

*Original Research Article***Grandparental Investment: The Influence of Reproductive Timing and Family Size**DAVID A. COALL,<sup>1\*</sup> MARC MEIER,<sup>1</sup> RALPH HERTWIG,<sup>1</sup> MICHAELA WÄNKE,<sup>1</sup> AND FRANÇOIS HÖPFLINGER<sup>2</sup><sup>1</sup>*Department of Psychology, University of Basel, Basel, Switzerland*<sup>2</sup>*Department of Sociology, University of Zürich, Zürich, Switzerland*

**ABSTRACT** The influence that grandparents have on the life history traits of their descendants has been studied extensively. However, no attention has been paid to the potential influence a grandparent's own reproductive history has on the investment they make in their grandchildren. We use data from 658 Swiss grandchildren and 591 of their grandparents to investigate whether grandparents' reproductive scheduling and family size influence the amount of investment grandparents make in a focal grandchild (shared contacts, occasions to meet, activities, discussions, interests, and important roles the grandparent plays). Grandparents who were younger when they had their first child had more children and grandchildren; this relationship strengthened after controlling for grandparental age, sex, lineage, and education (all  $P < 0.001$ ). Generally, having more children or grandchildren was associated with reduced levels of grandparental investment. After adjustment for a wide range of factors known to influence investment, having more children or grandchildren and having a first child or grandchild at a younger age were associated with reduced investment in 14 of 24 analyses (all  $P < 0.09$ ). The association between reproductive scheduling and investment was partially mediated by the grandparent's family size. Interestingly, these relationships were only present in data reported from the grandchild's point of view, not the grandparent's. This analysis provides preliminary evidence that grandparents' reproductive strategies have consequences for the amount of investment they make in their grandchildren. These results are examined in terms of the trade-offs between current and future reproduction and offspring quality and quantity. *Am. J. Hum. Biol.* 21:455–463, 2009. © 2009 Wiley-Liss, Inc.

Grandparents can play a crucial role in the lives of their grandchildren. However, as with any relationship, the extent of grandparental investment is highly variable (e.g., Euler and Weitzel, 1996; Laham et al., 2005; Michalski and Shackelford, 2005; Pashos and McBurney, 2008). Studies examining the underlying factors that contribute to this variability have been carried out by behavioral ecologists, psychologists, sociologists, and economists. To date, grandparental investment research has focused on the potential influences of genetic relatedness (e.g., Aldous, 1995), paternity certainty (e.g., Pollet et al., 2006), sex-specific reproductive strategies (e.g., Euler and Weitzel, 1996), the moderating role of parents (e.g., Pashos and McBurney, 2008), including mothers as links maintaining family ties (e.g., Monserud, 2008), grandparental age (Lahdenperä et al., 2004), physical resemblance (e.g., Michalski and Shackelford, 2005), the grandchild's reproductive value (e.g., Smith, 1991), and the grandchild's family size and birth order (Leonetti et al., 2005). Although grandparental investment, like parental investment, is often conceptualized as part of an individual's reproductive strategy (see Coall and Hertwig, submitted for publication), no attention has been paid to how grandparents' own reproductive histories, in terms of scheduling and family size, shape their ability, and inclination to invest in their grandchildren.

Evolutionary theory assumes that natural selection will have favored the allocation of parents' and grandparents' resources (e.g., energy, time) to reproduction and parental investment in a manner that maximizes their reproductive success. Life history theory makes predictions about how these resources will be allocated across the life cycle. Among the most commonly investigated life history traits are age and size at first reproduction, size and number of

offspring, and lifespan. Because resources that parents and grandparents have available to invest in reproduction (including in their descendants), growth, and maintenance are typically limited, decisions must be made about the best (fitness maximizing) way to invest. In multicellular organisms there is a developmental phase when no resources are invested in reproduction; at the age of first reproduction some resources are switched from growth and maintenance to reproduction. Because any unit of resource used for one purpose (e.g., reproduction) cannot be used for another (e.g., growth), organisms "decide" how to allocate their resources between competing life history goals, which inevitably creates vital trade-offs (see Borgerhoff Mulder, 1992; Chisholm, 1993, 1999; Clutton-Brock, 1991; Daan and Tinbergen, 1997; Hill, 1993; Hill and Kaplan, 1999; Lancaster, 1997; Low, 1978; Mace, 1998; Stearns, 1992).

One trade-off concerning reproductive timing is that between current and future reproduction. This trade-off predicts the optimal allocation of resources (given phylogenetic and ontogenetic constraints) to reproduction at any given age, based on the assumption that there is a

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trade-off between an individual's short-term (current) reproduction and his/her long-term (future) reproduction. Delaying reproduction and allocating resources to growth increases the potential for future reproduction. Therefore, it may be beneficial to delay reproduction if the cost of lost short-term reproduction is compensated by the gain in future reproduction. However, this balance is contingent on the environment. For example, under conditions of high-local mortality, reproducing earlier and having more offspring may be favored as a means of ensuring that the individual gets to reproduce at all and produce enough offspring to ensure that some survive (Borgerhoff Mulder, 1992; Hill, 1993; Stearns, 1992). Therefore, if grandparents develop in environments that promote a more current-oriented reproductive strategy, we predict that they would have their first child at a younger age and potentially have more children, which may also translate into having their first grandchild earlier and, ultimately, more grandchildren.

It is common for grandparental investment studies to explore the association between a grandparent's presence and their children's reproductive traits (see review by Mace and Sear, 2005). It is less common to examine the grandparents' *own* reproductive traits. Grandparental age has been associated with investment and does, at least partially, reflect reproductive timing. For example, in a historical Finnish population, Lahdenperä et al. (2004) found that grandchildren who had a grandmother alive when they were born were more likely to survive to 15 years of age. This association only held, however, if the grandmother was younger than 60 years of age at the grandchild's birth. This finding implies that grandmothers who reproduce earlier, and are younger and most likely healthier when they become grandparents, invest more in their grandchildren. To the best of our knowledge, however, ours is the first study to explicitly explore the contingency between grandparental reproductive timing and later investment.

If an individual reproduces earlier and produces more offspring, this reproductive strategy may have consequences for another life history trade-off: that between offspring size (quality) and number (quantity). The trade-off between offspring size and number holds that because natural selection has optimized the amount of resources a parent can allocate to reproduction across the life cycle and these resources are limited, any increase in the number of offspring decreases the resources available for each single one (Lack, 1947; Smith and Fretwell, 1974; Walker et al., 2008). One of the strongest factors influencing how much time parents spend interacting with their children is the number of children they have (Lawson and Mace, *in press*). Therefore, grandparents who reproduce earlier and have more children and grandchildren may of necessity have fewer resources per capita to subsequently devote to their children, and—our present focus—grandchildren.

Consistent with this trade-off, negative associations between the number of children and grandchildren grandparents have and the growth of their daughter's children have been found in natural fertility populations. In a study of the Oromo agropastoralists of Ethiopia, Gibson and Mace (2005) found that although children who lived in matrilineal households were 62% more likely to survive to 3 years of age than children from patrilineal households, their nutritional status was poorer (i.e., lower height for

age and weight-for-height) than the latter's. The authors proposed that in this low-resource environment "higher survival rates and increased family sizes may have further increased the competition for available resources between siblings" (Gibson and Mace, 2005, p 480). A woman's number of siblings has also been associated with the growth of her children. In a study of the Dogon from Mali, West Africa, Strassman (2008) found that as the number of maternal siblings increased the childhood growth rate slowed. This effect remained after adjustment for child's age, sex, village, survival status of various relatives, birth order, wealth rank, and polygyny.

Grandparental investment studies that include the grandchild's family size in their analyses also provide data consistent with a trade-off between offspring number and size. In a study of two Indian societies, the matrilineal Khasis and the patrilineal Bengalis, larger family sizes were associated with an increased risk of infant and child mortality, which is, at least in part, attributed to closely spaced births decreasing infant survival (Leonetti et al., 2005). Moreover, the beneficial influence of grandmothers on grandchild survival was most pronounced in the largest families where grandmothers appeared to buffer mothers against the trade-off between offspring size and number. It is clearly important to include the grandchild's family size in studies of grandparental investment and grandchild survival. However, if grandparental investment is conceptualized as part of grandparents' reproductive strategies, the analysis should not leave out the grandparent's own reproductive history and family size (number of children and grandchildren). This grandparental family size variable provides the best indicator of how many descendants a grandparent's investment may need to be shared among. Trade-offs are usually examined across one or two generations (Hill and Kaplan, 1999), whereas our proposed analysis involves three generations (but see Gillespie et al., 2008). However, if—as we are assuming—grandparental investment includes a range of behaviors that influence the health and survival of grandchildren and thus grandparental inclusive fitness (Sear and Mace, 2008), and that the fertility in one generation is likely to influence the survival and fertility in the next, and so on (Gillespie et al., 2008; Rogers, 1990), it makes sense to explore the consequences of fertility for fitness across three or more generations (Kaplan, 1994).

Our goal is to provide the first detailed analysis of the association between grandparents' past reproductive timing, their family size, and the time investments they make in a focal grandchild. We conduct this analysis using a Swiss sample of grandparents and grandchildren and their respective perceptions of the grandparent–grandchild relationship (Höpflinger et al., 2006). We will test three hypotheses: (a) that grandparents who have their first child and first grandchild at a younger age will have more children and grandchildren; (b) that grandparents who have more children and grandchildren will invest fewer resources in the focal grandchild; and (c) that grandparents who have their first child and first grandchild at a younger age will invest fewer resources in their focal grandchild, and this investment behavior is mediated by the influence of family size. In addition, due to the different effects of grandmothers' and grandfathers' investment on grandchild health (see Lahdenperä et al., 2004, 2007), which may also be reflected in different associations between grandparental reproductive timing, fam-

ily size, and investment, we will explore these associations separately for grandmothers and grandfathers.

## MATERIALS AND METHODS

### *Participants*

The data are from a Swiss study of adolescent grandchild–grandparent relationships conducted in 2004–2005 (see Höpfinger et al., 2006). Participants were 658 grandchildren who completed questionnaires about their relationships with each of their living grandparents, producing data on 1,759 grandparent–grandchild relationships. The grandchildren were recruited from schools in three urban regions and two language areas of Switzerland (Geneva [French], urban Valais, and Zurich [German]). They completed the questionnaires at home or at school. The grandchildren's parents were asked for the grandparent's contact details. Of the 788 grandparents who lived in Switzerland and for whom contact details were available, 591 (75%) completed a questionnaire that corresponded to that of the grandchild. Only the 580 purported biological grandparents were included in our analysis. The grandchildren were between 11 and 17 years of age (mean = 13.9, s.d. = 1.16) and 351 (51.7%) were female. The grandparents were between 48 and 110 years of age (mean = 74.0, s.d. = 8.55) and 354 (61%) were grandmothers.

### *Grandparent's reproductive timing and family size*

In separate questions, all grandparents were asked (a) how old they were when their first child and their first grandchild were born and (b) how many children and grandchildren they have had. No differentiation between type of child or grandchild (e.g., biological, adopted) was made in any of these questions.

### *Grandparent–grandchild relationship measures*

Grandparental investment was operationalized in terms of six aspects of the grandparent–grandchild relationship: frequency of contact; shared occasion when they met; shared activities; shared discussion topics; shared interests; and the important roles grandparents play. Each measure was available from both the grandparent's and grandchild's point of view and was created from multi-item scales. These measures are described later, first from the grandchild's questionnaire; any deviation from this in the grandparent questionnaires is highlighted.

Contacts assessed the kind and frequency of grandparent–grandchild interactions collapsed across three dimensions of contact: face-to-face, written, and telephone contact. Each item was rated on a four-point scale from “rarely/never” to “once a week or more.” Cronbach's alpha was calculated for each scale to evaluate its internal consistency, that is, how much the individual items of a scale are measuring the same construct (0.7 or higher is ideal). The sum scale of these contact items had a Cronbach's alpha of 0.47. Items examining contact by mobile phone, sms, and email were excluded because of low response rates. The grandparents' items and scales were identical (alpha = 0.39).

Occasions assessed on which occasions grandparents and grandchildren met on a five-item scale: at family celebrations; reunions or activities within the family; reunions or activities alone with the grandparent; holidays or

weekends with the family; and holidays or weekends alone with the grandparent. Each item was rated on a four-point scale from “never” to “often” (alpha = 0.74). The grandparents' items and scales were identical (alpha = 0.31).

Activities assessed the frequency of 14 shared activities: doing homework; going to a restaurant; attending the cinema, theater, or concert; visiting an exhibition or fair; going to festivals; shopping; playing sport; having discussions; watching television; playing games; reading; making crafts, gardening or cooking; traveling; and religious activities. The items “farming” and “other” were excluded. Each item was rated on a four-point scale from “very rarely or never” to “once a week or more” (alpha = 0.88). The grandparents' items and scales were identical (alpha = 0.86).

Discussions assessed with whom the grandchild discussed 10 topics: latest news; social problems; relationship to parents or siblings; relationship to friends; love affairs; school; leisure; intimacy; personal conflicts and secrets. The four possible responses (grandparent; someone within the family [father, mother, siblings]; one or more friends; and no one) were recoded into “with grandparent” and “not with grandparent” (alpha = 0.85). The grandparents' items were identical but the responses differed and were recoded as yes (“yes”) and no (“no, and I do not wish to talk with my grandchild about it”, or “no, and I want to talk with my grandchild about it”; alpha = 0.87).

Interests assesses whether the grandchild feels that the grandparent is interested in nine topics: the grandchild's friends; clothes; school achievement; way of talking; dealings with money; recreational activities; opinion; intimate life; and behavior within the family. To parallel the grandparent's question, these items were recoded into no (“never”) and yes (“seldom”, “often”, or “always”; alpha = 0.88). All of the grandparents' items were identical except “interested in your occupational life,” which replaced “interested in school achievement” (alpha = 0.82).

Important roles assessed the importance of the grandparent in eight situations: support you financially if you need it; give you psychological advice when you are in need; help with homework; there for you when you need them; suggest activities you could do (e.g., sport, cinema); help with your career choices; give advice for your private life; and make suggestions for your relationship with parents or siblings. Each item was rated on a four-point scale from “not important at all” to “very important” (alpha = 0.85). The grandparents' items and scales were identical (alpha = 0.84).

### *Other factors that influence grandparent–grandchild relationships*

Other variables known to influence grandparent–grandchild relationships (see Euler and Michalski, 2007) that were available in this dataset are detailed later. Residential distance (seven-point scale from “in the same apartment” to “in another country”) and grandparental health (five-point scale from “very bad” to “very good”) were available in both grandparent's and grandchild's questionnaires.

Grandparents rated the quality of their relationship with the grandchild's parents, which was coded as “very good” or “satisfactory” and “bad” due to low variability in responses. The grandparent's age, grandparental sex

TABLE 1. Regression of reproductive scheduling on family size<sup>a</sup>

	Number of children						Number of grandchildren					
	Grandmothers			Grandfathers			Grandmothers			Grandfathers		
	$\beta$	$\eta^2$ (%)	<i>P</i>	$\beta$	$\eta^2$ (%)	<i>P</i>	$\beta$	$\eta^2$ (%)	<i>P</i>	$\beta$	$\eta^2$ (%)	<i>P</i>
Age at first child	<b>-0.27</b>	<b>7.4</b>	<b>0.000</b>	<b>-0.15</b>	<b>2.1</b>	<b>0.030</b>	<b>-0.20</b>	<b>4.1</b>	<b>0.000</b>	<b>-0.12</b>	<b>1.5</b>	<b>0.070</b>
Adjusted model <sup>b</sup>	<b>-0.42</b>	<b>12.7</b>	<b>0.000</b>	<b>-0.33</b>	<b>8.0</b>	<b>0.000</b>	<b>-0.32</b>	<b>7.5</b>	<b>0.000</b>	<b>-0.30</b>	<b>6.5</b>	<b>0.000</b>
Age at first grandchild							<b>-0.26</b>	<b>6.9</b>	<b>0.000</b>	<b>-0.13</b>	<b>1.6</b>	<b>0.099</b>
Adjusted model <sup>b</sup>							<b>-0.50</b>	<b>16.6</b>	<b>0.000</b>	<b>-0.38</b>	<b>8.7</b>	<b>0.000</b>

All associations that are statistically significant at the 10% level are shown in bold.

<sup>a</sup>The statistics reported include the standardized beta coefficient ( $\beta$ ), partial eta squared as a percentage ( $\eta^2$ [%]), and the exact *P*-value (*P*).

<sup>b</sup>In these models grandparent's age, lineage, and education were adjusted.

(grandmother vs. grandfather), lineage (maternal vs. paternal), and education (six-point scale from "no education" to "university or technical college") were recorded in the grandparent's questionnaire, as were the grandparent's marital status ("married" or "widowed"), employment ("working" or "not working"), independence ("living in an apartment/house" or "living in a house/room for old people"), and whether or not they lived with their spouse.

Additional measures of the grandchild's family size, number of siblings and birth order (up to a maximum of 6), were taken from a question about who lives in the same household as the grandchild. The grandchild's age, sex, and the number of biological grandparents each grandchild has was taken from the grandchild's questionnaire. Finally, the grandchild's perception of the positive (caring, generous, hospitable, tolerant, dynamic, and humorous) and negative (strict, gets excited quickly, avaricious, and old-fashioned) characteristics of the grandparent were rated on a four-point scale from "no, does not apply to her/him at all" to "yes, applies very much" (negative characteristics alpha = 0.80, positive alpha = 0.52).

#### Statistical analysis

Pearson's product-moment correlations were used to examine associations between the grandparental investment variables and bivariate relationships between continuous predictor and outcome variables. Multiple linear regression tested for linear associations between predictors and outcome variables, allowing for the adjustment of potential mediating and confounding variables. These analyses focus on testing the hypotheses presented and do not explore the influence of all explanatory variables in detail. To this end, all regressions on grandparental investment are adjusted for a "basis model" (grandparent's age, sex, lineage, education, health, residential distance, marital status, independence, employment, cohabitation, positive and negative characteristics, relationships with the grandchild's parents, and number of living biological grandparents). To explore the role of family size in the association between reproductive timing and investment, number of children, grandchildren, grandchild's siblings, and birth order were added to the basis model in separate regressions. Regressions on the grandparental investment variables were run separately using data from the grandchild's and grandparent's point of view. In addition to the standardized beta coefficients ( $\beta$ ), partial eta square ( $\eta^2$ ) is the effect size reported and interpreted according to Cohen (1988) as small (0.01–0.09), medium (0.09–0.25), and large (0.25–1.0).

## RESULTS

### Grandparent's reproductive timing and family size

Our first hypothesis, that grandparents who have their first child and first grandchild at a younger age will have more children and grandchildren, was supported. An earlier age at first childbirth was strongly associated with having more children ( $\beta = -0.232$ ,  $P < 0.001$ ,  $\eta^2 = 5.4$ ) and more grandchildren ( $\beta = -0.180$ ,  $P < 0.001$ ,  $\eta^2 = 3.2$ ). These associations doubled in strength after adjustment for the grandparent's age, sex, lineage, and education: number of children ( $\beta = -0.401$ ,  $P < 0.001$ ,  $\eta^2 = 11.0$ ), number of grandchildren ( $\beta = -0.324$ ,  $P < 0.001$ ,  $\eta^2 = 7.1$ ). An earlier age at first grandchild was associated with having more grandchildren ( $\beta = -0.221$ ,  $P < 0.001$ ,  $\eta^2 = 4.9$ ); again, the strength of this association more than doubled after adjusting for the grandparent's age, sex, lineage, and education ( $\beta = -0.467$ ,  $P < 0.001$ ,  $\eta^2 = 13.6$ ). In the adjusted models age at first child or grandchild accounted for between 7 and 13% of the variance in family size. Table 1 shows that these associations were stronger for grandmothers than for grandfathers.

### Grandparent's and grandchild's family size and grandparental investment

Our second hypothesis, that grandparents who have more children and grandchildren will invest fewer resources in their focal grandchild, was generally supported (first four rows of Tables 2 and 3). From the grandchild's point of view, the existence of more grandchildren was associated with reduced grandparental investment across all six measures ( $\eta^2 = 1.6$ –4.0%). Moreover, after adjustment for the basis model the associations with contacts, activities, discussions, and interests remained significant ( $\eta^2 = 0.8$ –2.1%). Likewise, from the grandparent's point of view (Table 3), the association between number of grandchildren and investment was negative and significant for discussions, interests, and important roles ( $\eta^2 = 1.1$ –2.6%); however, none of these associations survived adjustment for the basis model. Having more children was associated with fewer contacts, occasions, activities, interests, and important roles for the grandchild's data ( $\eta^2 = 1.7$ –4.5%). Contacts, interests, and importance remained significant after adjustment for the basis model ( $\eta^2 = 1.3$ –2.5%). In the grandparent's data, having more children was associated with fewer contacts, activities, discussions, and important roles. Only contacts survived adjustment for the basis model ( $\eta^2 = 1.6$ %).

The bivariate associations between measures of the grandchild's family size (number of siblings and birth



order) and grandparental investment show weaker and less consistent relationships. From the grandchild's point of view, having more siblings and a higher birth order was significantly associated with reduced grandparental investment in 9 of 12 analyses ( $\eta^2 = 0.3\text{--}1.2\%$ ). In the grandparent's data, however, only 1 of the 12 analyses was significant: a higher birth order predicted fewer shared activities ( $\eta^2 = 2.6\%$ ).

#### *Grandparent's reproductive timing and grandparental investment*

Our third hypothesis, that grandparents who have their first child and first grandchild at a younger age will invest fewer resources in their focal grandchild, and that this association will be partly mediated by family size, was supported from the grandchild's point of view (see Table 2). In the bivariate analyses, an earlier age at first grandchild was associated with fewer contacts but more discussions and important roles. However, after adjustment for the basis model, from the grandchild's point of view, grandparents who were younger when they had their first grandchild had significantly fewer shared contacts, occasions, activities, and interests with their grandchild ( $\eta^2 = 0.8\text{--}4.5\%$ ). To explore the mediating role of family size the model was adjusted further for number of grandchildren, which substantially reduced the influence of age at first grandchild on all of the measures (on average by 62%). Adjusting for the grandchild's number of siblings also reduced all effect sizes but had a smaller influence (on average by 18%). Adjusting for the grandchild's birth order reduced the effect size in all analyses except for shared interests (on average by 52%).

Likewise, an earlier age at first child was associated with fewer shared contacts but more shared discussions in the bivariate analyses. After adjustment for the basis model, grandparents who were younger when they had their first child shared significantly fewer activities, interests, and important roles with their grandchild ( $\eta^2 = 0.7\text{--}3.1\%$ ). To examine the mediating role of family size the model was further adjusted for number of grandchildren and children, which reduced the strength of these three effects (on average by 38% and 34%, respectively); however, adjusting for the grandchild's number of siblings had little effect (6.3%). Adjusting for the grandchild's birth order only reduced the strength of the associations with activities and important roles (on average by 34%).

The association between reproductive scheduling and grandparental investment is less clear from the grandparent's point of view (see Table 3). In the bivariate analyses, earlier age at first grandchild was associated with more shared activities, discussions, interests, and more important roles ( $\eta^2 = 2.9\text{--}5.4\%$ ). However, after adjustment for the basis model, none of these associations remained significant. Further adjustment for number of grandchildren substantially increased the strength of these effects in all cases; however, only shared interests and important roles return to significance ( $\eta^2 = 1.4\text{--}1.6\%$ ). Likewise, adjusting for the grandchild's number of siblings and birth order had a similar but slightly weaker effect. An earlier age at first child was associated with more shared activities, discussions, interests, and more important roles ( $\eta^2 = 2.1\text{--}3.2\%$ ). After adjustment for the basis model, however, none of these associations remained significant. Further

adjustment for number of children, grandchildren, siblings, or birth order had no consistent effect.

When the analyses for hypothesis one and two are carried out separately for grandmothers and grandfathers (see Supporting Information Tables S1a–S1d), there is little quantitative difference between them.

## DISCUSSION

We have demonstrated for the first time that a grandparent's own reproductive scheduling and the number of descendants they have influence their grandparental investments. Interestingly, however, this effect only held from the grandchild's point of view. Specifically, we observed three main findings: first, grandparents who had their first child and grandchild at a younger age had more children and grandchildren. Second, grandparents who had more children and grandchildren generally invested fewer resources in their focal grandchild. Third, grandparents who had their first child and first grandchild at a younger age invested fewer resources in their focal grandchild and this was partially mediated by the number of children and grandchildren the grandparent had. All these effects held over and above other factors commonly known to influence grandparental investment. We are taking this as the first, tentative evidence that a grandparent's own reproductive strategy may influence the subsequent allocation of grandparental investment.

There is evidence from natural fertility populations that grandparents can offset maternal costs and influence their daughter's and daughter-in-law's reproductive scheduling, family size, and grandchild health (Gibson and Mace, 2005; Lahdenperä et al., 2004; Meehan, 2005). However, the influence of grandparents' own reproductive strategies on their intergenerational investment has not been examined. Our analyses are consistent with a trade-off between current and future reproduction that has consequences for grandparental investment, with individuals who start reproducing earlier having more children and grandchildren, and investing less in each grandchild. Interestingly, these associations appear to hold for both grandmothers and grandfathers.

The associations between earlier reproduction and less investment contrast with Lahdenperä et al.'s (2004) finding that younger grandmothers had a greater impact on their grandchildren's health than older grandmothers. It is likely these younger grandmothers were healthier and invested more because they could, a trend also found in contemporary Western studies (see Höpfinger et al., 2006). Our analysis shows that grandparental reproductive timing is associated with investment above and beyond the influences of grandparental age and health. Our dataset, however, does not allow us to explore the ecological and cultural factors that may be driving these associations. For example, individuals who develop under conditions of either high-local mortality rates or high-resource availability may be expected to start reproducing at a younger age and have more children (Chisholm and Coall, 2008; Cole, 1954; Ellison, 1994). Assuming that the environmental conditions do not change markedly, it is more likely that those individuals who developed in a higher mortality environment will go on to invest fewer resources in their descendants. Future investigations may be able to tease apart these potential pathways.

The role reproductive strategies play in grandparent–grandchild relationships has been explored in terms of sex-specific reproductive strategies. The concept of sex-specific reproductive strategies, according to which female mammals, generally speaking, pursue a high parental investment strategy and males, even in monogamous populations, pursue mixed mating strategies—sometimes focusing on parental investment and sometimes on additional mating opportunities (Trivers, 1972)—has been successfully incorporated into many studies of grandparental investment (e.g., Euler and Weitzel, 1996; Gibson and Mace, 2005; Huber and Breedlove, 2007; Huber et al., 2004; Leonetti et al., 2007; Meehan, 2005; Pashos and McBurney, 2008). However, focusing on these general reproductive strategies ignores the potentially important role that individual differences in reproductive timing and family size have on grandparental investment. This study shows that after controlling for, among other things, grandparental sex and lineage, reproductive scheduling, and family size influence grandparental investment. Although these effect sizes were generally small to medium, we believe that the fact these associations survived the wide range of control variables that were available in this dataset suggests that examining both sex-specific and individual reproductive strategies may be fruitful.

An increased family size is likely to reduce the availability of resources, in this case time, for each family member (see Hertwig et al., 2002; Van Bavel, 2006). Because of this, family size is often incorporated into grandparental investment studies (e.g., Gibson and Mace, 2005; Laham et al., 2005; Leonetti et al., 2005; Pollet et al., 2006) and is most commonly operationalized as the grandchild's number of siblings and birth order. In this study, family size was conceptualized as part of the grandparent's reproductive strategy and thus measured from the grandparents' point of view as their number of children and grandchildren. This study suggests that it is useful to examine measures of both the grandchild's and the grandparent's family size in investigations of grandparental investment. However, the grandparent's family size accounts for substantially more of the association between the grandparent's reproductive timing and subsequent investment than does the grandchild's family size. Interestingly, although birth order did not reduce the association between reproductive timing and investment in all cases, when it did it had a stronger influence than number of siblings. A larger family size not only increases the potential demand for investment by grandparents, it also increases the number of alternative investment opportunities grandparents have and thus their opportunity to invest differentially among investment options (Laham et al., 2005). A study examining grandparental investment among all of a grandparent's descendants may establish whether grandparents with alternative investment opportunities aim to invest equally across descendants (Hertwig et al., 2002) or preferentially allocate resources to some family members over others (Strohschein et al., 2008).

#### *Why do grandparents' and grandchildren's reports differ?*

One question arising from our analysis is: Why is the effect of reproductive timing and family size on grandparental investment only found in the reports of grandchildren but not in those of grandparents? If for a moment we take the information garnered from grandchildren as being

accurate—levels of investment do vary by reproductive timing and family size—then what biases the grandparents' reports? One possibility is that grandparents are little inclined to openly discriminate levels of investment between their grandchildren thus removing between-grandchild differences in investment (see Euler and Michalski, 2007; Euler and Weitzel, 1996; Michalski and Shackelford, 2005). Indeed, when grandparents are asked how emotionally close they feel to a focal grandchild compared with their other grandchildren, most (63%) said “about the same” and very few (13%) were at the extremes (“closer than most” or “less close than most”; Mueller et al., 2002). Again assuming these reports are biased, the bias can have at least two sources. First, it can reflect grandparents' desire to see themselves as relatively egalitarian in their allocation of resources. Relatedly, Zervas and Sherman (1994, p 31) argued that “as members of an egalitarian society, Americans typically espouse equal treatment of children by parents,” and by extension, by grandparents. Second, grandparents' reports of egalitarian treatment could purely be a consequence of mental account-keeping. Grandparents, especially those with a suite of grandchildren, may find keeping track of shared time spent with individual grandchildren difficult. If, instead, they used a general account-keeping system where contact with different grandchildren was pooled, and indeed on some occasions they may see all of their grandchildren together, then grandparents may be taking an average value for each grandchild, which again would be tantamount to removing between-grandchildren differences.

On the other hand, if we take the grandparents' point of view as being accurate—levels of investment do not vary by reproductive timing or family size—then what can trigger grandchildren's reports of unequal grandparental investment? As Hertwig et al. (2002) theoretically and empirically demonstrated, even if parents, and by extension, grandparents, attempt to invest equally at any given point in time, the amount of cumulative resources each child receives may still, as a consequence of birth order, be unequal. Paradoxically, such inequality could be the inevitable consequence of grandparental attempts to treat their grand children equally. Consequently, both grandparents' reports of egalitarian treatment at any given time and grandchildren's reports of unequal treatment can both be true at the same time (see Hertwig et al., 2002, for details).

On balance, we suggest that because grandparents do not command infinite resources, especially in terms of cognitive resources (e.g., time spent training and instructing children) and interpersonal resources (e.g., attention, time, love, affection), trade-offs exist between grandparental reproductive timing, family size and investment. At this point, we assume that these trade-offs are reflected in grandchildren's reports of grandparental investment. Consistent with this view, grandparental investment studies that use grandparents' reports show less agreement than studies using grandchildren's reports suggesting grandparental reports are less reliable (e.g., Michalski and Shackelford, 2005; Pollet et al., 2006). However, the causes of these differences remain interesting open questions that future research must address.

#### *Limitations*

The current dataset has the advantages that it includes a wide range of grandparent–grandchild relationship

measures that were available from both the grandchildren's and grandparents' points of view, and had a raft of potential confounding variables that could be taken into account. However, the data are limited by the fact that this study remains correlational, making cause and effect inferences impossible. Grandparents in this study were born between 1894 and 1956, and although we controlled for grandparental age to try and remove cohort effects, this may have been inadequate to account for different fertility rates and investment strategies that may be operating across this time period (see Mace, 2008).

Relatedly, our sample consists of living grandparents. Therefore, the association between earlier reproduction and having more descendants may emerge simply because those grandparents who started reproducing later have some of their grandchildren born after their own death. If this is the case, the negative associations between age at first child and grandchild and the number of children and grandchildren should be weaker in older grandparents. Although we cannot entirely rule out this possibility, our data speaks against it. Adjustment for grandparental age consistently strengthened, rather than weakened, the negative associations between reproductive timing and family size in our data.

Finally, although we adjusted for the grandparents' demographic factors (age, sex, education, employment status, marital status, independence, etc.), we did not have detailed information on grandparents' wealth, which has consequences for trade-offs between the number of siblings and the time that parents invest in their children (Lawson and Mace, in press).

To conclude, our data suggest that a grandparent's own reproductive scheduling (age at first child and first grandchild) and family size (number of children and grandchildren) influences their subsequent grandparental investment in a focal grandchild. These associations may be broadly interpreted as being consistent with the trade-offs between current and future reproduction and between offspring number and size. Future research may benefit from also conceptualizing grandparental investment as part of a grandparent's reproductive strategy and examining the ecological conditions that influence grandparents' reproductive strategies, which may ultimately have consequences for grandparent–grandchild relationships.

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#### LITERATURE CITED

- Aldous J. 1995. New views of grandparents in intergenerational context. *J Fam Issues* 16:104–122.
- Borgerhoff Mulder M. 1992. Reproductive decisions. In: Smith EA, Winterhalder B, editors. *Evolutionary ecology and human behavior*. New York (NY): Walter de Gruyter. p 339–373.
- Chisholm JS. 1993. Death, hope, and sex: life-history theory and the development of reproductive strategies. *Curr Anthropol* 34:1–24.
- Chisholm JS. 1999. *Death, hope, and sex*. Cambridge, England: Cambridge University Press.
- Chisholm JS, Coall DA. 2008. Not by bread alone: the role of psychosocial stress in age at first reproduction and health inequalities. In: Trevathan W, Smith EO, McKenna JJ, editors. *Evolutionary medicine and health*. Oxford, England: Oxford University Press. p 134–148.
- Clutton-Brock TH. 1991. *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Cohen J. 1988. *Statistical power analysis for the behavioral sciences*. Hillsdale, New Jersey: Erlbaum.
- Cole L. 1954. The population consequences of life history phenomena. *Q Rev Biol* 29:103–137.
- Daan S, Tinbergen JM. 1997. Adaptation of life histories. In: Krebs JR, Davies NB, editors. *Behavioural ecology: an evolutionary approach*. Oxford, England: Blackwell Science. p 311–333.
- Ellison P. 1994. Extinction and descent. *Hum Nat* 5:155–165.
- Euler HA, Michalski R. 2007. Grandparental and extended kin relationships. In: Salmon C, Shackelford TK, editors. *Family relationships: an evolutionary perspective*. Oxford, England: Oxford University Press. p 230–256.
- Euler HA, Weitzel B. 1996. Discriminative grandparental solicitude as reproductive strategy. *Hum Nat* 7:39–59.
- Gibson MA, Mace R. 2005. Helpful grandmothers in rural Ethiopia: a study of the effect of kin on child survival and growth. *Evol Hum Behav* 26:469–482.
- Gillespie DOS, Russell AF, Lummaa V. 2008. When fecundity does not equal fitness: evidence of an offspring quantity versus quality trade-off in pre-industrial humans. *Proc R Soc B* 275:713–722.
- Hertwig R, Davis JN, Sulloway FJ. 2002. Parental investment: how an equity motive can produce inequality. *Psychol Bull* 128:728–745.
- Hill K, Kaplan H. 1999. Life history traits in humans: theory and empirical studies. *Ann Rev Anthropol* 28:397–430.
- Hill K. 1993. Life history theory and evolutionary anthropology. *Evol Anthropol* 2:78–88.
- Höpfinger F, Hummel C, Hugentobler V. 2006. Teenage grandchildren and their grandparents in urban Switzerland. Available at: [http://www.nfp52.ch/e\\_dieprojekte.cfm?Projects.Command=detailsandget=13](http://www.nfp52.ch/e_dieprojekte.cfm?Projects.Command=detailsandget=13). Retrieved March 31, 2006.
- Huber BR, Breedlove WL. 2007. Evolutionary theory, kinship, and child-birth in cross-cultural perspective. *Cross-Cult Res* 41:196–219.
- Huber BR, Linhartova V, Cope D, Lacy M. 2004. Evolutionary theory and birth-related investment by kin in cross-cultural perspective. *World Cult* 15:60–79.
- Kaplan HS. 1994. Evolutionary and wealth flows theories of fertility: empirical tests and new hypotheses. *Popul Dev Rev* 20:752–791.
- Lack D. 1947. The significance of clutch size. I. Intraspecific variation. *Ibis* 89:302–352.
- Laham SM, Gonsalkorale K, von Hippel W. 2005. Darwinian grandparenting: Preferential investment in more certain kin. *Pers Soc Psychol Bull* 31:63–72.
- Lahdenperä M, Lummaa V, Helle S, Tremblay M, Russell AF. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428:178–181.
- Lahdenperä M, Russell AF, Lummaa V. 2007. Selection for long lifespan in men: Benefits of grandfathering? *Proc R Soc B* 274:2437–2444.
- Lancaster JB. 1997. The evolutionary history of human parental investment in relation to population growth and social stratification. In: Gowaty PA, editor. *Feminism and evolutionary biology*. New York: Chapman and Hall. p 466–489.
- Lawson DW, Mace R. Trade-offs in modern parenting: A longitudinal study of sibling competition for parental care. *Evol Hum Behav*. in press.
- Leonetti DL, Nath DC, Hemam NS, Neill DB. 2005. Kinship organization and the impact of grandmothers on reproductive success among the matrilineal Khasi and patrilineal Bengali of northeastern India. In: Voland E, Chasiotis A, Schiefelhövel W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. New Brunswick (NJ): Rutgers University Press. p 194–214.
- Leonetti DL, Nath DC, Hemam NS. 2007. In-law conflict. Women's reproductive lives and the roles of their mothers and husbands among the matrilineal Khasi. *Curr Anthropol* 48:861–890.
- Low BS. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. *Am Nat* 112:197–213.
- Mace R. 1998. The coevolution of human fertility and wealth inheritance strategies. *Philos Trans R Soc Lond B Biol Sci* 353:389–397.
- Mace R. 2008. Reproducing in cities. *Science* 310:764–766.
- Mace R, Sear R. 2005. Are humans cooperative breeders? In: Voland E, Chasiotis A, Schiefelhövel W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. New Brunswick (NJ): Rutgers University Press. p 143–159.

- Meehan CL. 2005. The effects of residential locality on parental and alloparental investment among the Aka foragers of the Central African Republic. *Hum Nat* 16:58–80.
- Michalski RL, Shackelford TK. 2005. Grandparental investment as a function of relational uncertainty and emotional closeness with parents. *Hum Nat* 16:292–304.
- Monserud MA. 2008. Intergenerational relationships and affectual solidarity between grandparents and young adults. *J Marr Fam* 70:182–195.
- Mueller MM, Wilhelm B, Elder GH Jr. 2002. Variations in grandparenting. *Res Aging* 24:360–388.
- Pashos A, McBurney DH. 2008. Kin relationships and the caregiving biases of grandparents, aunts and uncles: a two-generational questionnaire study. *Hum Nat* 19:311–330.
- Pollet TV, Nettle D, Nelissen M. 2006. Contact frequencies between grandparents and grandchildren in a modern society: estimates of the impact of paternity uncertainty. *J Cult Evol Psychol* 4:203–214.
- Rogers AR. 1990. Evolutionary economics of human reproduction. *Ethol Sociobiol* 11:479–495.
- Sear R, Mace R. 2008. Who keeps children alive? A review of the effects of kin on child survival. *Evol Hum Behav* 29:1–18.
- Smith MS. 1991. An evolutionary perspective on grandparent-grandchild relationships. In: Smith PK, editor. *The psychology of grandparenthood*. New York: Routledge. p 157–176.
- Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. *Am Nat* 108:499–506.
- Stearns SC. 1992. *The evolution of life histories*. Oxford, England: Oxford University Press.
- Strassman B. 2008. Menopause and the trade-off between offspring number and offspring quality. Paper presented at the International Union for the Scientific Study of Population entitled Trade-Offs in Female Life Histories: Raising New Questions in an Integrative Framework, 23–25 July, Bristol.
- Strohschein L, Gauthier AH, Campbell R, Kleparchuk C. 2008. Parenting as a dynamic process: a test of the resource dilution hypothesis. *J Marr Fam* 70:670–683.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and the descent of man 1871–1971*. Chicago: Aldine. pp 136–139.
- Van Bavel J. 2006. The effect of fertility limitation on intergenerational social mobility: the quality–quantity trade-off during the demographic transition. *J Biosoc Sci* 38:553–569.
- Walker RS, Gurven M, Burger O, Hamilton MJ. 2008. The trade-off between number and size of offspring in humans and other primates. *Proc R Soc B* 275:827–833.
- Zervas LJ, Sherman MF. 1994. The relationship between perceived parental favoritism and self-esteem. *J Genet Psychol* 169:281–288.