expect different responses between different grandparent types: compared to maternal grandparents (and maternal grandmothers in particular), the investment of paternal grandparents should be more facultative (Pollet et al. 2007; Pollet et al. 2013; Tanskanen & Danielsbacka 2019). As we know that maternal grandparents are willing to expend extra effort to invest in their grandchildren compared to other grandparent types (e.g., Pollet et al. 2007), we may thus expect the investment of maternal grandparents and maternal grandmothers in particular to be least sensitive while parental grandparents and paternal grandfathers in particular are predicted to be most sensitive also to changes in in their grandchildren's' early environment. Our main goal is not to contrast the differences between all the grandparental types but concentrate on two pre-planned hypotheses:

> Hypothesis 1: The more AELEs the grandchild has, the more the investment of paternal grandparents changes compared to maternal grandparents.

> Hypothesis 2: The more AELEs the grandchild has, the investment of maternal grandmother should change the least compared to other grandparent types.

To examine these hypotheses, we used nationally representative population-based data gathered from adolescent children in the UK and structural equation modeling (SEM) framework (Kline 2016). SEM has the benefits of allowing the fitting of complex structural models, the incorporation of measurement error into constructs of scientific interest using unobserved latent variables and enabling various sensitivity checks for robustness of the results to different modeling assumptions (e.g., to external model misspecification).

Methods & Materials

a) Data

We use the Involved Grandparenting and Child Well-Being 2007 survey, recruited by GfK National Opinion Polls, which is a nationally representative sample of English and Welsh adolescents aged 11–16 (see also Attar-Schwartz et al. 2009; Griggs, Tan, Buchanan, Attar-Schwartz, & Flouri, 2010; Tan, Buchanan, Flouri, Attar-Schwartz, & Griggs, 2010). In every selected school the classes were randomly chosen. Larger schools had a greater probability of being included in the final sample and the response rate is 68%. Respondents completed the questionnaire in a school classroom and the original sample included 1,566 adolescents (Attar-Schwartz et al., 2009; Buchanan, 2008). When filling in the questionnaire on grandparental investment, respondents were asked to answer questions for only those grandparents who were still alive. Hence, only those respondents who have at least one living grandparent (n = 1,488) were considered in the analyses. As commonly done in previous research, we also excluded those children from the analyses who were co-residing with their grandparents (n = 58). This was done because based on these data we cannot separate the cases where grandparents were the sole caretakers of grandchildren (in which case their investment is much more obligatory) from those cases of three-generation households. The total number of children included in the analyses was hence 1,430. For descriptive statistics, please see Table 1.

Measurement of grandchild's adverse early life experiences (AELEs). To measure grandchild's AELEs, Tiet et al.'s (2001) distal Adverse Life Events scale was used which records the number of adverse life events experienced prior to the last year. In its original formulation the Adverse Life Events scale consists of 25 possible events that children had little or no control over. However, the original scale included several events that were considered to be not severe enough to have a meaningful influence on grandparental investment. Therefore, only the following events (answered by yes/no) that directly involved the grandchild or her/his family were used to calculate the number of AELEs by the focal grandchild in earlier life: "someone in the family died", "there was a negative change in parent's financial situation", "family had drug/alcohol problem", "respondent got seriously sick or injured", "respondent was a victim of crime/violence/assault", "parents separated or divorced" and "one of the parents went to jail". In addition, we also included the question "have you ever qualified for free school meal (even if you don't have them)?" since children from low-income families receive free school meals in the UK and thus this variable also indicates the financial condition of the family. The resultant composite index for AELEs was thus a sum of eight indicators.

Grandparental investment. To measure grandparental investment on their grandchildren we used questions developed by Elder & Conger (2000), included in The Involved Grandparenting and Child Well-Being 2007 survey. From the list of all questions available we choose four questions that directly measured grandparental investment. These were "how often do you see them" (Q15), "their grandparents had looked after them" (Q26), "they could depend on their grandparents" (Q27), and "provided financial assistance or help" (Q38). The question Q26 was reverse-scaled to match the meaning and ordering of other scales. The questions Q26, Q27 and Q38 were measured on a 4-

point Likert-type scale ranging from 1 = *not at all / never* to 4 = *a lot / every day* and the question Q15 was measured on a 3-point Likert-type scale ranging from 1 = *never* to 3 = *usually.*

b) Statistical analysis

We applied structural equation modeling with multiple-indicator latent variables (SEM, Kline 2016) to examine how grandchildren's AELEs influenced grandparental investment on them. The benefits of SEM with latent variables instead of regular observed variable regression models include potentially more generalizable results owing to a more causally-oriented approach, handling of measurement error in latent constructs of interest that produces more consistent regression estimates, increased statistical power and more flexible representation of data by additional parameters (Thompson & Green 2015). In order to compare how grandparental investment among different grandparent types varies according to such AELEs, we needed first to establish measurement invariance (i.e., homogenous measurement properties) of our latent construct "grandparental investment" in all the grandparental groups examined (Vandenberg & Lance 2000). Analysis of measurement invariance showed that we had to rely on partial measurement invariance where one of the four factor loadings was non-invariant between the groups (see supplementary materials). We thus proceeded with a multi-group SEM where the model is simultaneously fitted to all four grandparent types.

The multi-group SEM fitted is shown in Figure 1. On the left, there is our response variable, a latent variable measuring "grandparental investment" on the grandchild using four effect indicators (i.e., the latent variable causes variation in its indicators) (Kline 2016). The question "provided financial assistance or help" was regarded as the most relevant measured variable and was thus used as a marker indicator for the latent variable by fixing its loading to unity. This sets the scale for the latent. The latent variable also has an error term (or disturbance) representing the fact that not all of its causes are modelled here (Kline 2016). In other words, the use of latent variables allows the inclusion of measurement error when we are measuring scientific constructs using multiple-indicator latent variables. On the right, there is our main predictor variable, adverse early life experiences of the grandchild that influences the latent “grandparental investment”. Furthermore, as precision covariates aiming to reduce error variance in “grandparental investment” (i.e., not causal confounders of the associations studied here, see e.g. Laubach et al. 2021), the model fitted included living distance between grandparents and the grandchild (in the same town, not in the same town but within 10 miles, further away in the UK, or overseas (= a reference category)), the number of other grandchildren (single grandchild (= a reference category), one to two grandchildren, more than three grandchildren, two to four grandchildren, more than four grandchildren, and more than six grandchildren), grandchild’s ethnicity (white (= a reference category), black or Afro-Caribbean, Asian, and mixed parentage), sex (female (= a reference), male), and grandparental age (<50 (= a reference category), 50-60, 60-70, and >70 years of age). All the categorical variables were dummy coded and grandchild age was grand mean-centred. All the regression parameters as well as latent variable intercepts (except for maternal grandmothers for identification purposes) and variances were allowed to vary between the grandparental types. As indicated by the measurement invariance analysis (see supplementary materials), a single residual covariance among the factor indicators was also included in the model.

The effect indicators of the latent variable “grandparental investment” were treated as ordinal variable modelled with probit link function. Hence, these loadings can be interpreted as the extent to which a one-unit increase in the latent variable score changes the predicted probit index in standard deviation units. In SEM with categorical latent variable indicators it is assumed that these categories of observed ordinal variables are determined by the thresholds (the number of categories in the observed variable minus one) in the underlying normally distributed latent variable (Kline 2016). These latent variables then become the indicators of the main latent variable, which are, in turn, associated with the ordinal observed variables by the respective threshold structure (Figure 1; Kline 2016).

To handle missing data in independent variables, we followed guidelines given in von Hippel (2018). By accepting a 5% change in the standard errors of the estimates, we imputed 62 data sets using multilevel variance covariance approach (because we had missing data on variables measured within and between grandchildren) using unrestricted model with Bayesian estimator (Asparouhov & Muthen 2010). Owing to multiple imputation, we used Wald's test instead of likelihood ratio test. Since the two preplanned tests were not orthogonal, we controlled for type I error rate by using false discovery rate (FDR) among the set of rejected hypotheses (Benjamini & Hochberg 1995). FDR, defined as the expected proportion of type I errors among all significant results, corrects for the expected proportion of type I errors by providing adjusted *P*-values. Mean and variance adjusted diagonally weighted least squares (WLSMV) estimator with a default delta parametrization was used for the estimation of multi-group SEM. Since we had multiple observations per grandchild (i.e., a maximum of four living grandparents), grandchild's identity was used as a design-based clustering factor to obtain unbiased estimates and robust standard errors (McNeish 2014).

We performed two robustness checks for model assumptions that could have affected our results. First, using a single-indicator latent variable approach to account for measurement error in our measure of adverse early life experiences, we examined the sensitivity of our results to artificially reduced reliability (down to 60% reliability) of the cumulative risk factor variable (Hayduk &

Littvay 2012). It is well known that measurement error in predictors attenuates their regression coefficients towards zero (e.g., Cole & Preacher 2014). Such lowered reliability (i.e., increased measurement error) might here include the factors missed by the original scale to represent grandchild's adverse early life experiences and for example errors of participants to understand the questions asked. In this approach, the original observed predictor (i.e., adverse early life experiences) is replaced by a latent variable for which cumulative risk has a unit loading while its error variance is set by multiplying its sample variance with desired level of reliability. Second, to evaluate the importance of unobserved confounding (i.e., a shared cause for both independent and dependent variables) on the association between grandparental investment and AELEs of grandchildren we applied the method recently described in Harring et al. (2017). In this method, the effect of potential unmeasured confounder(s) is mimicked by the use of a phantom variable that affects both the predictor (i.e., adverse early life experiences) and the outcome (i.e., grandparental investment) in the model. Phantom variables are latent variables without any indicators, precluding the need of actual data. Instead, the mean and variance of the phantom variables are fixed constants, usually set to zero and unity, respectively (Harring et al. 2017). The rationale is to examine how sensitive the original conclusions are when one adds the phantom variable into the model by varying the strength of the expected confounding. One potential confounder of the association between AELEs and grandparental investment that is unmeasured in these data is the socioeconomic status of grandparents, acting via or parallel to their children's (i.e., the parents of the grandchildren) socioeconomic status. It is likely that high socioeconomic status in grandparents acts by reducing the grandchildren's' AELEs and by increasing their investment in grandchildren. We thus concentrated on such a scenario. Note that, depending on the application, the confounder could as well be expected to exert positive or negative effects on both the independent and dependent variables or positive effect on the predictor and negative on the outcome. While the signs of the suspected confounder effects are usually rather straightforward to imagine, the strength of these effects are usually arbitrary without strong prior knowledge. Hence, using a range of values is recommended (Harring et al. 2017). Here, we started the process of fitting different values for the strength of confounding based on the observed associations between AELEs and investment among grandparents and by gradually increasing the strength of confounding until the confounding changed the statistical inference of the association of interest. Mplus 8.5 (Muthén and Muthén 2017) was used for all data analyses.

Results

The multi-group SEM showed almost statistically significant difference in the regression coefficient for AELEs on grandparental investment between maternal and paternal grandparents (Hypothesis 1: maternal grandparents: β (95% confidence intervals (CIs) = -0.012 (-0.032, 0.008), paternal grandparents β (95% CIs) = -0.040 (-0.064, -0.017), $\chi^2_1 = 3.371$, $P = 0.066$, $P_{\text{FDR-adjusted}} = 0.066$). Likewise, the investment of maternal grandmothers seemed somewhat less sensitive to the increased AELEs compared to other grandparents (Hypothesis 2: maternal grandmothers: β (95% CIs) = -0.003 (-0.028, 0.021), other grandparents: β (95% CIs) = -0.036 (-0.055, -0.016), χ^2_1 = 4.182, $P = 0.041$, $P_{\text{FDR-adjusted}} = 0.066$). These effect sizes can be evaluated in terms of predicted marginal effects of the question setting scale for the latent variable “investment” (i.e., “provided financial assistance or help”). For example, a grandchild who experienced none compared to all eight AELEs conditional probability of scoring “usually” (i.e., the highest category) was 53.4% and 49.6%, respectively, for the maternal grandparents (Figure 2A). For paternal grandparents, these percentages for zero and eight AELEs were 53.4% and 40.7%, respectively (Figure 2A). The corresponding numbers for the contrast between maternal grandmothers and other grandparents were 53.4% and 52.4% for maternal grandmothers and 53.4% and 42.0% other grandparents (Figure 2B).

When allowing free regression estimates for each grandparental type, we see a clear gradient in the association of AELEs on grandparental investment among different grandparent types (Table 2, see supplementary material for full results). The regression coefficient of AELEs on grandparental investment ranged from the least negative and statistically non-significant (i.e., no association between AELEs and grandparental investment) among maternal grandmothers and significantly the most negative among paternal grandfathers, with coefficients for maternal grandfathers and paternal grandmothers falling in between in this order.

Robustness checks showed that reducing the reliability of a variable measuring cumulative family risks down to 60% did not have any effect on the results (Table 3). The results of adding a confounder into the model that negatively affected the number of AELEs and positively grandparental investment on grandchildren by varying degree is given in Table 4. A confounder whose effect on both grandparental investment and AELEs was 0.25 and -0.25 units, respectively, was strong enough to change our statistical inference on the non-existing association between AELEs and grandparental investment among maternal grandmothers (β (95% CIs) = -0.003 (-0.028, 0.021)) to a significant *positive* association of AELEs on investment on grandchildren (β (95% CIs) = 0.029 (0.005, 0.053)). In other words, the effect of confounding would have to be approximately 83-times stronger compared to the estimated association between AELEs and maternal grandmother's investment in order to change our conclusion regarding that parameter. The corresponding values for changing our statistical inference for the association between AELEs and grandparent’s investment in maternal grandfathers, paternal grandmothers and paternal grandfathers were roughly 14-times, 3-times and 9-times stronger confounder effects, respectively (Table 4).

Discussion

Our goal was to challenge the currently held expectation in the social scientific literature that grandparents should increase their investment on grandchildren to meet the increased need with the opposite prediction arising from the evolutionary theory. Although our comparisons were on the borderline of conventional statistical significance after adjusting for multiple testing, the findings from the current data suggest that grandparents seem to reduce, not increase, their investment in grandchildren with an increasing number of AELEs. Moreover, it seems that maternal grandparents, and maternal grandmothers in particular, are rather insensitive in their investment in terms of AELEs of their grandchildren. Instead, paternal grandparents clearly reduced their investment on grandchildren when their grandchildren experienced more AELEs. These results appeared to be robust to potential measurement error in our measure of AELEs and the strength of confounding (i.e., bias due to omitted shared causes) would have to be much stronger than the associations found here between AELEs and grandparental investment to change our conclusions.

Our results thus lend support for the evolutionary prediction in grandparental literature that the investments made by grandparents should track the potential costs and benefits of such investments, which eventually determine the payoffs of these investments in terms of their grandchildren’s evolutionary fitness (i.e., their reproductive value measuring the fraction of a future population that has descendent from them) (Fisher 1930; Taylor 1990). In other words, high investment has likely poor inclusive fitness-payoffs when invested in a grandchild with low reproductive value and is thus selected against by natural selection. Given the wealth of evidence on how early life and childhood experiences affect adult phenotype in humans (e.g. Barker 2007; Ellis et al. 2009; Brumbach et al. 2009; Nettle et al. 2013; Szepsenwol et al. 2015; Maner et al. 2017; Herzog & Schmahl 2018), there probably exists a link between early environmental and social conditions and individual's reproductive value in our species. A common expectation among scholars in the fields examining these questions is that accelerated reproductive timing commonly related to adverse early life experiences or environmental conditions is adaptive by increasing their relative lifetime fitness (e.g. Nettle et al. 2013), thus contrasting our rationale of reduced reproductive value of individuals developing in adverse conditions. Yet, we do not know any study that would have formally studied or established such a link in humans, nor do theoretical life history models support such conclusions (Stearns & Koella 1986; Stearns & Rodrigues 2020). A recent long-term study in wild baboons failed to find to support for accelerated reproductive scheduling in response to early life adversity being adaptive in this species (Weibel et al. 2020). We need more studies associating early life conditions with multigenerational investment in humans. Such research, preferentially based on advanced demographic modeling as done in the case of sex allocation (Schindler et al. 2015), would probably benefit the field by making explicit predictions how grandparental investment should be expected to vary according to the reproductive value of grandchildren.

The current findings also strengthen the commonly held view of the important role played by maternal grandparents and the maternal grandmother in particular as investors in their grandchildren (Euler 2011; Daly & Perry 2017b). The novel contribution of the current research is that such patterns seem to hold also with respect to AELEs of the grandchildren. Those grandparents who are predicted to invest most in their grandchildren, i.e., maternal grandparents and maternal grandmothers in particular, seem to do so irrespective of the cues indicating declining reproductive value of those grandchildren. In contrast, paternal grandparents seem much more sensitive in their investment on their grandchildren's reduced fitness-payoffs by reducing their investment in them. From an evolutionary perspective, this may indicate that i) maternal grandparents and especially maternal grandmother can better tolerate the decreased fitness-payoffs in their grandchildren (e.g. owing to known relatedness) or ii) the costs of AELEs in grandchildren and in their family are disproportionally taking their toll on paternal grandparents.

The data used in the present study has several strengths. The adolescents were the respondents providing information on grandparental investment and background variables related to themselves, their family, and grandparents. Grandparents may not be the ideal source of such information because, as the norm in Western societies is to treat all children equally, they may try to present their investment as equal in all grandchildren (Coall & Hertwig 2010; Tanskanen & Danielsbacka 2019). Parents, in turn, may think of grandparents as couples, meaning they may not accurately report the amount of grandparental investment within lineages. Moreover, if one is interested in the investment of all four grandparent types, it would be very complicated to ask either grandparents or parents about the grandparental investment according to all the different grandparent-grandchild dyads. Because of these limitations related to surveying parents and grandparents, children could be regarded the most reliable source of information on biased grandparental investment (Euler and Weitzel 1996).

The conclusions drawn from these data are further strengthened by the modeling framework applied that enabled the evaluation of the two important threats to causal inference from correlative data: measurement error in predictors and confounding by omitted shared causes (i.e., causes of endogeneity) (Pearl 2009; Antonakis et al. 2010). Neither lowering the reliability of AELEs down to 60% nor modeling very strong confounding effects compared to the estimated association between AELEs and grandparental investment by grandparent type seem to change our statistical inference. Here we concentrated on a scenario, which we consider the most plausible, where a confounder or multiple confounders in concert reduced the AELEs and increased investment on grandchildren. Had we assumed the confounder to elect positive or negative effects on both AELEs and grandparental investment we would have observed increasingly negative estimates of the association between AELEs and investment in grandchildren among the grandparents. We do not however claim to have revealed causal effects here, since all the effects modeled were linear and causal inference is inherently non-parametric in nature (Pearl 2009).

The limitations of this research are related to the fact that we could not separate the factors affecting need of investment from those affecting the cost and benefits of investment using the current data at hand. These two need not to be synonymous as not all factors increasing the need for grandparental investment necessarily imply increased costs and benefits for grandparental investment. Moreover, it has recently been acknowledged that it is generally difficult to quantify and measure environmental unpredictability and harshness that could be relevant for individual development and its long-term consequences (Frankenhuis et al. 2019; Young et al. 2020). We however aimed to alleviate such concerns by using a cumulative measure of AELEs instead of relying on just a single or few events that may poorly capture the range of all external cues relevant for parental and grandparental investment (Taborsky 2017; Potticary & Duckworth 2020) and using a questionnaire that captures AELEs so far in the grandchildrens' lifetime. Furthermore, by modelling measurement error in our measure of AELEs we could show that our conclusions were robust to such a threat.

In conclusion, our results suggest that when considering the AELEs of grandchildren using a cumulative lifetime measure of adverse events instead of a single event or few events, there is more convincing evidence for a decrease in grandparental investment than increase in investment in grandchildren. An increase in grandparental investment with the increasing need from the grandchild's behalf has been commonly argued in social scientific literature but here we provide an alternative evolutionary rationale, based on the reproductive value (i.e., fitness) of grandchildren, as why we may expect a decrease in grandparental investment if grandchildren experience several AELEs. The between-grandparent patterns found here are also in line with the existing literature, showing the importance of maternal grandmothers as the main investors in grandchildren even in the cases when the grandchildren have already faced many hardships in their lives.

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Table 1. Descriptive statistics for the independent variables used in the study. MGM, MGF, PGM and PGF stand for maternal grandmothers, maternal grandfathers, paternal grandmothers and paternal grandfathers, respectively.

	mean	s.d.	min	max
Charachteristics of the grandchild				
Grandchild age (mean)	13.4	1.4		
Don't know / missing (%)	0.56			
Ethnicity (%)				
White	89.0			
Black or Afro-Caribbean	3.5			
Asian	2.1			
Mixed	2.2			
Don't know / missing	3.2			
Adverse early life experiences	1.6	1.4	0	8

	MGM	MGF	PGM	PGF
Charachteristics of the grandparent				
Number of other grandchildren (%)				
Respondent is the only grandchild	2.6	1.7	2.0	1.8
2 or 3	22.7	18.6	18.3	13.5
>3	53.4	40.9	44.6	33.6
Don't know / missing	21.2	38.8	35.2	51.1
Living distance between the grandparent and the grandchild (%)				
Overseas	7.1	5.1	5.2	4.1
Further away in the UK	18.8	16.4	20.0	15.5

Not in the same town but within 10 miles	20.6	15.0	18.0	14.5
In the same town	34.5	26.4	24.1	16.6
Don't know / missing	19.1	37.1	32.7	49.3
Grandparent age (%)				
<50 years	0.9	0.6	0.4	0.4
50-60 years	12.0	6.2	5.4	2.9
60-70 years	34.5	26.4	28.3	20.6
>70 years	24.6	22.0	22.9	19.6
Don't know / missing	28.0	45.0	43.0	56.6
Variables measuring grandparental investment				
"Do they give you money or help in any other way?" (%)				
Never	7.7	9.7	10.3	10.1
Occasionally	28.8	21.9	26.0	20.0
Usually	45.5	33.9	33.7	24.3
Missing	18.0	34.6	30.0	45.7
"How often do you see them?" (%)				
Never	4.9	5.5	5.9	6.6
Several times a year	30.8	25.4	33.5	25.5
Twice a week	30.2	22.8	23.4	17.6
Daily	16.4	10.7	6.4	3.7
Missing	17.7	35.6	30.8	46.6
"How often do your grandparents look after you?" (%)				
Every day	4.0	2.7	1.0	0.6
Once a week or so	20.8	15.2	12.8	9.3

Several times a year	32.9	23.9	26.4	18.6
Never	24.3	24.1	30.0	26.4
Missing	17.9	34.1	29.8	45.1
"How much can you depend on your grandparent to be there when you really need him/her?" (%)				
Not at all	8.9	9.7	12.1	11.5
A little	11.8	10.8	12.4	9.6
Sometimes	18.5	14.7	17.7	13.7
A lot	43.2	30.6	27.8	19.8
Missing	17.8	34.2	30.0	45.4

Table 2. Selected result of a multi-group structural equation model examining how cumulative risk factors experienced by the grandchild's family influenced grandparental investment among maternal grandmothers (MGM) and grandfathers (MGF) and paternal grandmothers (PGM) and grandfathers (PGF). For full results, please see the supplementary material Table S2. 95% CI denotes to 95% confidence intervals of the regression coefficients. Please note that the parameter estimates are on the probit scale.

	β	95% CI
Regression coefficient		
MGM	-0.003	-0.028, 0.021
MGF	-0.025	-0.057, 0.007
PGM	-0.032	-0.061, -0.002
PGF	-0.051	-0.088, -0.015

Table 2. Regression coefficients and their 95% confidence intervals (CI) examining how cumulative risk factors influenced grandparental investment (MGM = maternal grandmothers; MGF = maternal grandfathers; PGM = paternal grandmothers; PGF = paternal grandfathers) in relation to declining reliability, *R*, of variable measuring cumulative risk factors.

	MGM	MGF	PGM	PGF
R	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
1	-0.003 (-0.028, 0.021)	-0.025 (-0.057, 0.007)	-0.032 (-0.061, -0.002)	-0.051 (-0.088, -0.015)
0.95	-0.004 (-0.029, 0.147)	-0.026 (-0.059, 0.006)	-0.035 (-0.065, -0.004)	-0.056 (-0.092, -0.020)
0.90	-0.004 (-0.030, 0.022)	-0.028 (-0.062, 0.006)	-0.037 (-0.069, -0.005)	-0.059 (-0.097, -0.021)
0.85	-0.004 (-0.032, 0.024)	-0.030 (-0.066, 0.007)	-0.039 (-0.073, -0.005)	-0.063 (-0.103, -0.022)
0.80	-0.004 (-0.034, 0.025)	-0.031 (-0.070, 0.007)	-0.041 (-0.078, -0.005)	-0.066 (-0.110, -0.023)
0.75	-0.005 (-0.036, 0.027)	-0.033 (-0.074, 0.008)	-0.044 (-0.083, -0.005)	-0.071 (-0.117, -0.025)
0.70	-0.005 (-0.039, 0.029)	-0.036 (-0.080, 0.008)	-0.047 (-0.089, -0.006)	-0.076 (-0.126, -0.026)
0.65	-0.005 (-0.042, 0.031)	-0.038 (-0.086, 0.009)	-0.051 (-0.096, -0.006)	-0.082 (-0.136, -0.028)
0.60	-0.006 (-0.046, 0.034)	-0.042 (-0.093, 0.010)	-0.055 (-0.104, -0.007)	-0.089 (-0.147, -0.030)

Table 3. Regression coefficients and their 95% confidence intervals (CI) examining how cumulative risk factors influenced grandparental investment (MGM = maternal grandmothers; MGF = maternal grandfathers; PGM = paternal grandmothers; PGF = paternal grandfathers) in relation to varying strength of confounding. The bolded coefficients indicate the level of confounding that changes the statistical inference of the association between family risks and grandparental investment.

Confounding (Investment, risks)	MGM	MGF	PGM	PGF
	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
(0, 0)	-0.003 (-0.028, 0.021)	-0.025 (-0.057, 0.007)	-0.032 (-0.061, -0.002)	-0.051 (-0.088, -0.01
(0.001, -0.001)	-0.004 (-0.027, 0.020)	-0.025 (-0.056, 0.006)	-0.033 (-0.062, -0.004)	-0.053 (-0.088, -0.01
(0.01, -0.01)	-0.003 (-0.027, 0.020)	-0.025 (-0.056, 0.006)	-0.033 (-0.062, -0.004)	-0.053 (-0.088, -0.01
(0.05, -0.05)	-0.002 (-0.026, 0.021)	-0.024 (-0.055, 0.007)	-0.032 (-0.061, -0.003)	-0.052 (-0.086, -0.01
(0.1, -0.1)	0.002 (-0.022, 0.025)	-0.02 (-0.051, 0.011)	**-0.028 (-0.057, 0.001)**	-0.048 (-0.083, -0.01
(0.2, -0.2)	0.017 (-0.006, 0.041)	-0.005 (-0.036, 0.026)	-0.013 (-0.042, 0.017)	-0.033 (-0.067, 0.00
(0.25, -0.25)	**0.029 (0.005, 0.053)**	0.007 (-0.024, 0.038)	-0.001 (-0.03, 0.028)	-0.021 (-0.056, 0.01
(0.3, -0.3)	0.043 (0.019, 0.067)	0.021 (-0.01, 0.052)	0.013 (-0.016, 0.043)	-0.007 (-0.042, 0.02
(0.35, -0.35)	0.060 (0.036,0.084)	**0.037 (0.006, 0.064)**	0.030 (0.001, 0.060)	0.010 (-0.025, 0.04
(0.4, -0.4)	0.079 (0.055, 0.104)	0.057 (0.025, 0.088)	0.049 (0.020, 0.079)	0.029 (-0.006, 0.06
(0.5, -0.5)	0.101 (0.076, 0.126)	0.078 (0.046, 0.110)	0.071 (0.041, 0.102)	**0.051 (0.015, 0.087**

Figure legends

Figure 1. A graphical representation of the multi-group structural equation model used to examine how cumulative risk factors experienced by the grandchild's family influences grandparental investment on grandchildren depending on grandparental type. The same model is thus simultaneously fitted to all groups (i.e., for each grandparental type) but with potentially differing parameter estimates. Observed variables are represented as boxes and unobserved latent variables as circles. Triangle is the intercept parameter for latent variable mean (i.e., called the unit predictor). Single-headed straight arrows have three functions here: i) when pointing from a latent variable (i.e., "grandparental investment") to another latent variables (i.e., underlying normally-distributed latent variable for each observed question Q15, Q26, Q27 and Q38, y1*-y14*), they represent reflective linear loadings of the latent (λ's); ii) when pointing at observed or unobserved response variables, they represent structural path coefficients (β's) and; iii) when pointing at those underlying latent variables of the questions asked from grandchildren, they represent their unique residual errors (ε). Single-headed arrows with a step denote a non-linear association (modeled as probit link and thresholds (omitted for simplicity)) between the latent variables and their indicators. Double-headed arrow represents the error variances (i.e., disturbance) of the latent "grandparental investment" variable (ζ) and their covariances (Ψ).

Figure 2. Predicted marginal probabilities for grandchildren to score on the highest category (i.e., "usually") for the question setting scale for the latent variable "investment" in response to the number of their adverse early life experiences. A comparison between maternal and paternal grandparents (hypothesis 1) is given in panel A and a comparison between maternal grandmothers and other grandparents (hypothesis 2) in panel B.

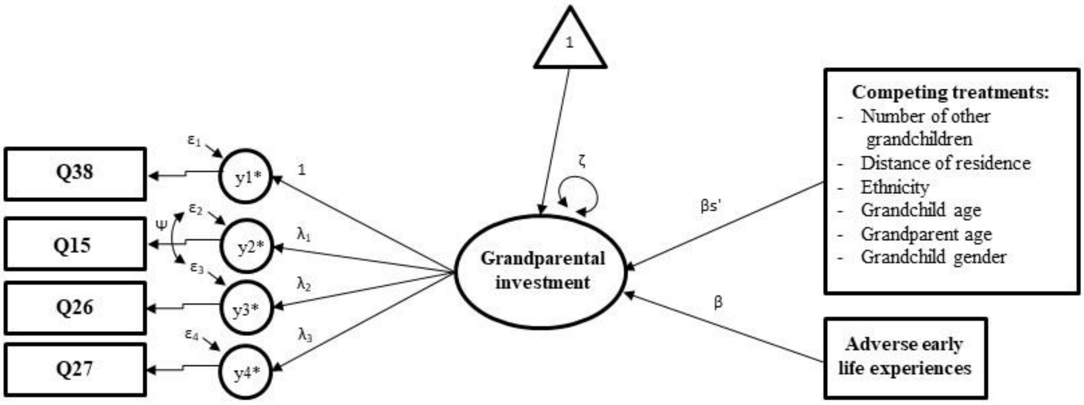

Figure 1 Helle et al

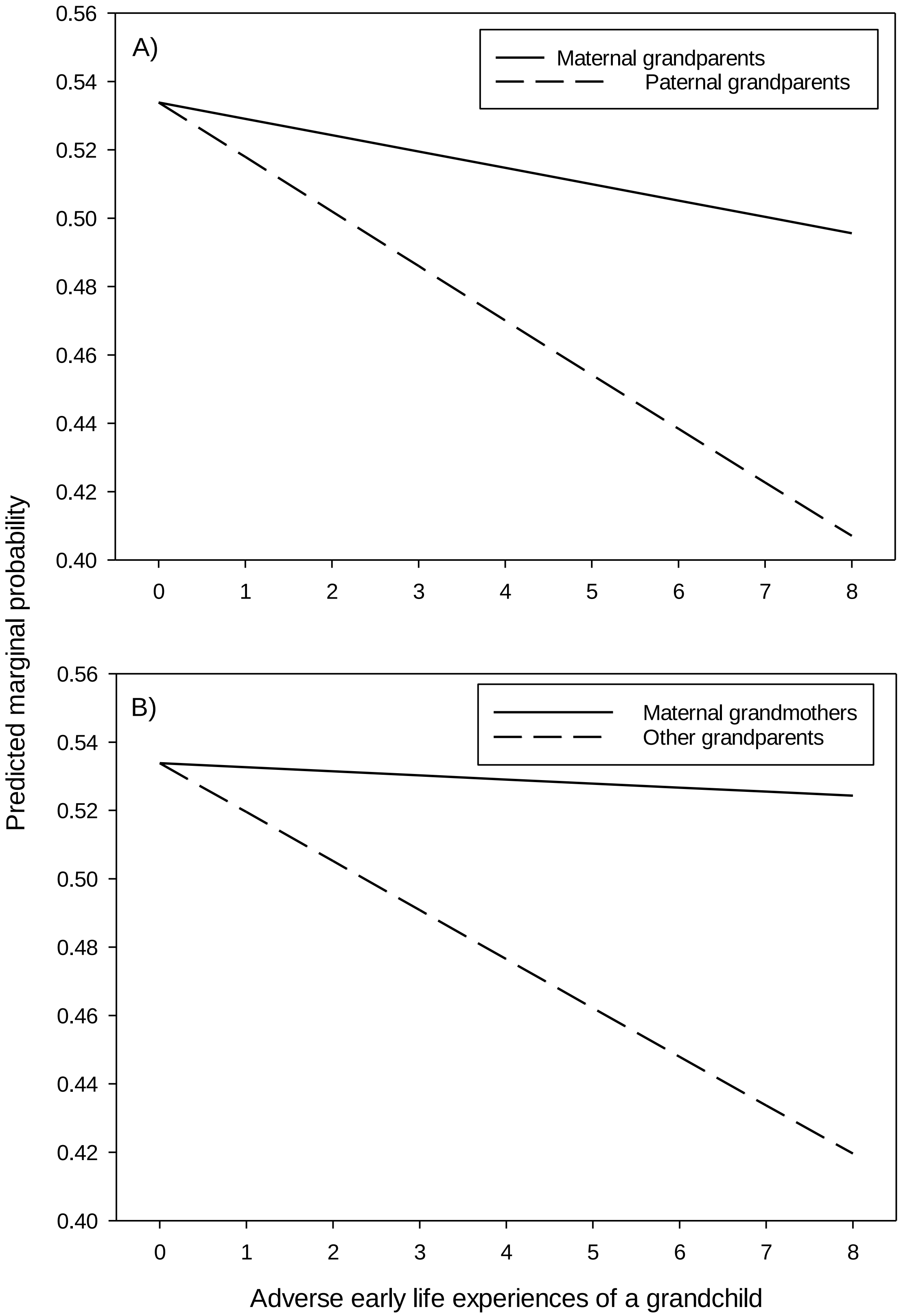

Figure 2 Helle et al.