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Statistical Self-Similarity in the Structural Organization of Human Forager Populations

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Introduction

From about 2.5 million years ago until the development of agriculture in the Near East ca. 12,000 years ago, all members of the Genus *Homo* were foragers; that is to say all resources, dietary or otherwise, were either hunted or gathered directly from the environment. As such, the study of contemporary foragers plays a prominent role in anthropology as foraging served as the primary socio-economic framework for the majority of human biological and cultural evolution. Importantly, although there is much cultural and behavioral diversity within the human foraging niche worldwide, foraging populations are usually 1) residentially mobile, in that they move camp several times a year (from an extreme of every few days, to once or twice a year), and 2) politically egalitarian, meaning that political structure is relatively simple in that political power is achievement-based, non-hereditary, and temporary. This second point is particularly important, as population structure is not simply the consequence of top-down political organization, but the bottom-up consequence of interactions between fitness-enhancing individuals.

Although population structure is recognized as fundamental to most evolutionary and ecological processes, remarkably little is known about the general structural properties of foraging populations due to the lack of available data. While anthropologists have long understood that the majority of foraging populations are internally structured, fissioning and fusing into different group sizes throughout the year due to resource availability and maintaining social bonds in fragmented populations, there have been few discussions of the potential underlying mechanisms involved. Traditionally, forager group sizes have been characterized by Birdsell's "magic numbers" of 25 and 500 for small and large groups, respectively (Kelly 1995). However, even though these numbers have almost become Anthropological lore there is little theoretical or empirical evidence to support their validity as global estimates (Kelly 1995). Moreover, recent studies of the grouping behavior of both human and non-human primates hint at a far deeper structural complexity than Birdsell's magic numbers suggest (Zhou *et al* 2005). These studies show that within the Order Primates, populations are commonly structured into a hierarchical

series of sub-groups, the size of which often correlates with neocortex volume (Hill and Dunbar 2002). Furthermore, using a mixture of experimental and available ethnographic data, these studies suggest that human social organization follows a similar hierarchical structure with a geometric series of group sizes at a constant scaling ratio of around 3.5 (Zhou *et al* 2005). This pattern implies self-similarity, a hallmark of an overall fractal structure.

The introduction of fractal statistics has been an important development in the life sciences, though rarely employed in the social sciences. Fractal structures are common in nature (Mandelbrot 1982) and have been central to understanding the mechanics of as diverse systems as river drainage networks (Rodriguez-Iturbe and Rinaldo 1997, Turcotte 1997), leaf structure (Pelletier and Sornette 2002), the human genome (Garte 2005), and ecological allometry (Brown *et al* 2002, 2004, Marquet *et al* 2005, West *et al* 1997, 1999, West and Brown 2005). Systems that exhibit fractal dimensions are often termed complex systems, or complex adaptive systems in biology. Such systems are characterized by telltale mathematical properties, or emergent structures, such as power law distributions and the structural self-similarity of component parts (either true or statistical). Recently, it has been proposed that fractal-like branching structures are a common feature of life (West *et al* 1997, 1999). In this model fractal structures emerge as a consequence of natural selection, which has designed the supply networks that sustain life to optimize efficiency by maximizing space and optimizing flow. Such systems are characterized by three features: 1) a self-similar branching structure; that 2) terminates in size-invariant units; and 3) is shaped by the process of natural selection (West *et al* 1999).

Research Questions

Given there is evidence to suggest that hierarchical population structures may be common to both non-human and human primates, there is reason to believe that forager population structure may exhibit fractal properties. In this paper we test the hypothesis that human foraging population structures are fractal, and that the fractal dimension γ is space-filling, such that $\gamma = 2$. We test this hypothesis in the wider context of examining whether human foraging populations are characterized by West *et al*'s (1999) three criteria of complex adaptive systems outlined above. We proceed first, by assuming individual foragers maximize space. This is a realistic assumption for any species that exhibits a positive territory size-fitness relationship and follows from fundamental principles of Darwinian evolution: If fitness is defined as the differential ability of organisms to convert resources into viable offspring, and if the primary determinant of resource availability is space, then space per individual will be maximized. There is empirical evidence that this is true for human foragers where juvenile survival to age at maturity (a key determinant of fitness) is correlated positively with home range size (data not shown). As there is no *a priori* reason that space-filling structures should be fractal (Murray 2001), we test our hypothesis by focusing on the potential self-similarity of the population structure. Our primary question of interest is then: As foragers optimize their use of space in order to maximize fitness, how is this reflected in population organization given the genetic and social structure of foraging populations, seasonally varying resource availability, the cost/benefit structure of social grouping, and intra-specific competition for finite resources?

Data

We synthesized newly available data from published sources (Binford 2001, Kelly 1995) representing a global sample of recent human forager populations (total number of populations $n = 348$; total number of sub-groups $N = 1555$) and analyzed the statistical properties of their

structure using Horton's Laws of network composition (Rodriguez-Iturbe and Rinaldo 1997, Turcotte 1997). Forager populations were separated into six levels of organization $\Omega = 6$. In the Horton-Strahler numbering system these levels of organization are termed Horton-Strahler orders ω_i , where $\omega_i \leq \Omega$ (Rodriguez-Iturbe and Rinaldo 1997):

- 1) Individuals ω_1 , the number of individuals per population.
- 2) Families ω_2 , the number of families per population; parents and dependent offspring.
- 3) Dispersed groups ω_3 , the smallest size of social foraging group per year, usually during the dry season.
- 4) Aggregated groups ω_4 , the largest aggregation of individuals per year, commonly during the winter months, though if water availability is scarce, aggregations can occur during the dry months, for example among aboriginal groups from the arid zone of central Australia. For more sedentary populations ω_4 is the size of semi-permanent villages that last for approximately two years (Binford 2001).
- 5) Multi-groups ω_5 , periodic large aggregations of individuals that occur every few years, commonly for marriage alliances, trading, information exchange etc. These aggregations are not subsistence-based (Binford 2001).
- 6) Total populations ω_6 , the largest social unit that individuals of ω_1 recognize as belonging to. Commonly populations are either discrete cultural or linguistic groups. By definition $\bar{N}(\omega_6) \equiv 1$ for all populations.

These levels of organization are anthropologically relevant, in that they are commonly used social units of analysis. Each order ω consists of N sub-groups. Let $\bar{N}(\omega_i)$ be the average number of subgroups of order ω_i in population n_i . For example, $\bar{N}(\omega_1)$ is the average number of individuals, and $\bar{N}(\omega_4)$ is the average number of aggregated groups in population n_i . Each population n has a territory size A km², such that the inverse density $(\bar{N}/A)^{-1} = D^{-1}$ gives the average area per individual in units of km². Assuming territories are approximately circular, it then follows that $\bar{L}_D = \sqrt{D^{-1}}$ gives the mean linear dimension of inverse density and $\bar{L}_A = \sqrt{A}$ gives the mean linear dimension of territory size for the total population. Frequency distributions of the numbers of individuals (and sub-groups) per order for all orders were log normal, such that data were normalized to the natural logarithmic scale, and the following analyses were conducted using geometric means and multiplicative variances (the exponentiated means and variances of the normalized data).

Methods

Our statistical analysis proceeded in four stages.

1) *Validity of analytical units*: The number of individuals N per organizational level ω were analyzed across the samples using one-way ANOVAs with Bonferonni adjustments to establish whether orders were statistically discrete, and therefore valid analytical units for this sample.

2) *Number of sub-groups per order (population structure)*: The potential self-similarity of population structure was examined by constructing Horton-Strahler bifurcation ratios between all sub-groups in all populations,

$$R_B = \frac{\bar{N}(\omega_i)}{\bar{N}(\omega_{i+1})}. \quad (1)$$

This procedure resulted in five lognormal distributions of bifurcation ratios ($R_{s,1}$ = families/individuals, $R_{s,2}$ = dispersed groups/families etc.). The geometric means $\bar{R}_{B,i}^*$ of these distributions were then examined by taking the overall mean $\langle \bar{R}_B^* \rangle$ and 99% confidence intervals of the five geometric means. Population structure was considered statistically self-similar if all $\bar{R}_{B,i}^*$'s fell within $\langle \bar{R}_B^* \rangle \pm 99\%$ confidence intervals.

3) *Linear dimension of sub-groups (spatial structure)*: Horton's length law,

$$R_L = \frac{\bar{L}(\omega_{i+1})}{\bar{L}(\omega_i)} \quad (2)$$

was approximated by the slope b of the linear regression equation

$$\log(\bar{L}_A) = \log(\bar{L}_D) + \omega b, \quad (3)$$

where \bar{L}_n and \bar{L}_D are averages over the entire sample. Estimates were required of equation 2 as the available data on human foragers includes spatial information only at the individual level ω_1 (density) and total population size ω_6 (total territory). Equation 3 approximates R_L by anchoring the slope at ω_1 and ω_6 , and therefore assumes R_L is constant between all orders, though the value of the slope b is free to vary.

4) *Ratio of population structure to spatial structure (fractal dimension)*: From equations 2 and 3, the average fractal dimension γ over all populations is then given by

$$\langle \gamma \rangle = \frac{\log(R_B)}{\log(R_L)} \quad (4)$$

such that if the population structure is fractal, $N \propto L^{\langle \gamma \rangle}$.

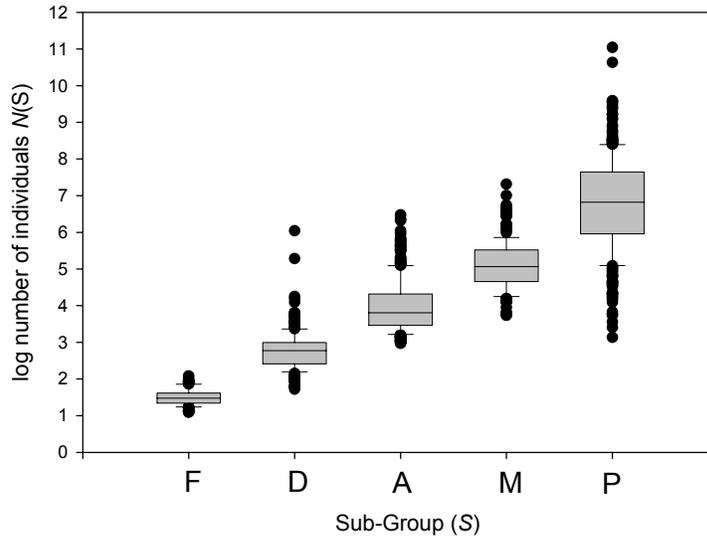


Figure 1. Boxplot of the mean number of subgroups per order $\bar{N}(\omega_i)$: F = family, D = dispersed group, A = aggregated group, M = multi-group, and P = population.

Results

Results are presented in order of the five stages of analysis.

1) All six orders ω were statistically discrete (ANOVA $F = 909.27$, $p < 0.001$, $df = 1197$, All Bonferonni comparisons $p < 0.01$, Figure 1) indicating that not only is the use of sub-group as the analytical unit anthropologically relevant, but also statistically relevant.

2) The bifurcation ratios between each sub-group are given in table 1. As $\langle \bar{R}_B^* \rangle = 3.8 \pm 0.8$, all $\bar{R}_{B,i}^*$'s fall within the 99% confidence intervals and we conclude population structure is statistically self-similar.

3) The slope of equation 3 was $b = 1.975 \pm 0.03$.

4) The resulting mean fractal dimension of the global sample of foraging populations included in this analysis is given by $\langle \gamma \rangle = \log(3.8) / \log(1.98) = 1.96 \pm 0.27$. As the confidence limits around the sample mean easily encompass the theoretical value $\gamma = 2$, we fail to reject the null hypothesis and conclude that across all samples, the structural properties of human forager populations are consistent with a space-filling fractal. Note that this result follows necessarily from result 2, and the assumption of individual space maximization (see "Introduction"). As the linear dimension L_D of population territory size A is $L_A = \sqrt{A}$ and the linear dimension L_D of the mean area per individual is estimated by $L_D = \sqrt{D^{-1}}$, where $D^{-1} = A/N$ there is a linear relationship between territory size A and population size N . Therefore, as long as R_L is a constant, the ratio $\log R_B / \log R_L = \gamma = 2$. In other words, as long as the population structure is self-similar the overall population organization will be fractal, and that fractal will be space filling given our estimation of $\sqrt{D^{-1}}$.

Table 1. Average number of sub-groups per order, individuals per sub-group, and bifurcation ratios.

Order	Sub-group	$\bar{N}(\omega_i)^+$	$\bar{N}(\omega_1)/\bar{N}(\omega_i)^*$	R_B^+
ω_1	Individual	869.65	1.00	-
ω_2	Family	165.14	5.27	4.5
ω_3	Dispersed Group	53.79	16.17	3.5
ω_4	Aggregated Group	16.04	54.21	3.0
ω_5	Multi-Group	4.48	194.13	3.4
ω_6	Population	1.00	869.65	4.6

Mean $R_B = 3.8 \pm 0.8$ 95% CI

⁺ Number of sub-groups per order

^{*} Number of individuals per sub-group

⁺ Bifurcation ratio, equation 1

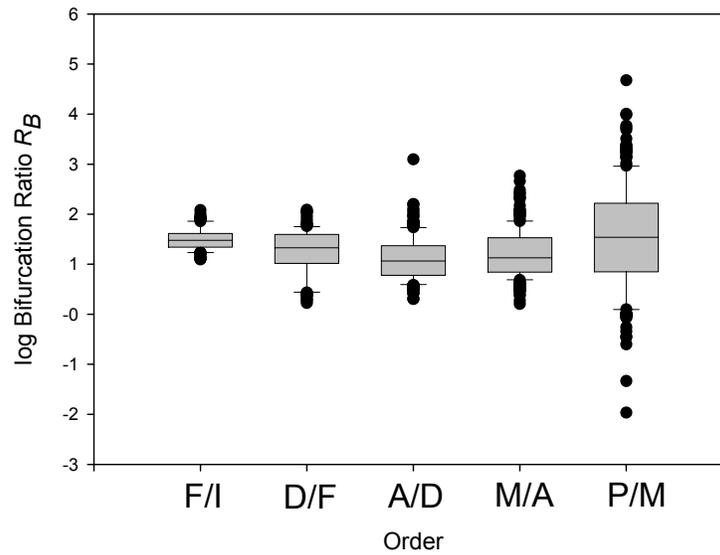


Figure 2. Boxplot of bifurcation ratios (equation 2) between sub-groups. I = individual, all other capital letters as in Figure 1.

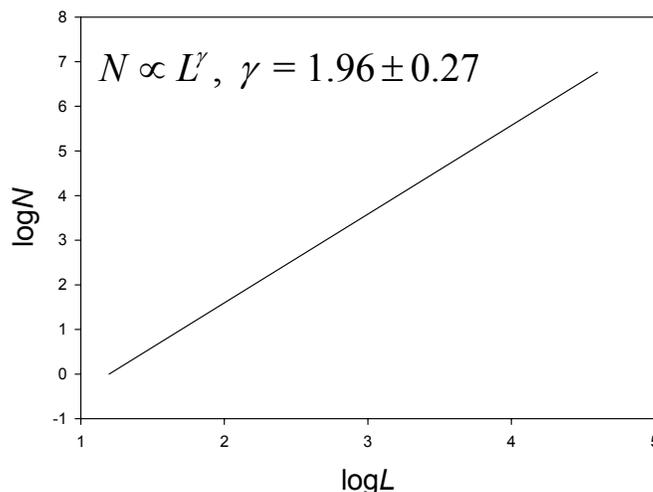


Figure 3. Log-log plot of the function describing the number of sub-groups per population as a function of the linear dimension of area, equation 4.

Discussion

Our analysis demonstrates that human forager populations are statistically self-similar, in that hierarchical sub-groupings are of the same size when suitably rescaled by some constant, and in our case that constant is given by equation 1, where $R_b \approx 4$. Further, our analysis demonstrates that the self-similarity of sub-groups results in a branching structure that can be described as a space-filling fractal with dimension $\gamma = 2$. However, an exact anthropological interpretation of $\gamma = 2$ is complicated by the fact that the structure we are concerned with is largely abstract. Unlike a river drainage basin, for example, which has both a measurable branching structure (streams) and currency (water flow), forager population structure has no such tangible form. An individual born into a population simultaneously belongs to several levels of social organization based on genetics (family), resource availability (dispersed and aggregated groups), and social structure (multi-groups and total populations), but move among these organizational levels through time as necessity dictates. The anthropological or biological currency that flows through the population resulting in this hierarchical branching structure must also be abstract, though tangible enough to have real-world consequences.

One such currency might be fitness. We began by assuming foragers maximize space in order to maximize fitness, given the Darwinian relationship between resource availability and the production of viable offspring. However, humans are not solitary animals, nor do they exist in totally homogenous environments. One of the most conspicuous aspects of the evolution of human behavior is sociality, and most foraging populations hunt and gather in small groups, which both maximizes return rates (measured as calories gained per unit time, or some equivalent currency) and allows for reciprocity through sharing, which buffers individuals from potentially catastrophic shortfalls in foraging returns. Therefore, social behavior is central to the human foraging dietary niche. Of course, at some point if group sizes ω_3 become too large, foraging returns decline per individual, leading to intra-specific competition and a loss in fitness, such that mean group size should approach an optimum over time. Additionally, in most parts of

the world resource availability varies throughout the year, requiring that individuals either disperse into smaller groups, or congregate into larger groups. This fission-fusion process must occur within the same evolutionary context, such that it is reasonable to assume there should be an optimal larger group size ω_4 as well as the smaller foraging group size ω_3 . However, above this point in the population structure, social aggregations are not resource based, and as such there is no reason to think that the sizes of multi-group aggregations ω_5 should be related to the lower level resource-based optima.

Implicit to the discussion thus far is that group behavior (foraging and sharing) optimizes fitness by maximizing an individual's access to resources. If fitness is optimized by other less tangible currencies in addition to resources, such as the sharing of knowledge, technological skills, and information as well as the creation of social alliances and political influence, these effects may constrain resource flow, and have effects on higher levels of social organization. There is some evidence to suggest that cognitive capacity in primates (and possibly other taxa, see Dunbar and Bever 1998) may constrain group size by limiting the amount of neural processes available to social interactions (Dunbar 1998, Zhou *et al* 2005). This pattern is evidenced by a consistent scaling relationship between the neocortex size of many primate species and the average size of social groups (Kudo and Dunbar 2001). Based on the neocortex size of humans Hill and Dunbar (2002) predict that human social groups should average around 150 individuals, and present experimental evidence to suggest this may be true for some sectors of modern societies. Interestingly, in the present study, the multi-group ω_5 is the largest social aggregation that occurs on a frequent basis, with $\bar{N}(\omega_5) \approx 164$, a figure remarkably close to the predicted value of 150. Additionally, the bifurcation ratio $R_B = 3.8 \pm 0.8$ in this study is statistically indistinguishable from that in Zhou *et al* (2005) of 3.5.

Regardless of whether or not population structure is an emergent property of the cognitive capacity of the human brain, a possible neocortex-group size scaling relationship predicts neither self-similarity *a priori*, nor the scaling of that self-similarity, $R_B = 3.8 \pm 0.8$. While an analytical approach to these questions is beyond the scope of this paper, we raise a few factors that may play a role in such an explanation. The first two orders of the population structure are the individual ω_1 and family ω_2 levels, and the bifurcation ratio between these levels $\bar{R}_{B,1}^* = 4.5$. This value is a function of several life history traits including the total fertility rate, juvenile survival to maturity, the female reproductive lifespan, and the mean age at first marriage. For example, if we assume a female is expected to give birth to an average of 5 offspring over her reproductive lifetime of about 25 years, the survival rate of which is about 60%, and the mean age at marriage is 20, in the first 20 years of her reproductive period she will produce 4 offspring, of which slightly more than 2 will be expected to survive. Assuming monogamous marriage partnerships, at any given time a family should average 2 parents, and about 2 dependent offspring, hence $\omega_2 = 4$. Central to human life history is the fact that offspring are entirely dependent on parental investment for the first few years of life and do not achieve independence until well into the second decade of life (Kaplan *et al* 2000). As such, families are the modular unit of forager population structure as it is not necessarily individuals that fission and fuse into different group sizes, but entire families. Therefore, we would expect that the number of individuals in successive orders of the population structure should be multiples of 4, though why this translates into a geometric series of around 4 is unclear.

A second insight into this pattern comes from the random model of drainage formation in the Horton-Strahler numbering scheme. In a random model the bifurcation ratios of a river basin

will approach $R_b = 4$ asymptotically, for large ω , regardless of substrate due to the mechanics of maximizing flow and minimizing friction (Rodriguez-Iturbe and Rinaldo 1997, Yekutieli and Mandelbrot 1994, Yekutieli *et al* 1994, but see Veitzer and Gupta 2000). As river drainages occur in two-dimensional space, the resulting fractal dimension of the random model is $\gamma = 2$. These numbers are statistically identical to the results of our analysis, suggesting that the self-similarity of forager population structure may be the result of analogous random processes occurring over time, due to the flow of fitness enhancing information and resources through the population, though the mechanisms involved will, of course, be very different in detail. Additionally, given the abstract nature of population structure, the asymptotic behavior of R_b may also be inappropriate.

Although the anthropological and biological mechanisms behind the self-similar structure of human forager populations remain elusive, the empirical scaling-relationship is robust. The implication that human group sizes may be related to the cognitive constraints of the primate neocortex, and fuelled by the evolution of the human foraging niche suggests this structure may have deep evolutionary roots. Of course, the evolutionary history of this population structure would be hard to establish solely from fossil hominid material, but may be a question addressed through a combination of archaeology, paleoanthropology, and paleoecology. The self-similarity, and fractal structure of this system demonstrate that human forager population structure is a complex adaptive system, where the structure is an emergent property of the behavior of the component parts. We suggest that the complex system explored in this paper bears a striking resemblance to broader families of complex adaptive systems, from protein networks to ecosystems that are characterized by hierarchical modularity (Hartwell *et al* 1999, Ravasz and Barabasi 2003, Ravasz *et al* 2002) and a consistent set of component mechanisms, including self-similar branching networks, and size-invariant units, shaped over evolutionary history by the process of natural selection (West *et al* 1997; 1999, Brown *et al* 2002).

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