



Dyble, M., Thompson, J., Smith, D., Salali, G. D., Chaudhary, N., Page, A. E., Vinicuis, L., Mace, R., & Migliano, A. B. (2016). Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups. *Current Biology*, 26(15), 2017-2021. <https://doi.org/10.1016/j.cub.2016.05.064>

Publisher's PDF, also known as Version of record

License (if available):  
Other

Link to published version (if available):  
[10.1016/j.cub.2016.05.064](https://doi.org/10.1016/j.cub.2016.05.064)

[Link to publication record in Explore Bristol Research](#)  
PDF-document

This is the final published version of the article (version of record). It first appeared online via Cell Press at <http://www.sciencedirect.com/science/article/pii/S0960982216305644> . Please refer to any applicable terms of use of the publisher.

## University of Bristol - Explore Bristol Research

### General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: <http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

# Current Biology

## Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups

### Highlights

- Networks of food sharing among two populations of hunter-gatherers are explored
- Food sharing is highly concentrated within small clusters of households
- These clusters represent one part of a multilevel social structure
- Living in a multilevel group allows access to important cooperative relationships

### Authors

Mark Dyble, James Thompson, Daniel Smith, ..., Lucio Vinicuis, Ruth Mace, Andrea Bamberg Migliano

### Correspondence

mark.dyble.12@ucl.ac.uk

### In Brief

Dyble et al. explore networks of food sharing among Agta and Mbendjele hunter-gatherers and identify three levels of social organization: the household, cluster, and camp. Their results suggest that this multilevel social system may provide individuals with access to the range of cooperative relationships that are vital in a foraging economy.



# Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups

Mark Dyble,<sup>1,\*</sup> James Thompson,<sup>1</sup> Daniel Smith,<sup>1</sup> Gul Deniz Salali,<sup>1</sup> Nikhil Chaudhary,<sup>1</sup> Abigail E. Page,<sup>1</sup> Lucio Vinicuis,<sup>1</sup> Ruth Mace,<sup>1</sup> and Andrea Bamberg Migliano<sup>1</sup>

<sup>1</sup>Anthropology, University College London, London WC1E 6BT, UK

\*Correspondence: [mark.dyble.12@ucl.ac.uk](mailto:mark.dyble.12@ucl.ac.uk)

<http://dx.doi.org/10.1016/j.cub.2016.05.064>

## SUMMARY

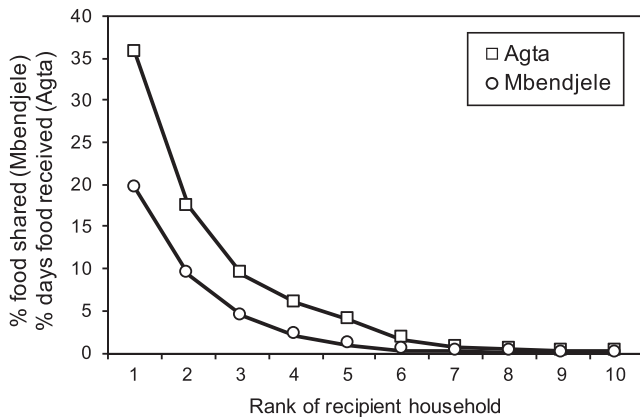
Like many other mammalian and primate societies [1–4], humans are said to live in multilevel social groups, with individuals situated in a series of hierarchically structured sub-groups [5, 6]. Although this multilevel social organization has been described among contemporary hunter-gatherers [5], questions 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)—reveals 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 that make offspring energetically demanding [9] and have moved to a dietary niche that 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 interdependent. 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  $62.54 \pm 24.84$  individuals or  $11.7 \pm 4.59$  households among the Agta ( $n = 319$  individuals) and  $41.12 \pm 6.37$  individuals or  $11.06 \pm 2.00$  households among the Mbendjele

( $n = 103$  individuals) (for full details, see [Tables S1](#) and [S2](#)). 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  $6.36 \pm 2.49$  individuals (range = 1–12) among the Agta and  $4.98 \pm 2.45$  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:  $r_s = 0.31$ ,  $p = 0.016$ ; Mbendjele: this  $r_s = 0.35$ ,  $p = 0.052$ ).

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  $23.25 \pm 8.08$  individuals or  $4.28 \pm 1.45$  households. Of the three Mbendjele camps, two contained three clusters, and



**Figure 1. Mean Intensity of Food Sharing with Other Households among the Agta and Mbendjele**

Agta (squares) and Mbendjele (circles); recipient households ranked by intensity of food sharing.

one contained four clusters. Mean experienced Mbendjele cluster size was  $14.73 \pm 6.21$  individuals and  $3.63 \pm 1.18$  households.

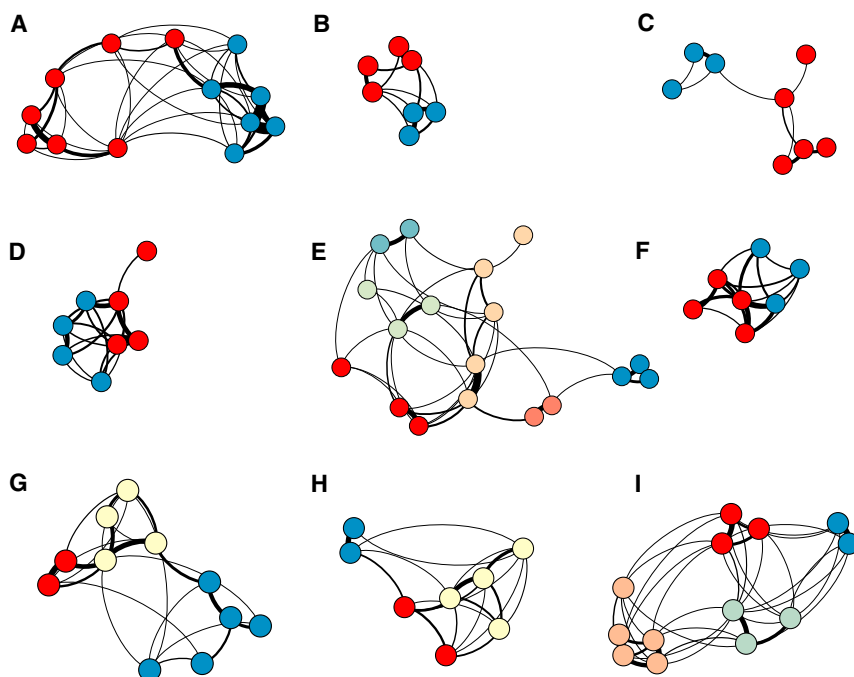
In order to determine the relatedness of individuals to members of their household, cluster, and camp, we conducted genealogical interviews with all adults and used these data to calculate the coefficient of relatedness ( $r$ ) between the 19,949 Agta and 4,934 Mbendjele dyads included in our sample. 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  $r = 0.10 \pm 0.09$ ,  $p < 0.001$ ; Mbendjele: mean  $r = 0.08 \pm 0.10$ ,  $p < 0.001$ ) and more closely related to individuals in their cluster than the wider camp (Agta: mean  $r = 0.04 \pm 0.04$ ,  $p < 0.001$ ; Mbendjele: mean  $r = 0.04 \pm 0.04$ ,  $p < 0.001$ ). 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%,  $n = 131$ ,  $p < 0.001$ ; Mbendjele grandparents: 40.6%,  $n = 32$ ,  $p = 0.024$ ; Agta aunts and uncles: 60.1%,  $n = 453$ ,  $p < 0.001$ ; Mbendjele aunts and uncles: 41.8%,  $n = 67$ ,  $p < 0.001$ )

### Food Production and Foraging among the Agta

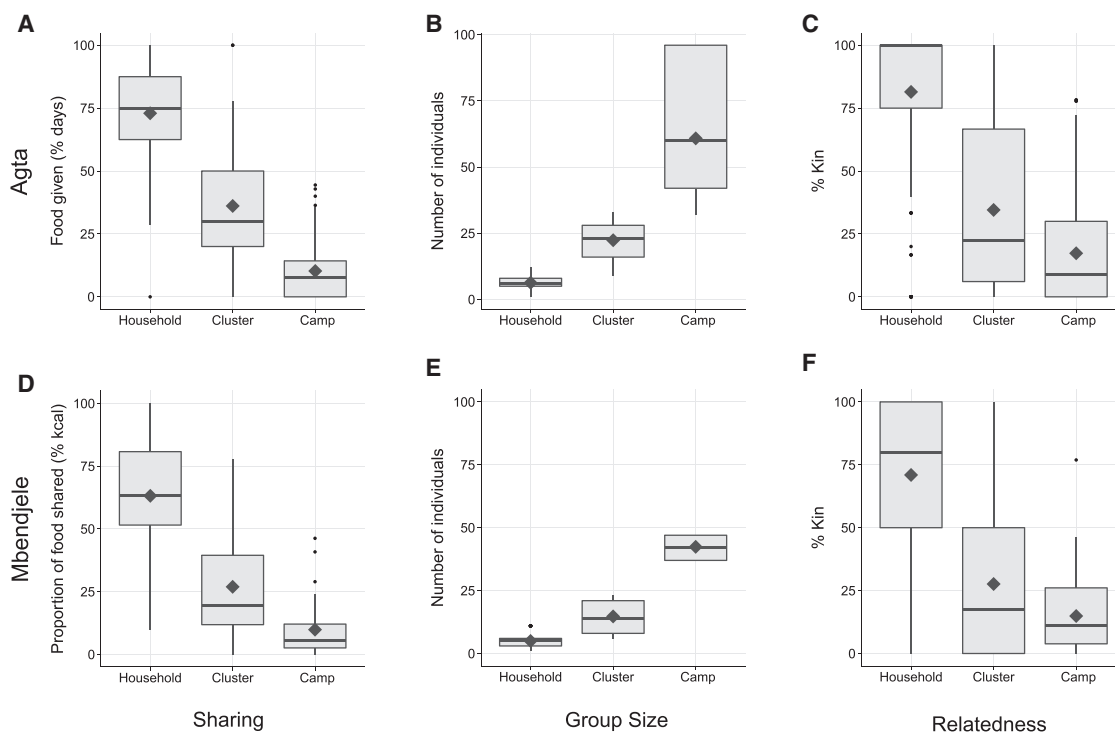
Among the Agta, we were able to supplement our data on food sharing with data on individual food production and foraging. The daily calorific productivity of married women (mean =  $-0.57 \pm 0.62$ ,  $n = 30$ ) was significantly lower than that of their husbands (mean =  $0.95 \pm 0.95$ , Wilcoxon matched pairs,  $W = 423$ ,  $p < 0.001$ , all women have one husband only; [Figure S1](#)) (data are standardized within camp; see [Experimental Procedures](#)). Mothers whose youngest child was under the age of 2 years had a markedly lower daily productivity ( $n = 26$ , mean =  $-0.82 \pm 0.28$ ) than mothers with a youngest child between the ages of 2 and 16 ( $n = 16$ , mean =  $-0.09 \pm 0.90$ ; 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



**Figure 2. Inter-household Food Sharing Networks for Six Agta and Three Mbendjele BaYaka Communities**

(A–I) 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. Further details for each camp are provided in [Table S1](#). See also [Tables S1](#) and [S3](#).



**Figure 3. Boxplots of Sharing, Group Size, and Relatedness across the Household, Cluster, and Camp among the Agta and Mbendjele**

(A–F) Boxplots of sharing, group size, and relatedness across the household, cluster, and camp among the Agta (A–C) and Mbendjele (D–F). 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](#).

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,  $r_s = 0.42$ ,  $p < 0.001$ ). There was also a significant positive relationship between package size and the number of households outside of the cluster receiving shares (Spearman correlation,  $r_s = 0.22$ ,  $p = 0.025$ ). 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 4,000 kcal, 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 =  $35.06\% \pm 2.62\%$ ,  $p = 0.006$ ) 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 =  $12.35\% \pm 2.44\%$ ,  $p < 0.001$ ). 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  $r < 0.0625$  (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 =  $65.33\% \pm 2.46\%$ ,  $p < 0.001$ ; expected proportion with non-kin =  $75.54\% \pm 2.22\%$ ,  $p < 0.001$ ).

## DISCUSSION

Despite their geographical separation and different foraging niches, communities of Agta and Mbendjele 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 as the long-term interpersonal 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 that are evident in hunter-gatherer food sharing [20–25]. These are (1) male-female complementarity and sex division of labor, as evident in within-household provisioning, (2) assistance from kin, which we observed within sharing clusters, and (3) 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-gatherers 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

All experiments and procedures were approved by the UCL Ethics Committee (UCLEthicscode3086/003). The Agta live in northeast Luzon, Philippines and, within our study area of Palanan, have a population of around 1,000. 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 these 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 were collected by J.T. through systematic observation of households rather than by interview. Households were observed over a series of 2–4 hr time blocks, with households observed for a total of 24 or 36 hr 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 members of the wider 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 [Supplemental Information](#) 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 and 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 was 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 is 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 (M-M), female-female (F-F), and male-female (M-F) co-foraging dyads (167 M-M, 61 F-F, and 120 M-F).

## SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, one figure, and five tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.05.064>.

## AUTHOR CONTRIBUTIONS

Conceptualization, A.B.M. and M.D.; Methodology, A.B.M., M.D., and J.T.; Investigation, M.D., A.B.M., J.T., A.E.P., D.S., G.D.S., and N.C.; Formal Analysis, M.D.; Writing, M.D., A.B.M., L.V., and R.M.; Funding Acquisition, A.B.M. and R.M.

## ACKNOWLEDGMENTS

This project was funded by the Leverhulme Trust grant RP2011-R-045 to A.B.M. and R.M. R.M. also received funds from European Research Council Advanced Grant AdG 249347. We thank A. Rey, P. Gerbault, J. Stevenson, J. Lewis, S. Viguier, K. Major, and R. and P. Schlaepfer for help in the field, as well as anonymous reviewers for valuable comments on the manuscript. We also thank our assistants in both Congo and the Philippines, as well as the Agta and Mbenjele communities.

Received: December 7, 2015

Revised: April 28, 2016

Accepted: May 26, 2016

Published: July 21, 2016

## REFERENCES

- Qi, X.G., Garber, P.A., Ji, W., Huang, Z.P., Huang, K., Zhang, P., Guo, S.T., Wang, X.W., He, G., Zhang, P., and Li, B.G. (2014). Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nat. Commun.* 5, 5296.
- Patzelt, A., Kopp, G.H., Ndao, I., Kalbitzer, U., Zinner, D., and Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proc. Natl. Acad. Sci. USA* 111, 14740–14745.
- Cantor, M., Shoemaker, L.G., Cabral, R.B., Flores, C.O., Varga, M., and Whitehead, H. (2015). Multilevel animal societies can emerge from cultural transmission. *Nat. Commun.* 6, 8091.
- Hill, R.A., Bentley, R.A., and Dunbar, R.I.M. (2008). Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. *Biol. Lett.* 4, 748–751.
- Hamilton, M.J., Milne, B.T., Walker, R.S., Burger, O., and Brown, J.H. (2007). The complex structure of hunter-gatherer social networks. *Proc. Biol. Sci.* 274, 2195–2202.
- Zhou, W.X., Sornette, D., Hill, R.A., and Dunbar, R.I.M. (2005). Discrete hierarchical organization of social group sizes. *Proc. Biol. Sci.* 272, 439–444.
- Hooper, P.L., Gurven, M., and Kaplan, H.S. (2014). Social and economic underpinnings of human biodemography. In *Sociality, Hierarchy, Health: Comparative Biodemography: A Collection of Papers*, M. Weinstein, and M.A. Lane, eds. (Washington, DC: National Academies Press), pp. 169–196.
- Hooper, P.L., Demps, K., Gurven, M., Gerkey, D., and Kaplan, H. (2015). Skills, division of labour and economies of scale among Amazonian hunters and South Indian honey collectors. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20150008.
- Kaplan, H., Hill, K., Lancaster, J., and Hurtado, A.M. (2000). A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* 9, 156–185.
- Winterhalder, B. (1986). Diet choice, risk, and food sharing in a stochastic environment. *J. Anthropol. Archaeol.* 5, 369–392.
- Hill, K., and Hurtado, A.M. (2009). Cooperative breeding in South American hunter-gatherers. *Proc. Biol. Sci.* 276, 3863–3870.
- Gurven, M. (2004). To give and to give not: the behavioral ecology of human food transfers. *Behav. Brain Sci.* 27, 543–583.
- Brandes, U., Dellinger, D., Gaertler, M., Gorke, R., Hofer, M., Nikoloski, Z., and Wagner, D. (2008). On modularity clustering. *IEEE Trans. Knowl. Data Eng.* 20, 172–188.
- Kaplan, H., Hill, K., Cadelina, R.V., Hayden, B., Hyndman, D.C., Preston, R.J., Smith, E.A., Stuart, D.E., and Yesner, D.R. (1985). Food sharing among Ache foragers: tests of explanatory hypotheses. *Curr. Anthropol.* 26, 223–246.
- Gurven, M. (2004). Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter-gatherers. *Behav. Ecol. Sociobiol.* 56, 366–380.
- McElreath, R., and Koster, J. (2014). Using multilevel models to estimate variation in foraging returns. Effects of failure rate, harvest size, age, and individual heterogeneity. *Hum. Nat.* 25, 100–120.
- Mace, R. (2000). Evolutionary ecology of human life history. *Anim. Behav.* 59, 1–10.
- Dyble, M., Salali, G.D., Chaudhary, N., Page, A., Smith, D., Thompson, J., Vinicius, L., Mace, R., and Migliano, A.B. (2015). Sex equality can explain the unique social structure of hunter-gatherer bands. *Science* 348, 796–798.
- Hill, K.R., Walker, R.S., Bozicević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., Marlowe, F., Wiessner, P., and Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331, 1286–1289.
- Hawkes, K., O'Connell, J.F., Jones, N.G., Alvarez, H., and Charnov, E.L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. USA* 95, 1336–1339.
- Allen-Arave, W., Gurven, M., and Hill, K. (2008). Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evol. Hum. Behav.* 29, 305–318.
- Wood, B.M., and Marlowe, F.W. (2013). Household and kin provisioning by Hadza men. *Hum. Nat.* 24, 280–317.
- Hooper, P.L., Gurven, M., Winking, J., and Kaplan, H.S. (2015). Inclusive fitness and differential productivity across the life course determine inter-generational transfers in a small-scale human society. *Proc. Biol. Sci.* 282, 20142808.
- Jaeggi, A.V., and Gurven, M. (2013). Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proc. Biol. Sci.* 280, 20131615.
- Ziker, J., and Schnegg, M. (2005). Food sharing at meals: Kinship, reciprocity, and clustering in the taimyr autonomous okrug, northern Russia. *Hum. Nat.* 16, 178–210.
- Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* 22, 469–493.
- Dunbar, R.I.M. (1996). Determinants of group size in primates: a general model. In *Evolution of Culture and Language in Primates and Humans*, J. Maynard Smith, G. Runciman, and R.I.M. Dunbar, eds. (Oxford: Oxford University Press), pp. 33–57.
- Hill, K.R., Wood, B.M., Baggio, J., Hurtado, A.M., and Boyd, R.T. (2014). Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PLoS ONE* 9, e102806.
- Migliano, A.B., Page, A., Gomez-Gardenes, J., Viguier, S., Dyble, M., Thompson, J., Chaudhary, N., Salali, G.D., Smith, D., Strods, J., et al. (2016). High-resolution maps of hunter-gatherer social networks reveal human adaptation for cultural exchange. *bioRxiv*. <http://dx.doi.org/10.1101/040154>.
- Hamilton, M.J., Milne, B.T., Walker, R.S., and Brown, J.H. (2007). Nonlinear scaling of space use in human hunter-gatherers. *Proc. Natl. Acad. Sci. USA* 104, 4765–4769.
- Lewis, H.M., Vinicius, L., Strods, J., Mace, R., and Migliano, A.B. (2014). High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nat. Commun.* 5, 5789.
- Chaudhary, N., Salali, G.D., Thompson, J., Dyble, M., Page, A., Smith, D., Mace, R., and Migliano, A.B. (2015). Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka Pygmies. *R Soc Open Sci* 2, 150054.
- Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal. Complex Syst.* 1695, 1–9.