Beyond the here and now: Hunter-gatherer socio-spatial complexity and the evolution of language

For Philosophical Transactions of the Royal Society, B

Author Name	ORCID	Affiliations	Email
Brian M. Wood	0000-0002-8187-9429	Department of Anthropology, University of California, Los Angeles	brianwood@anthro.ucla.edu
		Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary	
		Anthropology	
David A. Raichlen	0000-0002-4940-7886	Department of Biological Sciences & Department of Anthropology, University of Southern California	draichle@usc.edu
Herman Pontzer	0000-0003-2397-6543	Dept of Evolutionary Anthropology, Duke University	Herman.pontzer@duke.edu
		Duke Global Health Institute, Duke University	
Jacob A. Harris	0000-0001-5398-7871	School of Interdisciplinary Forensics, Arizona State University	Jacob.a.harris@asu.edu
M. Katherine Sayre	0000-0003-2554-4058	Department of Anthropology, University of California, Santa Barbara	margaret.sayre@gmail.com
Bunga Paolo		Mangola, Tanzania	
Mariamu Anyawire		Mangola, Tanzania	mariamu.anyawire@gmail.com
Audax ZP Mabulla	0000-0001-9591-5497	University of Dar es Salaam, Department of Archaeology and Heritage	aumabu@gmail.com



Abstract

Human evolutionary ecology stands to benefit by integrating theory and methods developed in movement ecology, and in turn, to make contributions to the broader field of movement ecology by leveraging our species' distinct attributes. In this paper, we review data and evolutionary models suggesting that major changes in socio-spatial behavior accompanied the evolution of language. To illustrate and explore these issues, we present a comparison of GPS measures of the socio-spatial behavior of Hadza hunter-gatherers of northern Tanzania to those of olive baboons (*Papio anubis*), a comparatively small-brained primate that is also savanna-adapted. While standard spatial metrics show modest differences, measures of spatial diversity, landscape exploration, and spatiotemporal displacement between individuals differ markedly. Groups of Hadza foragers rapidly accumulate a vast, diverse knowledge pool about places and things over the horizon, contrasting with the baboon's narrower and more homogeneous pool of ecological information. The larger and more complex socio-spatial world illustrated by the Hadza is one where heightened cognitive abilities for spatial and episodic memory, navigation, perspective taking, and communication about things beyond the here and now all have clear value.

Introduction

Evolutionary anthropologists, linguists, and cognitive scientists have suggested that changes in socio-spatial behavior accompanied the evolution of key attributes of *Homo sapiens*, including our large brains, advanced cognitive capabilities, and language (Kaplan et al. 2000; Dunbar 1998; González-Forero and Gardner 2018). These evolutionary models motivate research into functional relationships between spatial behavior, social structure, cognition, and communication, aligned with the socio-spatial interface framework advocated by Webber et al. (2023). Humans and our hominin ancestors are extreme outliers in our dependence on socially-transmitted information (Boyd, Richerson, and Henrich 2011). Following the causal paths outlined by Webber et al. (2023), we thus expect distinct patterns of spatial behavior to have emerged in our species, relative to other primates. Specifically, we hypothesize that patterns of spatial behavior have arisen that facilitate increased collection and sharing of ecological information. To examine this idea, Part 1 of this paper presents a targeted review of relevant theory and data. In Part 2, we provide an empirical comparison, using GPS data collected at a similar scale and resolution, of the movement and interaction patterns of human huntergatherers and olive baboons living in a similar savannah-woodland habitat.

Part I. The Evolution of Human Spatial Behavior and Language

Reconstructing the evolution of hominin spatial behavior is challenging, because data attesting to ancestral human landscape use is scant and fragmentary. Tentative models of the past are built through a merging of theory with data derived from studies of primatology, fossil anatomy, geology, archaeology, and ethnography. Primatological research documents the range of challenges that early hominins likely confronted, inspiring hypotheses about how adaptations to these challenges shaped human evolution. Studies of great apes are particularly relevant for phylogenetic reconstructions of early hominins.

Chimpanzees, bonobos, and gorillas all specialize in acquiring ripe fruit, and prefer rainforest habitats with short dry seasons (Nelson and Hamilton 2017). The last common ancestor of humans and African apes likely had similar dietary and habitat preferences (Ungar and Teaford 2002). Since the Late Miocene, global cooling, drying, and increased seasonality have led to the spread of grasslands and open woodlands across much of Africa (Herbert et al. 2016). Stable carbon isotopes from fossil soils indicate that over the past 6 million years, hominins in eastern Africa lived in open environments with less than 40% woody cover (Cerling et al. 2011).

Remains of early hominins in the period between 7 mya and 4 mya have been found in central and east Africa, and have been placed within the genera *Sahelanthropus*, *Orrorin*, and *Ardipithecus* (Daver et al. 2022; Richmond and Jungers 2008). Anatomical interpretations of these earliest hominins remain a focus of debate, but they appear to have been bipedal, with the skulls of *Sahelanthropus* and *Ardipithecus* indicating great ape-sized brains (Zollikofer et al. 2005; Suwa et al. 2009). Unambiguous evidence for bipedalism is found in the anatomy of *Australopithecus* species after 4 mya (Leakey and Hay 1979). When modeling how these early hominins made a living and ranged through landscapes, large primates living in open environments are especially relevant. In a less fruit-rich environment, one strategy is to consume large amounts of lower-quality vegetation. When facing seasonal fruit shortfalls, mountain gorillas, for instance, focus on abundant but low-quality fibrous leaves and terrestrial herbaceous vegetation (THV) and maintain a smaller daily travel distances than other apes (Robbins and McNeilage 2003; Watts 1984; Fossey and Harcourt 1977; Ganas and Robbins 2005). A similar strategy might have been adopted by the megadont hominin *Paranthropus* group (3-1 mya), which likely exploited low-quality C4 vegetation (Cerling et al. 2011; O'Brien, Hebdon, and Faith 2023).

Another strategy in response to decreased fruit abundance is to expand one's search for higher quality foods. Evidence for an analogous strategy is seen in comparisons of chimpanzee communities. Compared to those living in fruit-rich rainforests, chimpanzees at the far western and eastern edges of the species' range, in the savanna woodlands of Senegal and Tanzania (Mt. Assarik, Fongoli, and Ugalla, Tanzania), cover more territory, and have the largest home ranges recorded for any non-human primate (Ogawa et al. 2007; Baldwin, McGrew, and Tutin 1982).

Baboons are also a widely-used primate model for early hominins (Devore and Washburn 1963; Hamilton, Copeland, and Nelson 2024). They are an apt model for considering the ranging and sociality of australopithecines because both taxa are large-bodied, sexually dimorphic, catarrhine primates (Strum 1991). Olive baboons are ecologically diverse and widespread, inhabiting both forest and savannah habitats across Africa. Many *Australopithecus* remains have been recovered from the East African Rift Valley (Schwartz and Tattersall 2005), a region where today baboons thrive, and no great ape populations are found. For thinking about how the risks, resources, and physical features of this habitat would have influenced the spatial and social behavior of australopithecines, further consideration of the baboon model is warranted. Comparing the spatial behavior of humans and baboons today may provide insights into how our species' unique cognitive abilities, technologies, and language have changed the manner in which we make adaptive use of these landscapes, relative to a more primitive ancestral species.

Language is our species' most distinctive adaptation (Darwin 1871). A core feature of language is that it permits efficient communication about spatially and temporally remote events beyond the here and now (Hauser, Chomsky, and Fitch 2002; Bickerton 2009; Hockett 1960). The linguist Charles Hockett (Hockett 1960) argued that an exceptional feature of human language was its capacity for *displacement* -- the ability to communicate about things that are out of sight or in the past or future. By contrast, signals used in non-human communication systems typically refer to things in the immediate environment of the sender or receiver, such as the presence of a predator or a food source. Hockett considered some capacity for displaced communication to be a key precursor to the development of more complex symbolic communication. More recently, linguist Derek Bickerton (2009) highlighted the extreme rarity of displacement in animal communication systems. He argued that this feature was pivotal in the early evolution of human language. Bickerton proposed that the capacity for displacement likely evolved for sharing information about food sources located beyond the direct sensory perception of message recipients. Displacement is the feature of language we focus on here because it refers to the *where* and *when* of meanings being expressed in language, and the adaptive benefits of this rare, essential language feature hinge on how individuals interact across space and time. We hypothesize that this core feature of language is necessary only in social groups where individuals interact with others who have recently acquired dissimilar ecological and spatial information. Below, we test the prediction that human hunter-gatherer movement patterns more strongly satisfy this criteria than those observed in olive baboons.

Part 2: Human hunter-gatherer and olive baboon movement patterns

Motivated by an interest in spatial information acquisition and sharing, we use GPS measures to estimate the spatial information that individuals are exposed to. Strandburg-Peshkin et al. (2015) deployed GPS collars and tracked the movement of a troop of olive baboons at Kenya's Mpala field station over 14 days, and then shared the GPS data publicly via moveBank (Kranstauber et al. 2011). These baboon movement data now provide a valuable benchmark for cross-species and cross-community comparisons. No such data are available for any great ape. The Hadza hunter-gatherer GPS data that we analyze here is the same sample used in Wood et al. (2021), which records the movement of 179 Hadza research participants (87 females and 92 males) over 2,048 person-days of travel, ranging in age from 2 to 84 years (mean = 36, SD = 19). We refer readers to that open-access publication for full details of the sample and methods. In studies of people, ethical considerations limit the open distribution of detailed location data, highlighting the importance of quantitative, standardized data summaries in order to balance the goals of knowledge dissemination with privacy and ethical concerns.

Results

We next compare measures of daily travel, inter-individual proximity, inter-individual differences in exposure to spatial information, and collective measures of landscape exploration.

Daily Travel and Inter-Individual Proximity

The average day range for the Mpala baboons was 10.58 km (n=250, SD=1.81), higher than day ranges reported for this species in prior research (Johnson et al. 2015), likely owing to the high temporal resolution of the GPS data. This value is quite similar to the average day range of adult Hadza, which is 11 km on average for adults (males and females combined) between the ages of 18 and 50 (Wood et al. 2021). In the figure below, we plot the track of the baboon whose day range most closely matched the sample average, and her proximity to other group members throughout the day.

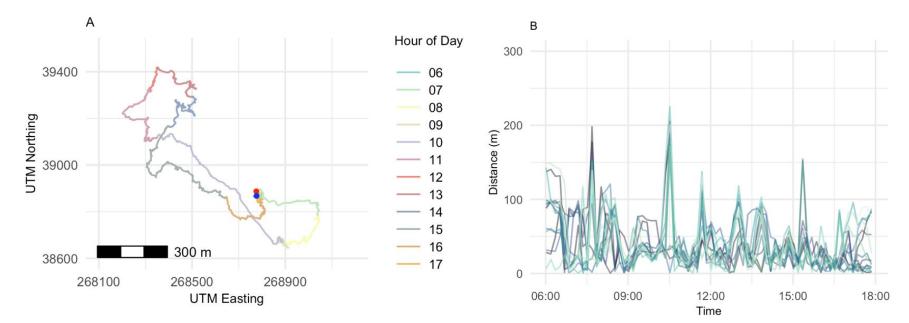


Figure 1. A) The path of an adult female olive baboon at Mpala who traveled 10.6 km on 2012-08-12, over the course of 12 hours. Her path on this day began at the location indicated by the red dot, and ended at that shown by the blue dot, only 20 meters distant. B) Proximity between this female and all other group members throughout the day, sampled at 10-minute intervals for visual clarity. Each line in B) represents her proximity to a different group member.

The Mpala baboons were central place foragers whose travel was usually tethered to the sleeping sites from which they departed in the morning and returned to at the end of the day. Across the baboon sample, the median distance between a day's start and end points of travel was only 58 meters (SD=85). Olive baboon sleeping sites are usually carefully selected for their safety and proximity to water, and are often on cliffs or high in trees, where group members are afforded greater visibility and safety from predators (Hamilton 1982).

In an early study of wild baboons, Washburn and DeVore (1961) wrote that "whether by day or night, individual baboons do not wander away from the troop, even for a few hours ... once an animal is separated from the troop the chances of death are high" (ibid: 66). Indeed, the Mpala baboons seldom ventured far from one another (Figure 1B). In the baboon sample, the median inter-individual distance was 23.1 meters (mean= 33.5, SD = 32.9, max = 407.2, n = 18,881,268). Among the Hadza, the median inter-individual distance was 301.5 meters (Fig 2A; mean=1545.8, SD = 2341.2, max=17,347.3, n = 106,429,818).

In Hadza settlements, or camps, it is normal for people to depart camp in the early morning, traveling in parties of variable sizes, searching for and harvesting resources, followed by a return back to camp in the afternoon or evening. A small subset of camp members might stay in the bush hunting all night, or leave on short visits to neighboring camps (Marlowe, 2010). These typical patterns of movement mean that the splitting and merging of Hadza social groups, reflected in inter-individual proximities, are highly structured across time, forming a general pattern of early day aggregation, daytime dispersal, and evening re-aggregation. This forms a notable contrast with baboons, where cohesive groups are observed across all hours of the day (Figure 2B); there is even a trend seen in the baboon GPS data of greater dispersion at dawn and in the evening.

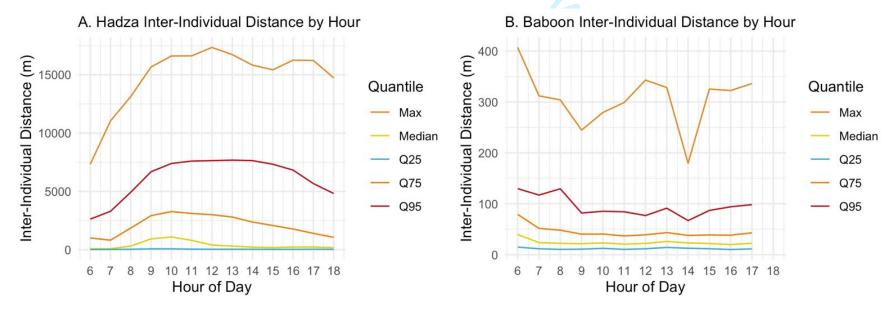
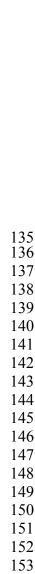


Figure 2. A) Hadza inter-individual proximities by hour (n=102,854,437) and B) Mpala baboon inter-individual proximities by hour (n=18,881,268). Please note large difference in y-axis scales.

Hadza camps are inviting places where a range of activities occur including rest, food preparation, meals, childcare, socializing, play, tool maintenance, conversation, and storytelling (Marlowe 2010). The importance of these in-camp social activities is reflected in the greater amount of time that Hadza spend very near their day's first GPS point, which was usually at the wearer's hearth (Figure 6). Twenty-five percent of the Hadza's total GPS points (i.e. 25% of their total observed time) was within 24 meters of their day's starting point, and 50% of their total time was spent within 88 meters of this point (Figure 3).



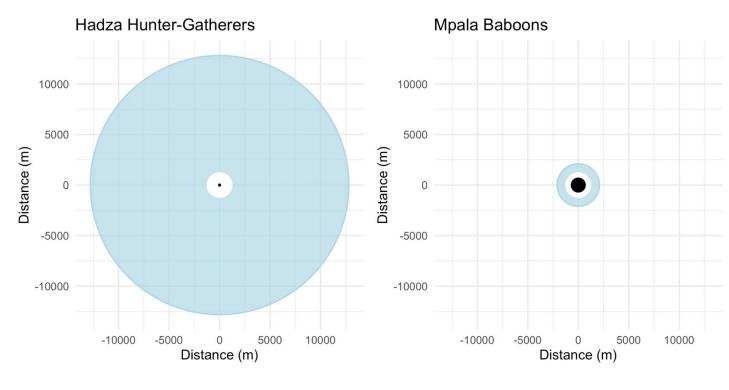


Figure 3. Time spent at different distances from each day's starting point in the Hadza hunter-gatherer and Mpala baboon samples. The black circles in the center of each plot encompass 50% of all GPS points, i.e. 50% of all recorded time, of each sample. The white circles encompass 75% of all GPS points, and the blue circles encompass 100% of each sample.

By contrast, in the olive baboon sample, the first quartile of their recorded distances extends to locations 243 meters distant from their day's starting point, and the median logged distance was 679 meters from that point. These data also attest to how much further the Hadza travel from their "central places". No baboon traveled further than 2.1 kilometers from their day's starting point, whereas 17% of the Hadza's time was spent in locations more distant than this, and the maximum distance reached by a Hadza in this sample was 12.8 kilometers. In summary, these data show that Hadza both spend more time very close to their central place, and more time very far that place (Figure 3).

Inter-Individual Differences in Exposure to Spatial Information

Here we present measures of whether individuals explore the same or different parts of the landscape on each day, which we consider a proxy for differences in exposure to spatial and ecological information. These analyses are based on raster representations of the landscape, in which we record every 10 m² cell visited by each individual, each day. For each dyad on each day, the fraction of their landscape use that is *shared* is that fraction of the total visited landscape that was visited by both individuals, and the fraction that is *different* is that proportion which was visited by one of the dyad members but not both. Our calculations show that dyads of Mpala olive baboons are much more similar in their patterns of landscape use and exposure to spatial information than are dyads of Hadza hunter-gatherers. The median shared fraction of the landscape visited per day was 0.35 in Mpala baboon dyads and just 0.04 in Hadza dyads (Figure 4).

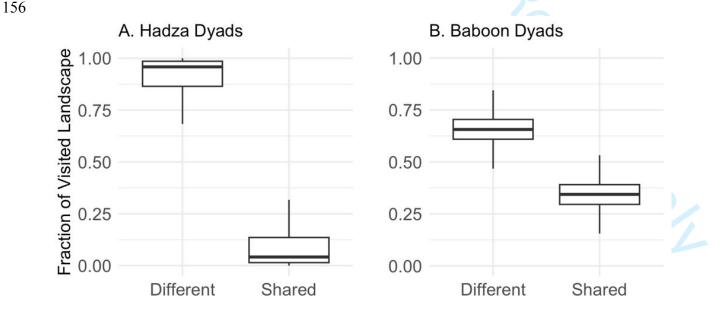


Figure 4. Dyadic measures of similarity and difference in daily landscape use by A) Hadza hunter-gatherers (n=13,656 dyads) and B) Mpala baboons (n=2,240 dyads). See methods section "Dyadic Measures of Landscape Visitation" for details of how these values were calculated.

These data show that Hadza who live in the same camp experience much greater spatial displacement from one another each day (Figure 2) and that dyads of Hadza who live and interact daily in the same group visit highly distinct areas of the landscape, relative to baboons (Figure 4). This confirms our prediction that within Hadza groups, individuals would acquire more individually-distinct (i.e. dissimilar) sets of spatial and ecological information. The Hadza's spatial behavior thus creates more possibilities for individuals to share information that is novel to others, because it was beyond others' range of travel and direct sensory perception that day.

Collective Measures of Landscape Exploration

We next consider how spatial exploration, and by extension, ecological and spatial information, accumulates in the group across individuals. We calculated the cumulative sum of total unique land visited each day, progressively considering how this value changes as we sum from 1 to N individuals whose travel was monitored each day.

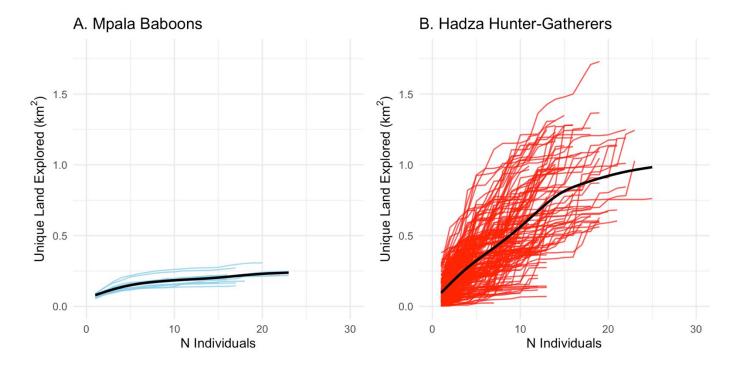


Figure 5. The cumulative amount of unique land explored per day, as a function of group size. Each line represents a unique calendar day, and its slope represents the relationship between unique land explored and additional group members. The black line represents a generalized additive model of the expected trend, fit to the data using a cubic spline.

The cohesive ranging of baboons creates a relatively homogeneous spatial and ecological experience for group members. The low slope of the trend line in Figure 5A means that additional group members provide little gain in spatial exposure, or by extension, unique spatial knowledge, at the collective level. Conversely, the Hadza's more diverse travel results in a much steeper gain of exposure to unique areas of the landscape, producing a larger and more diverse pool of spatial information at the group level.

Sex Differences in Landscape Use

A sexual division of labor, in which each gender is associated with different economic roles, is a universal feature of hunter-gatherer societies (Kelly 2013; Venkataraman et al. 2024). The sexual division of labor is one factor that helps explain why hunter-gatherers like the Hadza are expected to exhibit greater intragroup diversity in patterns of landscape use compared to non-human primates. Hadza men focus on hunting more widely dispersed and mobile resources (mammals, birds, and wild bee colonies) whereas Hadza women focus on gathering immobile and more abundant plant resources (tubers, fruit, and greens). A prior study of Hadza movement ecology (Wood et al. 2021) found that the paths that women followed while foraging out of camp were shorter and more linear, while those of Hadza men were longer and more sinuous. Here we present a comparison of geographic segregation by sex/gender. Using raster analysis, we calculated the total landscape visited, and then partitioned it into the fraction only visited by males, only visited by females, and that visited by both males and females.

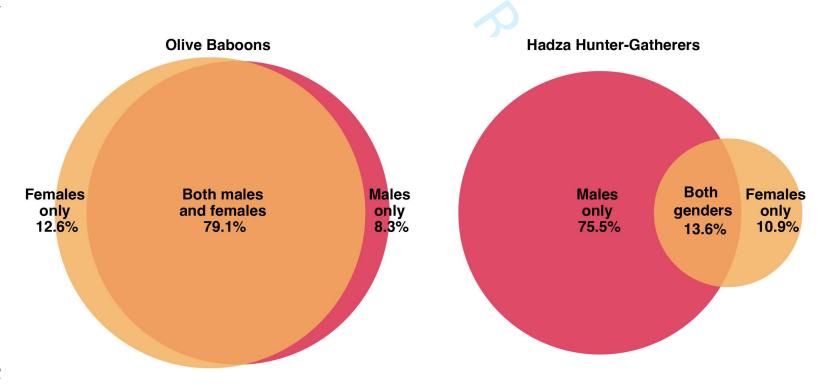


Figure 6. Similarity and difference in landscape use, aggregated by gender / sex. The Hadza measures are the average values in a study of 12 camps (Wood et al. 2021).

Figure 6 shows that gender strongly structures patterns of Hadza landscape use, and on average only 13.6% of the total landscape visited was visited by both males and females. This pattern arises because Hadza men traveled further, and usually traveled alone, whereas Hadza women traveled in groups and to fewer areas of the landscape (Wood et al. 2021). Sex is much less predictive of landscape use in baboons, and both males and females visited 79.1% of the total visited landscape at Mpala.

Discussion and Conclusion

While both Hadza hunter-gatherers and Mpala baboons inhabit similar environments in the Rift Valley and engage in central place foraging with similar daily travel distances, notable differences exist in their social interactions, travel diversity, and the accumulation of spatial and ecological knowledge at the group level. The Hadza's diverse travel patterns create opportunities for frequent interactions where individuals can share ecological information that others are unaware of. By contrast, among Mpala baboons, the "ecological news" gathered by one group member is largely equivalent to others'. The evolution of more Hadza-like patterns, we suggest, would generate conditions more conducive to communication about places and events beyond the here and now, a key adaptive feature of language.

The scenario we envision as conducive to the evolution of language involves central place foragers who travel widely and disperse during the day, and then aggregate afterward. Under what conditions would it be beneficial for such individuals to share ecological information? We have not focused on that question here, but Bickerton (2009) argued that a hominin dietary shift towards more hunting and scavenging would have generated new opportunities for mutualistic cooperation, and thus a context where individuals who could communicate with and recruit conspecifics for the defense, processing, and carrying of large animal carcasses would benefit. Because hunter-gatherers cooperate in many foraging activities, the evolution of language to coordinate joint action for harvesting resources is a compelling idea (Hill 2002; Kraft et al. 2022; Jang et al. 2024). Theoretically, one can imagine different temporal and spatial scales of dispersal and aggregation, different sorts of ecological features and adaptive challenges that may warrant cooperation and communication, and differences in the social composition of groups that would impact the costs and benefits of sharing news. This is all ripe territory for modeling, and agent-based models of social learning and information transmission are well suited to exploring these possibilities (e.g. Garg et al. (2021)).

How did the highly diverse ranging patterns of hunter-gatherers arise? As noted by Marlowe (2005), the evolution of technology -- including sharpened sticks, pikes, and spears would have improved hominin extractive foraging and hunting, predator defense, and likely changed patterns of travel. The Hadza's bows, arrows, knives, axes, and digging sticks both make their hunting and gathering more effective and protect them from the same predators that afflict baboons. The

development of such technologies is likely to have co-evolved with greater individual spatial autonomy and socio-spatial diversity, and thus, generated more contexts for the adaptive sharing of ecological information, recruitment, and spatial coordination in general. A shift towards more technologically-aided extractive foraging is likely to have also selected for larger brains (Kaplan et al. 2000). Rosati (2017) provides several examples of how foraging strategies predict cognitive traits of primates, and calls for renewed attention into how diet, foraging strategies, and ranging behaviors might influence cognition. Rosati also notes that human hunter-gatherers appear exceptional in terms of their ranging and the degree to which socially acquired information (culture) is employed in foraging strategies.

Language and storytelling are human universals, and many ethnographic studies have documented storytelling in hunter-gatherer camps (e.g. Blurton Jones and Konner 1976). Marlowe describes Hadza storytelling as both a form of entertainment and a way to convey vital information (Marlowe 2010:66). Scalise Sugiyama (2001) argues that acquiring locally adapted foraging knowledge is a key function of narrative storytelling in hunter-gatherers. In her study of Ju/hoansi storytelling, Wiessner (2014) notes that economic plans are a frequent topic discussed during daylight hours, and that events of the day are also retold by firelight at night. In their study of Agta storytelling, Smith et al. (2017) note that narrative stories often convey messages that are important for coordinating behavior and planning foraging activities. These observations align closely with our experiences in Hadza camps, where, regardless of one's luck in foraging, everyone returns to camp with a story to share.

Methods and Materials

All the code needed to reproduce this paper's figures and text-reported results are shared via the Open Science Foundation (https://osf.io/c6gr5/ DOI: 10.17605/OSF.IO/C6GR5).

Hadza GPS Data

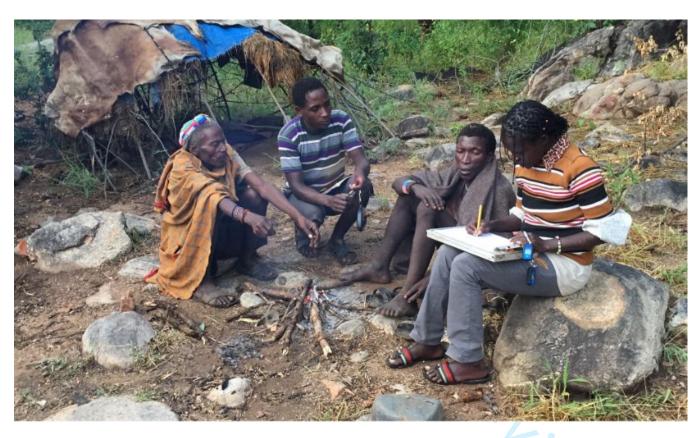


Figure 8. Co-authors BP and MA collecting GPS data using lightweight Canmore GPS devices.

Before participating in the study, all participants were informed about the research and gave their consent. This research received authorization from the Institutional Review Boards at Harvard University, Yale University, Hunter College, the University of Arizona, and the University of California, Los Angeles, as well as from the Tanzania Commission for Science and Technology and the National Institute for Medical Research in Tanzania. GPS data were collected in 15 Hadza camps between 2005 and 2018 where the residents were subsisting from hunting and gathering for the vast majority of their diet. The sample includes 2,078 person-days of travel, and 179 participants (87 female, 92 male, mean age=36). The GPS data record individuals locations every five seconds. On average, devices were put on at 07:46 and stopped recording at 18:58. Full details of the methods are shared in open access publication Wood et al. (2021).

Mpala Olive Baboon GPS Data

The baboon GPS data were collected in August 2012 and shared in moveBank. The original raw data recorded individual locations once per second, and we have resampled the data to a resolution of one location per five seconds, in order to make the temporal resolution equivalent to the Hadza data. In the moveBank data, there is one individual who has spatial data but has no corresponding demographic data provided, which is the individual 2459. This individual has been dropped from the analyses. Four other days of GPS data were excluded: the GPS data of individual 2452 on 2012-08-14 was excluded because the GPS readings were clearly in error, and the device only recorded locations for 9.5 hours that day, while all other individuals had their locations recorded for 11.9 hours. The locations of individual 2432 on 2012-08-05 were excluded because this track only recorded for 1.55 hours. The locations of individual 2450 on 2012-08-05 were excluded because they only recorded 7.1 hours of data.

Inter-individual Proximities

We calculated inter-individual proximities every five seconds on each day, for every possible dyad of individuals. Using this large dataset, we then made simple calculations of the mean, median, and standard deviation in proximity across all times and dyads, within each study location. Data from each study location was then stratified by hour (e.g. hour 7 covers 7:00:00 until 7:59:59) and quantiles of dyad distances calculated for each hour.

Dyadic Measure of Landscape Visitation

The landscape visited by each individual on each day ($L_{i,d}$) was calculated from the GPS data using the function *rasterize* in the R package *raster* (Hijmans 2019). Using these raster representations, we then measured the similarity and difference in landscape areas visited each day for each dyad. For this calculation, each 10 m² raster cell in the landscape was analyzed for each day and for each dyad (i, j) and placed into one of four sets:

- a) Visited by neither *i* nor *j*.
- b) Visited only by *i*
- c) Visited only by *j*
- d) Visited by both i and j.

Counts of the raster cells in each of these sets were made (n_a, n_b, n_c, n_d) , and a count of all cells visited by any member of the dyad $(n_e = n_b + n_c + n_d)$. The measure "fraction different" represents the fraction of the visited landscape that was visited by only one member of the dyad, and is calculated as $(n_b + n_c) / n_e$. The measure "fraction similar" is calculated as n_d / n_e and represents the fraction of the dyad-visited landscape that was visited by both members of the dyad.

Cumulative Measures of Landscape Exploration

For each study community, and for each day, we assessed the relationship between the number of individuals included in the analysis and the cumulative size of the landscape visited by that number of considered individuals. Within each day, we generated a random order of individual IDs that dictated the order by which subjects' GPS data would be entered into the analysis. For the first individual considered within a day, all the 10 m²

raster cells intersected by this individuals' path of travel are included in the cumulative metric of total landscape visitation. For the second individual, we carried out a union of the first and second individuals' rasters of land visitation, and then summed the number of raster cells in that union. We continued this process for each day until all the paths of travel for all individuals had been entered into the cumulative sum.

Sex Differences in Landscape Use

For the Mpala baboon data, we identified all the 10 m² raster cells intersected by all male tracks, and all the cells intersected by all the female tracks. Set operations were then used calculate amount of visited landscape that was visited only by males, only by females, or by both males and females. The same analyses were carried out for 12 different Hadza camps and the results across these samples averaged (Wood et al. 2021: Table 1).

Acknowledgements

We thank the Hadza community for their hospitality and support, D. Peterson, T. Peterson, C. Schmelling, N. Dowling and C. Wood. We thank A. Strandburg-Peshkin, D. Farine, I. Couzin, and M. Crofoot for collecting and sharing the Mpala Olive Baboon data.

Bibliography

Baldwin, P. J., W. C. McGrew, and C. E. G. Tutin

1982 Wide-Ranging Chimpanzees at Mt. Assirik, Senegal. International Journal of Primatology 3(4): 367–385.

Bickerton, Derek

2009 Adam's Tongue: How Humans Made Language, How Language Made Humans. Macmillan.

Boyd, Robert, Peter J. Richerson, and Joseph Henrich

2011 The Cultural Niche: Why Social Learning Is Essential for Human Adaptation. Proceedings of the National Academy of Sciences 108(supplement_2). Proceedings of the National Academy of Sciences: 10918–10925.

Daver, G., F. Guy, H. T. Mackaye, et al.

2022 Postcranial Evidence of Late Miocene Hominin Bipedalism in Chad. Nature 609(7925). Nature Publishing Group: 94–100.

Devore, I, and S.L. Washburn

1963 Social Behavior of Baboons and Early Man. *In* The Social Life of Early Man Pp. 91–105. Aldine.

Dunbar, Robin I. M.

1998 The Social Brain Hypothesis. Evolutionary Anthropology: Issues, News, and Reviews 6(5): 178–190.

Fossey, D, and A Harcourt

1977 Feeding Ecology of Free-Ranging Mountain Gorilla. *In* Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes Pp. 415–447. London: Academic Press.

Ganas, Jessica, and Martha M. Robbins
2005 Ranging Behavior of the Mountain Gorillas (Gorilla Beringei Beringei) in Bwindi Impenetrable National Park, Uganda: A Test of the Ecological Constraints
Model. Behavioral Ecology and Sociobiology 58(3): 277–288.

Garg, Ketika, Cecilia Padilla-Iglesias, Nicolás Restrepo Ochoa, and V. Bleu Knight

2021 Hunter-Gatherer Foraging Networks Promote Information Transmission. bioRxiv: The Preprint Server for Biology. Cold Spring Harbor Laboratory.

https://www.biorxiv.org/content/early/2021/04/29/2021.04.29.442031.

342 González-Forero, Mauricio, and Andy Gardner

2018 Inference of Ecological and Social Drivers of Human Brain-Size Evolution. Nature 557(7706). Nature Publishing Group: 554–557.

Hamilton, Marian I., Sandi R. Copeland, and Sherry V. Nelson 2024 A Reanalysis of Strontium Isotope Ratios as Indicators

2024 A Reanalysis of Strontium Isotope Ratios as Indicators of Dispersal in South African Hominins. Journal of Human Evolution 187: 103480.

348 Hamilton, William J.

1982 Baboon Sleeping Site Preferences and Relationships to Primate Grouping Patterns. American Journal of Primatology 3(1–4): 41–53.

351 Hauser, Marc D., Noam Chomsky, and W. Tecumseh Fitch

352 2002 The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? Science 298(5598). American Association for the Advancement of Science:

353 1569–1579.

355 Hijmans, Robert J.

2019 Raster: Geographic Data Analysis and Modeling. https://CRAN.R-project.org/package=raster.

358 Hill, K.

2002 Altruistic Cooperation during Foraging by the Ache, and the Evolved Human Predisposition to Cooperate. Human Nature-an Interdisciplinary Biosocial Perspective 13(1): 105–128.

361362 Hockett, Charles F

363 1960 The Origin of Speech. Scientific American 203(3). JSTOR: 88–97.

364365 Jang, Haneul, Cody T. Ross, Adam H. Boyette, et al.

2024 Women's Subsistence Networks Scaffold Cultural Transmission among BaYaka Foragers in the Congo Basin. Science Advances 10(2). American
 Association for the Advancement of Science: eadj2543.

Johnson, Caspian, Alex K. Piel, Dan Forman, Fiona A. Stewart, and Andrew J. King

370 2015 The Ecological Determinants of Baboon Troop Movements at Local and Continental Scales. Movement Ecology 3(1): 14.

372 Kaplan, H., K. Hill, J. Lancaster, and A. M. Hurtado

373 2000 A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity. Evolutionary Anthropology 9(4): 156–185.

375 Kelly, Robert L

376 2013 The Lifeways of Hunter-Gatherers: The Foraging Spectrum. Cambridge University Press.

378 Kraft, Thomas S., Daniel K. Cummings, Vivek V. Venkataraman, et al.

2022 Female Cooperative Labour Networks in Hunter–Gatherers and Horticulturalists. Philosophical Transactions of the Royal Society B: Biological Sciences

380 378(1868). Royal Society: 20210431.

Leakey, Mary D, and Richard L Hay

1979 Pliocene Footprints in the Laetolil Beds at Laetoli, Northern Tanzania. Nature 278(5702). Nature Publishing Group UK London: 317–323.

Marlowe, Frank W

2005 Hunter-Gatherers and Human Evolution. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews 14(2). Wiley Online Library: 54–67.

Marlowe, Frank W.

 2010 The Hadza: Hunter-Gatherers of Tanzania. University of California Press.

Ogawa, Hideshi, Gen'ich Idani, Jim Moore, Lilian Pintea, and Adriana Hernandez-Aguilar

 Richmond, Brian G, and William L Jungers 2008 Orrorin Tugenensis Femoral Morphology and the Evolution of Hominin Bipedalism. Science (New York, N.Y.) 319(5870). American Association for the Advancement of Science: 1662–1665.

2007 Sleeping Parties and Nest Distribution of Chimpanzees in the Savanna Woodland, Ugalla, Tanzania. International Journal of Primatology 28(6): 1397–1412.

Robbins, Martha M, and Alastair McNeilage

Home Range and Frugivory Patterns of Mountain Gorillas in Bwindi Impenetrable National Park, Uganda. International Journal of Primatology 24. Springer: 467–491.

Rosati, Alexandra G.

 2017 Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. Trends in Cognitive Sciences 21(9): 691–702.

Schwartz, Jeffery H, and I Tattersall

2005 The Human Fossil Record. Vol. 4: Craniodental Morphology of Early Hominids (Genera, Australopithecus, Paranthropus, Orrorin), and Overview. NJ: John Wiley & Sons.

Strum

1991 Weight and Age in Wild Olive Baboons. American Journal of Primatology 25(4): 219–237.

Suwa, Gen, Berhane Asfaw, Reiko T Kono, et al.

2009 The Ardipithecus Ramidus Skull and Its Implications for Hominid Origins. Science (New York, N.Y.) 326(5949). American Association for the Advancement of Science: 68-68e7.

Ungar, Peter, and Mark Teaford

 2002 Human Diet: Its Origin and Evolution. USA: Bloomsbury Publishing.

Venkataraman, Vivek V., Jordie Hoffman, Kyle Farquharson, et al.

Female Foragers Sometimes Hunt, yet Gendered Divisions of Labor Are Real: A Comment on Anderson et al. (2023) The Myth of Man the Hunter.

Evolution and Human Behavior. https://www.sciencedirect.com/science/article/pii/S1090513824000497.

Watts, David P 1984 Composition and Variability of Mountain Gorilla Diets in the Central Virungas. American Journal of Primatology 7(4). Wiley Online Library: 323–356.

Webber, Quinn MR, Gregory F Albery, Damien R Farine, et al.

2023 Behavioural Ecology at the Spatial–Social Interface. Biological Reviews 98(3). Wiley Online Library: 868–886.

Wood, Brian M., Jacob A. Harris, David A. Raichlen, et al.

 2021 Gendered Movement Ecology and Landscape Use in Hadza Hunter-Gatherers. Nature Human Behaviour 5(4): 436–446.

Zollikofer, Christoph PE, Marcia S Ponce de León, Daniel E Lieberman, et al.

 2005 Virtual Cranial Reconstruction of Sahelanthropus Tchadensis. Nature 434(7034). Nature Publishing Group UK London: 755–759.

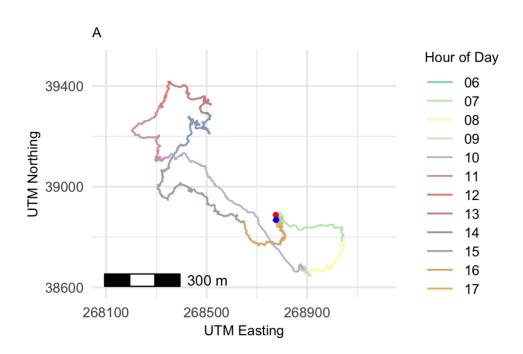


Figure 1. A) The path of an adult female olive baboon at Mpala who traveled 10.6 km on 2012-08-12, over the course of 12 hours. Her path on this day began at the location indicated by the red dot, and ended at that shown by the blue dot, only 20 meters distant. B) Proximity between this female and all other group members throughout the day, sampled at 10-minute intervals for visual clarity. Each line in B) represents her proximity to a different group member.

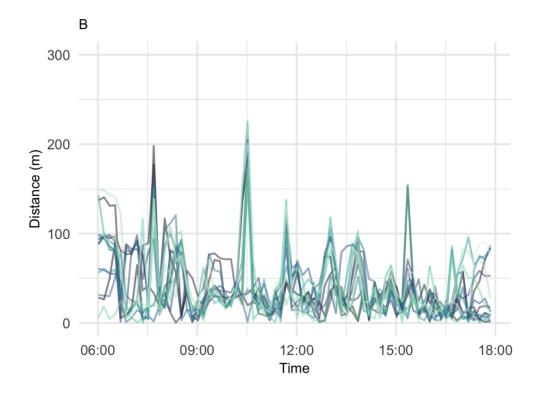


Figure 1. A) The path of an adult female olive baboon at Mpala who traveled 10.6 km on 2012-08-12, over the course of 12 hours. Her path on this day began at the location indicated by the red dot, and ended at that shown by the blue dot, only 20 meters distant. B) Proximity between this female and all other group members throughout the day, sampled at 10-minute intervals for visual clarity. Each line in B) represents her proximity to a different group member.

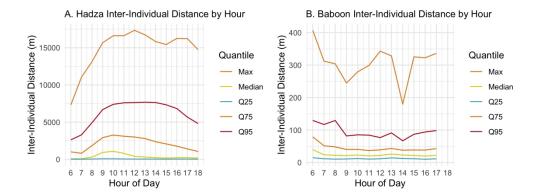


Figure 2. A) Hadza inter-individual proximities by hour (n=102,854,437) and B) Mpala baboon inter-individual proximities by hour (n=18,881,268). Please note large difference in y-axis scales.

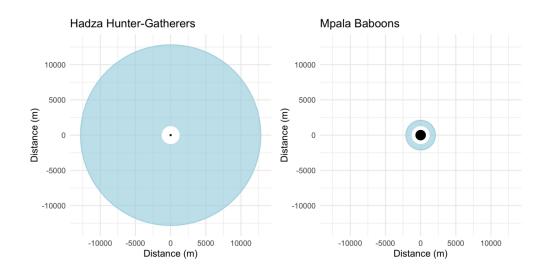


Figure 3. Time spent at different distances from each day's starting point in the Hadza hunter-gatherer and Mpala baboon samples. The black circles in the center of each plot encompass 50% of all GPS points, i.e. 50% of all recorded time, of each sample. The white circles encompass 75% of all GPS points, and the blue circles encompass 100% of each sample.

846x423mm (72 x 72 DPI)

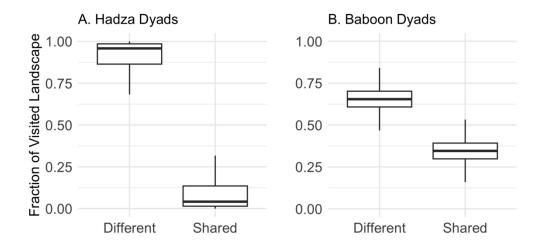


Figure 4. Dyadic measures of similarity and difference in daily landscape use by A) Hadza hunter-gatherers (n=13,656 dyads) and B) Mpala baboons (n=2,240 dyads). See methods section "Dyadic Measures of Landscape Visitation" for details of how these values were calculated.

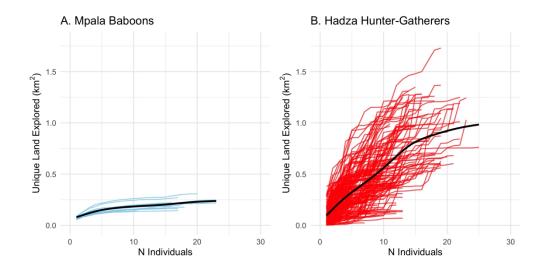


Figure 5. The cumulative amount of unique land explored per day, as a function of group size. Each line represents a unique calendar day, and its slope represents the relationship between unique land explored and additional group members. The black line represents a generalized additive model of the expected trend, fit to the data using a cubic spline.

705x352mm (72 x 72 DPI)

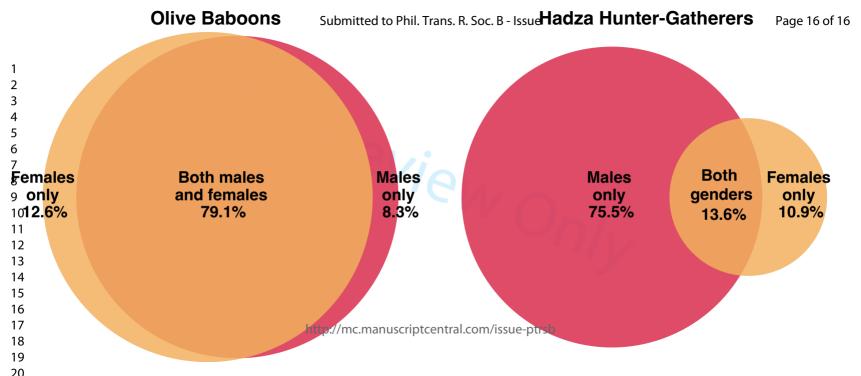




Figure 8. Co-authors BP and MA collecting GPS data using lightweight Canmore GPS devices. 143x85mm~(144~x~144~DPI)