



Matrilateral Bias in Human Grandmothering

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Children receive more care and resources from their maternal grandmothers than from their paternal grandmothers. This asymmetry is the “matrilateral bias” in grandmaternal investment. Here, we synopsise the evolutionary theories that predict such a bias, and review evidence of its cross-cultural generality and magnitude. Evolutionists have long maintained that investing in a daughter’s child yields greater fitness returns, on average, than investing in a son’s child because of paternity uncertainty: the son’s putative progeny may have been sired by someone else. Recent theoretical work has identified an additional natural selective basis for the matrilateral bias that may be no less important: supporting grandchildren lightens the load on their mother, increasing her capacity to pursue her fitness in other ways, and if she invests those gains either in her natal relatives or in children of a former or future partner, fitness returns accrue to the maternal, but not the paternal, grandmother. In modern democracies, where kinship is reckoned bilaterally and no postmarital residence norms restrict grandmaternal access to grandchildren, many studies have found large matrilateral biases in contact, childcare, and emotional closeness. In other societies, patrilineal ideology and postmarital residence with the husband’s kin (virilocality) might be expected to have produced a patrilateral bias instead, but the available evidence refutes this hypothesis. In hunter-gatherers, regardless of professed norms concerning kinship and residence, mothers get needed help at and after childbirth from their mothers, not their mothers-in-law. In traditional agricultural and pastoral societies, patrilineal and virilocal norms are common, but young mothers still turn to their natal families for crucial help, and several studies have documented benefits, including reduced child mortality, associated with access to maternal, but not paternal, grandmothers. Even in rural China and Bangladesh, where women’s links to their natal families are formally severed at marriage, critical matrilateral assistance persists “under the radar.” Our review is limited to grandmothers, but the relevant evolutionary theories are not, and there is empirical evidence that the matrilateral bias extends to other kin, too. We propose that it is an evolved aspect of human nature.

Keywords: alloparents, grandmothers, inclusive fitness, kinship, matrilateral, nepotism, paternity uncertainty, patrilateral

INTRODUCTION

Childcare by grandmothers in developed countries is the focus of a large literature. How much care do grandmothers provide, how many serve as their grandchildren’s primary caregivers, and what are the consequences? A remarkable feature of this literature is its scant attention to *laterality*: the distinction between maternal and paternal relatives. Many broad-ranging reviews of the literature

have ignored this variable (e.g., Cherlin and Furstenberg, 1992; Pebley and Rudkin, 1999; Fuller-Thomson and Minkler, 2001; Hayslip and Kaminski, 2005; Fruhauf and Hayslip, 2013; Choi et al., 2016), as have hundreds of empirical studies, large and small.

This neglect is unfortunate. There are compelling theoretical reasons to anticipate that laterality will affect how grandmothers and other relatives invest in children, and evolutionary anthropologists, demographers, and psychologists have amassed abundant relevant evidence from a broad array of societies. In general, maternal kin provide more “alloparental” care and resources than their patrilineal counterparts, and when apparent impacts have been assessed, their presence and participation impart greater benefits. Here, we review this body of work, focusing, for conciseness, on grandmothers.

THE RELEVANT EVOLUTIONARY THEORIES

Natural selection favors traits promoting *inclusive fitness*, the expected replication of one’s particular genetic variants (Hamilton, 1964). Since close kin share genes, “nepotistic” motives and behavior that contribute to the survival and eventual reproduction of the actor’s relatives are ubiquitous in social animals (West et al., 2007).

With minor exceptions, each grandparental gene has a 25% chance of having a descendant copy in a given grandchild, regardless of the sex of the intermediate parent. If this were the whole story, natural selection would favor treating the children of one’s daughters and one’s sons as if they were equally valuable. But there are complications. Where paternity is mistakable due to the crypticity of fertilization and the gap between conception and birth, the subjective value of a male relative’s child should be discounted by the probability that the putative father is not the actual sire. Evolutionists have, therefore, sought—and found—evidence that laterality affects kin solicitude and investment in humans and other animals.

Unfortunately, the term “paternity uncertainty” is used ambiguously, referring to two quantities that should be distinguished. The first is the species- or population-specific rate of “extra-pair” paternity (“cuckoldry”), which helps explain “fixed” differences between taxa in such matters as whether male birds incubate their partners’ eggs (e.g., Møller and Birkhead, 1993). The second is a psychological variable, responsive to *cues* of paternity probability including the timing of a mate’s absences and the phenotypic resemblance of father and offspring, which helps explain individual differences in such things as male participation in feeding the young (e.g., Schroeder et al., 2016). As a result of a history of natural selection, both the population parameter and the individual difference variable influence paternal care, mate guarding, patrilineal kin investment, and other social phenomena in many species (Daly and Wilson, 1988).

Recently, Perry and Daly (2017) have identified a further selective basis for a matrilineal bias in alloparenting. Because the costs of parenting are paid primarily by mothers, not fathers, in all societies and alloparents alleviate that burden (Hrdy, 2009),

their help constitutes a *de facto* investment in the mother as well as her children. Child-rearing assistance raises the mother’s *nepotistic value* (NV): her residual capacity to promote her own fitness through any and all avenues. If the mother’s NV gains are invested back into the same child or its full siblings, both grandmothers accrue inclusive fitness benefits that could repay alloparental investments. If, however, an assisted mother invests her NV gains in natal kin such as her nieces and nephews, or in extant or future children who are *not* the progeny of her current mate, fitness benefits accrue to her genetic relatives, but not her in-laws. Matrilineal kin are, therefore, selected to be more enthusiastic alloparents than patrilineal kin regardless of paternity uncertainty.

In contrast to the literature on human alloparenting, students of cooperatively breeding birds have long understood that inclusive fitness returns from alloparenting might accrue, in part, from its effects on the survival and subsequent reproduction of related breeders (Heinsohn, 2004). However, analyses of “load lightening” and its effects in birds have not incorporated the possibility that the assisted breeders might then provide help to kin of the original helpers, perhaps because helping is a pre-reproductive life stage in most cooperatively breeding birds and collateral nepotism on the part of those who have already attained the status of breeders is rare. The human life course, however, is very different from that of birds, with plenty of opportunity for former reproductives to act as helpers later, and this eventual nepotistic payback probably played a significant role in the evolution of the matrilineal bias (Perry and Daly, 2017), a possibility reinforced by recent evidence that misattributed paternity is much rarer than previously supposed (Anderson, 2006; Larmuseau et al., 2016; Sear, 2016).

Finally, according to the “grandmother hypothesis” (Hawkes and Coxworth, 2013), senior women have evolved to be grandmothering specialists. The human female’s efficacious postreproductive lifespan is unique; in all other primates, reproductive capability and other physiological systems tend to fail more or less simultaneously. This suggests past selection for delaying human female senescence, which can only have occurred if women continued to contribute to their fitness after menopause. One way they do that is by tending and providing for weaned grandchildren, freeing their daughters to nurse infants or reproduce again sooner. This hypothesis need not preclude adaptive investment by paternal grandmothers (PGMs) as well as maternal grandmothers (MGMs), but Hawkes and colleagues give primacy to the latter, partly on the basis of ethnographic evidence of mother–daughter cooperation at and after childbirth, and partly because of technical details of their life history model (Hawkes et al., 1998).

GRANDMOTHERING AMONG HUNTER-GATHERERS

Hunter-gatherers (foragers) provide a model of the social and ecological contexts of human evolution, and it is therefore instructive to consider what is known about grandmothering in such societies. Indeed, Hawkes’ “grandmother hypothesis” was

inspired by the Hadza women of Tanzania, who collect many more calories than they consume, increase their foraging effort and surplus caloric accrual after menopause, and work hardest when their daughters have newborns (Hawkes et al., 1997). Moreover, despite foraging for over 5 hours a day, MGMs find the time to provide more hands-on childcare than anyone other than the parents (Marlowe, 2005).

Hadza camp composition is fluid, and grandmothers go where their help is needed. Senior women are present significantly more often in camps where they have adult daughters rather than sons, and they make themselves most available when those daughters are nursing (Blurton Jones et al., 2005). PGMs also provide childcare, but much less than MGMs (Marlowe, 2005), coming forward mainly if the MGM is deceased (Blurton Jones et al., 2005).

The Hadza are just one society, and hunter-gatherer practices are diverse. The aboriginal societies of Australia, for example, stand out for a high incidence of polygynous marriage, which goes hand in hand with a male preference for residing on patrilocal territory. Although Australian kinship clearly incorporates both male and female lines of descent, Denham (2015) notes that early male anthropologists stressed the former because their informants were men, whereas genealogies collected from women paint a different picture, stressing female lines. According to Peterson (1978), young aboriginal men aspire to live on their fathers' lands, but when they marry, they often find themselves residing matrilocally instead. Recent studies concur. Among the Martu of Western Australia, married women have more natal kin in their residential camps than do married men, and this is especially true for the youngest mothers, who cannot yet use older children to help care for younger siblings (Scelza and Bliege Bird, 2008). The story is apparently similar among the Alyawarra of central Australia, where Denham (2015) further suggests that MGMs help more than PGMs partly because the former are 14 years younger, on average; this is an important consideration, but his data also show that a matrilateral bias in alloparental assistance is not limited to grandmothers.

Anthropologists formerly generalized that hunter-gatherers were patrilineal in descent reckoning and inheritance, and virilocal (patrilocal) in postmarital residence (e.g., Service, 1962). This stereotype was overturned in the 1960s, and if any generalization remains, it is that almost all hunter-gatherers affiliate with and depend on both maternal and paternal kin (Alvarez, 2004; Kramer and Greaves, 2011; Kelly, 2013). *In toto*, the literature still indicates a preponderance of virilocality, but as in Australia, this may reflect male informants portraying their preference for living close to patrilineal allies as normative, rather than the behavioral reality. Kelly's (Kelly, 2013) thorough review of "hunter-gatherer lifeways" shows that even in nominally virilocal societies, actual residence practices are fluid and variable, young mothers routinely prefer their own mothers as birth attendants, and matrilateral kin play large alloparental roles. An intensive study of Aka hunter-gatherers in central Africa, who purportedly reside in patrilocal clans, illustrates these points. When Meehan (2005) interviewed 15 mothers of infants, 7 were residing matrilocally and 8 patrilocally, but none actually preferred the latter option: 13 said that given the choice, they would be with their mothers,

where they and their children would get better care, and two professed indifference. Observational data confirmed that the infants indeed received significantly more care from maternal relatives when residing matrilocally than was provided by paternal kin when they dwelt virilocally. More research is needed, but current evidence suggests that a preponderance of matrilateral assistance is ubiquitous among hunter-gatherers, not exceptional.

GRANDMOTHERING IN AGRICULTURAL AND PASTORAL SOCIETIES

Patrilineal ideologies legitimizing father-to-son inheritance of land and livestock arose when people began to practice animal husbandry and agriculture. Then, marriage itself began to be treated as a transfer of proprietary entitlements to the bride's labor and reproductive capacity from her natal patrilineage to that of her husband (Wilson and Daly, 1992).

Unsurprisingly, patrilineal ideology is associated with virilocal residence. Brides are often expected to leave home to reside with and serve their new in-laws. Judd (1989), for example, describes "classic" marriage practices in China as follows:

[T]he norm for Chinese women who married ... was a definitive rupture with their natal families. The anticipation of this break caused women to be viewed as only temporary and marginal members of their natal families ... the step the bride took that day could never be undone. Whatever her future circumstances or difficulties, she would never return to her natal family except as a visitor. (Judd, 1989, pp. 525–526)

Similar practices reportedly prevail in the Bengali society of north-east India and Bangladesh, among Muslims and Hindus alike. In rural Bangladesh, according to one account,

the custom of patrilocal marriage removes a newly married woman from her family of birth and places her in her husband's locality. Preference for lineage and village exogamy attenuates a woman's ties with her family of birth and reduces the possibility that her family will intervene on her behalf after marriage. (Cain et al., 1979, p. 406)

In such societies, the only available targets for grandmaternal care would seem to be the children of sons. Nevertheless, although PGMs do indeed have more contact with their grandchildren than MGMs, the situation in both of these societies is more complex than stereotype implies, and matrilateral bonds are surprisingly robust.

Using data from a 2002 survey, Zeng and Xie (2014) found that paternal grandparents outnumbered maternal by about 18 to 1 in rural Chinese households where children dwelt with both parents. However, Chen et al. (2011) report a much smaller difference on the basis of five waves of data from the *China Health & Nutrition Survey (CHNS)* conducted between 1991 and 2004: 35% of households with young children contained one or both

paternal grandparents and another 10% included maternal grandparents. The apparent contradiction between these reports derives largely from a rural-urban difference, with city-dwellers having stronger matrilateral ties, and also from the fact that Chen et al.'s data include households in which grandparents were the children's primary caregivers. It has undeniably been normative that Chinese grandparents should care primarily for their sons' children (see also Kaptijn et al., 2013), but this patrilateral bias is on the wane. There is some evidence that MGMs now provide more child care than PGMs in urban centers and that this is true even in "4-2-1" families in which a child is the sole grandchild for all four grandparents (Zhang, 2016).

Is the involvement of MGMs a novelty? Perhaps not. In the 1980s, when effects of newly implemented economic market reforms and the one-child policy can scarcely have begun to be felt, Judd's fieldwork in Shandong province uncovered some striking departures from the patrilocal norms:

I unexpectedly found married women resident in their natal families, daughters-in-law who were missing from their marital families (and still resident with their natal families), and young married women who had taken up residence with their husbands but returned daily to their natal families. Inquiry elicited the response that this was their custom (*xiguan*) and tradition (*chuantong*) and ample confirmation that these practices were common. (Judd, 1989, p. 526)

This is noteworthy because Shandong is a stronghold of Taoist and Confucian traditions. What Judd's observations may indicate is that expressions of patrilineal, virilocal ideology constitute a moralistic chiding that is more prescriptive than descriptive, and that matrilateral affiliation and support have long been important "under the radar."

Research in Bangladesh invites a similar interpretation. Perry (2017a) conducted interviews with two groups of mothers raising dependent children in intact first marriages in a rural county: 40 residing with their husbands, and 46 whose husbands were absent migrant laborers. Although patrilocal residence was universally acknowledged as normative, over 45% of both groups actually resided elsewhere. A common life trajectory was to initially reside with the husband's parents after marriage, to later establish a separate household within the same paternal family compound, and finally, to leave to dwell neolocally. Interviewees agreed that pregnant women prefer to return to their mothers' homes to give birth, where mother and child receive better care than at the mother-in-law's, and those who indeed went home to give birth often stayed for many months, a practice said to be long-standing and traditional (see also Edhborgh et al., 2015; Perry, 2017b). Twenty-two percent of the women whose husbands were migrant laborers (but none of those whose husbands were present) were living with their own mothers when interviewed. These estimates should be unbiased, because the two samples of potential interviewees were drawn randomly and there were almost no refusals.

Each mother was asked who was the secondary provider of childcare after herself. PGMs were the primary nominees,

constituting 24% of those named, while 10% were MGMs, which is unsurprising given the prevalence of virilocal residence. More interestingly, when accessibility was controlled, evidence for a matrilateral investment bias emerged. For example, *every* MGM who actually resided in the same compound was nominated as her grandchild's secondary caregiver, but the same was not true for PGMs. Moreover, the main providers of material help from outside the child's immediate household were overwhelmingly matrilateral relatives. Perhaps most telling is the fact that having the MGM present in the home and/or serving as secondary caregiver was a significant positive predictor of children's educational attainment, net of family income, and other potential confounds, whereas patrilocal residence was a significant negative predictor of child height and weight (Perry, 2017a).

Perry (2016) reported further findings from interviews of the caregivers of children whose natal families had been disrupted by parental death or divorce. The Bengali kinship system makes children members of their patrilineage and not of any matriline (Inden and Nicholas, 1977), and widows usually remained in the deceased husband's compound to safeguard their children's patrimony, but even so, MGMs undertook primary care of these children more frequently than did PGMs. In sum, as in China, uterine kinship plays a crucial "under the radar" role in the support of children in Bangladesh, and this appears to be especially true in difficult circumstances.

Research in small-scale, traditional agricultural and pastoral societies has produced similar findings. The Himba, a semi-nomadic pastoralist group in Namibia, provide a remarkable example of the importance of women's natal family ties in an ostensibly virilocal society. According to Scelza (2011), when an adult woman marries, a small brideprice is paid, and the newlyweds take up residence "either with the husband's kin or, once the man has come into his inheritance, in a neolocal camp." Nevertheless, over 60% of currently married adult women happened to be residing among natal kin when interviewed, partly because of frequent prolonged visits and fluidity of camp membership, and partly because women usually returned to their mothers to give birth and stayed for many months. The MGM assisted at childbirth in 67% of 432 births, and a matrilateral relative in over 90%; the PGM attended in fewer than 5% of cases.

Gibson and Mace (2005) investigated grandmaternal involvement and its apparent effects among the predominantly virilocal agropastoralist Oromo of Ethiopia, using both census data for several thousand villagers and time budget data from repeated "spot sampling" of 58 households. According to the census data, most women moved at marriage to their husbands' villages, but having an accessible MGM was predictive of improved child survival and growth, whereas PGMs had no such effects. In the observational data, women visited their married daughters' homes much more than those of their sons, even when all parties dwelt in the same village, and they pitched in with heavy domestic tasks more than PGMs. Even senior women who had sons with children close at hand and daughters with children in another village still visited and helped out more at the latter's homes.

Finally, there is a substantial body of historical and demographic evidence concerning the predictors of child mortality in natural-fertility populations. In the absence of observational data,

causal inference is conjectural, but the general tendency is to find that a living, accessible MGM has more beneficial “effects” than other kin (Sear and Mace, 2008; Fox et al., 2010). It is particularly striking that this is true even in patrilineal societies in which MGMs typically have less access to their grandchildren than PGMs (Strassmann and Garrard, 2011).

In sum, the elevated levels of patrilineal affiliation and ideology associated with agricultural lifeways have not erased the matrilateral bias in grandmothering.

GRANDMOTHERING IN MODERN DEMOCRACIES

Technologically advanced democracies have properties that permit strong tests of laterality biases in kin solicitude. Descent reckoning is bilateral, and neolocal postmarital residence is normative in both the prescriptive and statistical senses of “norms.” With few pressures favoring lateralized family relationships, the expression of preferences should be relatively unconstrained.

Grandparents often act as children’s primary caregivers for reasons that include parental incarceration, incompetence, abuse or neglect, and work-related demands. In the United States, 2.7 million grandparents were the primary caregivers of one or more minor grandchildren in 2010 (U.S. Bureau of the Census, 2012). But despite a large literature on grandparental care (much of which implicitly treats the phenomenon as consisting entirely of MGMs stepping in for mothers), we have been unable to find quantitative estimates of the relative roles of maternal and paternal grandparents as custodial caregivers. Just two studies of custodial care in a child protection context have attended to this distinction. Perry et al. (2014) found that over 40% of all kin placements by one Canadian child protection agency were with MGMs: maternal and paternal grandparental *couples* came forward in almost identical numbers, but the maternal side predominated among grandmothers with new partners unrelated to the child, and their predominance became extreme in the case of single grandmothers. Assuming that step-grandfathers are often unenthusiastic about taking in unrelated children, and that child-rearing without a partner is especially demanding, these findings suggest that MGMs are less deterred by various negatives than PGMs. This conclusion is further supported by two additional findings: care-providing MGMs were especially likely to have serious health problems of their own (Perry and Daly, 2013), and yet placements with paternal kin “broke down” at twice the rate of those with maternal kin (Perry et al., 2014). Recent analyses of U.S. data by Helton et al. (2017) tell a similar story: maternal grandparents provide more care than their paternal counterparts, and despite having higher incidences of various challenges, they were apparently less likely to mistreat the grandchildren entrusted to their care.

Other research on grandparent–grandchild relations in the modern west has relied on surveys and interview data. Smith (1981, 1991) was the first to seek a matrilateral bias on the grounds of paternity uncertainty. Pursuing a conjecture by Dawkins (1976), he hypothesized that people would “invest in grandchildren in the descending order: (1) maternal grandmothers; (2) paternal grandmothers and maternal grandfathers;

and (3) paternal grandfathers” because these three groupings have zero, one, and two uncertain links, respectively (Smith, 1991, p. 158). Smith recruited Canadian grandparents in the Toronto and Vancouver areas for a questionnaire study, and to ensure a “conservative” test of his hypothesis, he excluded respondents who actually dwelt with a grandchild or had a child who had divorced. The following summary is confined to his results for 439 grandmothers who met these criteria. Women with grandchildren through both daughters and sons spent 44% more time with the former (Cohen’s $d = 0.26$), although they dwelt an identical average distance away. In those with grandchildren through a daughter or son but not both, the difference was reduced but not abolished: MGMs spent 33% more time with their grandchildren than did PGMs (Cohen’s $d = 0.21$).

Can we trust such self-report data? People may systematically exaggerate their commitment to close kin, but we see no reason why this should apply differentially to matrilateral *versus* patrilineal relatives. Similarly, although Smith’s sample was surely vulnerable to recruitment and/or volunteering biases, there is again no obvious reason why such biases should create a spurious laterality bias or inflate an existing one. If anything, social desirability biases might encourage denying “favoritism,” and recruiting people for study of their relationships with their grandchildren should select for relationships that are closer than average, leading the researcher to *underestimate* any genuine biases.

When samples collected by diverse methods provide convergent evidence, confidence in the validity of apparent contrasts increases. Consider, for example, the results of Smith’s original Canadian study *versus* a later one by Salmon (1999). Smith’s MGMs and PGMs reported that they dwelt at the same average distance from their grandchildren, but Salmon’s undergraduate subjects reported that their MGMs lived 176 km away, on average, *versus* just 65 km for their PGMs. The inconsistency probably derives from the studies’ different recruitment strategies and implies that both samples cannot be representative. Nevertheless, even without correcting for effects of distance, Salmon’s subjects reported seeing their MGMs 36% more often than their PGMs (Cohen’s $d = 0.36$), a difference similar to that reported by Smith and even larger in terms of effect size.

Even before Smith, researchers with no evolutionary overview had reported that American children feel closer, on average, to their MGMs than to their PGMs (e.g., Kahana and Kahana, 1970; Hoffman, 1980; Hartshorne and Manaster, 1982), and after Smith, studies in several countries have replicated his frequency of contact results (e.g., Eisenberg, 1988; Uhlenberg and Hammill, 1998; Laham et al., 2005), and/or demonstrated other sorts of biased engagement and investment favoring the maternal side (e.g., Eisenberg, 1988; Tyszkowa, 1991; Boon and Brussoni, 1996; Euler and Weitzel, 1996; Salmon, 1999; Dubas, 2001; Chrastil et al., 2006; Pashos and McBurney, 2008; Bishop et al., 2009; Kirchengast and Putz, 2016).

The most compelling data come from large nationally representative surveys. Willingness to participate remains a potential source of bias, but such research should be less vulnerable to bias than studies of undergraduates or other targeted groups. Pollet et al. (2006) analyzed data from the *Netherlands Kinship Panel*

Study, selecting respondents who had a grandchild younger than 16 living with the parent who was the respondent's child. Controlling for proximity and other potential confounds, they found that MGMs were about 7 times more likely than PGMs to see the grandchild a few times a week (and 13 times more likely to see the child daily) as opposed to rarely (less than monthly); these are odds ratios and should not be mistaken for simple relative frequencies, but they bespeak a large difference. Pollet et al. (2007) furthermore showed that contact with grandchildren falls away more steeply with distance for PGMs than MGMs, a contrast they epitomized by saying that MGMs “go the extra mile” for the children.

Pollet et al. (2008) used different analytic methods on data from the British *Millennium Cohort Study*. Confining analysis to cases in which grandchildren were 9- to 12-month olds and living with both birth parents, and all four grandparents were alive and unseparated, they found the usual laterality difference in frequency of contact, but reported a “small” effect size (Cohen's $d = 0.2$). However, Cohen's d is not a good effect size metric for ordinal data like these. According to the paper's Table 1, 46.4% of 7,467 MGMs were in contact with their infant grandchildren at least three times a week, *versus* 27.3% of 7,469 PGMs, yielding an odds ratio of 2.3, arguably a rather large difference.

Danielsbacka et al. (2011) analyzed data from 13 European countries participating in the *Survey of Health, Ageing and Retirement in Europe*, and found a consistent tendency for MGMs to provide more care than PGMs. There were large national differences in grandparental child care, which was most prevalent in southern Europe, but the matrilateral bias was ubiquitous, regardless of national differences in family policy or culture. Women with grandchildren through both daughters and sons were about twice as likely to look after their daughters' children as their sons', net of other influences.

Ho (2015) conducted econometric analyses of data from the nationally representative US *Health & Retirement* study to determine what variables predict both direct care of grandchildren and monetary transfers. Rather than comparing MGMs *versus* PGMs directly, Ho treated that contrast as one predictor in multivariate analyses, along with proximity, the grandparent's age, health, wage, wealth, and numbers of children and grandchildren, and the parents' ages and marital status. Preferential investment of both care and money in daughters' children was strong and significant among both single grandmothers and grandparent couples, but not single grandfathers. Indeed, laterality was the best predictor of grandparental caregiving other than coresiding in the same household, and the third best predictor of monetary transfers after grandparental wealth and single motherhood of the grandchild. Another compelling econometric analysis is that of Duflo (2003), who showed that the receipt of pensions by South African MGMs, but not PGMs (or grandfathers on either side), had a positive effect on the grandchildren's height-for-age and weight-for-height; this study is unique in that it used no self-report measures and did not require caregiver participation.

We know of only two studies that have been interpreted as showing a patrilateral bias in grandmothering. Both were conducted in rural communities where patrilineal inheritance

of family farms was important, and neither provides persuasive evidence for preferential treatment of the children of sons. First, a study of rural families in IA, USA (King and Elder, 1995) is often cited as one where grandchildren had stronger ties to PGMs than to MGMs, but this misrepresents the actual findings. The study's primary focus was comparing farm-dwellers to town-dwellers. On the farm, children indeed resided closer to and had more frequent contact with their PGMs, but they nevertheless rated the MGM slightly higher with respect to the level of “support” that they had received from her and the quality of their relationship. In town-dwellers, proximity still favored the PGM, but contact, support, and relationship quality ratings all favored the MGM. No statistical tests of laterality were presented, but some of the MGM's advantages were of a magnitude comparable to the significant differences in farm-town comparisons. Thus, insofar as this study speaks to laterality at all, it appears to document the usual matrilateral bias in grandmother-grandchild bonds, and those who have cited it as a counterexample are mistaken.

Finally, Pashos (2000) found that rural Greeks reported having received more childcare prior to age seven from PGMs than from MGMs, which is again unsurprising. (Urban Greeks reported the reverse.) More provocatively, Pashos further concluded that the rural Greek PGMs provided more grandchild care than MGMs even when they lived “equally far away.” Looking more closely, however, Pashos's distance coding was too crude to warrant that conclusion: residence in the same household, “in the same town,” or in a “neighboring village” were all coded as equally, maximally, close at hand. Thus, it remains unknown whether even this one case truly represents a rare reversal of the usual preference. What is *not* in doubt is that there is, in general, a very large matrilateral bias in grandmothering in modern democracies.

CONCLUSION

A matrilateral bias in grandmothering is widespread and, where outcome data are available, it is consequential. Mothers get more help from their own mothers than from their mothers-in-law in societies ranging from hunter-gatherers to the modern west.

If paternity uncertainty and the differential fitness returns from boosting the NV of relatives *versus* in-laws are indeed the evolutionary engines of the matrilateral bias, as Perry and Daly (2017) have proposed, their relevance is not limited to grandmothers. The logic extends to matrilateral *versus* patrilateral kin in general, and there is already considerable evidence for matrilateral investment biases by grandfathers (many of the studies cited in Section “Grandmothering in Modern Democracies”), aunts and uncles (e.g., Gaulin et al., 1997; Perry, 2017a), and cousins (e.g., Jeon and Buss, 2007).

It seems, then, that effects of laterality on investment in kin are not culturally arbitrary and devoid of intrinsic directionality. We believe that the evidence that we have reviewed here, in conjunction with the theories of paternity uncertainty and maternal load-lightening, support the view that a matrilateral bias in nepotistic inclinations is an evolved aspect of human social psychology and behavior. But regardless of whether

this interpretation is correct, laterality matters. Family studies researchers working in traditions that have ignored this variable should start recording it and incorporating it into their analyses.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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