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Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure

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Contemporary humans exhibit spectacular biological success derived from cumulative culture and cooperation. The origins of these traits may be related to our ancestral group structure. Because humans lived as foragers for 95% of our species' history, we analyzed co-residence patterns among 32 present-day foraging societies (total $n = 5067$ individuals, mean experienced band size = 28.2 adults). We found that hunter-gatherers display a unique social structure where (i) either sex may disperse or remain in their natal group, (ii) adult brothers and sisters often co-reside, and (iii) most individuals in residential groups are genetically unrelated. These patterns produce large interaction networks of unrelated adults and suggest that inclusive fitness cannot explain extensive cooperation in hunter-gatherer bands. However, large social networks may help to explain why humans evolved capacities for social learning that resulted in cumulative culture.

Our ancestors lived as hunter-gatherers until the beginning of the Holocene; during that time, they spread across the globe and developed features that distinguish us as an outlier among life forms on this planet (1). Our biological success appears to be based on both cooperation with non-kin and exceptional reliance on cultural transmission, yet critical questions remain about why these traits emerged in humans but not other animals. Contemporary hunter-gatherers often show extensive cooperation among members of a residential unit (referred to here as a “band”) in ways not paralleled by any other primate. This includes band-wide food sharing (2); high levels of allomaternal child care (3); daily cooperative food acquisition, construction, and maintenance of living spaces and transportation of children and possessions (4); and provisioning of public goods on a daily basis. The widespread flow of goods and services within hunter-gatherer bands coevolved with a life history that included slow juvenile growth, late sexual maturity, high fertility, high adult survivorship, and a long post-reproductive life span (1, 5, 6). The combination of juvenile allomaternal provisioning, adult shared energy budgets, and helper-dependent life history

traits has led some to label hunter-gatherers as cooperative breeders (7, 8).

Evolutionary behavioral scientists have attempted to understand how cooperative temperament might spread in small-scale human societies and how it might account for “prosocial” and “other-regarding” behaviors (9), exceptional social cognition and shared intentionality (10), orientation toward teaching and learning (11), a taste for equitable distribution (12), and a widespread willingness to punish norm violators, even when not directly affected by the noncooperative behavior (13). These traits appear to be derived in *Homo* because they are rare or absent in other apes (14).

If hunter-gatherers engage in extensive cooperation within residential bands, we must determine the composition of these units to assess how such behavior could have evolved. Traditionally, anthropologists have suggested that hunter-gatherer co-residence is almost entirely based on kinship [e.g., (15, 16)], and evolutionary psychologists have embraced this idea in order to develop “mismatch hypotheses” about cooperation among non-kin in modern societies (17). Evolutionary researchers have also argued both that female philopatry and maternal grandmother provisioning is ancestral (5) and that male philopatry, typical of other African hominoids (18, 19) and leading to adult male provisioning (8), is the ancestral human pattern. If either of these is correct, and if foraging bands are mainly collections of close kin, inclusive fitness gains might be the primary motivator of ancestral human cooperation.

Chapais (18) recently developed an alternative model of ancestral human social structure derived from pair-bonding and paternal investment within chimpanzee-like social groups. He suggested that the affiliation of several unrelated males to the same female (related as daughter, sister, wife, son's wife, or brother's wife) could ameliorate

hostile relations across ancestral male philopatric groups, and could allow for cross-group visiting and opportunistic co-residence by kin of either sex and frequent interactions with affines. This model predicts lifetime cooperation and frequent co-residence of adult brothers and sisters as a unique feature of human society [(18), p. 129]. These features result in metagroups (“tribes”) composed of multiple residential bands that exchange spouses [(18), pp. 216–228]. Most important, the resultant social structure would lead to a high number of co-resident adults who are not genetically related [(18), pp. 235–243]. If this model is correct, and if most band members are not closely linked by either kinship or shared genetic descendants, a variety of mechanisms that promote dyadic and indirect reciprocity (19, 20) or favor social sanctioning of noncooperators (21, 22) may be required to explain the emergence of extensive cooperation in ancestral human societies.

Hunter-gatherer residential patterns are also critical for assessing models of cultural evolution. If friendly visiting between groups is common and social network sizes are large, frequent interaction allows for increased observation of rare innovations that are unlikely to be discovered by individual learning. Under these conditions, costly social learning mechanisms are more likely to evolve (21), and cultural traits are more likely to accumulate complexity and efficiency (23). Thus, the emergence of metagroup social structure might explain why humans, but not other social-learning animals, evolved the cognitive mechanisms that produce cumulative culture, and why *H. sapiens* were able to replace other hominins as they spread out of Africa (24).

Cross-cultural analysis. We analyzed data on band composition collected from published literature and unpublished field notes for a worldwide sample of 32 hunter-gatherer societies (25). Tabulations of the mean number of primary adult kin (i.e., parents, siblings, and offspring) that co-reside in bands clearly support the bisexual philopatry and dispersal model of co-residence. We found no significant difference in the mean number of parents living with adult sons versus daughters in 19 societies (Table 1). In a minority of societies, parents were statistically more likely to co-reside with adult offspring of one sex (seven societies with sons, six societies with daughters), but even in these societies many parents lived with adult offspring of the other sex.

Likewise, adult brothers and sisters frequently co-reside in all societies; thus, men often co-reside with male in-laws (fig. S1). In about half of the societies, men and women lived with no more same-sex adult siblings than opposite-sex siblings (table S1, 18 of 32 societies). The pattern of frequent brother-sister co-residence is not just due to bride service (in which new husbands live with parents-in-law and work for them) but is evident across the entire adult life span, even in groups that show preferential clustering of male kin, and

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even when controlling for mortality effects by considering only living siblings (Fig. 1).

Despite the common occurrence of brother-sister co-residence, statistical analysis also illustrates a greater tendency for close kin of men to co-reside than for close female kin to live together. For example, the mean number of adult brothers residing with each other is significantly higher than the mean number of adult sisters co-residing in 17 societies, but vice versa in only three societies (Table 1), and the total number of co-residing primary kin of males is typically higher than the number of co-residing primary kin of females (Table 1 and fig. S1).

The data demonstrate that primary kin associations are typical, but that most adult band members are not close kin in any of the societies in our sample. The mean total number of co-resident adult primary kin per band is only 1.8 for these 32 societies (range 0.45 to 5.27, Table 1). This represents only a small proportion (7%) of the total co-resident adults in the censused bands

(mean experienced band size = 28.2). To determine exactly who the remaining band members are, we require complete genealogical and marital information on all adults in the population (available only for the Ache and Ju/'hoansi). We analyzed the complete composition of 58 precontact Ache bands ($n = 980$ adults) using demographic and marital databases (26), and one of us (P.W.) tabulated relationships for all adult dyads in six bands of Ju/'hoansi foragers ($n = 89$ adults).

Even though Ache bands are larger than Ju/'hoansi bands (21 versus 15 adults), typical band composition from a randomly chosen adult ego's point of view shows a common pattern: First, ego and his/her primary and distant kin connected by up to five meiotic links (genetic coefficient of relatedness $r = 1$ to 0.03125) make up only about 25% of the adults who co-reside in Ache and Ju/'hoansi bands (Fig. 2 and table S2). Smaller Ju/'hoansi bands contain a greater proportion of primary kin, whereas larger Ache bands

contain a higher proportion of distant kin. Second, spouse and spouse's kin constitute about 16% of the adults in these bands. Thus, primary and distant kin of a family unit make up only about 40% of the co-resident adult members of a band. Among the individuals genetically unrelated to either spouse or ego, the spouses of ego's primary kin often carry the same kinship term as spouse's primary kin (e.g., brother-in-law, sister-in-law, etc.) and may be treated equally. These make up about 6% of adult band members. Other adults connected through a multiple-linked chain of distant genetic and marriage ties (i.e., "distant affines" such as cousin's spouse or "affines of affines" such as spouse's brother's wife's brother) make up about half the co-resident adults members of a band. Finally, about one-quarter of the individuals in a band are not linked directly to ego by any known genealogical or marriage tie. It is noteworthy that flexible bilocal residence leads to neither sex being surrounded mainly by kin (table S3).

Table 1. Mean number of co-residing adult primary kin for men and women, with societies sorted from most to least virilocal (male-biased) co-residence. Significant differences were determined by resampling. The mean experienced band size is the mean of all band sizes weighted by the number of individuals who lived in bands of that size.

Society	Men's parents	Women's parents	Men's brothers	Men's sisters	Women's brothers	Women's sisters	Men's primary kin	Women's primary kin	Mean experienced band size
Gunwinggu	1.26*	0.30	2.50*	0.75	0.60	0.60	5.27*	2.20	18.0
Labrador Inuit	0.24	0.14	0.36*	0.18	0.11	0.00	0.93*	0.45	24.1
Semang	0.76*	0.21	0.72*	0.44	0.46	0.00	2.40*	1.18	19.3
Iglulik	0.60*	0.23	0.56*	0.19	0.18	0.13	1.74*	0.97	25.5
Belcher Island	0.15	0.10	0.50*	0.45	0.43	0.10	1.25*	0.73	11.9
Mbuti	0.57*	0.21	0.59*	0.37	0.33	0.27	1.88*	1.21	32.9
Hiwi	0.54	0.44	1.58*	0.58	0.55	0.51	3.13*	2.05	36.7
Angmagsalik	0.75*	0.20	0.25	0.25	0.20	0.20	1.63	1.10	17.0
Ainu	0.15	0.24	0.89*	0.57	0.53	0.34	1.78*	1.33	14.9
Ache	0.50*	0.36	0.59*	0.33	0.34	0.16	1.77*	1.36	20.7
Paliyan	0.28	0.16	0.48*	0.57	0.63	0.21	1.57	1.21	25.0
Nunamuit	0.37	0.38	0.88*	0.79	0.75	0.52	2.44*	2.00	64.9
Aka	0.56	0.49	0.51*	0.27	0.21	0.33	1.86	1.55	16.6
Chenchu	0.44*	0.25	0.45*	0.40	0.37	0.21	1.52	1.28	17.6
Netsilik	0.39	0.32	0.27*	0.19	0.18	0.06	1.15	0.97	17.0
Agta	0.35	0.27	0.42*	0.37	0.35	0.27	1.42	1.22	12.8
Slavey	0.50	0.46	1.00	0.29	0.27	0.53	2.14	1.86	22.3
Ojibwa	0.52	0.43	0.78*	0.75	0.71	0.44	2.45*	2.13	56.6
Wanindiljaugwa	0.07	0.33†	1.56	1.54	1.37	1.46	3.61	3.16	21.4
Copper	0.20	0.40†	0.33*	0.13	0.13	0.07	0.96	0.90	16.3
Dogrib	0.89	0.94	1.23	1.23	1.16	1.04	4.20	4.12	81.6
Ju/'hoansi	0.71	0.62	0.37	0.50	0.46	0.31	2.15	2.14	14.5
Shoshoni	0.11	0.11	0.37	0.24	0.21	0.33	0.78	0.81	7.3
Batak	0.53	0.53	0.69	0.58	0.73	0.53	2.25	2.42	42.6
Alyawarra	0.57	0.60	0.65	0.44	0.33	0.88	2.21	2.43	39.2
Vedda	0.40	0.88†	0.60	0.30	0.33	0.44	1.90	2.31	11.6
Paiute	0.16	0.52†	0.32	0.21	0.21	0.21	1.03	1.28	11.7
Apache	0.49	0.56	0.29	0.32	0.33	0.48†	1.55	1.96†	18.6
Takamiut	0.47	0.76	0.67	0.33	0.31	0.88	2.07	2.64	15.9
Hadza	0.38	0.40	0.32	0.42	0.38	0.68†	1.43	1.93†	35.1
Hill Pandaram	0.16	0.50†	0.16	0.24	0.27	0.18	0.84	1.31†	5.8
Miwuyt	0.06	0.30†	0.11	0.22	0.17	0.42†	0.56	1.10†	11.9
Average	0.44	0.39	0.66*	0.45	0.42	0.40	1.93	1.67	28.2

*Significantly more kin co-residing with men ($P < 0.05$).

†Significantly more kin co-residing with women ($P < 0.05$).

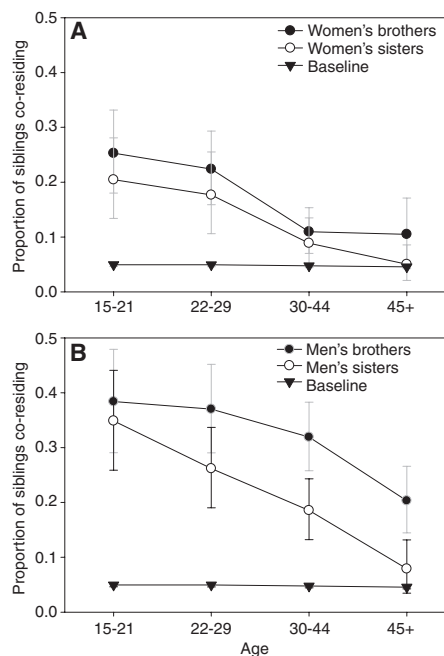


Fig. 1. Comparison of same-sex and cross-sex sibling co-residence contingent on survival by age for precontact Ache women (A) and men (B). Data points show mean proportions per age group of surviving siblings who co-reside. Bars indicate 95% confidence intervals; triangles mark the baseline proportion of co-residence for all adults in the population who are more than three genealogical steps removed (and not married to each other). Brother-brother and brother-sister co-residence is common throughout the life span, but after their 30s, women are no more likely to co-reside with another living sister than with any randomly selected, unrelated adult.

Conclusion. Formerly, anthropologists believed that hunter-gatherers lived in patrilocal bands composed mainly of close kin (15). Here, we present a statistical analysis of hunter-gatherer band composition based on actual residence rather than cultural rules. We show that bisexual philopatry and dispersal are typical and result in frequent adult brother-sister co-residence. This social pattern is not reported for any other primate or vertebrate, as far as we know. We hypothesize that monogamous pair bonding, paternal recognition within cooperatively breeding social units (8), and bisexual dispersal facilitate frequent and friendly intergroup relations (18) and migration and low group genetic relatedness of band co-residents.

The hunter-gatherer social structure we describe has important implications for theories about the evolution of cooperation and cultural capacity. First, bands are mainly composed of individuals either distantly related by kinship and/or marriage or unrelated altogether. In our sample of 32 societies, primary kin generally make up less than 10% of a residential band. For example, in the Ache we estimate the mean genetic coefficient of relatedness (Hamilton's r) between

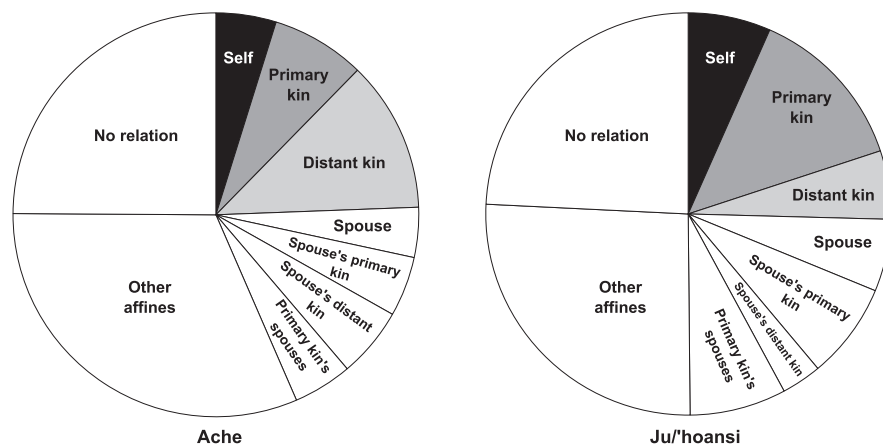


Fig. 2. Mean band composition from adult ego's point of view for 58 Ache bands and 6 Ju/'hoansi bands (data in table S2). The category "distant affines" includes spouses of distant kin, distant kin of spouse, and affines of affines. The category "No relation" includes all adult dyads that cannot be connected in five or fewer total steps of kinship and marriage with no more than two marriage links in the chain of connection. The shaded region shows all band members genetically related to ego.

adults in 58 precontact bands to be only 0.054 ($n = 19,634$ dyads, $SE = 0.0001$). This agrees with Ache informants who reported that during the precontact period they often lived with people described as "friends, not relatives." The Ju/'hoansi results in Fig. 2 suggest that mean relatedness in other groups is not too different from the Ache. Thus, we cannot necessarily assume that cognitive features such as inequality aversion and enhanced prosocial emotions evolved in ancestral environments composed mainly of close kin. Given the constant flow of individuals between groups, genetic group selection at the level of the band also seems improbable. Instead, cultural group selection (27) may lead to the spread of cooperative institutions within ethnic groups, which might then create a context favoring the genetic evolution of prosocial cognitive mechanisms through individual-level selection.

Second, mathematical models suggest that large interaction networks may be required for culture to accumulate (21, 23). In small populations, cultural innovations can be lost because of infrequent interaction between potential models and imitators and/or stochastic events that eliminate models with particular cultural knowledge. For example, one of the authors (K.R.H.) observed that the Northern Ache, isolated from their ancestral core territory in the 19th century, were unable to make fire by the time they were contacted in the 1970s. However, older informants stated that their parents and grandparents had told them that their ancestors could make fire, and had partially described to them the technique, even though none had ever observed it directly. In contrast, the Southern Ache groups did maintain fire-making knowledge until their first contact in the late 20th century. Likewise, Tasmanians failed to maintain previously known methods for fishing when their island was cut off from mainland Australia in the early Holocene (23), and fishing technology in Polynesia shows reduced complexity

on islands with smaller populations (28). In contrast, Wiessner [(29) and references therein] conducted studies on style and social information in material culture among Kalahari Bushman bands from four language families connected by intermarriage, exchange partnerships, and visiting. She found that tapered bone points were rapidly replaced everywhere by iron tips when fence wire became available in the 20th century, and that new point styles emerged and became relatively homogeneous within language groups over a period of 40 years.

When people reside together, they have frequent opportunities to observe innovations, evaluate their success, and imitate traits judged most successful or most common. Our analyses suggest that the increased network size that follows a unique shift in ancestral human residential structure may have led to greater exposure to novel ideas worth copying, and may explain why humans, but not other animals, evolved costly social learning mechanisms (such as high-fidelity over-imitation or conformity-biased transmission) that may have resulted in cumulative cultural evolution (21). This unique expansion of network size in our hominin ancestors can be detected archaeologically by the emergence of long-distance flows of tools and raw materials that appear at least as early as the middle Pleistocene (30).

The extent to which modern hunter-gatherer patterns represent ancestral patterns is a complex question. For example, most of our sample societies were censused after the elimination of warfare, and many had been geographically displaced or lived in environments that had been substantially depleted of large game. All modern hunter-gatherers use projectile weapons that were not available to our distant ancestors. Without causal models of residential association that consider the impacts of technology, warfare, cooperative hunting, territorial inheritance, depletion, and demographic crashes, we should be cautious about

the use of specific modern groups as analogs for past patterns. Nonetheless, the robustness of our main result suggests that our foraging ancestors evolved a novel social structure that emphasized bilateral kin associations, frequent brother-sister affiliation, important affinal alliances, and co-residence with many unrelated individuals. How this social structure evolved, and how it in turn affected cooperation and cultural capacity—and the role of language in all these features—were key to understanding the emergence of human uniqueness.

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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S12

Figs. S1 to S3

References

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Ordered and Dynamic Assembly of Single Spliceosomes

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The spliceosome is the complex macromolecular machine responsible for removing introns from precursors to messenger RNAs (pre-mRNAs). We combined yeast genetic engineering, chemical biology, and multiwavelength fluorescence microscopy to follow assembly of single spliceosomes in real time in whole-cell extracts. We find that individual spliceosomal subcomplexes associate with pre-mRNA sequentially via an ordered pathway to yield functional spliceosomes and that association of every subcomplex is reversible. Further, early subcomplex binding events do not fully commit a pre-mRNA to splicing; rather, commitment increases as assembly proceeds. These findings have important implications for the regulation of alternative splicing. This experimental strategy should prove widely useful for mechanistic analysis of other macromolecular machines in environments approaching the complexity of living cells.

The spliceosome is a complex macromolecular machine responsible for removing introns from nascent transcripts via pre-mRNA (precursor to mRNA) splicing (1). The spliceosome is composed of five small nuclear RNAs (snRNAs) and ~100 core proteins minimally required for activity in vitro (2). The snRNAs

and many core proteins are arranged into stable subcomplexes constituting small nuclear ribonucleoprotein particles [U1 and U2 small nuclear ribonucleoproteins (snRNPs) and the U4/U6.U5 tri-snRNP] and the multiprotein Prp19-complex (NTC). Although association of U1 with pre-mRNA can occur in the absence of adenosine triphosphate (ATP), stable association of all other subcomplexes requires ATP hydrolysis. Intron excision occurs after the spliceosome has been fully assembled and activated by additional structural rearrangements (3).

Current models of spliceosome assembly, activation, and catalysis generally depict it as an ordered (U1 → U2 → tri-snRNP → NTC → activation → catalysis), one-way process (3). Yet deviations from the ordered assembly model have been reported (4–6), with some studies suggesting that both spliceosome assembly and catalysis are dynamic and reversible (7–9). None of these studies, however, directly examined the ki-

netics of subcomplex association with pre-mRNA. We monitored subcomplex dynamics during spliceosome assembly in real time by combining yeast genetic engineering, chemical biology, and a multiwavelength fluorescence technique, colocalization single-molecule spectroscopy (CoSMoS) (10).

Labeling spliceosome subcomplexes. We previously established that splicing of single pre-mRNA molecules can be monitored by multiwavelength total internal reflection fluorescence (TIRF) microscopy in the complex environment of *Saccharomyces cerevisiae* whole-cell extract (yeast WCE) (11). To enable kinetic analysis of spliceosome assembly, we have now developed methods to introduce fluorophores into individual spliceosomal subcomplexes in WCE. Protein labeling was accomplished using homologous recombination to fuse either a SNAP (an alkyl-guanine S-transferase) (12) or an *Escherichia coli* DHFR (dihydrofolate reductase) tag (13) onto the C terminus of numerous spliceosomal proteins. These tags enabled us to incorporate bright, photostable organic dyes into the subcomplexes and to avoid the poor photon output and blinking behavior of single fluorescent proteins (14). Integration of two orthogonal tags allows for simultaneous monitoring of two different subcomplexes by CoSMoS (Fig. 1). To ensure functionality of the tagged species, we tagged only essential proteins and verified that the resultant strains (table S1) had growth rates and in vitro splicing activities comparable to the parental strain (figs. S1 to S3). By using several selectable markers, we were able to incorporate up to three tags into a single strain. Multiple tags present in the same subcomplex minimized artifacts due to incomplete labeling, photobleaching, and/or long-lived dark-state formation of single fluorophores (15).

DHFR tags were labeled by adding excess (20 nM) fluorophore-trimethoprim (TMP) con-

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