A model explaining the matrilateral bias in alloparental investment

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Maternal grandmothers invest more in childcare than paternal grandmothers. This bias is large where the expression of preferences is unconstrained by residential and lineage norms, and is detectable even where marriage removes women from their natal families. We maintain that the standard evolutionary explanation, paternity uncertainty, is incomplete, and present an expanded model incorporating effects of alloparents on the mother as well as on her children. Alloparenting lightens a mother's load and increases her residual nepotistic value: her expected fitness from later investments in personal reproduction and in her natal relatives. The mother's mother derives fitness from all such investments, whereas her mother-in-law gains only from further investment in children sired by her son, and thus has less incentive to assist the mother even if paternity is certain. This logic extends to kin other than grandmothers. We generate several hypotheses for future research.

alloparent | matrilateral bias | grandmother | kinship laterality | family relations

Animals have evolved to cherish kin and invest in their survival and well-being because doing so promoted inclusive fitness (expected genetic posterity) in the social and material environments in which those nepotistic inclinations evolved (1, 2). In humans, alloparental assistance by grandmothers and other relatives is so cross-culturally prevalent and profound in its effects that many theorists consider it a cornerstone of our species' social evolution (3–8).

The inclusive fitness returns from investing in a related child should be unaffected by whether the kinship link is through male or female relatives. Nevertheless, many studies indicate that maternal kin, especially grandmothers, invest more in children than do their counterparts on the paternal side, an asymmetry that we refer to as the "matrilateral bias" in alloparental assistance. With only a few exceptions, to which we will return, evolutionists have attributed this bias to paternity uncertainty resulting from the crypticity of fertilization and the interval between conception and birth. According to this theory, valuation of a male relative's child should be discounted by the probability that the putative father is not in fact the sire. We maintain that this theory is incomplete, and propose an expanded model incorporating additional evolutionary grounds for the matrilateral bias.

The organization of our discussion is as follows. First, we briefly review evidence that the matrilateral bias is widespread, large, and consequential, focusing on grandmothers, who are the most frequent and best studied helpers. Second, we formalize the predominant explanation of the matrilateral bias as an evolved response to paternity uncertainty, and then lay out an evolutionary model that predicts biased alloparental investment regardless of paternity certainty. Third, we explain how our model differs from some earlier suggestions that the matrilateral bias is not explained by paternity uncertainty alone. Finally, we show how the model points the way to testable hypotheses.

For conciseness, we restrict discussion to comparisons between maternal and paternal grandmothers (MGMs and PGMs, respectively), but essentially the same logic applies to grandfathers, aunts, uncles, and cousins, all of whom also exhibit a matrilateral bias (9–12). To facilitate the exposition, we use the abbreviations and terminology explained in Table 1.

The Matrilateral Bias in Human Grandmothering

A number of demographic studies indicate that the presence of MGMs, but not necessarily PGMs, tends to be positively associated with child survival in natural-fertility populations (see refs. 7, 13, and 14 for reviews). It is particularly striking that this is true even in patrilocal societies in which MGMs typically have less access to the grandchild (GC) than do PGMs, a result that has been interpreted as due to local resource competition within patrilineal family compounds (14). These findings suggest that MGMs provide more support than PGMs, but the data are demographic rather than observational, and differential outcomes associated with MGM vs. PGM presence need not reflect differences in their behavioral contributions (14–16).

More direct evidence of differential solicitude comes from interviews, questionnaires, and observational studies. Such research has been conducted mainly in so-called WEIRD (Western, educated, industrialized, rich, democratic) societies (17), which may be deemed a limitation but is also a strength. In traditional societies, grandparent (GP)–GC contact is often constrained by lineage-based ideologies and residence patterns. In contrast, in WEIRD societies kinship reckoning is bilateral and newlyweds typically reside neolocally rather than with either marriage partner's family of origin, facilitating the expression of relatively unconstrained GP preferences.

The first investigator to predict a matrilateral bias in GP–GC relations on the grounds of paternity uncertainty was Smith (18, 19), who found that bilineal Canadian grandmothers (GMs) reported spending 44% more time with their unilineal (U) GCs than their agnatic (A) GCs, despite residing an identical average distance away. Even among UGMs, the difference remained

Table 1. Abbreviations and terminology for GP–GC relationships

Abbreviation	Explanation
GP, GM, GF	Grandparent, Grandmother, Grandfather
MGP, MGM, MGF	Maternal GP, GM, GF (i.e., a parent of one's mother)
PGP, PGM, PGF	Paternal GP, GM, GF (i.e., a parent of one's father)
GC	Grandchild
UGC	Uterine grandchild (i.e., a child of one's daughter)
AGC	Agnatic grandchild (i.e., a child of one's son)
Bilineal GP (GM, GF)	GP (GM, GF) who has both uterine and agnatic grandchildren
Unilineal GP (GM, GF)	GP (GM, GF) who has uterine or agnatic grandchildren, but not both

substantial. Many subsequent studies have replicated Smith's results, or have demonstrated other sorts of biased engagement and investment favoring the maternal side. When questions focus specifically on grandmaternal investments in GC, effects of laterality tend to be even larger than when questions focus on mere contact.

GMs often act as children's primary caregivers when mothers cannot, but most research reports on this topic have ignored laterality. We know of just two exceptions. One was a study of kinship care in a Canadian child-protection context, where MGMs provided over 40% of all placements with family members (20). Maternal grandparent (MGP) couples only slightly outnumbered paternal grandparents (PGPs), but the laterality difference was larger for care-giving GMs whose spouses were unrelated to the child, and very much larger again among single GMs. These results suggest that MGMs are more committed and less easily deterred than PGMs, an interpretation reinforced by several additional findings: care-providing MGMs were more likely than PGMs to be poor, to have little education, and to have serious health problems of their own, and yet placements with paternal kin were twice as likely as those with maternal kin to break down (20). The second relevant study used data from a nationally representative sample of child-protection cases in the United States (21). Placements with MGPs outnumbered those with PGPs by almost 3:1, and the MGPs were again less educated and more often impoverished (but not less healthy) than their paternal counterparts; nevertheless, the incidence of investigations of further child maltreatment in the grandparental home was higher with PGPs than with MGPs (21).

Perhaps the most compelling evidence of differential care and solicitude comes from large nationally representative surveys, which consistently find that MGMs report investing more than PGMs in their GCs, often to a substantial degree. Examples include analyses of data from the Netherlands Kinship Panel Study (22, 23), the British Millennium Cohort Study (24, 25), the US Health & Retirement study (26), and the 13 European countries that participated in the Survey of Health, Aging, and Retirement in Europe (27). Furthermore, a clever econometric analysis that is unique in its nonreliance on the testimony of family members has shown that the receipt of pensions by South African MGMs, but not by PGMs or grandfathers (GFs), has a positive effect on GC height-for-age and weight-for-height (28).

In traditional societies, virilocal residence, whereby a bride moves to her husband's town, farm, camp, or family compound, is common and is strongly associated with patrilineal descent reckoning. Marriage may then entail the transfer of rights to a bride's reproduction and labor from her natal patrilineage to that of her husband, and even her sequestration in the home of her in-laws. In such cultural settings, it would seem that AGCs must be the only available targets for alloparenting by GMs, but although children indeed have more contact with their PGMs than their MGMs, the situation is often more complicated than stereotypes suggest, and matrilateral bonds are surprisingly robust. In a study of the predominantly virilocal agropastoralist Oromo people of Ethiopia, for example, MGMs were much more frequent visitors to their GCs' homes, and pitched in with heavier domestic tasks, than PGMs; even women who had AGCs in the same village and UGCs farther afield still visited and helped out more at the latter's home (29). Among the Himba, seminomadic Namibian pastoralists, newlyweds initially take up residence with the husband's family, but in an interview study, most currently married adult women were found to be residing with their natal kin, partly because of frequent prolonged visits and fluidity of camp membership, and partly because women returned to their mothers to give birth and remained for up to a year (30).

In rural Bangladesh, both virilocal marriage and *purdah*, the seclusion of women, are normative, but in a recent study, almost half of all intact families with young children actually resided elsewhere. PGMs outnumbered MGMs as secondary caregivers, but to a lesser degree than would be expected on the basis of residential proximity, and having the MGM present in the home or providing direct childcare was a positive predictor of children's educational attainment, net of family income, and other potential confounds, whereas virilocal residence was a negative predictor of child height and weight (31). Like the Himba, Bangladeshi women often return to their natal family homes and stay for many months before and after childbirth (32, 33). When parents had divorced or died, MGMs assumed the role of primary caregiver slightly more frequently than did PGMs, even though Bengali kinship deems children members of their patrilineage and widows usually remained in their in-laws' family compound to safeguard their children's patrimony (34).

China also has strong patrilineal and virilocal norms, and PGMs very often reside with and help care for their AGCs (35, 36). However, MGMs also live with and provide out-of-home care for their GCs in surprising numbers (35), and there is some evidence that MGMs now provide more child care than PGMs in urban centers (37). Is MGM involvement a novelty? A study of rural village life in the 1980s in Shandong province, a stronghold of Taoist and Confucian traditions, suggests otherwise: Judd (38) found that many married women resided with their natal families while others visited them daily, and her informants maintained that these were longstanding traditions. These observations suggest that in China, as in Bangladesh, significant matrilateral affiliation and support may exist "under the radar" of an overtly patrilineal, virilocal ideology.

In the data from Western democracies, virilocal rural communities in the United States and Greece have provided two purported exceptions to the generality of the matrilateral bias. The first, a study of families in Iowa in which farm-dwelling children had more frequent contact with their PGMs than their MGMs (39), has been cited repeatedly as an instance of patrilateral bias, but this is misleading: the children actually rated the MGM higher with respect to the "support" she provided and the quality of the GM–GC relationship. The other example is one in which rural residents in Greece reported having received more care as children from PGMs than from MGMs, whereas urban residents reported the reverse (40). Pashos (40, 41) maintains that these rural Greek PGMs provided more childcare than MGMs, even when the two lived "equally far away," which, if true, would constitute a unique demonstration of preferential investment in AGCs. However, the distance measure for this analysis was too crude to warrant such a strong conclusion: residence in the same household, "in the same town," or in a "neighboring village" were all scored as equally, maximally, close at hand, leaving the question of a preferential caregiving net of differences in accessibility unresolved.

In sum, the available data from societies with virilocal residence norms indicate that despite geographical and ideological impediments to uterine family contact, MGMs remain heavily involved in the lives of their GCs, and that their role relative to that of PGMs often increases when help is most needed, whether because of poverty, imminent childbirth, or parental death or divorce (29–33, 37, 38).

Why the Matrilateral Bias?

In animals with internal fertilization, the identification of fathers is susceptible to error. The risk that a mate's offspring may have been sired by a rival constitutes a selection pressure against the evolution of both paternal care and nepotistic feelings toward kin related through males (42). Paternity uncertainty thus provides a candidate explanation for the matrilateral bias, as portrayed in Model 1, where investments in UGCs and AGCs yield identical fitness returns for GMs only when the probability of paternity is 1.0.

Evolutionary psychologists, anthropologists, and biologists have embraced this explanation. Their reports of laterality biases routinely frame the research as tests of the predicted effects of paternity uncertainty and interpret the findings as confirmations of its impact (9, 18, 19, 22, 23, 27, 43–45). However, Model 1 is incomplete, because it captures only one of several reasons why caring for UGCs versus AGCs may yield different fitness payoffs.

Alloparental assistance presumably increases the expected fitness of the children being cared for, and in Model 1 that is the sole medium by which the GM also gains fitness. However, alloparental aid also constitutes an investment in the children's mother, reducing her load. Many authors have recognized that alloparents relieve the demands on human mothers (e.g., refs. 3–7, 46, and 47), but none have incorporated the downstream effects of this relief into a model of how natural selection acts on alloparenting. It is not simply the mother's reproductive value (48) that benefits from alloparental assistance, but her nepotistic value (NV). Reproductive value is a pre-Hamiltonian concept, which refers only to expected future reproduction, and it therefore falls to zero by menopause, when a woman's capacity to promote her fitness is still substantial (3–5, 49). NV is an expanded concept that refers to one's expected future inclusive fitness effect through any and all channels (50). The argument that alloparental assistance elevates parental NV applies with lesser force to fathers, because it is a cross-culturally universal feature of human reproduction that the burden of childcare is borne mainly by women. A more extensive model incorporating potential effects of alloparents on the NV of both mother and father is presented in Model S1 and Table S1 and its implications are explored in our concluding remarks.

There are various ways in which a mother may expend the NV gains that accrue to her as a result of having been helped, many of which also yield fitness benefits for her own mother (the

MGM), but not for her mother-in-law (the PGM), as outlined in Table 2. Note that the items enumerated in Table 2 are distinct components that add up to her total NV; women can expend their embodied capital in other ways, but if they do not provide inclusive fitness payoffs, they are not components of NV, by definition. Only nepotistic investment in the woman's father's kin (item 8 in Table 2) contributes to her own inclusive fitness but not to her mother's.

These payoff asymmetries increase the extent to which MGMs derive greater fitness from grandmothering than do PGMs, and warrant an expansion of Model 1, in which the GCs were treated as the sole beneficiaries of GM investment. In our revised Model 2, the beneficiaries of GM investment are both the GCs and their mother, whose own mother then garners an inclusive fitness return from the mother's NV expenditures 1 through 7 (as enumerated in Table 2), whereas her mother-in-law's fitness benefits only from expenditures on item 1 (hence "Prop$_1$" in Model 2).

Not Just Paternity Uncertainty?

In contrast to the literature on human alloparenting, investigators of cooperatively breeding birds have explicitly noted that inclusive fitness returns from alloparenting may accrue, in part, from elevating the survival and subsequent reproduction of the assisted parents. This "load-lightening" hypothesis has a long history and substantial empirical support in certain species (51, 52). To the best of our knowledge, however, even in the bird literature, analyses of load-lightening and its effects have never incorporated the additional element of future nepotistic investments in the common kin of parents and their helpers (items 5–8 in Table 2). This omission is probably explained by the fact that helping is a prereproductive 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 is, of course, very different from that of birds, with plenty of opportunity for former reproductives, especially GPs, to act as helpers later. Most evolution-minded researchers have nevertheless attributed the matrilateral bias among human alloparents to paternity uncertainty alone. However, a few have dissented, arguing that additional considerations may be relevant. Euler et al. (53, 54), for example, have proposed that matrilateral biases derive not just from paternity uncertainty but also from "sex-specific reproductive strategies": MGPs are motivated to advance their daughter's agenda, which is dominated by parental investment, and PGPs to advance their son's agenda, which aims for status and polygynous opportunity.

Invoking sex-specific strategies helps dispose of a distraction that has muddied the literature, namely a supposed prediction from the paternity uncertainty model that PGMs and maternal grandfathers (MGFs) should invest equally in GCs because both have one certain and one uncertain genetic link. However, there is no logical reason why attributing the effects of laterality to paternity uncertainty should preclude additional effects of sex differences. That said, we cannot see how the concept of sex-specific reproductive strategies helps explain the matrilateral bias itself. How would withholding investment from an AGC enable a PGM to better promote her son's polygynous career? And why would acting in accordance with her sex-specific strategy cause a bilineal GM to derive greater fitness from providing child care for her UGC than for her AGC?

Taking a different tack, Mace and Sear (55, 56) have suggested that matrilateral biases derive not only from paternity uncertainty, but also from the fact that a daughter is "irreplaceable," whereas a new daughter-in-law can take the place of one who dies. This argument recognizes that GM assistance may enhance maternal survival, but it overlooks both the inclusive fitness value of collateral nepotism and the crucial consideration that when it is instead the children's father who dies, his widow's

$$\Delta\omega_{MGM} = 0.25 * \Delta\omega_{UGC}$$

$$\Delta\omega_{PGM} = 0.25 * \Delta\omega_{AGC} * p(pat)$$

$\Delta\omega$ = change in fitness.

p(pat) = probability of paternity = [1 - (probability of "cuckoldry")].

Other abbreviations as in Table 1.

Model 1. Differential fitness gains from investment in uterine vs. agnatic GC as a result of paternity uncertainty.

Table 2. Ways in which a mother can expend her gains in nepotistic value for her own inclusive fitness benefit, and their effects on the fitness of her mother and mother-in-law

Inclusive fitness value for her mother (MGM)	Fitness-promoting components of a woman's allocation of her reproductive and nepotistic efforts	Inclusive fitness value for her mother-in-law (PGM)
√	1. Investment in children sired by current partner.	√
√	2. Investment in children sired by former partner(s).	—
√	3. Investment in children sired by future partner(s).	—
√	4. Investment in children sired by cuckolder(s).	—
√	5. Nepotistic investment in siblings.	—
√	6. Nepotistic investment in nieces and nephews.	—
√	7. Nepotistic investment in matrilateral cousins and distant kin.	—
—	8. Nepotistic investment in patrilateral cousins and distant kin.	—

further reproduction yields fitness for her own mother but not for his. In contrast, Voland and Beise (57) have explicitly noted that mother-in-law/daughter-in-law conflicts derive in part from high rates of widowhood and remarriage in our species' evolutionary past, whence "the reproductive interests of mothers-in-law in their daughters-in-law are limited to a much narrower period of time than that of the latters' own mothers." However, this point was made with regard to apparent effects of mothers vs. mothers-in-law on women's survival, not alloparental efforts, and the idea of shared fitness interests was again limited to direct reproduction (items 2–4 in Table 2), while overlooking collateral nepotism (items 5–7 in Table 2).

Others doubt that the matrilateral bias has any adaptive basis. Survey data indicating more childcare by MGPs in the Netherlands and by PGPs in China, for example, have inspired one research group to reject evolutionary arguments and conclude that "discriminative grandparental investments are better understood as the outcome of cultural prescriptions and economic motives" (36). We maintain, to the contrary, that in China and elsewhere, cultural prescriptions constrain the expression of matrilateral preferences but do not reverse them. Another proposal is that the matrilateral bias is largely, perhaps entirely, a statistical artifact of the fact that MGPs tend to be younger than PGPs and therefore tend to have more years of lifespan overlap with their GCs (58). This explanation is contradicted by many findings, including the large uterine bias in the allocation of care by bilineal GMs (e.g., ref. 19).

Could the matrilateral bias nevertheless be a functionless byproduct of strong mother–daughter bonds? The "grandmother hypothesis" (3–5, 49) can be read as supporting such a conjecture, because it attributes the efficacy of postmenopausal women to selection for grandmothering that is typically envisioned as taking place in a context of sustained mother–daughter affiliation. [A formerly fashionable model whereby human social psychology

supposedly evolved in a context of patrilineal affiliation and female dispersal has fallen out of favor, largely because the evidence now indicates that matrilateral kinship ties are ubiquitous and crucial in contemporary hunter-gatherer lifeways (59, 60)]. However, interpreting the matrilateral bias as a functionless byproduct of uniquely strong mother–daughter bonds does not sit well with the fact that GMs in all societies do care for their sons' children, albeit to a lesser degree than for those of their daughters, nor with evidence that mother–son relationships are no less close than those between mothers and daughters (e.g., refs. 61 and 62). McBurney et al. further maintain that the byproduct hypothesis creates a false opposition between complementary levels of analysis, writing "Pashos interprets the proximate cause of the matrilateral bias in western cultures to be the stronger family bonds of women compared with those of men. Indeed, we believe that this phenomenon may well be the proximate cause of matrilateral bias; our question concerns the ultimate cause, for which paternity certainty is the only current contender" (ref. 10, p. 399).

Paternity uncertainty has two related but distinct meanings in the social evolution literature. The first is a population parameter: the incidence of misattributed or "extra-pair" paternity. This is the more straightforward interpretation of $p(pat)$ in Models 1 and 2, but there is a second meaning, as well: paternity uncertainty may refer to a psychological variable that responds to cues such as the timing of a mate's absences and the phenotypic resemblance between fathers and offspring. Both the population parameter and the psychological variable have been hypothesized to affect paternal care, mate guarding, patrilateral kin investment, and other social phenomena, as a result of a history of natural selection (63), and there is substantial nonhuman evidence that both are important. The former is invoked to explain differences between taxa in such matters as whether male birds incubate their partners' eggs (64); the latter is invoked to explain facultative variation within taxa, such as how much food individual males deliver to nestlings (65).

Both meanings of paternity uncertainty have informed treatments of the matrilateral bias. Assuming paternity uncertainty to be the sole basis for the bias (as in Model 1), some authors have proposed that we can estimate a species-specific incidence of misattributed paternity from contemporary behavioral manifestations of the bias (9, 66). This logic effectively treats paternity uncertainty as a population parameter, corresponding to the average ancestral cuckoldry rate over some selectively relevant period in human evolution. Conversely, if one proposes that the variable magnitude of matrilateral biases should track societal variability in the enforcement of female fidelity, one is assuming flexible, facultative responses to the local social ecology, and interpreting paternity uncertainty as a psychological variable.

The dual meanings of population parameter and psychological variable may be applicable not just to paternity uncertainty, but also to the additional elements in Model 2. Nepotistic investment

$$\Delta\omega_{MGM} = 0.25 * \Delta\omega_{UGC} + \left[0.5 * \sum_{i=1}^{7} (Prop_i) * \Delta NV_{Mo}\right]$$

$$\Delta\omega_{PGM} = 0.25 * \Delta\omega_{AGC} * p(pat) + [0.5 * Prop_1 * \Delta NV_{Mo}]$$

$\Delta\omega$ = effect on fitness of GM's investment

ΔNV_{Mo} = effect on mother's nepotistic value of GM's investment

$Prop_i$ = proportion of mother's NV gains expended on item i in Table 2

$p(pat)$ = probability of paternity = [1 - (probability of "cuckoldry")]

Other abbreviations as in Table 1

Model 2. Differential fitness gains from investment in uterine vs. agnatic GC as a result of both paternity uncertainty and the impact of GM's alloparental contributions on the mother's residual nepotistic value.

in natal kin, for example, has arguably affected the evolution of the matrilateral bias by virtue of its average selective effects in the past, but there are also cues of variable opportunities for such nepotism that vary situationally and cross-culturally, to which prospective alloparents may respond flexibly.

Testable Hypotheses

The paternity uncertainty model (Model 1) assumes that allo-parents gain fitness only through effects on expected fitness of the children in whom they invest. Our expanded Model 2 adds potential inclusive fitness returns that alloparents might derive from raising the expected fitness of the children's mother, as well. Can these additional returns be credited with a major role in the evolution and expression of the matrilateral bias, over and above the effects of paternity uncertainty alone?

One reason for suspecting that the answer may be "yes" is provided by recent re-evaluations of the evidence on human cuckoldry rates. Contradicting earlier claims based largely on biased samples of paternity exclusion data, the best estimates are now on the order of 1–2% (67, 68), which suggests a lesser role for paternity uncertainty in the evolution and expression of large matrilateral biases in alloparenting than has previously been supposed.

How important are the elements that Model 2 adds to Model 1? This general question can be translated into a set of specific testable hypotheses:

Hypothesis 1: Having been the recipient of alloparental assistance has a positive effect on a woman's survival and future reproduction.

Hypothesis 2: Having been the recipient of alloparental assistance has a positive effect on a woman's chances of reproducing with a new partner after being widowed or divorced, yielding inclusive fitness benefits for matrilateral, but not for patrilateral, alloparents.

Hypothesis 3: Having been the recipient of alloparental assistance as a young mother has a positive effect on the beneficiary's investments in her natal family later in life.

Existing studies lend support to hypothesis 1 (e.g., ref. 69), but we are unaware of any evidence bearing directly on hypotheses 2 and 3. There is, however, evidence that mortality and divorce rates have been sufficiently high among hunter-gatherers that women often, perhaps typically, had two or more husbands before menopause (70–72), suggesting that the asymmetrical benefits to matrilateral versus patrilateral alloparents proposed by hypothesis 2 may be important. There is also evidence that maternal aunts sometimes make substantial investments in their nieces and nephews (72), suggesting that hypothesis 3 may also capture an important contributing factor to the matrilateral bias.

Strong tests of these hypotheses will typically require longitudinal data and valid measures of alloparental contributions; the negative association between PGM presence and child survival in several studies (13, 14) proves that indirect proxy measures of alloparenting are inadequate. These hypotheses should be tested in hunter-gatherers and other natural-fertility populations, where evolutionarily relevant contingencies between alloparenting and its fitness consequences are most likely to persist. To the degree that alloparenting and the matrilateral bias reflect flexible responses to cues of possible fitness returns, however, the three hypotheses may be predictive of behavior in modern low-fertility societies, too. The possibility of facultative response also suggests additional questions for future research. Is the matrilateral bias bigger where divorce and widowhood are more frequent? Does matrilateral alloparenting increase when the mother has collateral kin who may need help later, whereas patrilateral alloparenting does not and perhaps even declines? And how does the strength of kin recognition cues (73) affect the magnitude of the matrilateral bias?

In Model 2 we incorporated the effects of "load-lightening" on mothers, but not fathers, on the grounds that the former are everywhere the primary caretakers of children. However, fathers also provide childcare, and a more complete model (Model S1) incorporates effects on them, too, with the matrilateral bias then attributed to the effects of paternity uncertainty plus the difference between the effects of maternal and paternal NV gains on the two GMs. Such a model leads to further testable hypotheses, especially if we suppose that the matrilateral bias is flexible and facultative. For example, in societies in which fathers provide substantial childcare and alloparents demonstrably lighten their load, the matrilateral bias should be relatively small.

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