

Networks of food sharing reveal the functional significance of multilevel sociality in two hunter-gatherer groups

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Summary

Like many other mammalian and primate societies [1–4], humans are said to live in multilevel social groups, with individuals situated in a series of hierarchically structured sub-groups [5,6]. Although this multilevel social organization has been described among contemporary hunter-gatherers [5], questions remain as to the benefits that individuals derive from living in such groups. Here, we show that food sharing among two populations of contemporary hunter-gatherers - the Palanan Agta (Philippines) and Mbendjele BaYaka (Republic of Congo) - reveal similar multilevel social structures, with individuals situated in households, within sharing clusters of 3-4 households, within the wider residential camps, which vary in size. We suggest that these groupings serve to facilitate inter-sexual provisioning, kin provisioning, and risk reduction reciprocity, three levels of cooperation argued to be fundamental in human societies [7,8]. Humans have a suite of derived life history characteristics including a long childhood and short inter-birth intervals which make offspring energetically demanding [9], and have moved to a dietary niche which often involves the exploitation of difficult to acquire foods with highly variable return rates [10–12]. This means that human foragers face both day-to-day and more long-term energetic deficits that conspire to make humans energetically inter-dependent. We suggest that a multilevel social organization allows individuals access to both the food sharing partners required to buffer themselves against energetic shortfalls and the cooperative partners required for skill based tasks such as cooperative foraging.

Results

We collected data on inter-household food sharing among six Agta and three Mbendjele camps. Mean (\pm SD) experienced camp size was 62.54 ± 24.84 individuals or 11.7 ± 4.59 households among the Agta ($n = 319$ individuals), and 41.12 ± 6.37 individuals or 11.06 ± 2.00 households among the Mbendjele ($n = 103$ individuals) (for full details, see Tables S1-2). Households were defined as the occupants of single dwelling. 49 of 61 Agta

households and 20 of 32 Mbendjele households consisted of an adult couple plus any dependent children, although there are many variations and extensions on this (for a full breakdown of household composition, see table S3). The mean experienced household size (\pm SD) was 6.36 ± 2.49 individuals (range = 1-12) among the Agta, and 4.98 ± 2.45 individuals (range = 1-11) among the Mbendjele. Among the Agta, 74.1% of food packages ($n = 1,540$) consumed by households were produced by household members. Across Mbendjele households ($n = 32$), the mean (\pm SD) proportion of calories consumed that were produced by household members was $60.55 \pm 20.49\%$ (see Experimental Procedures for more details on differences in data collection protocols). In both communities, there was a positive association between the number of dependents within households and the net number of food packages received (Spearman correlations; Agta: $r_s = .31$, $p = 0.016$; Mbendjele: this $r_s = .35$, $p = 0.052$).

Households typically had a small number of strong food sharing relationships (Figure 1), with a mean (\pm SD) of $88.3 \pm 16.3\%$ Agta household sharing ($n = 61$ households) and $89.1 \pm 10.4\%$ of Mbendjele household sharing ($n = 32$ households) occurring with just three other households. In order to determine whether these concentrated sharing relationships represented consistent clusters, we constructed weighted networks of inter-household food sharing where nodes represent households, and edges represent the extent of food sharing between each household dyad. Across the nine study camps, clustering coefficients ranged from 0.39 to 0.84 (see Table S1). For each camp network we used a community-detection algorithm to explore all possible graph partitions and identify the partition that maximized modularity [13] (Figure 2). Clusters defined in this way encompassed the majority of food sharing, with the average Agta household giving food to households in their cluster on $37.1 \pm 27.0\%$ of days, as compared to $10.3 \pm 12.5\%$ of days to households outside of their cluster (Figure 3A), and with Mbendjele households giving $26.9 \pm 21.1\%$ of their calorific production to households in their cluster, as compared to $9.9 \pm 11.5\%$ to households outside of their cluster (Figure 3D). Large camps contained a larger number of clusters as opposed to larger clusters (Figure 2, Table S1). Among the Agta, five of the six study camps contained two clusters, while the largest camp contained six. The mean experienced cluster size (\pm SD) among the Agta was 23.25 ± 8.08 individuals or 4.28 ± 1.45 households. Of the three Mbendjele camps, two contained three clusters, and one contained four clusters. Mean experienced Mbendjele cluster size was 14.73 ± 6.21 individuals and 3.63 ± 1.18 households.

In order to determine the relatedness of individuals to members of their household, cluster, and camp, we conducted genealogical interviews with all adults and used these data to calculate the coefficient of relatedness (r) between the 19,949 Agta and 4,934 Mbendjele dyads included in our sample. Permutation tests were used to generate sampling distributions that we compare to observed values (100,000 repeats, see Experimental

Procedures). Among both study populations, individuals were more closely related to members of their household (Agta: mean (\pm SD) $r = 0.39 \pm 0.14$, $n = 319$; Mbendjele: mean $r = 0.33 \pm 0.18$, $n = 103$) than to individuals within their cluster (Agta: mean $r = 0.10 \pm 0.09$, $p < .001$; Mbendjele: mean $r = 0.08 \pm 0.10$, $p < .001$) and more closely related to individuals in their cluster than the wider camp (Agta: mean $r = 0.04 \pm 0.04$, $p < .001$; Mbendjele: mean $r = 0.04 \pm 0.04$, $p < .001$). The difference in relatedness to the cluster and camp was also significant in both populations when household membership was fixed (see Supplemental Information). Among both populations, ties between children (<13 years of age) and their grandparents and between children and their aunts and uncles were significantly more likely to be found within the household or cluster than the wider camp (Agta grandparents: 67.2%, $n = 131$, $p < .001$; Mbendjele grandparents: 40.6%, $n = 32$, $p = 0.024$; Agta aunts/uncles: 60.1%, $n = 453$, $p < .001$; Mbendjele aunts/uncles: 41.8%, $n = 67$, $p < .001$)

Food production and foraging among the Agta

Among the Agta, we were able to supplement our data on food sharing with data on individual food production and foraging. The daily calorific productivity of married women (mean = -0.57 ± 0.62 , $n = 30$) was significantly lower than that of their husbands (mean = 0.95 ± 0.95 , Wilcoxon matched pairs, $W = 423$, $p < .001$, all women have one husband only, Figure S1) (data is standardized within camp, see Experimental Procedures). Mothers whose youngest child was under the age of two years had a markedly lower daily productivity ($n = 26$, mean = -0.82 ± 0.28) than mothers with a youngest child between the ages of two and sixteen ($n = 16$, mean = -0.09 ± 0.90 ; Wilcoxon rank sum test, $W = 101$, $p = 0.005$), suggesting that the sex difference in productivity may be a reflection of the energetic and time demands of mothering, and that food sharing within households represents inter-sexual provisioning.

If the majority of food sharing occurs within the household and cluster, what benefits do individuals derive from living in camps in terms of food sharing and production? First, as in other hunter-gatherer populations [14,15] sharing with the wider camp may represent the risk-reduction sharing of larger package size foods. Of the 106 food packages for which both calorific value and food sharing distributions were known in the Agta, there was a significant correlation between the calorific value of food packages and the number of households who received shares (Spearman correlation, $r_s = .42$, $p < .001$). There was also a significant positive relationship between package size and the number of households outside of the cluster receiving shares (Spearman correlation, $r_s = .22$, $p = 0.025$). Although foods of large package size were obtained less often, they contribute a significant amount to the

Agta diet (Table S4). For example, while only 16.7% of 497 food packages were larger than 4,000kcal, these packages contributed 62.1% of all calories returned to camp. Permutation tests revealed that Agta households were more likely to receive food from the cluster on days when they produced nothing themselves ($n = 220$, observed proportion = 41.82%, expected proportion = $35.06\% \pm 2.62\%$, $p = .006$) and were more likely to receive food from outside the cluster on days when they produced nothing themselves and received nothing from the cluster ($n = 128$, observed proportion = 21.10%, expected proportion = $12.35\% \pm 2.44\%$, $p < .001$). Living in a camp may also increase the number of foraging partners available to individuals and foraging with individuals from the wider camp may serve to reduce variation in foraging returns within the cluster [10]. Of our sample of 348 Agta adult co-foraging events, 41.1% occurred with individuals outside of the cluster and 60.1% with individuals with a coefficient of relatedness of $r < .0625$ (excluding spouses) (Table S5). Permutation tests, however, suggest that these proportions are lower than would be expected by chance (expected proportion outside of the cluster = $65.33\% \pm 2.46\%$, $p < .001$; expected proportion with non-kin = $75.54\% \pm 2.22\%$, $p < .001$).

Discussion

Despite their geographical separation and different foraging niches, communities of Agta and Mbandjele hunter-gatherers are structured in similar ways, with individuals situated within households, within food sharing clusters of around 3-4 households, within a wider camp. Camps vary in size, and in larger camps there are more clusters, rather than larger clusters. We suggest that this multilevel social organization allows individuals access to the range of social relationships required to mitigate against day-to-day variability in foraging success inherent in the human foraging economy [10,16], as well the long-term inter-personal dependency to which humans are committed due to our costly life-history niche [9,17]. Although small-scale hunter-gatherers tend to live in groups of low relatedness [18,19], this multilevel social structure means that individuals do not interact with all campmates equally, and are able to maintain a relatively constant number of close kin inside their clusters.

While previous studies have demonstrated that human groups often have a multilevel social organization [5,6], our work is the first to explore how this distinctive social organization relates to cooperation in important economic and social domains. The three levels of social organization we identify may correspond to the three kinds of cooperative relationships that Hooper and colleagues argue were important in human evolutionary history [7,8], and which are evident in hunter-gatherer food sharing [20–25]. These are (a) male-female complementarity and sex division of labour, as evident in within-household provisioning, (b) assistance from kin, which we observed

within sharing clusters, and (c) cooperation with both related and unrelated individuals, as observed in the selection of foraging partners. Although overall camp size varied, the size of households and food sharing clusters were similar across the two hunter-gatherer groups we studied. These similarities suggest that multi-level sociality might reflect male-female complementarity and assistance from kin, central adaptations of hunter-gatherer populations. Of course, foraging and food sharing are unlikely to be the only forces shaping the size and structure of hunter-gatherer communities. For example, group size in humans and non-human primates may be related to time and cognitive constraints, between-group competition, and differences in predation and food distribution [26,27]. Camp size may also relate to the efficiency of cultural transmission [28,29] and the use of space [30,31]. We suggest that multilevel social organization in humans may have evolved, in part, to allow individuals access to the range of cooperative relationships required to facilitate the energetic provisioning necessary to overcome the risks of our foraging niche and costly life-histories.

Experimental Procedures:

The Agta live in northeast Luzon, Philippines and, within our study area of Palanan, have a population of around one thousand. Riverine and marine spearfishing provides the primary source of animal protein for the Agta, supplemented by inter-tidal foraging, hunting, honey collecting, and gathering wild foods. The Mbendjele are a subgroup of the BaYaka who live in an area spanning northern Republic of Congo and southern Central African Republic. The three Mbendjele camps described in this paper are situated in the Sangha and Likouala regions of the Republic of Congo. Among the Mbendjele, hunting in the forest is the primary source of animal protein. Both populations live in camps of fluid membership containing a large proportion of unrelated individuals and both have a multi-local residential system [18,32]. Both the Agta and Mbendjele engage in the trade of wild for cultivated foods. In the case of the Agta this is typically the trade of fish for rice, while among the Mbendjele, trade is typically of meat for manioc and alcohol.

Data on inter-household food sharing were collected using different methodologies among the Agta and Mbendjele. Among the Agta, M.D. and A.B.M. conducted short interviews at the end of each day with at least one adult member of each household. We asked which households they, as a household, had given food to, or received food from. In order to solicit more accurate responses, we first asked what food the household had eaten during the day and from whom they had received it. We supplemented this data with our own observations of food sharing

in camp. Sharing included both cooked and uncooked food and, in total, we collected sharing data over 103 days across six Agta camps. Among the Mbendjele, food sharing data was collected by J.T. through systematic observation of households, rather than by interview. Households were observed over a series of two to four-hour time blocks, with households observed for a total of 24 or 36 hours depending on the camp. Observations were evenly distributed between 6 a.m. and 6 p.m. and spread over several days. During observation periods, a record was made of all food produced by the household. If division of resource packages occurred, all recipient households were identified. For all food cooked and consumed by the household, the type and amount of food were recorded and, again, all those who ate the food were identified. For both populations, data were collected from February to August 2014. Analysis of food sharing networks was conducted in R.3.1.1 using functions available in the ‘igraph’ package [33]. Since our networks were relatively small, we were able to use a community detection algorithm (the function ‘optimal.community’) which iterates through all possible graph partitions and returns the partition that maximized modularity – the proportion of edges that fall within clusters minus the expected fraction that would fall within clusters if the edges were distributed randomly [13]. In all tests, social layers were defined exclusive of their sub-units. Experienced group sizes were calculated by weighting the mean of group sizes by the number of individuals in each group.

In order to establish relatedness between individuals, we conducted genealogical interviews with all adults in our study camps. To evaluate the statistical significance of differences in relatedness and the composition of the household, cluster, and camp, permutation tests were conducted in R3.1.1 using scripts written by M.D. For each individual, we calculated the difference in mean coefficient of relatedness to individuals in their household versus their cluster and in their cluster versus the camp. We then compared these values to an expected frequency distribution generated by resampling from the original data. To produce the expected distributions we randomized dyadic relatedness 100,000 times and in each case calculated the mean difference in relatedness of individuals to members of their household versus their cluster, and to members of their cluster versus the of the camp. We then compared our observed relatedness values with 95% confidence intervals from these distributions of randomized means to test the null hypotheses that individuals were no more closely related to their household than their cluster, and no more closely related to their cluster than the rest of the camp. We also conducted a permutation test (100,000 permutations) in which household composition was fixed at observed values but where households were randomly assigned to clusters. Even when this was the case, the observed difference in relatedness of individuals to their cluster versus their camp was significantly greater than expected (see SI for full results). Permutation tests were

also used to evaluate the statistical significance of the frequencies of ties between children (under 13 years) and their grandparents and aunts/uncles. In this case, the procedure described above was employed with 100,000 repetitions but with only ties including children included, and with categorical relatedness of these children with the resident adults in their cluster being shuffled. For correlations of the number of dependents per household and net household income, net income was calculated as the total number of packages or calories given, minus the number received, divided by the total number given and received.

Data on food production and co-foraging were collected among the Agta by M.D. who collected data on 878 person foraging days across the six camps for which we also collected food-sharing data. Where possible, the weight of foods returned to camp were recorded and calorific values were estimated using the USDA National Nutrient Database. From this, mean daily productivity was calculated for every individual. We then standardized foraging returns within each camp since seasonal variation in foraging returns resulted in between-camp differences in productivity and because the trade of fish for rice means that the raw calorific value of foraging returns are not necessarily representative of the actual calorific contribution to the diet. To assess whether the receipt of food shares from the cluster and wider camp were related to each other and to household production, we conducted a permutations test in which we generated expected distributions by resampling 100,000 times from the 656 household observation days for which we had both food sharing and food production data. We also used permutations tests to assess the composition of foraging parties, resampling from the original data 100,000 times and assessing the statistical significance of our observed data by comparing the observed values to the expected frequency distribution. In each permutation, we maintained the observed proportion of male-male, female-female, and male-female co-foraging dyads (167 M-M, 61 F-F, and 120 M-F).

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Figure 1: Mean intensity of food sharing with other households among the Agta (squares) and Mbendjele (circles). Recipient households ranked by intensity of food sharing.

Figure 2. Inter-household food sharing networks for six Agta (A-F) and three Mbendjele BaYaka (G-I) communities. Node colors reflect cluster membership defined by the frequency of food sharing between households. Networks were produced in Gephi using a Force Atlas layout. Descriptives for each camp are provided in Table S1. See also Tables S1 and S3.

Figure 3: Box plots of sharing, group size and relatedness across the household, cluster, and camp among the Agta (*top*) and Mbendjele (*bottom*). Group size represents experienced group size where each individual is treated as a separate observation. For all Agta panels, $n = 319$ individuals. For all Mbendjele panels, $n = 120$ individuals. Diamonds represent the mean values. See also Figure S1 and Tables S2, S4, and S5.