The expendable male hypothesis

Siobhán M. Mattison[1], Robert J. Quinlan[2], Darragh Hare[1]

[1]University of New Mexico, Department of Anthropology
[2]Washington State University, Department of Anthropology

Abstract: Matrilineal descent confers lineage membership via the female line. In matrilineal descent systems, men share lineage membership not with their own children, but with their sisters' children. The theoretically influential concept of the matrilineal puzzle posits that men experience tension between the desire to exert control over their natal kin (i.e., the lineage to which they belong) and over their affinal kin (i.e., their spouses and their biological children). The rationale for this puzzle rests on two fundamental assumptions: (i) that men are always in positions of authority over women; and (ii) that men are interested in the outcomes of parenting. In this paper, we suggest that the 'matrilineal puzzle' does not exist from an evolutionary perspective. Instead, we examine what ecological conditions might render men expendable within local kinship configurations - specifically when (i) women, without significant assistance from men, are capable of meeting the subsistence needs of their families; and (ii) men have little to gain from parental investment in children. We conclude that the expendable male hypothesis may explain the evolution of matrilineal descent in numerous cases, and by noting that female-centered approaches that call into doubt assumptions inherent to male-centered models of kinship are justified in evolutionary perspective.

Keywords: kinship; matrifocality; matriliny; gender; parental investment; mating systems

"…for some females there exist important advantages for male care ... For many females male parental care has small or negligible effects on female reproductive success, suggesting that as a general explanation for social monogamy, the Male Care is Essential Hypothesis is inadequate." – Gowaty 1996 [1]

1.0 Introduction.

Matriliny is common in both human [cf. 2] and non-human animals [3], yet is considered problematic in the former. The problem created by human matriliny is exclusive to males, who are said to invest more in their nieces and nephews than in their own children. Such avuncular investment violates a fundamental expectation based on Hamilton's rule [4] that, all else equal, altruism (investment in another individual at some short-term cost to oneself) should be directed toward more closely related kin. Several solutions have been proposed to what has been dubbed the 'matrilineal puzzle' [5], based on i) paternity certainty, ii) the differential impacts of resources on male versus female reproductive success (RS), and iii) other considerations affecting the benefits of avuncular support of sororal nieces and nephews. In this paper, we present the expendable male hypothesis, which questions fundamental ethnographic and evolutionary premises of the 'matrilineal puzzle'. We propose that well known principles defined by theories of parental investment and cooperative breeding can explain differential male investments in their own and others' children. Our fundamental claim – which must be empirically validated – is that it is seldom adaptive for males to invest in nieces and nephews to the detriment of their own biological children. Rather, a range of ecological, economic, and social factors result in female control of shared resources and poor returns to investment in pair-bonds.

We present our argument as follows. First, we provide a definition of matriliny that emphasizes cooperation among females. Next, we review the extensive animal literature on female philopatry, concluding that it offers limited insight into the evolution of matriliny given matriliny's ubiquity in mammals and consequent lack of detailed data on causes. We examine some cross-cultural trends in matriliny including "incipient" matriliny (i.e., "matrifocality") when cultural "ideals" otherwise prescribe patrilineal organization. We offer critical examination of dominant hypotheses for matriliny including the roles of paternity certainty and daughter-biased investment. These earlier models offer promising leads that we use to recast matriliny as the expendable male hypothesis, in which matriliny results from environments that favor female control of resources and limited male investment in offspring.

1.1 Defining matriliny

Matriliny is ambiguously defined [6,7], variously incorporating notions of genealogical descent, corporate descent ("lineality"), inheritance, post-marital residence ("locality"), and female-biased cooperative kinship networks. In non-human animals (hereafter, "animals"), relevant domains of kinship mostly overlap, but this is not always the case in humans. A major goal of

this article is to characterize the limitations of the matrilineal puzzle as an evolutionary problem; thus, we consider here domains of kinship that define matriliny across species. In particular, we define matriliny as a *system of behaviors that bias investment toward matrilineally related kin* [see also 8]. Our definition includes inheritance of resources, rank, title, or information and other forms of cooperation that are biased toward matrilineally related kin. The focus on observable behavior [9,10] separates our definition from more ambiguous metrics of matrilineality such as corporate descent, which arguably apply only to humans and, while affording greater opportunities for certain forms of cooperation among relatives, do not effectively militate against alternatives [e.g., 11]. Finally, our definition requires observation of *actual* behaviors as opposed to stated norms. Kinship behaviors frequently defy norms [12,13] and natural selection acts on behaviors – not norms – because different behaviors generate differential fitness outcomes.

2.0 Matriliny in Comparative Perspective.

2.1 Explanations of Matriliny in Animals

> "Female philopatry enhances the potential for cooperative relationships to arise through kin selection, and may thus facilitate the development of social bonds and the formation of social groups." – Silk 2007:540 [14]

Matriliny as defined above is common among gregarious animals. For example, ongoing affiliative relationships or territorial overlap among female kin arise in cetaceans, canids, ungulates, in the primates, birds, and rodents. Matrilineal behavior varies considerably across these species, however. Matrilineal killer whales (*Orcinus orca*) transmit cultural information with high fidelity through natalocal matrilines [15]. An adult cheetah (*Acinonyx jubatus*) female ceases to interact with her mother while continuing to reside on (i.e., inheriting) her mother's territory [16]. Diverse matrilineal species, from farm cats (*Felis catus*) [17], to lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) [18], to African elephants (*Loxodonta africana*) [19], engage in communal suckling, whereby lactating females feed related and unrelated young. These different expressions of matriliny suggest that the costs and benefits of matrilineal sociality are variable in animals and warrant empirical and theoretical attention [see also 20].

Yet the causes of matriliny, per se, have been little explored in ethology. Rather, causes must be inferred from arguments concerning the factors selecting for female philopatry, on the one hand, and the benefits of sociality, on the other. For example, an influential model of primate sociality [21] posits that female philopatry and nepotistic relationships allow co-resident females to better defend patchily distributed resources, whereas female dispersal is favored when resources are more evenly distributed. This socioecological model has been extended to other mammals [22] and to incorporate additional ecological factors selecting for or against sex-biased philopatry and sociality (e.g., predation, inbreeding, pathogen exposure) [23,24]. In all cases, strong biases in favor of female philopatry and nepotistic relationships among females are attributed fundamentally to the inclusive fitness benefits derived from living with kin [14].

Why such benefits are discussed in relation to *female* sociality isn't made explicit in these arguments, but may are likely derived from the expectation that female decisions in mammals are predicated fundamentally on the distribution of resources whereas male decisions center on the distribution of females [22].

By defaulting to a female perspective, such causal arguments potentially conflate female philopatry with nepotistic relationships among philopatric females. In particular, it is not clear in these explanations whether the proposed causal factors – resource distribution, inbreeding avoidance, etc. – favor female philopatry, nepotistic female cooperation, or nepotistic female cooperation *given* female philopatry. Moreover, costs and benefits of philopatry and dispersal extend to both males and females, so it is unclear why these explanations focus exclusively on females. We suspect that this may be motivated by the widespread nature of female philopatry among mammals [25,26], which may render matriliny relatively 'uninteresting' to explain. A bipartite theory that builds matriliny from first principles – i.e., that considers the factors favoring female (or natal) philopatry as well as female sociality – would provide clarity, even if such an endeavor may not be simple. There remains little consensus as to which factors (e.g., predation, inbreeding) favor male- versus female-biased dispersal [27,28]. Moreover, female philopatry and nepotistic relationships may be mutually reinforcing, creating a chicken and egg problem when considering how these features evolve as an integrated social system (i.e., as matriliny).

Suffice to say that female-biased philopatry is neither necessary nor sufficient to cause matrilineal social organization. Numerous animals are female-philopatric and not necessarily matrilineal, for example mountain lions (*Puma concolor* [29]) and wolverines (*Gulo gulo* [30]). Moreover, matrilineal social organization is seen in species favoring different dispersal patterns. Natal philopatry (aka natalocality, in humans) also provides opportunities for female kin to continue affiliative associations [6,26,31] and matriliny has been reported in natal philopatric species, including canids, felids, viverrids, hyanids, and cetaceans. Even female-biased dispersal does not prevent matrifocal kinship behaviors. For example, although male-biased dispersal is more common in non-human primates, related females often emigrate together to nearby populations or otherwise build female-centered affiliative alliances within new groups [32]. Finally, rates of dispersal vary considerably within systems of sex-biased dispersal [22,27], affording the opportunity for building and maintaining matrilineal alliances, even in species where such alliances are not normative [32].

We propose that a broad theory of matriliny must consider the consequences of decision-making among both males and females, within specific socio-ecological contexts, involving when to cooperate, with whom, and in what ways. We build upon insights from ethology to consider costs and benefits of allocare to different care providers in relation to different recipients [3] in different socio-ecological environments [33]. Because much of the controversy in human studies of matriliny surrounds the relative costs and benefits of avuncular versus paternal support of juveniles (see 2.2, "Explanations of Matriliny in Humans"), we note here

limited scholarship investigating avuncular investment in nieces and nephews in animals. The absence of such scholarship would be easy to chalk up to dispersal patterns if a single sex reliably dispersed prior to maturity, but both natal philopatry [26] and delayed dispersal [34] open the scope for avuncular investment in nieces and nephews in animals. Indeed, in a number of well described matrilineal species, adult males have been reported to provide allocare. Yet, while common, male allocare seems to be restricted to care of siblings or to their own putative offspring [35]. Even the male-female "friendships" that have been associated with non-paternal care of offspring in some primates may provide benefits to males through accruing status or access to mates [e.g., 36–38]. In short, whereas avuncular support of nieces and nephews is widely reported in human societies, we were not able to find clear comparisons in mammalian societies, matrilineal or otherwise.

We also note a striking difference between animal and human perspectives on matriliny, which involves the extent to which matriliny is viewed as problematic versus neutral or beneficial. In particular, the vast majority of ethnographic and evolutionary scholarship views human matriliny as problematic, particularly regarding men's investment in sisters' children rather than in their own. By contrast, much of the animal literature treats matriliny neutrally or describes benefits made possible by stable matrilineal structures. Such benefits include female longevity and accumulated ecological knowledge [39,40], cumulative culture [e.g., 15], infant survivorship [41], and even decreased aggression [26,see also 6]. Matriliny is not sufficient on its own to generate such benefits, yet the stability provided by female-centered kinship may be more likely to generate the conditions to reap the benefits of longevity than more unstable structures associated with looser kinship generated by bonds among patri-kin [42]. The multi-generational structure apparent in some mammalian matrilineal species may also facilitate cumulative cultural complexity. Indeed, eusociality is present only in matrilineal societies (e.g., eusocial insects and naked mole-rats (*Heterocephalus glaber*)); cooperation is so complete in these species that they have been dubbed "superorganisms" to reflect the shared goals of individual members [43].

2.2 Explanations of Matriliny in Humans

Female-biased kinship is considered rare in human societies: the Standard Cross-Cultural Sample reports matriliny as the institutional mode of descent in just 17% of societies and uxorilocal residence constitutes only 16% of the societies surveyed in the Worldwide Ethnographic Atlas [44]. The extent of overlap between matrilocal residence and matrilineal descent is considerable: 70% of matrilineal societies are also uxorilocal (see Surowiec and Creanza, this issue). These statistics belie the complex expression of matrilineal behavior, however. For example, matrilineal inheritance does not proceed via a single route of transmission: resources may be inherited directly from mother (or parents) to daughters, as among the matrilineal Chewa of Africa [45] or, as among 8-9% of cases in the Standard Cross-Cultural Sample, from maternal uncle (MB) to sororal nephew (ZS) [8]. Cooperation among kin

related through females is also much more extensive than the above would suggest. Viri- and neo-locality do not preclude investment in children by matrilateral kin in WEIRD (Western, Educated, Industrialized, Rich, and Democratic) [46,47] or small-scale societies [48]. Indeed, many societies default to matrifocal social organization even under strong norms of patriliny [e.g., 49].

It is therefore surprising that while matriliny is considered evolutionarily neutral or beneficial (maybe even unremarkable) in animal ethological circles, it is widely considered problematic in studies of humans. Dubbed the 'matrilineal puzzle' by Audrey Richards [5], the problem surrounds the allocation of male authority, which is officially granted to men over their natal households (i.e., because they fill the important role of MB), but simultaneously exerted by a man over his spouse and children. This problem does not affect male authority in patrilineal kinship systems, because men's authority over their natal kin, spouse, and children overlap as in-marrying women are incorporated into their husband's patrilineage (an in-marrying man is socially inferior to his wife's brother and not ordinarily considered part of his wife's lineage following marriage in matrilineal systems). Even for evolutionary scholars, human matriliny is often considered puzzling: if ethnographic reports are accurate, then uncles may be misallocating investments in their nieces and nephews [50], who are only half as related to a man as are the man's biological children. Such a pattern of investment defies the logic of Hamilton's rule, which predicts, all else being equal, greater investment in more closely related kin [4].

To the extent that evolutionary anthropologists agree that matriliny is puzzling, attempts to 'solve' the puzzle have invoked three main considerations: i) the effects of paternity certainty on the allocation of male parental investment; ii) sex-based differences in the rate at which resources are translated into reproductive success; and iii) other considerations affecting the benefits of avuncular support of sororal nieces and nephews. We describe each of the proposed solutions, in turn, before recasting the matrilineal puzzle in light of the expendable male hypothesis.

Paternity uncertainty represents the oldest and most common explanation of matrilineal inheritance and cooperative behavior. Alexander [51] was the first evolutionary anthropologist to describe what is, in fact, 'one of the oldest hypotheses in social science' [52] in evolutionary terms. The adage, "Mommy's baby; Daddy's, maybe" captures the source of a fundamental difference between male and female reproduction in mammals: for mammalian females, genetic parentage is virtually assured, whereas there is nearly always room to doubt a male's parentage. The paternity certainty hypothesis posits that, if a male's parentage is very insecure, he may do better in terms of inclusive fitness to invest in his matrilateral nieces and nephews, to whom genetic relatedness is assured [8,51,53–57]. The level of uncertainty necessary to produce the conditions under which men are more related to their nieces and nephews (i.e., the 'paternity threshold' [55,57]) ranges from a probability of paternity (P) of 0.268 [55] to 0.33 [53,56] in the short-term, to 0.46 if the compounding geometric effects of paternity on

217 relatedness over several generations are considered [52], to an upper bound of 0.5 if
218 assumptions about the nature of cuckoldry are relaxed [57]. Such levels are almost certainly
219 unrealistically low [12,45,50,57], all falling well below published estimates of paternity in
220 human societies [58,59]. Finally, the paternity uncertainty hypothesis, if correct, would require
221 its own explanation accounting for the socioecological factors leading to multiple mating in
222 females [60]. In contrast, as described below, the expendable male hypothesis suggests that
223 low paternity certainty is acceptable to men and women in matrilineal systems because the
224 socio-ecologies that produce matriliny do not require significant male support of offspring.

225 A second class of explanations incorporates the differential impact of subsistence on male
226 versus female RS. Following the logic of the Trivers-Willard hypothesis [61], the matriliny-as-
227 daughter-biased investment hypothesis [45] posits that parents should direct wealth toward
228 the sex that is most capable of translating wealth into reproductive success. Because female RS
229 has a lower ceiling compared to male RS and because RS is typically more variable in males than
230 in females [62,but see 63], the slope of the RS-wealth relationship is often steeper for males
231 (Figure 1A [64]). Although each unit of investment yields higher marginal returns via male
232 offspring under this scenario [65], parents who are of low socio-economic status and whose
233 sons are likely to fail to reproduce gain absolutely more from investing in daughters [e.g.,
234 64,see also 66]. Many forms of wealth are thought to result in steeper fitness gains through
235 males [67] – both livestock and productive land are usually more beneficial to males than
236 females, for example, because males are able to use such resources to attract additional mates
237 [45,50,68]. However, some resources may not be particularly conducive to steep gains in
238 reproductive success in either sex; in which case, the hypothesis says, paternity uncertainty in
239 sons' offspring renders it beneficial to invest in daughters (Figure 1b).

240 Although two studies of matriliny have described results that support the MDBI hypothesis
241 [45,50] and numerous other findings are consistent with subsistence being crucial to the
242 evolution of sex-biased kinship , by focusing on vertical transmission between parents and
243 their children, the MDBI hypothesis in fact fails to solve the most vexing problem in the
244 evolution of matrilineal kinship – i.e., avuncular investment in sororal nieces and nephews [50].
245 More recent hypotheses have modeled the 'father versus uncle' problem directly, incorporating
246 paternity certainty, the effects of subsistence on inheritance, and additional considerations,
247 such as the effects of polygyny and polyandry [8] and the number of communally breeding
248 sisters in a man's natal household [31], to describe additional benefits that males might accrue
249 through avuncular investments in sororal nieces and nephews. A final model [72] is the first
250 model in recent years to propose a solution to the puzzle that does not invoke paternity
251 certainty; rather, it focuses on the how the functional form (diminishing versus linear) linking
252 yield to labor affects the returns associated with investing in nieces and nephews over one's
253 own children. In what follows, we describe a fourth 'solution' that proposes that, at least in
254 some instances, the matrilineal puzzle is an ethnographic artifact and that men's investments in
255 children follow straightforward evolutionary predictions based on parental investment and
256 cooperative breeding theories.

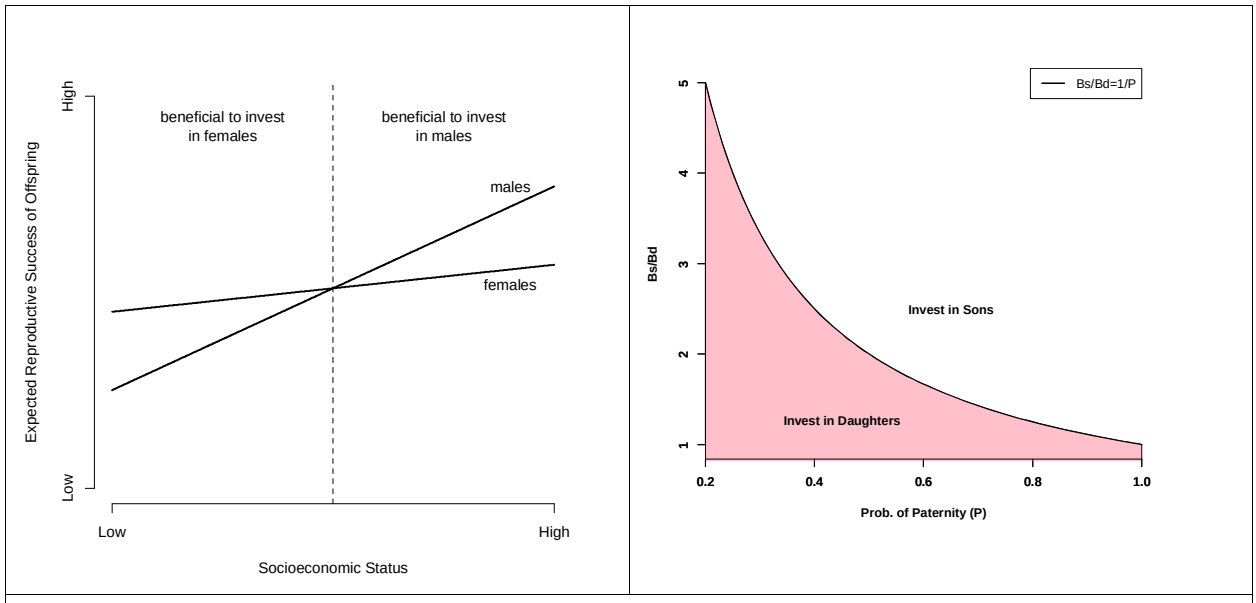

Figure 1. Investments in daughters versus sons. A. Trivers-Willard. The fitness ceiling is lower for females than for males. According to the Trivers-Willard hypothesis, under certain circumstances, this leads to steeper marginal gains to fitness from resources to males. In such cases, poorly resourced parents may benefit from investing in daughters whereas richly resourced parents may benefit from investing in sons (redrawn from [64]). **B. Matriliny as daughter-biased investment (MDBI)**. The MDBI hypothesis incorporates the differential effects of resources on male and female fitness shown in A and the effect of paternity certainty to predict when parents will invest in daughters (matriliny) versus sons (patriliny). The area in pink shows that parents will invest in daughters whenever the additional benefit of investing in sons does not compensate for risk of non-paternity in sons' offspring (redrawn from [50] based on [45]).

3.0 Problematic Assumptions of the Matrilineal Puzzle

The matrilineal puzzle relies on two assumptions that, if nullified, invalidate the basis of the puzzle: first, that men are always in positions of authority over women; and second, that men are interested in the outcomes of parenting. For behavioral ecologists, the problem surrounds avuncular investment in sororal nieces and nephews – transmission of resources (e.g., inheritance) from mother's brother (MB) to sister's son (ZS), without theoretical gymnastics to solve issues surrounding paternity certainty, contradicts the key expectation that a man should invest in more closely related kin. We tackle each of these issues in turn.

3.1 Male Authority

Ethnographic material on matrilineal societies suggests that ties of affiliation through females (e.g., 'suckled at the same breast') and limited involvement of fathers is often normative [5,e.g., 73–75]. Although one might expect this to render men's roles somewhat peripheral, extant literature suggests instead that men wield authority not as fathers, but as mother's brothers.

Among the matrilineal Bantu societies, for example, "…authority passes to the dead man's brothers or to his sisters' sons, or to the sons of his maternal nieces." [5] and "…in most societies authority over households, or a group of households, is usually in the hands of men, not women, as are most of the important political offices" [5]. Flinn (1981) documented a number of compatible examples, including the mother's brother acting as head of household among the Djuka (citing Kahn 1931), wealth and social position being inherited from maternal uncle to nephew among the Trobrianders (citing Malinowski 1961), and the mother's brother holding the greatest obligation to provide support and assistance to children among the Plateau Tonga (citing Colson 1961).

Some ethnographers have questioned the premise that male authority is universal or at least that it is universally applied in all domains of kinship in matrilineal systems [76–78]. Moreover, even in extended family avunculate households, norms stipulate that only one brother of the sibling set act as household head, leaving most men in subordinate positions within households. Furthermore, as behavioral ecologists, it behooves us to ask whether a normative emphasis on male authority plays out in actual patterns of behavior and, perhaps more crucially, what *variation* in behavior tells us about how the *distribution* of 'authority' reflects sex biases in cooperation. We contend that, at least in some cases, male authority is nominal rather than real and that the ethnographic and normative emphases on male authority overlook a more stable and central importance of females to provisioning and childrearing [see also 79]. For example, Mattison [50] argued that the nominal transmission of resources from MB to ZS among the matrilineal Mosuo obscures de facto transmission down the female line; men's authority over such resources amounts to usufruct access to land and household resources during their lifetime. The Mosuo also reveal significant heterogeneity in who claims to be household head (户主): male household heads accounted for only ~25 per cent of households residing in areas adhering to a more 'traditional' matrilineal lifeway [11]. Moreover, the phrasing of questions in her study had a significant impact on whether male or female authority was emphasized; when Mattison asked who *generally* was the most important decision-maker in a household, the answer was nearly always the mother's brother; when she asked who was most important in a person's *own* household, answers varied, but females were commonly listed as heads of house. This underscores that even very careful ethnographic reports of normative behavior may overstate the importance of a general norm.

For comparison, in Caribbean communities, norms or cultural models invariably emphasize male-headed households and patrilineal inheritance, when actual household organization is often strongly female-centered. Women (even married women) exert substantial control over household resources, and inheritance is highly variable [80–84]. Men can and do head households and control family resources in some Caribbean families; however, greater gender-specific risks for Caribbean men can make many men unattractive as mates with potentially poor returns on women's investment in conjugal relationships [49]. Hence, by our definition, Caribbean matrifocality is a form of latent or "incipient" matriliny that suggests the likelihood of

the *prevalence* of matrilineal behavior in numerous societies nominally adhering to conflicting kinship norms [see also 85]. The Caribbean case further highlights the difficulty of using cultural "traits" (such as patrilineal descent) as the basis of cross-cultural comparison in the study matriliny [e.g., 86]. The behavioral ecological focus on actual behavior provides a means of understanding the evolutionary costs and benefits of female-centered kinship at higher resolution than does reliance on "ideal culture," often the focus of classic ethnography and cross-cultural work. Although norms and institutions may be products of selection and constrain individual decision-making [87], including kinship behavior [52,57], we focus on actual patterns of investment as a more tractable and surprisingly under-studied component of the matrilineal puzzle.

3.2 Male Investment

Whereas the majority of evolutionary work on matriliny takes for granted that men invest significantly in their sororal nieces and nephews, we propose that many men in matrilineal and matrifocal societies may have little interest in childrearing and provide correspondingly low investments therein, negating this second premise of the matrilineal puzzle. Relative to most mammals, male provisioning of offspring in humans is extensive [e.g., 88]. Male provisioning is correspondingly central to a number of influential theories explaining the evolution of human adaptive complex, which posit that large brains, lengthy juvenile dependence, and nuclear families were made possible and resulted from hunted meat being provided by males to sexually exclusive female partners and their children [summarized in 89]. The observation that men frequently invest in children should obviously not imply that they always do so [e.g., 90,91], yet it seems that there has been an uncritical acceptance of this premise in defining the matrilineal puzzle in evolutionary terms. A quote from Hartung [52] illustrates the problem. In setting up the premise for the matrilineal puzzle, he writes: "Relative to most male mammals, human males give their offspring an exceptional amount of parental investment (Trivers 1972). Accordingly, husbands risk investing a significant component of reproductive success in other men's children if wives engage in extramarital sex." Alexander's [53] solution to the matrilineal puzzle also focuses on misallocated male investment: "…lowered confidence of paternity causes a man's sister's offspring to assume increased importance **as recipients of nepotistic benefits**…" (emphasis added).

Yet, what if sometimes males in matrilineal kinship systems act like drones in honey bee colonies? That is to say, what if the ethnography does not line up with actual behavior [12] and men are, in fact, doing relatively little to contribute to the welfare of their biological offspring or to that of their sororal nieces and nephews? The association between matriliny and protracted male absences (e.g., due to fishing [70], warfare [e.g., 92], or historical involvement in major trade routes [93]) means that men are frequently not in a position to invest directly into their households, natal or affinal. Mattison's ethnographic work among the matrilineal Mosuo concurs with prior descriptions of this population as one with a significant imbalance in female and male workload. In particular, although men engage in occasional heavy labor and

obligations related to ritual and political office, women do the vast majority of day-to-day work, including planting, harvesting, and childcare, and also serve as village heads and in other governmental and non-governmental positions [94,95]. Indeed, the limited systematic evidence that we are aware of that addresses workload using behavioral observations is consistent with a lopsided sexual division of labor: Wu et al. [31] report lower levels of observed farming behavior by Mosuo males than by Mosuo females and by Han (majority, patrilineal Chinese) males. He et al. report that "Mosuo males are allowed to reside with their mothers and sisters, who feed them while they do relatively low levels of household domestic or agricultural labor" [96]. Similarly, unmarried men in matrifocal Dominica spend about 17% of their daylight time working (manual labor and childcare) compared with 25% for married men, 50% for women, and 26% for girls 11 to 15 years old [97]. All of this evidence points to the need to verify empirically the contributions that men make to their natal and affinal households – if male authority and investment in the natal household is limited, then the basis for the matrilineal puzzle is invalidated and we must ask different questions about men's involvement in household economics.

4.0 The Expendable Male Hypothesis

> "…most students of the evolution of mating systems experienced a strong intuitive commitment to the idea that females were handicapped without male help." (Gowaty 1996: 488)

> "…the males [of multi-male, multi-female primate societies] have apparently evolved to maximize matings, accepting a low confidence of paternity and showing less parental care than in other social groups" (Alexander 1974: 331)

Based on the foregoing discussion, the expendable male hypothesis posits as its fundamental premises that the matrilineal puzzle: (i) does not exist; (ii) that males do not decide whether to invest in nieces or nephews *or* in their own biological children; (iii) rather, males *either* invest little in parenting on the whole *or* they invest more intensely in their own biological children, when paternity is more certain; and (iv) that male investments in natal kin may be motivated less by genetic relatedness and more by (a) other benefits reaped through cooperation (e.g., reciprocity), or (b) constraints that promote cooperative breeding among natal kin (e.g., 'helpers at the nest'/ecological constraints). Finally, (v) matriliny prevails in environments in which women's efforts are sufficient to meet their families' needs. Therefore, in some environments, women's investment in conjugal families may present unacceptable returns if ecologically expensive men [98,99] put household welfare at risk [100].

Many aspects of matrilineal and matrifocal kinship may disincentivize paternal investment in biological offspring. Male parental investment is likely when a) paternity is more certain, b) opportunity costs of care are low, and c) paternal investment enhances offspring fitness [88,101–103]. It has already been established that paternity certainty may be low for many males in matrilineal systems, whether due to protracted absences (e.g., warfare), residence

387 systems such as natal philopatry that prevent effective mate guarding [cf. 104], etc. Another
388 perspective on paternity is that, in the absence of strong investments into offspring, men may
389 have little *interest* in whether paternity is assured. Ecologies [45,70] and institutions [12,49,52]
390 that limit or decrease the impact of men's investments on offspring fitness are as likely to lead
391 to low paternity certainty as the other way around [see 105]. Mating markets are undoubtedly
392 broader in such contexts, as women balance the benefits of multiple mating against fidelity [60]
393 and men pursue mating opportunities that face little competition from parental responsibilities.
394 We do not wish to imply that matriliny entirely precludes paternal investment – we have shown
395 previously that in one economically transitional matrilineal context, fathers play important roles
396 [101] – rather, we contend that direct investment in childcare by males is often limited due to
397 constraints that make such investments less beneficial than other behavioral strategies.

398 Consistent with this view are observations that when men have control over resources or make
399 significant investments in childcare, such resources are used *not* to benefit their natal kin, but
400 to advance their own reproductive agendas. Ethnographers have noted the tendencies of
401 matrilineal men to invest in their biological children. In the Trobriand Islanders, for example,
402 Malinowski noted a 'strong tendency of surreptitious patrilineal transmission of property and
403 influence' [cited in 12]. Among the Nayar, who, like the Mosuo, were famous for a near-
404 complete absence of fathers and husbands, Gough reported that 'a man is said to have been
405 especially fond of a child whom he knew with reasonable certainty to be his own' [Gough
406 1961a:364, cited in 12]. Richards [5] observed that 'in many matrilineal societies, a man
407 typically must give his heritable possessions such as land to his sister's children but is more
408 likely to be involved in the day-to-day care of his putative offspring and that "men of wealth
409 and distinction are able to reverse the usual rules of residence". Pre-Communist Mosuo also
410 illustrate this tendency: against a backdrop of middle- and lower-class matrilineal
411 horticulturalists, upper-class families investing significant resources in their wives and children
412 were patrilineal [93,106]. We are aware of limited quantitative evidence addressing men's
413 investments in nieces and nephews versus to their spousal households, but note that Wu and
414 colleagues' [31] results reveal that even unmarried Mosuo men invest almost as much labor in
415 their spousal households as in their natal households and that married Mosuo men were more
416 likely to be observed working on any farm than unmarried men. We suspect that this may be
417 due to increasing demands on men's labor by their affinal households [11,96,105].

418 But why do men labor in their natal households at all? What do they do for their natal
419 households? If women's returns on investment in relationships with men are highly variable,
420 and if the gendered division of labor requires any male input, then investment in male kin
421 (brothers and uncles) could yield a higher inclusive fitness return than investment in a conjugal
422 union. Men also provide an inclusive fitness benefit to the natal household that is unrelated to
423 labor: mating. Ruth Mace's research group has argued extensively that reproductive conflict
424 underlies patterns of cooperation among the Mosuo [31,96,107,108] and have pointed to the
425 benefits of male mating within this context, speculating that "mothers may help adult sons stay
426 in the natal household to enable them to mate more freely and/or do relatively less work than

427 if they moved into their wife's household." [96]. In this view, matrilineal men assume roles that
428 are analogous to the drone in honey bee society, providing relatively little in the way of labor,
429 but delivering significant benefits if successful on the mating market.

430 But surely, matrilineal men are less idle than honey bee drones? Undoubtedly, male effort
431 varies over the lifespan and lies on a spectrum from very little to very great [109]. Indeed,
432 although we have seen many an idle man in our respective field sites, we have also observed
433 men being quite helpful, including within their natal households [see also 31,101]. Even
434 unmarried rural Caribbean men, who spend significantly less time working than do married
435 men or even their pre-adolescent nieces, periodically take on extremely energy-intensive tasks
436 requiring considerable upper body strength, such as forest clearing, which can be a substantial
437 benefit to the natal household. Alexander [53] long ago proposed a number of other under-
438 appreciated factors motivating avuncular investments in nieces and nephews: the net benefit of
439 investment in nieces and nephews increases "if the males involved are: (1) young and childless
440 brothers, (2) brothers estranged from other wives, (3) unusually wealthy or powerful brothers,
441 or (4) brothers who are for other reasons unlikely to be successful with their own offspring".
442 We would add to this that male effort in their natal households need not relate directly to allo-
443 care of sisters' children to be beneficial – men may, for example, be underwriting the costs of
444 their own subsistence in the household [3,110] or providing labor in return for reciprocal
445 benefits delivered from other members of the household. Thus, although we may need to seek
446 explanations that venture beyond kin selection and paternity certainty to understand the
447 variation in male investments [49,111], we may not require new explanations to solve a puzzle
448 that does not exist.

449 As a final point of the expendable male hypothesis, we argue that the variability in male
450 investments in their natal and affinal households in matrifocal societies is made possible by a
451 labor force that largely consists of female kin [79]. This labor force provides a sufficient basis for
452 subsistence and supports the development of male and female descendants. Furthermore, the
453 ability of women to provide the resources necessary to support their descendants
454 disincentivizes additional male investment because it decreases offspring sensitivity to paternal
455 investments in children [see 'The Female Competence Hypothesis' in 1]. This argument
456 reignites the idea that the relative contributions of men versus women to subsistence plays a
457 role in determining whether kinship systems are female- or male-biased [12,69,112–114] by
458 considering how female contributions to subsistence impact male motivations to provide
459 additional care [1,115]. Significant support from affinal men is helpful in certain contexts (e.g.,
460 when children become very expensive to rear)[116], but is not necessary to meet basic
461 subsistence needs in matrifocal contexts [cf. 117]. Rather, as male support becomes useful,
462 kinship systems are anticipated to transition toward patrilineal (if assistance from kin is
463 required) or nuclear (if households are self-sufficient) [11,105] as "the more potential parental
464 effort (i.e., altruism, e.g., heritable possessions and paternal care …) a male has, the more
465 adaptive it is for him to establish high confidence of paternity and dispense benefits to his own
466 offspring" [12].

5.0 Summary and Conclusion

We offer an initial articulation of the expendable male hypothesis and propose that this hypothesis can circumvent the long-standing matrilineal puzzle by denying that it is a puzzle at all and proposing instead that matriliny can evolve and remain stable in particular social and ecological circumstances. The expendable male hypothesis predicts that males *either* invest little in their natal households to offset costs of belonging to a household, *or* they invest significantly in children to whom paternity is reasonably assured and whose wellbeing they can significantly improve (e.g., when male investments appreciably enhance female care). It also predicts that males *do not invest significantly in nieces/nephews* at the expense of investing in their own children. We argue further that established evolutionary theories of parental investment, cooperative breeding, and kin selection can explain variability in human male investments. The expendable male hypothesis therefore connects human matriliny to matriliny in other gregarious mammals, among whom male help is context-dependent, and almost never primarily focused on avuncular support of nieces and nephews. In these species, ecological constraints can render male investment in their own offspring either not possible or not useful, so selection favors investment in natal kin. We welcome theoretical refinement as well as empirical tests of the expendable male hypothesis to help uncover the social and ecological conditions that favor matriliny within and across animal societies.

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