

that we would want to add to our model, based on C&H's discussions:

a. Grandparental investment will be indifferent to the age of the grandchild (see target article, sect. 3.4, para. 1).

b. Grandparental investment is independent of grandparent-grandchild exchange and sensitive to grandparent-child exchange (sect. 4.1).

c. Bequests are motivated by a different calculus than *in vivo* investments. Grandparents have no motivation to diverge from the equal division norm in death, based on our model.

d. Grandparents who make a clear investment in one set of grandchildren are likely to have fewer depressive symptoms and reduced cognitive impairment (sect. 8.2, paras. 1–3).

All told, this is a topic that is ripe for a productive assessment of the relative merits of evolutionary and rational choice theories of individual behavior. The same is true for the much better appreciated phenomenon of declining fertility in developed societies. C&H advert to the demographic transition in their essay, but fail to point out that there is no satisfactory evolutionary explanation of it. Rational choice theory fares better in this respect (Friedman et al. 1994).

ACKNOWLEDGMENT

The authors are grateful for the comments of Satoshi Kanazawa.

An evolutionary perspective can help unify disparate accounts of grandparental investment

doi:10.1017/S0140525X09991634

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Abstract: Coall & Hertwig (C&H) bring attention to alternative accounts of grandparental investment from economics, evolutionary anthropology, psychology, and sociology, which have yet to be reconciled. We attempt to help integrate some of the disparate perspectives by expanding the scope of the evolutionary perspective, highlighting some gaps, and discussing problems with the authors' treatment of grandparents in traditional societies.

Coall & Hertwig (C&H) offer a comprehensive survey of literature pertaining to grandparental "altruism" and call for an integration of disparate perspectives. Although the scope and coherence of a unified theoretical approach are not clearly defined, the authors are to be commended for raising important issues. We argue that evolutionary and rational actor perspectives could be expanded to provide a framework that encompasses both ultimate and proximate-level explanations.

Highly encephalized brains, slow growth, and long lives are derived features of human life history, with juvenile dependency, complex skill development, and grandparenting as key components. If the function of post-reproductive lifespan is to improve fitness of descendant kin, a wide range of cognitive and behavioral traits that focus attention on perceiving and responding to needs of particular kin is expected. Emotions, like motivations, could further modulate behaviors that either benefit or burden particular kin. Psychological studies of wisdom among older adults in modern societies (Baltes et al. 1992) and of kin-favoring dispositions despite age-related physical decline (Carstensen & Lockenhoff 2003) are consistent with an evolutionary perspective. Norms and institutions might

help facilitate delivery of benefits, even when co-residence is unlikely, as codified in inheritance rules. Norms and institutions are considered features of the sociological domain and emotions as part of psychology, yet evolutionary theory and economics are required to make sense of why norms, institutions, and emotions occur in particular forms and expressions. The evolutionary study of emotions and norms is a rich industry.

Evolution has led to a long human lifespan with a substantial post-reproductive phase, yet, despite the adaptive value that grandparenthood must have provided our ancestors, the authors point out a conundrum: Grandparents in the past overlapped with grandchildren for a brief period but with large fitness impact, whereas longer-living grandparents today have more overlap and thereby greater potential to help, but few grandchildren. As a consequence, grandparents in the past increased fitness by reducing infant mortality, but today mostly have only "soft" impacts on well-being and cognition. We feel that (1) the contrast made between past and present *opportunity* is overstated, and (2) differences in investment patterns depend on marginal benefits of grandparental help, which varies among societies based on differences in fertility, production patterns, co-residence, and inheritance.

Contrary to the statement that grandparental opportunity is strongest today, evidence suggests that the opportunity to help grandchildren was higher among our hunter-gatherer ancestors. First, while mortality and fertility are lower today, age at first marriage is also much later, and so Westerners become grandparents about 12 years later on average than do hunter-gatherers. Thus, the average number of years lived as a grandparent may not be very different between groups (Table 1). Second, hunter-gatherers are more likely to be co-resident with grandchildren and the total number of grandchildren to potentially impact is higher (fertility of hunter-gatherers is 4–8 births).

Third, support for the idea that grandparents in traditional societies increase fitness has relied on historical demographic datasets to measure the impact of their presence on early life mortality. Anthropological studies of grandparental contributions focus primarily on food production of older adults. To our knowledge, caloric production (or any other grandparental behavior) has yet to be causally linked to child welfare in any of these studies. Despite the popularity and importance of the Grandmother Hypothesis and alternate explanations of post-menopausal lifespan, all studies of grandparental impacts on kin fitness are indirect, based on whether a grandparent was alive or dead, or in rare cases, co-resident, in a given year. To what extent is the early weaning of infants, higher infant and child survivorship, and earlier reproduction, influenced by grandparents? Until these pathways are studied, phenotypic correlations may confound any observed positive relationship between living grandparents and kin survivorship or fertility. Without an understanding of the proximate mechanisms by which grandparents likely improved kin welfare, detailed predictions about what grandparents should be doing today (and whether their behavior is maladaptive) are difficult to make.

Fitness is impacted by accumulating and transferring material, embodied, and relational wealth, and societies vary in the extent to which each of these is inherited and needed for cultural and biological "success" (Borgerhoff Mulder et al. 2009). Grandparents should facultatively adjust their aid behavior where they can have the highest marginal benefit at lowest personal cost. Whether in small-scale societies or modern post-industrial ones, we suspect that the greatest impact of grandparents may be realized during rare, but fitness-relevant, periods. The authors describe postpartum depression and teenage pregnancy in modern societies as examples. We mention a few others here based on ten years of fieldwork among Tsimane forager-horticulturalists of Bolivia. Tsimane grandparents are often primary caretakers when parents die: 17% of adult Tsimane interviewees had a parent die before age 18, and 19% of these went to live with a

Table 1 (Gurven & Schniter). *Demographic parameters for hunter-gatherers and modern populations*

Population	Age at first birth (AFB)	Remaining life expectancy, (e_{AFB})	Age at first grandparenting (AFGB)	Remaining life expectancy, (e_{AFGB})	Total fertility rate (TFR)
Hunter-gatherers	19	36	38	25	5.4
Acculturated hunter-gatherers	19	44	38	30	5.5
Spain, 2002–2007	29.3	53	58.6	26	1.28
United States, 2004	25.0	54	50	31	2.09

Data Sources: Hunter-gatherers: Gurven and Kaplan (2007), Hewlett (1991); Spain: Instituto Valenciano de Investigaciones Económicas (Goehlich, <http://www.ivie.es>); United States: National Center for Health Statistics (http://www.cdc.gov/nchs/data/nvsr/nvsr57/nvsr57_14.pdf).

grandparent (9.8% with maternal, 9.0% with paternal). Even when not holding leadership positions, older adults mediate conflicts between different kin factions, which helps to promote coordination in activities so as to more efficiently reap gains from divisions of labor and economies of scale. While the “soft” impact of grandparents in traditional societies has not been described, we suspect that further inquiry may reveal that the marginal impact of grandparents is not primarily in the form of calories. Grandparents are named as important transmitters of Tsimane skills and knowledge (Gurven & Kaplan 2008; Schniter 2009); they account for 8% of identified contributors to early-life skill acquisition. They are twice as likely to be named for rare but important skills, such as making pottery, punishing bad behavior, singing traditional songs, and telling old stories and myths.

Finally, an evolutionary perspective emphasizes not only grandparents’ cumulative fitness impacts, but also the increasing costs on descendants with age. Few hunter-gatherers and horticulturalists live beyond the seventh decade of life. Among Tsimane, we observed that grandparents in their 70’s no longer make net-transfers of food to grandchildren. Whether the complementary contributions listed above are sufficient to slow the decline in utility is an open question, but we suspect that net utility is negative by the late 70’s. In pre-industrial societies where production is costly and resource competition is high, geronticide and neglect are commonly practiced (Maxwell et al. 1984). Elderly populations today, whose knowledge and traditions may be devalued, given rapid cultural change, show increasing evidence of neglect and abuse (Lachs & Pillemer 2004). Intervention programs that focus on the marginal benefits grandparents can offer may be helpful for strengthening familial care networks and building communities (Denham & Smith 1989). The total value of grandparents as fallback caretakers, educators, mediators, storytellers, and as sources of wisdom is too important as social insurance to risk losing, even in modern societies.

Grandparental transfers and kin selection

doi:10.1017/S0140525X09991646

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Abstract: In the analysis of intergenerational transfer, several improvements can be made. First, following kin selection theory, grandparents have kin other than grandchildren in which to invest and therefore any investigation into grandparents should take this perspective. Secondly, how transfers actually enhance the survivorship of younger relatives such as grandchildren must be better measured,

especially in the ethnographic literature. Finally, the problem of indirect investments or targeting must be considered.

Coall & Hertwig (C&H) present a wonderfully comprehensive and admirable review on the investing roles that grandparents play in traditional and modern societies. I would direct any of my students to this article if they were beginning research on the topic. Given that the article is so comprehensive, I restrict my comments to the history of this research in anthropology, especially as it relates to kin selection theory and some measurement issues that would better assess the ways in which grandparents matter.

There are several strands of research in evolutionary anthropology that deal with the role that grandmothers may play in enhancing the fertility of their children and survival of their grandchildren, beginning with the work of Turke (1989) and Kaplan (1994) on intergenerational resource transfers, the literature on “helpers at the nest” (for a review, see Hames & Draper 2004), as well as reviews of the grandmother literature (Sear & Mace 2008). To a limited extent, the theme of extended family intergenerational transfers is picked up by the authors in section 8.2 (under the heading of the “one-way street?”) and elsewhere. Turke and Kaplan criticized the work of the influential development demographer Caldwell (1976), who argued that high fertility in the developing world is a kind of social security mechanism whereby the elderly through high fertility produce children and eventually grandchildren who will support them in their old age. This strategy functions as insurance in social systems that lack effective social security. Turke and Kaplan note that Caldwell’s model is a challenge to evolutionary demography and kin selection theory because the fitness concerns of family members, especially grandparents, should lead to a flow of wealth and resources from those who have low reproductive value to those who have greater reproductive value, adjusted by the coefficient of relatedness. If the flow were opposite, from younger to older, the fitness of the younger would be reduced, as well as the inclusive fitness of the older generation. The literature C&H review tends to support Turke and Kaplan’s view in the modern context, but we need more research in the developing world, as exemplified by the research reviewed by Sear and Mace (2008).

The next research thread moved the focus from the extended family to a close examination of the impact of grandparents and was initiated by Hawkes and colleagues, beginning with their work on Hadza grandmothers (Hawkes et al. 1989). These researchers argued that menopause was designed by natural selection to channel resources to grandoffspring. This insight generated a large amount of high quality research on grandmother effects on the survivorship of grandoffspring and the fertility of their children. C&H point out that much of this research is summarized in Hrdy’s conceptualization of communal breeding (Hrdy 2005a) and in the general literature on helpers at the nest.