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SUPPLEMENTARY MATERIALS

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HUMAN BEHAVIOR

Sex equality can explain the unique social structure of hunter-gatherer bands

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The social organization of mobile hunter-gatherers has several derived features, including low within-camp relatedness and fluid meta-groups. Although these features have been proposed to have provided the selective context for the evolution of human hypercooperation and cumulative culture, how such a distinctive social system may have emerged remains unclear. We present an agent-based model suggesting that, even if all individuals in a community seek to live with as many kin as possible, within-camp relatedness is reduced if men and women have equal influence in selecting camp members. Our model closely approximates observed patterns of co-residence among Agta and Mbendjele BaYaka hunter-gatherers. Our results suggest that pair-bonding and increased sex egalitarianism in human evolutionary history may have had a transformative effect on human social organization.

Contemporary mobile hunter-gatherers cooperate extensively with unrelated individuals across multiple social and economic domains. Many communities of mobile hunter-gatherers (hereafter hunter-gatherers) share food extensively within camp and hunt, gather, and fish cooperatively (1). Alloparenting is also commonplace (2, 3). The importance of cooperative activities is reflected in many hunter-gatherer societies by a pervasive ethic of egalitarianism (4, 5). Like a number of nonhuman primate species, humans live in multimale, multifemale groups (6). However, we maintain enduring pair bonds, resulting in what have been described as “multifamily” groups (7). In addition, and in contrast to the bounded and territorial groups of chimpanzees (8, 9), bonobos (10), and gorillas (11), contemporary hunter-gatherers have fluid social networks where family units are relatively autonomous, with couples and their children moving often between bands (12), living with kin of either the husband or the wife. This residence pattern has been described as either “bilocal” or “multilocal” (13).

As well as being highly mobile, contemporary hunter-gatherer camps include a significant proportion of unrelated individuals (14) and are less closely related than groups of non-foraging small-scale societies (15). Given the inclusive fitness benefits of living with kin, why hunter-gatherers live with unrelated individuals is a puzzle, even more so if one considers that hunter-gatherers show a preference for living with siblings (13) and preferentially include kin in their campmate choices and social networks (16). Therefore, the mechanisms by which contemporary hunter-gatherers attempt to maximize co-residence and cooperation with kin, but nonetheless end up residing mostly with unrelated individuals, remain unclear.

Here, we offer a solution for this apparent paradox by demonstrating that, even where all individuals are actively assorting with kin, within-group relatedness is reduced if both sexes have influence over camp composition, as is the case among egalitarian, multilocal hunter-gatherers. We present a simulation of camp assortment where individuals attempt to reside with as many kin as possible under two conditions. In the egalitarian condition, men and women have equal influence on camp composition, whereas in the non-egalitarian condition, only one sex has influence. We compared the results with previously unpublished data from two hunter-gatherer groups, the Palanan Agta ($N = 4055$ dyads) and Mbendjele BaYaka (5) ($N = 1863$ dyads), as well as one farming population, the Paranan ($N = 1049$ dyads). We demonstrate that low within-camp relatedness emerges naturally from men and women seeking to maximize the presence of related kin. In contrast, in societies where decision-making on co-residence rests on one sex only, as in the case of patrilocal farmers, low relatedness does not emerge. Our model offers a mechanism that reconciles individual-level preferences for kin with reduced camp-level relatedness. Assuming that extant hunter-gatherers live in social structures resembling the ones existing in past hominins, our model explains how the shift from an ancestral hierarchical, female-dispersal system to a multilocal, egalitarian one would provide the selective context for expanded social networks, cumulative culture, and cooperation among unrelated individuals.

Among the Agta, we collected data from 191 adults across 11 camps, coding a total of 4055 dyadic relationships. Among the Mbendjele, we collected data from 103 adults across nine camps, totaling 1863 dyadic relationships. Mean experienced camp size was 18.09 adults ($SD = 8.62$) for the Mbendjele and 21.23 adults ($SD = 8.61$) for the Agta. Both populations were multilocal, with

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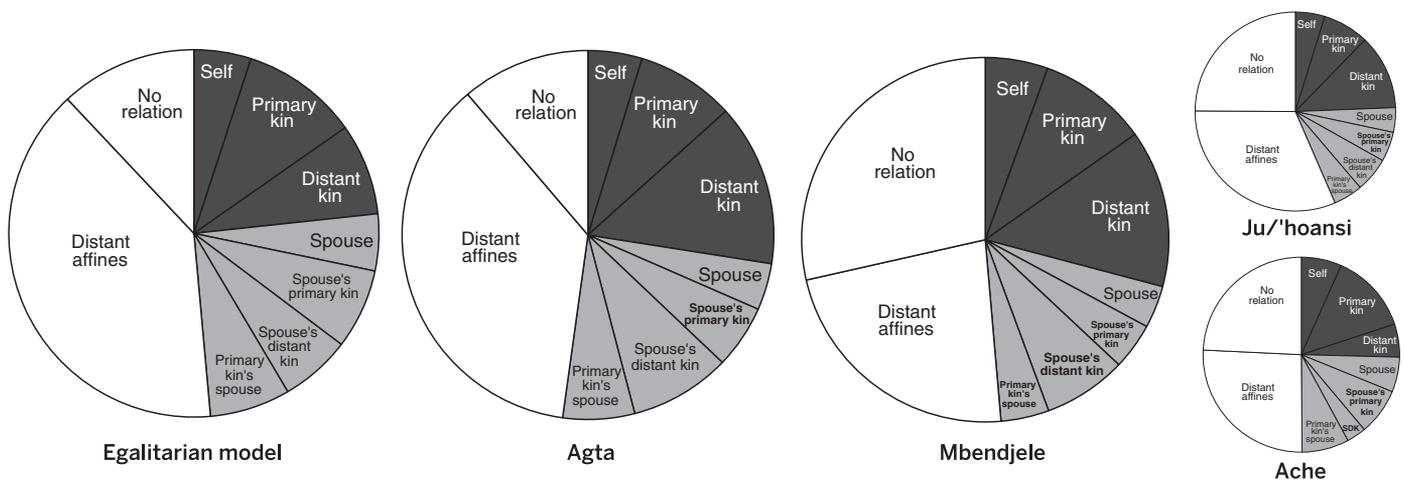


Fig. 1. Co-residence patterns across modeled and observed egalitarian populations. Chart area represents the proportion of all dyads across nine categories of relatedness for the egalitarian model (left), Agta (middle left), Mbendjele (middle right), Ache (bottom right), and Ju/'hoansi (top right). Ache and Ju/'hoansi data redrawn from Hill *et al.* (2011).

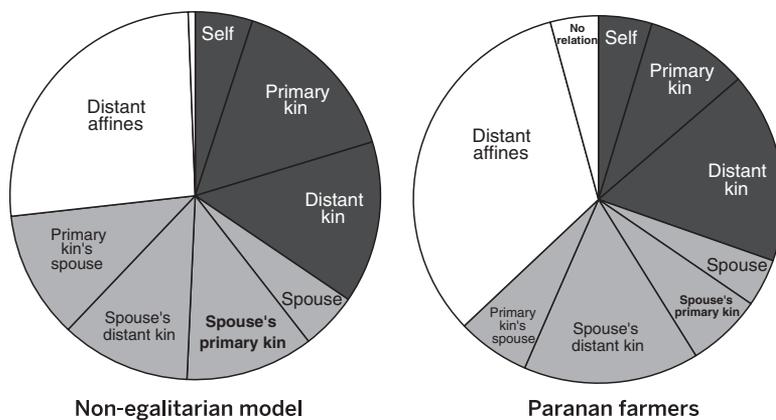


Fig. 2. Co-residence patterns across modeled and observed non-egalitarian populations. Chart area represents the proportion of all dyads across nine categories of relatedness for the non-egalitarian model (left) and Paranan (right).

husbands and wives living with similar numbers of consanguineal (genetic) kin (table S1 and fig. S1). In both groups, around 25% of dyads represented consanguineal kin, 25% were close affinal kin, and around 50% of dyads were distant affinal kin or unrelated individuals (Fig. 1 and table S2). These results are similar to those reported for the Ache and Ju/'hoansi by Hill and colleagues (14) (see Fig. 1).

In contrast to the unbiased residence patterns of the Agta and Mbendjele, Paranan farmers ($n = 49$ adults, 1049 dyads) demonstrate a significant male bias in residence, with men living with a larger number of primary kin ($n = 23$, mean = 2.65, SD = 2.29) than women ($n = 26$, mean = 1.27, SD = 2.05; $P = 0.031$). Despite having a comparable group size of 21.4 adults (SD = 9.30), the Paranan live with fewer unrelated individuals than the hunter-gatherers (4.2% versus 16.7%) ($\chi^2 = 108.93$, $P < 0.001$) (Fig. 2).

Although it is possible that low within-camp relatedness could result from random dispersal, with households moving randomly between camps

and living with related individuals only by chance, our results do not suggest that this is the case. Rather, the observed frequency of primary kin co-residence was significantly higher than would be expected if individuals assorted randomly across camps (Mbendjele, $\chi^2 = 451.62$, $P < 0.001$; Agta, $\chi^2 = 982.00$, $P < 0.001$). Thus, hunter-gatherer co-residence patterns are notable not only in their low-relatedness but because this low relatedness occurs despite the positive assortment of kin.

We developed a model to understand how hunter-gatherers come to co-reside with a large number of unrelated individuals at the group level, despite a preference toward living with kin at the individual level. We ran two versions of the model: one egalitarian, where both husband and wife have equal influence over where their household resides, and a non-egalitarian one, where only one sex has influence. Even at relatively small population sizes, these two conditions result in large differences in group composition. Across 100 simulations at a population size of 20, for example, there was a significantly larger

proportion of unrelated dyads in the modeled egalitarian camps ($12.0\% \pm 8.4$ SD) compared with the non-egalitarian, single-sex dispersal camps ($0.6\% \pm 1.5$) ($\chi^2 = 4372.36$, $P < 0.001$; Figs. 1 and 2). Although it is known that group relatedness decreases with increased group size (15), modeled egalitarian camps show higher proportions of unrelated individuals irrespective of camp size (Fig. 3).

The modeled co-residence patterns also mirror our observed data. The proportion of unrelated dyads in the model at a comparable group size ($n = 20$ agents) ($12.0\% \pm 8.4$) was not significantly different from the observed proportion of unrelated co-residence among the Agta (11.2% , $\chi^2 = 1.98$, $P = 0.16$). Although the Mbendjele had significantly larger numbers of unrelated individuals in the camps (28.6%) than predicted by the model ($\chi^2 = 440.76$, $P < 0.001$), this was in the direction consistent with our hypothesis. The observed proportion of unrelated dyads among the Paranan (4.2%) was larger than the modeled proportion ($0.6\% \pm 1.5$, $\chi^2 = 183.41$, $P < 0.001$), but it was lower than either of the observed hunter-gatherer populations (see above) and the egalitarian model ($\chi^2 = 58.65$, $P < 0.001$).

Our results suggest that pair-bonding alone is not sufficient to explain the low levels of relatedness seen in hunter-gatherer groups. Rather, both pair-bonding and sex equality in residential decision-making act together to constrain the overall relatedness of groups, leading to the co-residence of individuals unrelated through either genetic or affinal ties.

It has been proposed elsewhere that the combination of pair-bonding, cooperation among unrelated males, and increased mobility derived from male alliances could account for the low relatedness of hunter-gatherer camps (7). We argue instead that low within-camp relatedness is a consequence of sex equality in hunter-gatherer couples, with husbands and wives having an equal influence over camp composition. Given sex equality, we have shown that unrelated individuals come to

co-reside even when they display a strong individual preference to live with kin, exemplified in hunter-gatherers by the frequent co-residence of brothers and sisters (14) and the higher frequency of related individuals in campmate and gift networks (16). Therefore, our simulations provide a mechanism for the emergence of low within-camp relatedness in hunter-gatherers by solving the apparent contradiction between individual-level preferences for living with kin and group-level co-residence with non-kin. Gender inequality reappeared in humans with the transition to agriculture and pastoralism (17). Once heritable resources, such as land and livestock, became important determinants of reproductive success, sex-biased inheritance and lineal systems started to arise, leading to wealth and sex inequalities (18). This predicted effect was demonstrated in our non-egalitarian model and data from Paranan agriculturalists. Our results also provide further evidence that multilocality, rather than patrilocality, is the norm among mobile hunter-gatherers.

Understanding hunter-gatherer sex egalitarianism and the shift from hierarchical male philopatry typical of chimpanzees and bonobos to a multilocal residence pattern is key to theories of human social evolution. A possible clue for the evolution of sex equality in the hominin lineage was the increase in the cost of human reproduction associated with larger brain sizes in early *Homo* (19). Higher offspring costs would require investment from both mothers and fathers (20), as seen among extant hunter-gatherers (3, 21). The need for biparental investment predicts increased sex equality (22), which is reflected in the high frequency of monogamy and the reproductive schedules of male hunter-gatherers, who

typically stop reproducing early and exhibit long life spans after their last reproduction. This pattern contrasts with that of male farmers and pastoralists, whose reproductive spans extend well into late life (23). The recognition of affinal ties throughout our long life span has been argued to be an important step in human social evolution, and household residence may also be influenced by a tug of war between a husband and his affinal kin, who may want to live with their daughter or sister (7). The possibility of recruiting help from both maternal and paternal kin by moving camps might have been an important adaptation to meet reproductive costs in unpredictable environments—for example, by increasing the frequency of co-residence with grandmothers, who have an important provisioning role in many hunter-gatherer societies (24). Increased reproductive costs, cooperative breeding, and sex equality in residential decision-making can explain why hunter-gatherer parents live in groups containing multiple mated pairs, why hunter-gatherers recruit help both from related and unrelated individuals, and why hunter-gatherer camps exhibit low levels of relatedness.

Sex equality and the resulting low within-camp relatedness had many important consequences. Co-residence with unrelated individuals set the selective environment for the evolution of hyper-cooperation and prosociality (25). Sex equality suggests a scenario where cooperation among unrelated individuals can evolve in the absence of wealth accumulation, reproductive inequalities, and intergroup warfare (26). Couples freely moving between camps and sharing interests with kin and affines would be able to maintain cooperation without the need for more complex sys-

tems, such as cultural group selection and altruistic punishment (27).

Last, this social system may have allowed hunter-gatherers to extend their social networks, buffering environmental risk and promoting levels of information exchange required for cumulative culture (28–31).

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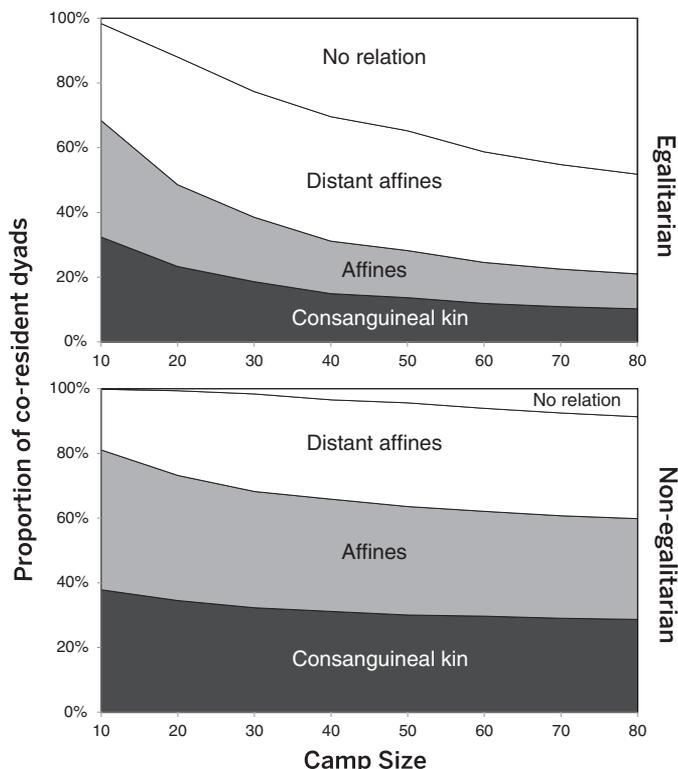
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SUPPLEMENTARY MATERIALS

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Fig. 3. Modeling relatedness, equality, and group size. Results of the egalitarian model (top) and non-egalitarian model (bottom) at camp sizes between 10 and 80. From bottom to top, areas represent consanguineal (genetic) kin, affinal kin, distant affinal kin, and unrelated individuals. Exact proportions are given in tables S3 and S4.



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