

Collective Computation, Information Flow, and the Emergence of Hunter-Gatherer Small-Worlds

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Abstract: Two key features of human sociality are anatomically complex brains with neuron-dense cerebral cortices, and the propensity to form complex social networks with non-kin. Complex brains and complex social networks facilitate flows of fitness-enhancing energy and information at multiple scales of social organization. Here, we consider how these flows interact to shape the emergence of macroscopic regularities in hunter-gatherer macroecology relative to other mammals and non-human primates. Collective computation is the processing of information by complex adaptive systems to generate inferences in order to solve adaptive problems. In hunter-gatherer societies the adaptive problem is to resolve uncertainty in generative models used to predict complex environments in order to maximize inclusive fitness. The macroecological solution is to link complex brains in social networks to form collective brains that perform collective computations. By developing theory and analyzing data, the author shows hunter-gatherers bands of ~16 people, or ~4 co-residing families, form the largest collective brains of any social mammal. Moreover, because individuals, families, and bands interact at multiple time scales, these fission-fusion dynamics lead to the emergence of the macroscopic regularities in hunter-gatherer macroecology we observe in cross-cultural data. These results show how computation is distributed across spatially-extended social networks forming decentralized knowledge systems characteristic of hunter-gatherer societies. The flow of information at scales far beyond daily interactions leads to the emergence of small-worlds where highly clustered local interactions are embedded within much larger, but sparsely connected multilevel metapopulations.

Key words: complex adaptive systems; hierarchically modular networks; collective brains; macroecology; allometry; mammals; primates

1 Introduction

A central goal of evolutionary anthropology is to develop mechanistic theories that explain how flows of energy and information between humans and their environments create the diversity we observe in the archaeological and ethnographic records. There are multiple theoretical approaches to this problem. Some of the first formal work in this area used the mathematics of population genetics to model the interaction of

cultural and genetic transmission processes in human populations^[1, 2], leading to rich theories of dual-inheritance, cultural evolution, and cumulative culture^[3, 4]. Despite parallel developments in human behavioral ecology^[5, 6], it was not until the development of niche construction in the 1990s that the importance of ecology to cultural evolutionary theory was fully realized^[7–9]. More recent work considers the impact of networked interactions on the transmission of information in both human and non-human systems^[10–13]. Related research in complex adaptive social systems describes how networks of social interactions lead to the emergence of the nonlinear scaling behavior that characterizes the growth and size of many human social systems^[14–20].

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Similarly, studies of information transmission in hunter-gatherer societies now often focus on the complex structure of social networks^[21–24]. Detailed insights come from ethnographic case studies that explicitly model the flows and consequences of information transmission through real-world interaction networks including the fitness consequences of network position^[25], the role of cooperation^[26], the shared knowledge of plants^[27], the importance of story-telling^[28, 29], and the accelerated pace of cultural evolution in multilevel social networks^[30].

In this paper the author hopes to contribute another perspective to this research by taking a complex adaptive systems approach designed to understand how computation, energy, and sociality interact to shape large-scale macroscopic regularities of hunter-gatherer macroecology. Specifically, this paper asks how energy and information flows at the individual level scale up to shape the large-scale organization of hunter-gatherer metapopulations. The processing of energy and information across levels of social organization is what we refer to here as *collective computation*. More generally, collective computation is the ability of complex adaptive systems to compute solutions to problems by accumulating, aggregating, and deploying information across scales^[31]. For example, the brain performs collective computations by aggregating the firing of individual neurons to perform complex behavioral responses to external stimuli^[32, 33]. Collective computation plays a central role in Bayesian theories of the brain where sensory information that the brain receives from interacting with the world is used to update models built from prior experience^[34]. Predictions are then made by deploying updated information to produce increasingly accurate generative models of the world with obvious fitness consequences^[35–37].

Computations are energetically expensive, and so the costs of information processing are integrated into the energy budgets of complex adaptive systems, from the increased metabolic costs of fueling large human brains^[38] to the ecological costs of supporting populations^[18]. These trade-offs lead to the optimizations we are interested in here. The costs and benefits of large brains play a central role in evolution of human ecology at all scales, from the scheduling of the human life history^[39] and the optimization of foraging

behaviors^[40], to the formation of social networks and their distribution across landscapes^[18, 23]. Indeed, the propensity of humans to form social networks has been central to the evolution of human ecology as cooperation and learning aggregate and amplify the knowledge, skill, and experience accrued by individuals over their lifetimes.

1.1 Hunter-gatherer complex adaptive systems

Hunter-gatherer societies are perhaps definitive examples of complex adaptive systems^[41]. Hunter-gatherer populations self-organize to form multiscale societies^[42] composed of autonomous agents seeking to maximize inclusive fitness by interacting with each other and their environments. Time-scale separation in rates of interaction at these multiple scales leads to the emergence of macroscopic regularities that appear in data as correlations across multiple levels of social organization and the environmental regulatory systems on which they rely^[18]. Hunter-gatherer societies are thus best thought of as metapopulations formed by the constant interaction of families, groups, and subpopulations, as individuals seek to optimize their time, energy, and opportunity budgets. Human behavioral ecologists have built deep mechanistic theories of these optimizations including foraging behavior, time allocation, social learning, parental investment, and patch residence time, many of which are summarized in Ref. [40]. While behavioral ecology models derive these optimizations, collective computation is the process by which statistically sufficient regularities are extracted from environmental signals and used to evaluate decision variables. The macroecological perspective we pursue here coarse-grains over these local optimizations to focus on how social groups solve the overall adaptive problem of predicting regularities in stochastic environments through collective computation.

1.2 Traditional knowledge as collective computation

A common feature of many ethnohistoric hunter-gatherer societies are *knowledge systems*^[43] that integrate social, ecological, and environmental information into cohesive cultural belief traditions^[44–46]. Here, knowledge accumulated over generations essential to survival and cultural identity are encoded into norms of behavior, craft, kinship, mythology, art,

and ritual^[29, 47–49]. The resulting traditions of belief are central to hunter-gatherer adaptations and are transmitted rigorously and systematically across generations. The “Dreaming” traditions common to many Aboriginal Australian hunter-gatherers provide a prime example^[50]. In Dreaming cultures, from birth, individuals are embedded in living landscapes of mythical events and inherit custodial obligations to a particular region of the landscape and all the sacred knowledge it contains^[51]. Landscapes are overlain by networks of songlines, or dreaming tracks, created by the epic journeys of Ancestral beings as they travelled across the country forming rivers, mountains, springs, plants, and animals^[52]. Dreaming tracks often extend across the territories of neighboring groups and some traverse the entire continent. These songline networks form mental maps that link locations, people, and resources in space and can only be traversed by memorizing the appropriate song cycles^[51, 53, 54] in a tradition often described as “singing up” the landscape^[55]. Stars and constellations are then used to build star maps facilitating travel along dreaming tracks^[56–58]. People thus have the ability to travel far beyond their familiar landscapes by learning the appropriate song cycles from the appropriate custodians of the landscapes they will be traversing. Dreaming tracks, star maps, and song cycles create multidimensional virtual worlds through which individuals navigate their social, biological, and physical environments. Thus, all individuals from birth are nodes in a vast network that extends across the entire continent, the properties of which are encoded in local belief systems and maintained for millennia^[51]. These traditions allow individuals to build detailed inferential models of resources, people, and landscapes far beyond local experience. In this sense, a dreaming tradition is a collective computation that solves the adaptive problem of detecting, extracting, and storing regularities from a dynamic, stochastic, fluctuating social and physical environment, by encoding accumulated information into culturally-inherited knowledge systems.

1.3 Tinbergen’s four questions

The goal of this paper is to develop an intuition into the role collective computation and information flow plays in structuring hunter-gatherer macroecology at multiple spatial-temporal scales. To do this the paper focuses on the cross-cultural analysis of hunter-gatherer societies

and their comparison to non-human primates (hereafter primates, unless otherwise stated) and non-primate mammals (hereafter mammals, unless otherwise stated). A useful framework for our discussion is to consider how Niko Tinbergen’s four questions^[59] apply to the ecological and evolutionary role of collective computation in hunter-gatherer societies :

(1) Phylogeny: What is the evolutionary history of collective computation in hunter-gatherer societies?

(2) Causation: How is collective computation performed in hunter-gatherer societies?

(3) Function: What is the adaptive function of collective computation in hunter-gatherer societies?

(4) Ontogeny: How is collective computation integrated into the life history of hunter-gatherers?

The remainder of this paper examines collective computation in hunter-gatherer societies by quantifying how individual computation scales up in social groups to form what is sometimes termed the *collective brain*^[60]. The paper starts by considering the computational scaling of mammalian, primate, and human brains. Next a model is derived to describe the allometric scaling of group size across mammals, primates, and hunter-gatherers. The scaling of individual computation and social groups are then combined to form collective brains and the resulting organization of hunter-gatherer macroecology. At the end of the paper we summarize answers to Tinbergen’s questions.

2 Data and Method

2.1 Datasets and sources

To address the phylogenetic, causative, functional, and ontogenetic role of collective computation in hunter-gatherer societies, the paper uses three comparative dataset: (1) mammal brain composition; (2) mammal species ecology; and (3) cross-cultural hunter-gatherer macroecology. The first is data on mammal brain composition from Herculano-Houzel that includes various metrics of brain size including counts of neurons in various parts of the brain for 39 species^[61]. The second dataset is a combined macroecological database compiled by the author from published sources. These data focused on various ecological traits of mammal species. Mammal body mass, group size, population density, and home range size came primarily from the PanTHERIA database^[62], with additional

group size data from Jetz et al.^[63]. Home range data came from Kelt and van Vuren^[64]. Primate group sizes came from Dunbar et al.^[65]. Additional body mass data were extracted from the Amniote database^[66]. Mammal brain mass data came from a combination of Isler and van Schaik^[67], Sol et al.^[68], and Barton and Capellini^[69]. Data were examined and cleaned: obvious outliers and errors in the datasets were followed up through original sources, comparison to additional published sources and/or respected online sources, including Animal Diversity Web and the IUCN Red List of Threatened Species. These data were included in the analyses if verified, and if not they were omitted. The third dataset is the Binford cross-cultural hunter-gatherer database^[70], which includes social group size estimates at five levels of social organization, in addition to estimates of population density, and territory size for 339 populations. These data were compiled by Binford and his research team over many years and consist of metrics derived from the ethnographic literature generated over the 20th century.

2.2 Macroecological modeling approach

We take a macroecological approach to the comparative analyses of brain anatomy, species ecology, and hunter-gatherer socioecology. Macroecology is the study of complex adaptive systems in ecology. Macroecology is a top-down theoretical approach focusing on the statistics of the interaction of organisms with their environments across multiple scales of organization and observation, and how these influence the abundance, diversity, and distribution of biological species as they compete for space^[71]. For comparative analyses across species the independent variable in macroecological studies is commonly a measure of mass; in this paper, either some measure of brain mass or body mass (i.e. body size). For cross-cultural comparative analyses of hunter-gatherer societies the independent variable is population size. A standard goal in scaling analysis is understanding how the dependent variable responds to a change in the independent variable; i.e., how does a focal property of the system change in response to a change in size of the system?

In macroecology, body size is considered a fundamental variable as it sets the metabolic demand of an organism – the rate at which an organism uptakes, transforms, and expends energy to support life

functions—including the scheduling of life history and many aspects of behavioral ecology^[71, 72]. Body size also correlates closely with brain size^[73], and so brain size correlates closely with an organism’s metabolic rate and life history. However, it is also important to understand how aspects of brain anatomy vary with aspects of brain size across species^[38]. Of course, there is a sense in which while the metabolic cost of the brain is a significant proportion of the whole organism metabolic budget (~20%–25% in humans), ultimately the metabolic cost of performing all brain-related functions *is* the whole organism metabolic rate.

Body size is therefore a useful comparative independent variable as it captures many fundamental aspects of a species ecology^[72]. Moreover, it serves as a basis for building rich axiomatic, mechanistic theories of energy flows in ecology and allows us to predict the expected value of a trait for a given body size, and whether observed data are consistent with predictions. So, for humans we can then ask what the predicted ecology of a mammal (or a primate) of our body size should be from fundamental ecological principles. Any deviations from expectations therefore point to specific ecological and evolutionary mechanisms, highlighting the particular ways human ecology may differ from other animals in some respects, but may be entirely predictable in other respects.

Within the human species, body size can be effectively held constant, at least on size scales relevant to allometric scaling across species^[74]. As such, the relevant change of scale is not an *inter-specific* change in body size, but an *intra-specific* change in the number of individuals with similar body sizes (i.e., group size, or population size, for example). Note then that population size can still be considered a measure of population biomass. So, the questions of interest in human macroecology is how some aspect of the ecology of a human population changes across populations of different sizes (or total biomass).

2.3 Statistical approach

For the allometry of brain mass, cortical mass, and neuron count we use OLS regression as the sample size ($n = 39$) does not provide enough power for a mixed model controlling for order, or a full phylogenetically-controlled model. These data are divided simply into primate species vs. other mammal species, as this is the primary question of interest in this

section of the paper. Similarly, for the analyses of mammal species, again, the data are divided into primates and other mammals and measures the allometries with OLS regression. This is to be consistent with the brain anatomy data, as we later combine the results of the two analyses and so they must be subject to the same statistical treatment. However, we also provide results of a mixed linear model of the cross-species data where mammal order is introduced as a random effect. The effect sizes of mammal order in this model are consistent with the OLS results. For the cross-cultural data, we use one-way ANOVAs where appropriate and fixed effects models when we are interested in the differential scaling across pre-defined groups, such as group sizes at the various levels of hunter-gatherer metapopulations, or across ecosystem types. All statistical results are provided either in figures or tables.

As the sample sizes and scales of resolution differ widely across the three datasets we do not control attempt to control for phylogenetic autocorrelation in either the mammal or the hunter-gatherer data. There are published phylogenies for mammals^[75], but there are no equivalent phylogenetic trees that capture the evolutionary relatedness of hunter-gatherer societies. Therefore, for consistency, we do not attempt to control for phylogeny in either case.

Statistical tests and figures are generated in the R statistical computing environment^[76]. Basic statistics use the R base package. Mixed linear models use the lme4 package^[77] and the merTools package^[78]. All data are available as supplementary material attached to this paper.

3 Results

3.1 Currencies, optimizations, and gambits

The assumption, or phenotypic gambit, made here is that fitness-maximizing foragers reduce the uncertainty in the models they construct of their worlds by updating prior beliefs with new information they extract from their environments. By definition, a net gain in information is a net decrease in model uncertainty^[32] leading to increased predictability and improved inferences of the world^[35]. The goal is to minimize surprisal by maximizing the mutual information between the model used to generate inferences about the

environment and the actual physical structure of the environment. Ethnographic examples may include models used to predict the location of resources in time and space, or macroscopic features of the environment used to inform mobility decisions, such as when to leave a patch. Thus uncertainty-minimizers optimize metabolic budgets by minimizing energy and time costs. By accumulating relevant information about the environment in the form of sufficient statistics, uncertainty-minimizers generate increasingly predictive models of their world, which are used to compute increasingly effective inferences. Larger groups of cooperators have the potential to accumulate increasing amounts of information, but will necessarily incur increasing energy costs in finite environments. As such, group sizes, and the broader structure of social networks emerge from scale-dependent trade-offs between the benefits of information processing versus the ecological costs of maintaining the aggregate metabolic demand of group members.

This paper focuses on the fundamental currencies of energy and information and their optimization in hunter-gatherer populations. A common measure of energy in biological systems is metabolism, which is defined as the uptake, transformation, and expenditure of energy by an organism to fund the ecological demands of growth, maintenance, reproduction, and motility^[72]. Collective computation is the natural informational counterpart to metabolism in complex adaptive systems. In this paper, we generalize the definition given by Brush et al.^[31], where collective computation is the accumulation, aggregation, and deployment of information in order to make inferences about the world that solve adaptive problems.

3.2 Tinbergen's first question: Phylogeny

Tinbergen's first question considers the evolutionary origins of collective computation in hunter-gatherer societies. Answering this requires us to consider the deep evolutionary history of collective computation in primates and mammals. We begin by considering collective computation at the individual level. The fundamental units of computation in the brain are neurons, which transmit information to other nerve, muscle, and gland cells. Neurons are responsible for receiving and transmitting sensory input from the external world which is used to create and update models

that allow organisms to make inferences of their environments^[34]. The differential ability to compute accurate inferences about the world is central to biological fitness^[32, 79].

There are tight correlations between body mass, metabolic rate, and brain mass across mammals^[73], and humans have particularly large brains for a mammal with an average adult body mass of ~ 60 kg^[80]. However, the uniqueness of the human brain is the number of neurons in the cerebral cortex rather than the total number of neurons in the brain (~ 86 billion)^[38, 80, 81]. The number of neurons in the mammalian cortex correlates positively with cognitive ability measured as task performance in behavioral experiments, and so following Herculano-Houzel^[82], here we use the number of cortical neurons in the mammal brain as a basic measure of cognitive ability, and thus cognitive computation. We

use these data in Ref. [61] to develop an intuition into the differential scaling of cognitive computation across mammals (denoted by subscript m), primates (denoted by subscript p), and humans.

We describe the scaling relationship between a dependent variable, Y , and an independent variable, X , as a power law, which has the mathematical form,

$$Y(X) = aX^\beta \quad (1)$$

where a is a normalization constant and β is a scaling exponent describing how Y responds to a change in X ; both parameters are time and scale invariant. Note that power laws are flexible functions as they allow for both linear ($\beta = 1$) and nonlinear ($\beta \neq 1$) responses.

Figure 1a and Table 1 shows the scalings of brain mass, B , and body mass, M , where $B \propto M^\beta$. For primates $\beta_p = 0.90$ (0.74–1.06), and for other mammals $\beta_m = 0.72$

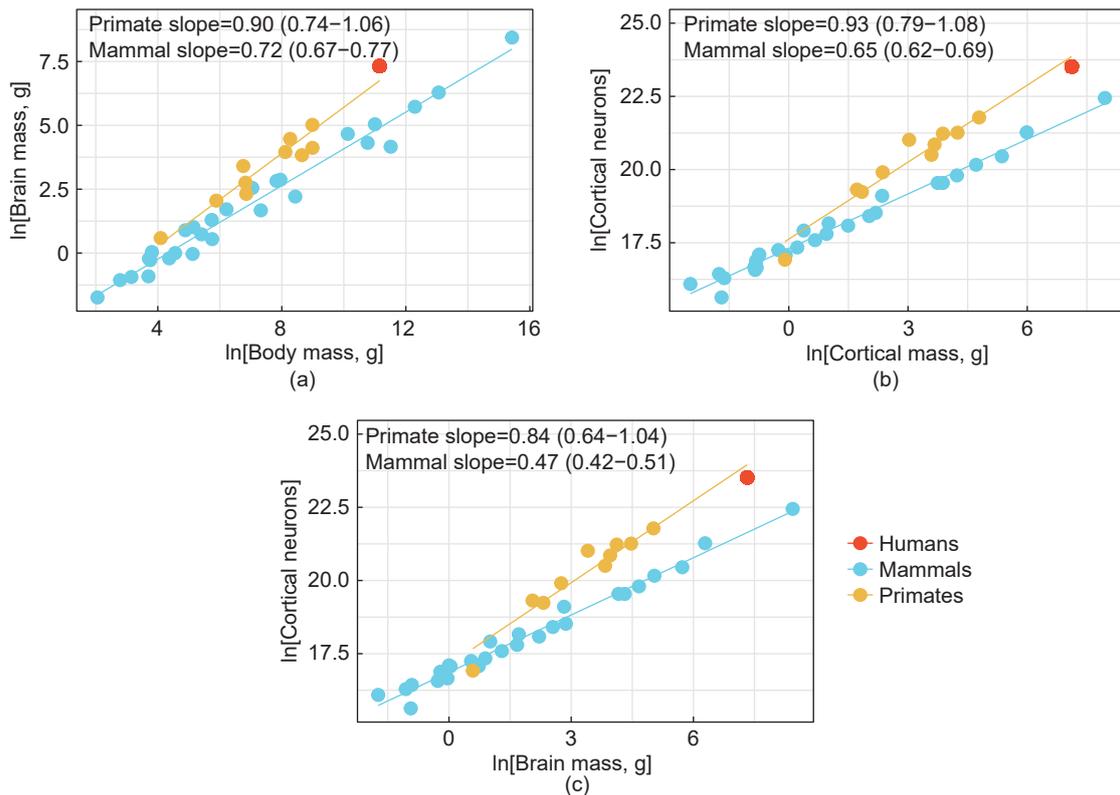


Fig. 1 Allometric scaling of brain mass, cortical mass, and cortical neurons across non-primate mammals (blue points), non-human primates (orange points), and humans (red point) using data from Herculano-Houzel et al.^[61] (a) Brain mass increases with body mass slightly faster in primates than other mammals, though the difference in slopes is non-significant (see main text for statistical results). The human brain is large for an equivalently-sized mammal, but only slightly larger than expected for an equivalently-sized primate. (b) The number of cortical neurons increases with cortical mass faster in primates than in other mammals, and so primate brains have a much higher density of neurons in their cortices than other mammals. (c) The number of cortical neurons increases with brain mass nearly twice as fast in primates than in other mammals. Human brains have a near predictable number of cortical neurons for a primate, but more importantly they have more cortical neurons than any other mammal in the dataset.

Table 1 Brain mass, cortical mass, and cortical neuron allometry.

	Dependent variable					
	ln[Body mass, M]		ln[Cortical neurons, C]			
	Mammal	Primate	Mammal	Primate	Mammal	Primate
$\ln M$	0.72 *** (0.67, 0.77)	0.90 *** (0.74, 1.06)	– –	– –	0.47 *** (0.42, 0.51)	0.84 *** (0.64, 1.04)
$\ln B$	– –	– –	0.65 *** (0.62, 0.69)	0.93 *** (0.79, 1.08)	– –	– –
Constant	–3.11 *** (–3.47, –2.76)	–3.32 *** (–4.59, –2.06)	16.86 *** (16.76, 16.97)	17.12 *** (16.55, 17.70)	14.85 *** (14.52, 15.18)	14.02 *** (12.44, 15.61)
Number of observations	28	11	28	11	28	11
R^2	0.97	0.93	0.98	0.95	0.95	0.88
Residual Std. Error (SE)	0.43	0.49	0.24	0.41	0.40	0.61
F statistic	943.28 ***	122.17 ***	1341.41 ***	161.81 ***	460.49 ***	67.47 ***

Note: *** denotes $p < 0.01$.

(0.67–0.77). Though primate brain mass increases with body mass faster than in other mammals, the difference between the slopes is not statistically significant at the 95% level ($t_{35} = 1.97$ and $p = 0.06$).

Figure 1b and Table 1 show the scaling of the number of cortical neurons, C , and cortical mass, B_c , where $C \propto B_c^\alpha$. For primates $\alpha_p = 0.93$ (0.79–1.08) and for other mammals $\alpha_m = 0.65$ (0.62–0.69). Here, the number of cortical neurons increases with cortical mass significantly faster in primates than in other mammals ($t_{35} = 1.97$ and $p = 0.001$), and so the density of neurons in primate cortices is significantly greater than in other mammals.

Figure 1c and Table 1 show the number of cortical neurons, C , scales with brain mass, B , where $C \propto B^\gamma$. For primates $\gamma_p = 0.84$ (0.64–1.04) and for mammals $\gamma_m = 0.47$ (0.42–0.51), so the number of neurons in primate brains increase significantly faster than in other mammals ($t_{35} = 3.05$ and $p = 0.004$). Humans have the most cortical neurons of all species in the dataset.

The number of cortical neurons in primate brains increases with body mass nearly twice as fast as other mammals, but it is important to note that humans have a predictable number of cortical neurons for a 60 kg primate. Recalling Kleiber’s Law, $E \propto M^{3/4}$, where E is the basal metabolic rate of a typical individual in a species, and M is the average adult body mass, then the cognitive return on whole organism metabolic investment in primates is $C_p \propto E_p^{1.12}$, which is nearly twice that in other mammals, $C_m \propto E_m^{0.62}$. So, a doubling of the metabolic rate in a primate results in a ~110% increase in neurons, whereas the same doubling in other

mammals results in only a ~60% increase in neurons. Moreover, the cognitive return on metabolic investment is superlinear in primates and sublinear in other mammals.

As a consequence of Kleiber’s Law, mammals with larger body masses have slower reproductive rates, but increased life spans^[72] resulting in body-size invariant life-time reproductive effort across mammals^[83] and humans^[84]. However, Kleiber’s Law also describes economies of scale where mass-specific metabolic efficiency increases with body mass, and so natural selection will favor increased body masses if the result is to decrease mortality, even if reproductive rates are reduced. The neuron scaling results presented here show that in primates larger body mass correlates with disproportionate increases in cognitive ability compared to other mammals. As a large-bodied primate, humans inherited an evolutionary legacy of neuron-dense cerebral cortices.

3.3 Tinbergen’s second question: Function

3.3.1 Social group size allometry

Tinbergen’s second question concerns the adaptive function of collective computation in hunter-gatherer societies. To answer this, we describe how cognitive ability scales up allometrically in groups by developing a macroecological model of group size. Social group size can be defined in many ways as there are many reasons social mammals live in groups^[85–87]. One method of estimating the average size of social groups is the average number of conspecifics (related or not) an individual encounters while performing daily tasks^[62].

As such, group size S is a function of the encounter rate of an individual with conspecifics λ over the home range H . Assuming the encounter rate of conspecifics λ is proportional to population density D , then

$$S \propto \lambda H \propto DH \quad (2)$$

As is well-known in mammal ecology, the scaling of population density and body mass is described by Damuth's Law^[88], $D \propto M^{\beta_D}$ where $\beta_D = -3/4$, and home range scales as $H \propto M^{\beta_H}$, where $\beta_H = 1$ ^[63]. In Damuth's Law, population density is defined as $D = N/A$, where N is the number of individuals and A is a sampled area, measured in units l^2 , where l could be meters or kilometers. Note that we can equivalently write l^{d_s} , where d_s is the dimension of the area sampled. Therefore, in a 3-dimensional environment, the area A in Damuth's Law has an additional spatial dimension, and so we can

write $D \propto M^{(-\beta_D)(d_s/d_e)} \propto M^{-1/2}$, where d_e is the foraging dimension of the environment. Following Formula (2) we then have an expression for group size as a function of body mass and the dimension of the foraging environment,

$$S(M) \propto M^{(d_s/d_e)\beta_D + \beta_H} \quad (3)$$

which in 2 dimensions gives $S \propto M^{1/4}$, and in 3 dimensions $S \propto M^{1/2}$. Formula (3) predicts that for a given body mass, group sizes are larger in species that forage in three dimensions than species that forage in 2 dimensions, a prediction we confirm in data below.

The parameters in Formula (3) are estimated from inter-specific mammal species data. Figure 2a and Table 2 show that for both primates and other mammals, home ranges scale approximately linearly with body mass,

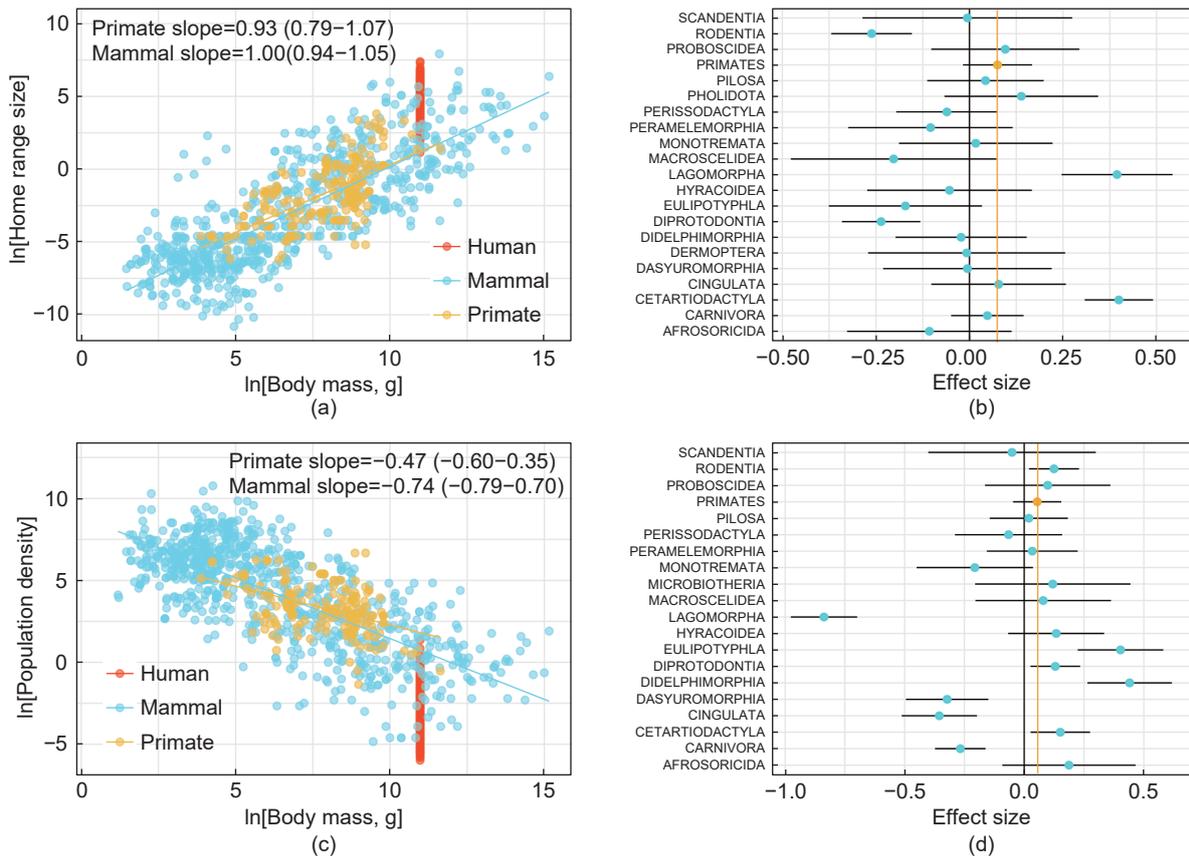


Fig. 2 Allometric scaling of home range and population density in humans (red), primates (orange), and mammals (blue). In the panels on the left, the fitted functions are OLS regressions and the slope parameters given in the panels. The panels on the right are the effect sizes for each mammal order from a mixed linear model of the data used to generate the figure on the left. The vertical line is a zero effect and the orange vertical line is the primate effect size. (a) Home ranges increase approximately linearly with body mass in both primates and mammals (see Table 3 for details in the following). Hunter-gatherers have large home ranges for their body mass. (b) The primate effect size is similar to other mammal orders. (c) Primate population densities decrease with body mass more shallowly than other mammals, but hunter-gatherers have especially low population densities for both mammals and primates. (d) The primate effect size is similar to other mammal orders.

Table 2 Home range and population density.

	Dependent variable			
	ln[Home range, H]		ln[Population density, D]	
	Mammal	Primate	Mammal	Primate
$\ln M$	1.00 *** (0.94, 1.05)	0.93 *** (0.79, 1.07)	-0.74 *** (-0.79, -0.70)	-0.47 *** (-0.60, -0.35)
Constant	-9.78 *** (-10.18, -9.38)	-9.00 *** (-10.13, -7.86)	8.87 *** (8.55, 9.20)	7.03 *** (6.06, 8.00)
Number of observations	719	225	832	212
R^2	0.65	0.42	0.55	0.22
Residual SE	2.24	1.57	2.06	1.27
F statistic	1320.44 ***	164.72 ***	1012.25 ***	58.39 ***

Note: *** denotes $p < 0.01$.

$H \propto M^1$, and Fig. 2b shows that population density in mammals scales as $D_m \propto M_m^{-0.74}$, whereas for primates $D_p \propto M_p^{-0.47}$ (see Table 2 for confidence intervals and test statistics). So, across primates and mammals home ranges scale approximately linearly with body mass, but within those home ranges, for a given body mass, population densities are higher in primates than other mammals, consistent with the dimension of their respective foraging niches. Figure 3a shows that, as predicted, primate group sizes scale with body mass as $S_p \propto M_p^{0.46}$, whereas social group sizes in other mammals scale a little shallower than expected, at $S_m \propto M_m^{0.14}$. Interestingly, hunter-gatherer band sizes (the equivalent of mammal social group sizes in a home range), are considerably smaller than expected for a primate, but larger than expected for other mammals. Small band sizes would be consistent with the fact hunter-gatherers generally forage in niches that are close to 2-dimensional, with the possible exception of high canopy forests, fishing, or excavating roots, tubers, and fossorial animals, for example. As such, primates maintain larger group sizes by the increased resource supply rates and decreased competition of 3-dimensional foraging niches. Hunter-gatherer group sizes are constrained by 2-dimensional foraging niches leading to increased intraspecific competition exacerbated by the specialized food resources in the human diet. However, as we will explore below, hunter-gatherers integrate these small local groups into much larger networks facilitating flows of energy and information far beyond local interactions.

3.3.2 Constructing the collective brain

Following Muthukrishna and Henrich^[60] this paper uses the term *collective brain* to refer to the collective

computational power of a social group: the collective brain, G , is simply the product of the species-specific group size, S , and the average number of cortical neurons, C , in the brain of each individual in the group, and so $G = SC$. In hunter-gatherers, the collective brain is the average number of cortical neurons in the human brain and the average band size of a society. Following Formula (3) we then have a general expression for the collective brain,

$$G(M) = SC \propto M^{(d_s/d_e)\beta_D + \beta_H + \beta_N} \quad (4)$$

which in non-primate mammals predicts

$$\hat{G}(M)_m = S_m C_m \propto M^{1/4+1/2} \propto M^{3/4} \quad (5)$$

and in primates,

$$\hat{G}(M)_p = S_p C_p \propto M^{1/2+3/4} \propto M^{5/4} \quad (6)$$

As such, collective brains in non-primate mammals are predicted to scale sublinearly with body mass, whereas in primates collective brains are predicted to scale superlinearly. Given the scaling results in Tables 1 and 3 we find in mammals,

$$G(M)_m = S_m C_m \propto M^{0.45+0.14} \propto M^{0.59} \quad (7)$$

and in primates,

$$G(M)_p = S_p C_p \propto M^{0.74+0.46} \propto M^{1.20} \quad (8)$$

Empirically, the computational power of primate social groups increases with body mass twice as fast than in other mammals: doubling the body size of a mammal increases the computational power of a group by 60%; doubling the body size of a primate increases the computational power of a social group by 120%. To visualize this scaling relationship, Fig. 3e shows the estimated collective brain (i.e., converting mammal brain masses in the dataset to the estimated number of

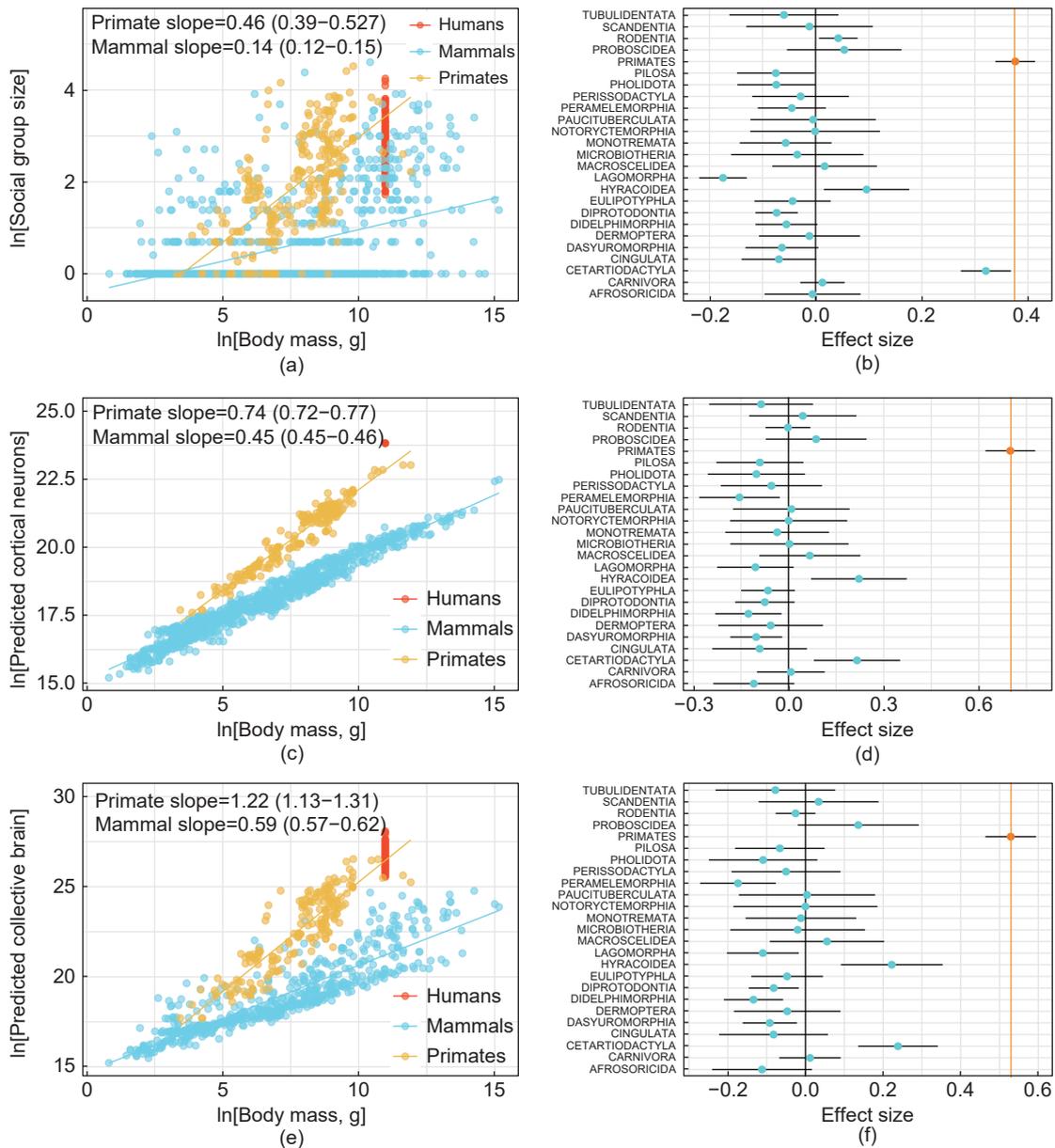


Fig. 3 Allometric scaling of collective features of groups by body size across hunter-gatherers (red), primates (orange), and mammals (blue). In the panels on the left, the fitted functions are OLS regressions and the slope parameters are in the upper left. The panels on the right are the effect sizes for each mammal order from a mixed linear model of the data on the left. The vertical line is a zero effect and the orange vertical line is the primate effect size. In each case, the positive random effect size for mammals is much greater than any other mammal order. (a) The allometry of group size and body size is 3-fold steeper in primates than other mammals, and hunter-gatherers have a broad range of band sizes. (b) The random effect for primates shows the primate group size allometry is much steeper than other mammal orders with the exception of cetartiodactyls (even-toed ungulates). (c) The allometry of the estimated number of cortical neurons in the brain is much steeper in primates than other mammals, and humans have more cortical neurons for their body size than other primates. (d) The random effect for primates indicates the response of a change in the number cortical neurons to a change in body size is much greater in primates than other mammals. (e) The allometry of the estimated collective brain (group size \times cortical neurons) in mammals, primates, and humans. (f) The effect size for primates is much greater than other mammal orders, showing that the collective brain of primate groups increases significantly faster than any other mammal. Hunter-gatherer collective brain sizes are much as predicted for a primate of our body size as smaller than predicted group sizes are compensated by larger than predicted cortical neurons. The primate allometry is twice as steep as other mammals. Nevertheless, human hunter-gatherers have the largest collective brains of all species in the dataset.

Table 3 Group size, estimated number of cortical neurons, and estimated collective brain mass.

	Dependent variable					
	ln[Group size, S]		ln[Cortical neurons, C]		ln[Collective brain, G]	
	Mammal	Primate	Mammal	Primate	Mammal	Primate
$\ln M$	0.14 *** (0.12, 0.15)	0.46 *** (0.39, 0.52)	0.45 *** (0.45, 0.46)	0.74 *** (0.72, 0.77)	0.59 *** (0.57, 0.62)	1.22 *** (1.13, 1.31)
Constant	-0.41 *** (-0.54, -0.29)	-1.60 *** (-2.11, -1.08)	15.16 *** (15.11, 15.20)	14.72 *** (14.51, 14.92)	14.72 *** (14.54, 14.91)	13.08 *** (12.38, 13.78)
Number of observations	1,035	290	961	227	584	202
R^2	0.20	0.39	0.96	0.94	0.79	0.79
Resid SE	0.83	0.85	0.27	0.30	0.92	0.99
F statistic	265.02 ***	186.40 ***	22 038.22 ***	3272.10 ***	2210.72 ***	733.11 ***

Note: *** denotes $p < 0.01$.

cortical neurons using the scaling parameters in Table 1) as a function of body mass in primates, mammals, and human hunter-gatherers. Hunter-gatherer bands have the predicted collective brain for a primate of ~ 60 kg as small social group sizes (Fig. 3a) are compensated by encephalized brains (Fig. 1a). Figure 3e shows that hunter-gatherers have the largest collective brains of any mammal.

3.4 Tinbergen's third question: Causation

3.4.1 Hunter-gatherer metapopulation structure

Tinbergen's third question asks how collective computation is performed in hunter-gatherer societies. To answer this, first we examine the ways in which neighboring hunter-gatherer bands are connected and integrated into larger social networks. Hunter-gatherer populations are multiscale societies where bands composed of co-residing families are connected to others across the landscape forming large-scale, low density, and decentralized metapopulations. Empirically, these multiscale societies form self-similar, hierarchically modular networks^[23] as shown in Fig. 4. The kinship ties that bind families are extended to non-kin within co-residing bands by norms of reciprocal altruism and resource sharing^[89]. Bands typically move multiple times over the course of a year as local foraging patches are depleted^[90]. Moreover, individuals move through the broader social network in several ways: families may choose to relocate to another band or form a new band; individuals often visit friends and relatives in other bands; or husbands and wives change bands after marriage. As such, there is a constant demographic churn at the local level. At an aggregate level, in some environments (particularly hot and cold deserts) bands may seasonally disaggregate into individual families,

and at other times local bands may aggregate into large temporary camps. Periodically, perhaps every few years, multiple bands may aggregate for mass events, such as puberty ceremonies, or communal foraging events, such as rabbit drives or bison jumps (see Refs. [91, 92]). Hunter-gatherer metapopulations are connected by fission-fusion dynamics at all levels and timescales of the social network which serve to cycle information (both social and genetic) far beyond the daily interactions of individuals within bands. For example, Ache foragers of northern Paraguay and the Hadza foragers of Tanzania interact with around 1000 people over their lifetimes, which may constitute much of the entire metapopulation^[24].

3.4.2 Hunter-gatherer hierarchical modularity

A hunter-gatherer metapopulation consists of Ω levels, labelled from the lowest level ω_1 (families), the second level ω_2 (bands), up to the highest level Ω , the metapopulation. The number of individuals, or average group size, at each level is denoted S_ω , and so S_Ω is the total number of individuals in the metapopulation. Statistically, the branching ratio across all levels is constant, $\theta = S_{\omega+1}/S_\omega \approx 4$, in which case hunter-gatherer metapopulations form self-similar hierarchically modular networks^[23]: that is to say, on average there are four individuals in a family (S_1), four families in a band (S_2), four bands in a regional cluster of bands (S_3), four clusters form a subpopulation (S_4), and four subpopulations form the greater metapopulation, S_Ω (Figs. 4a and 5). Importantly however, as this branching ratio is an average across hundreds of populations, the observed branching ratio of any individual population may differ considerably from the average. It is interesting to note that the branching structure of these networks does not vary across different

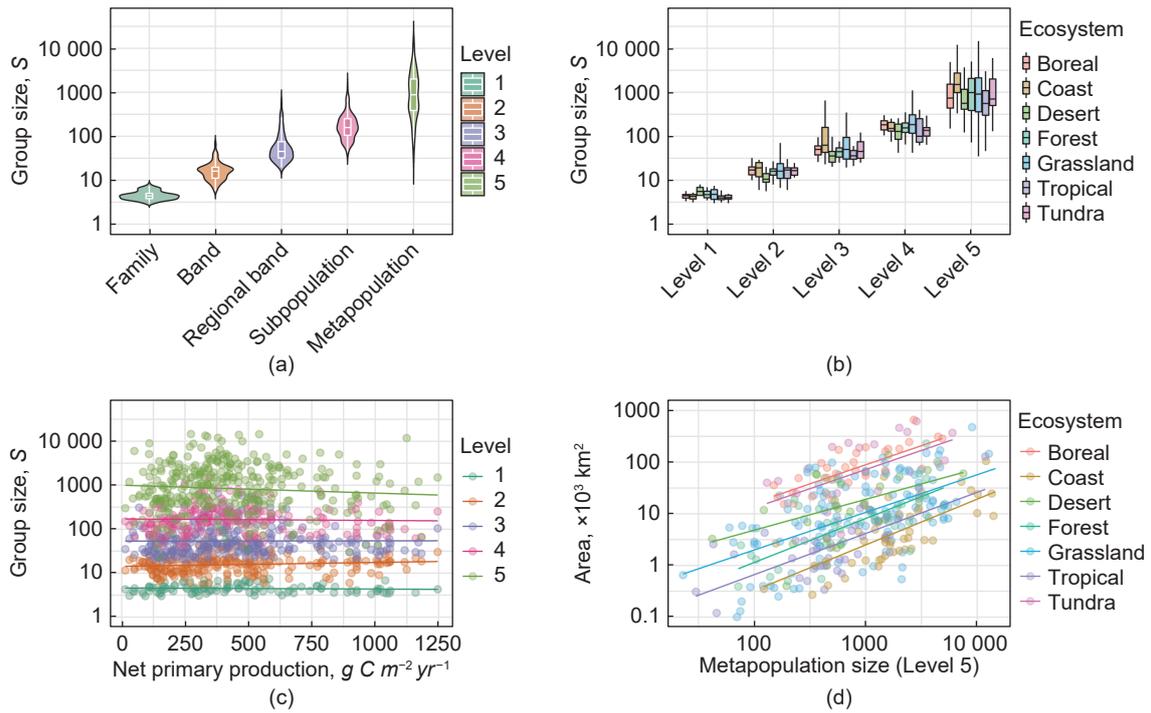


Fig. 4 Hierarchically modular structure of hunter-gatherer networks using data from Binford ($n = 339$)^[70]. (a) Social group sizes at five levels of social organization for 339 populations show a geometric series. (b) The same social group size data at each of the five levels plotted by the ecosystem of the population, showing the geometric increase in group size holds across habitats. For statistical results, see Table 4 in the following. (c) Social group size at each level plotted as a function of the net primary production of the environment for each population, showing that the variation in group size within each level is independent of environmental productivity. For statistical details see Table 5 in the following. (d) Hunter-gatherer territory size plotted as a function of total population size (Level 5), plotted by ecosystem type for each population. Across ecosystems hunter-gatherer populations are structured by self-similar networks, and exhibit economies of scale in space-use where larger networks. For statistical results, see Table 6 in the following.

environments. Figure 4b and Table 3 illustrate this invariance: an ANOVA shows the average size of social groups at the five levels does not vary across ecosystem types, and in Fig. 4c and Table 4 the regression model shows the variation within group sizes across the levels of the network is independent of local environmental productivity, measured as net primary production ($g C m^{-2} yr^{-1}$).

3.4.3 Hunter-gatherer small worlds

Hierarchically modular networks have small-world-like properties here dense clusters of local connections are linked by sparse global connections^[93]. Amongst individuals co-residing with multiple families in a band, daily interactions between are likely frequent and ubiquitous. Assume all co-residing individuals, S , in a band, $\omega = 2$, interact with each other, then the expected connectivity is given by the number of edges, K , which in a fully-connected bi-directional network is

$$K_2 = S_2(S_2 - 1) \approx S^2 \quad (9)$$

However, above the band level interactions between individuals in the metapopulation are far less frequent. If we assume inter-band connectivity is minimized then it can be shown that connections between bands are proportional to the branching ratio θ , and so we have

$$K_\omega = \theta(S_\omega - 1) \approx S_\omega^1 \quad (10)$$

in which case inter-band connectivity is linear in S for $\omega > 2$. This leads to the modular network structures shown in Fig. 5, generated from the average properties of the Binford data used in this paper: internally bands are fully connected, but each band is minimally connected to other neighboring bands creating a statistically self-similar hierarchical modular network.

3.5 Tinbergen's fourth question: Ontogeny

3.5.1 Hunter-gatherer family formation

Tinbergen's fourth questions ask how collective computation is integrated into the ontogeny of hunter-gatherers and their societies. To begin, human

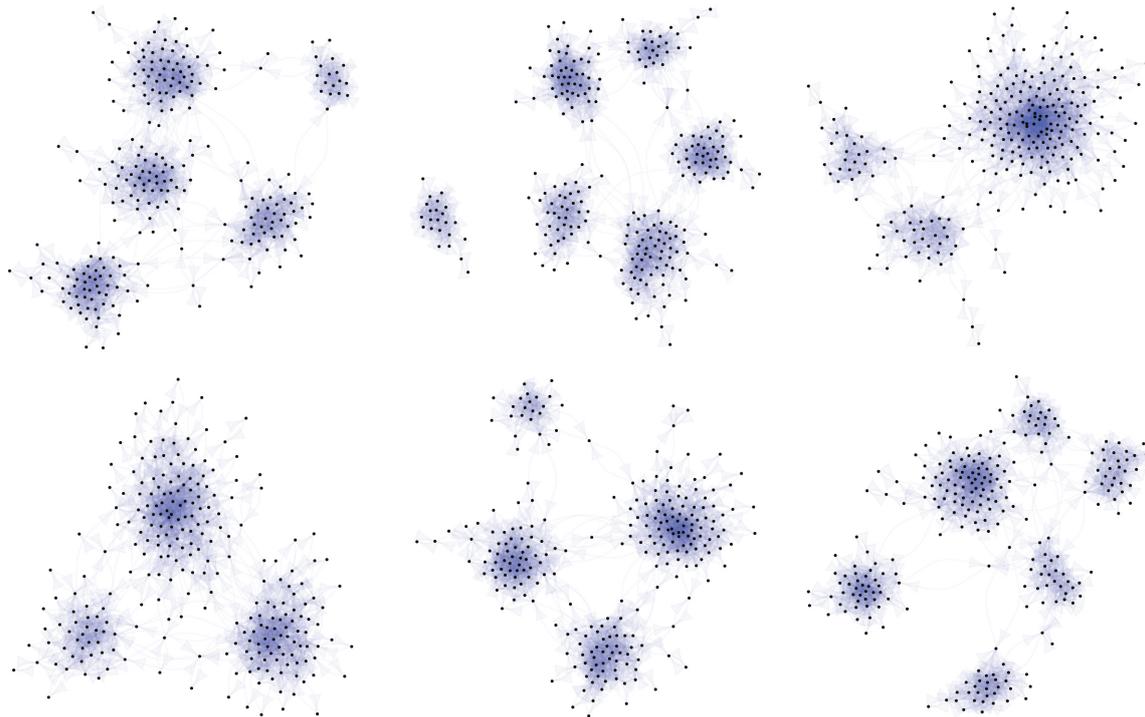


Fig. 5 Network structure of six simulated hunter-gatherer metapopulations visualized as hierarchical modular networks using the branching statistics from Fig. 4. In each simulated metapopulation the nodes in the networks are families ($n = 256$) linked by multiple levels of interaction to form the subpopulations of the greater metapopulation. Fusion-fusion dynamics occur at multiple levels of the hierarchy as individuals, families, and bands move, interact, aggregate, and disperse at various timescales. The frequency of local interactions forms the modularity of the subpopulations, which vary in number. Each family exists in a small-world of dense local interactions, but is connected to the larger network by sparse global interactions. As a result, all families are connected to all others by short path lengths that extend across the entire metapopulation (generated using the EcoNetGen package in R^[79]).

Table 4 ANOVA table of social group size by organizational level and ecosystem.

	D_f	Sum S_q	Mean S_q	F value	$P_r (>F)$
Level	4	3575.79	893.95	1361.89	0.0000
Ecosystem	6	45.28	7.55	11.50	0.0000
Level: ecosystem	24	21.49	0.90	1.36	0.1129
Residual	1156	758.80	0.66	–	–

family formation is driven by the interplay of expensive brains, complex foraging niches, offspring-provisioning, high infant mortality rates, high inputs of childcare, and so necessary divisions of tasks and labor by age and gender among closely-related kin^[39, 94, 95]. Further, in hunter-gatherer societies the kinship ties that bind families are extended beyond the family to non-kin: alloparenting is essential to childcare^[96, 97], and groups of families create long-term inter-dependent networks of reciprocal altruism where key resources (particularly meat) are shared altruistically, with the understanding that shared resources will be reciprocated in the future^[90, 98, 99]. As such, hunter-gatherer family

formation emerges from the evolution of the human life history, which evolved within an ultra-social environment that includes fitness-enhancing inputs from non-kin. The ability to form, negotiate, and police such social networks requires cognitive inputs and computations over the entire collective.

3.5.2 Hunter-gatherer band size

Bands emerge from the economic ties that bind co-residing families^[100, 101], but there is no consensus on the mechanisms that ultimately constrain the number of families that co-reside^[24, 40, 101, 102]. However, it is useful to consider how the two fundamental currencies of energy and information may come into play in limiting

Table 5 Hunter-gatherer social group size across levels by net primary productivity NPP.

	Dependent variable
	ln[Social group size, S_ω]
NPP	-0.0001 (-0.001, 0.0005)
Level 2	1.14 *** (0.79, 1.48)
Level 3	2.45 *** (2.12, 2.79)
Level 4	3.62 *** (3.27, 3.97)
Level 5	5.38 *** (5.06, 5.71)
NPP: Level 2	0.0003 (-0.0004, 0.001)
NPP: Level 3	0.0001 (-0.001, 0.001)
NPP: Level 4	-0.0000 (-0.001, 0.001)
NPP: Level 5	-0.0004 (-0.001, 0.0003)
Constant	1.52 *** (1.24, 1.80)
Number of observations	1191
R^2	0.81
Residual SE	0.83
F statistic	572.35 ***

Note: *** denotes $p < 0.01$.

Table 6 Linear model of hunter-gatherer territory size by population size and ecosystem type.

	Dependent variable
	ln(Territory size, A)
ln S_5	0.74 *** (0.32, 1.16)
$ECOSYSTEM_{Coast}$	-4.59 ** (-8.19, -0.98)
$ECOSYSTEM_{Desert}$	-0.56 (-4.47, 3.35)
$ECOSYSTEM_{Forest}$	-3.17 * (-6.70, 0.36)
$ECOSYSTEM_{Grassland}$	-2.28 (-5.29, 0.72)
$ECOSYSTEM_{Tropical}$	-3.46 * (-6.92, -0.01)
$ECOSYSTEM_{Tundra}$	-0.22 (-4.63, 4.19)
ln $p:ECOSYSTEM_{Coast}$	0.15 (-0.37, 0.66)
ln $p:ECOSYSTEM_{Desert}$	-0.14 (-0.73, 0.44)
ln $p:ECOSYSTEM_{Forest}$	0.11 (-0.41, 0.63)
ln $p:ECOSYSTEM_{Grassland}$	0.02 (-0.42, 0.47)
ln $p:ECOSYSTEM_{Tropical}$	0.06 (-0.47, 0.58)
ln $p:ECOSYSTEM_{Tundra}$	0.001 (-0.65, 0.65)
Constant	34.21 *** (3.47, 9.11)
Number of observations	339
R^2	0.58
Residual SE	1.19
F statistic	34.21 ***

Note: * denotes $p < 0.1$; ** denotes $p < 0.05$; *** denotes $p < 0.01$.

the number of co-residing families. Consider the finite nature of energy available to human foragers. Data show that hunter-gatherers adjust population *density* rather than population *size* in response to the level of environmental productivity on local landscapes^[18, 91, 101]

(Fig. 4c), and so the size of the social group, S , is invariant to environmental productivity. However, home range size, H (the area required by a group of foragers to encounter the resources needed to meet their combined energy budget), varies with environmental productivity^[18]. As such, the level of intraspecific competition – the number of individuals cooperating and competing – is invariant to local environmental productivity. While competition is invariant, resources are finite ultimately limiting return rates and therefore the ability to maintain the energy demands of foragers and their dependents. Even if we assume total energy return rates, r , from cooperative foraging are superlinear ($r \propto S^{\beta_r}$, where $\beta_r > 1$), following Eq. (9) then the energy cost of competition e in a band will go as $e \propto S^2$, and so competition outpaces cooperation with increasing group size. The net return is then $n = r - e \propto r_0 S^{\beta_r} - e_0 S^2$, where $1 < \beta_r < 2$ and $r_0 > e_0$ (see Figs. 4a and 4b), which the data suggest is maximized at ~ 16 individuals. The upper limit of band sizes is then set where $r - e = 0$: the largest band size in the data set is 70 people in the Niitsitapi (Blackfoot), an equestrian society of the North American Plains.

As group size increases, not only there is increasing intraspecific competition over finite resources, but there is also an increasing risk of free riders. To detect free riders an individual must monitor not only their interactions with others, but all interactions in the group as a whole, as a free rider may cooperate with some and defect with others. If we assume the cost of monitoring a link in the network is a constant, c_0 , then, following Eq. (9), the per capita cost, c , of monitoring all the interactions, K , in a group goes as $c = c_0 K = c_0 S^2$. So, like energy, the per capita informational benefits of cooperation will necessarily be less than quadratic, as the exchange of information between individuals cannot be perfect^[18, 103]. That is, if there the benefit of cooperating partners is positive but not perfect, then benefits will increase as, $b = b_0 S^{\beta_b}$, where $\beta_b < 2$. Therefore, the initial informational benefits to cooperation ($b_0 > c_0$) are quickly outpaced by the costs of policing group interactions. Hunter-gatherer band sizes are thus limited both by competition over energy and imperfect information exchange, independent of environmental productivity.

Average band sizes of ~ 16 individuals correspond to ~ 4 co-residing families. However, by maintaining links

with neighboring bands, families exist in a small-world of dense local connections linked to many other small-worlds throughout the network by short path lengths; dispersed, low density hunter-gatherer metapopulations are bound by the strength of weak ties^[104]. Equations 9 and 10 suggest that the cost of maintaining links between bands is much less than within bands as the interaction frequency is far less. As such, the decentralized, modular, and hierarchical network structure of hunter-gatherer metapopulations maintains global connectivity but reduces the connectivity costs by minimizing the links that allow people, material, and information to flow through the network at multiple scales.

4 Discussion

The empirical results in this paper show that hunter-gatherer bands composed of a handful of co-residing cooperating families form powerful collective brains^[60] with higher computational capacity than any other social group of primates or other mammals. This is because human brains are not only large for a mammal of our body size, human cerebral cortices have particularly high neuronal densities compared to other mammal species^[38]. As neuronal density in the cerebral cortex correlates with cognitive ability^[83], human brains are particularly efficient at information processing^[32]. Current perspectives in theoretical evolutionary neuroscience suggest these cognitive computations are used to build inferential models of complex external worlds, allowing for the prediction of environmental uncertainty, and therefore the maximization of inclusive fitness^[34, 35, 80]. Individual computational capacity is aggregated within bands, which are then aggregated to form distributed cognitive networks at higher levels of aggregation in the multiscale metapopulation^[105, 106]. Thus, collective computation at multiple levels is an inherent aspect of the evolution of human life history, behavioral ecology, and macroecology, as fitness-enhancing contributions from non-kin play an important role in human evolutionary ecology^[39].

This paper highlights the central role collective computation plays in the organization of hunter-gatherer macroecology. The complex adaptive system approach taken here shows how top-down, comparative analyses add an additional and complementary perspective to the bottom-up approaches traditionally developed in anthropology which often identify the roles particular

sets of transmission rules, cultural norms, or behaviors play in structuring social systems at much larger scales. Macroecology explicitly places the human traits of interest to anthropologists within the broader context of the energetic and biophysical principles that shape the ecology of all other organisms. In this way macroecology establishes a principled comparative baseline along which we can observe human systems and measure their deviations from other species.

Despite the enormous diversity of hunter-gatherer societies in the ethnographic record, cross-cultural data show remarkable macroscopic regularities in the scale and structure of hunter-gatherer societies across different environments, reflecting an invariance in the flow of information across different environments. The multiscale structure of metapopulations emerges from fission-fusion dynamics as individuals, families, and bands move through a nested hierarchy of social groups at multiple levels of social organization at various time scales. These dynamics form a fluid, hierarchically modular social network where individuals, genes, and social information cycle at scales far beyond the local scale of daily interactions among co-residing families^[24, 107, 108]. This complex structure is ultimately shaped by energy constraints on the flow of information among social groups at different levels of social organization resulting in scale-dependent optimizations, modularity, and time-scale separation in dynamics^[109].

A key feature of this social structure is the formation of co-residing families in bands. Band size is a trade-off between the collective benefit of increasingly predictive models that resolve environmental uncertainty versus the ecological maintenance costs of supporting group members, and the policing costs of detecting free riders. Data and theory show that the average size of hunter-gatherer bands in the ethnographic record is smaller than predicted for a 60 kg primate; the primate scaling parameters in Table 2 predict hunter-gatherer band sizes of ~ 32 , whereas the empirical average across cultures is ~ 16 , half the predicted value^[23, 101] (but see Ref. [100]). Smaller than predicted social group sizes are compensated by larger than predicted human brain masses such that the collective brain *mass* of a hunter-gatherer band is much as predicted for a 60 kg primate, and is among the largest of any mammal, regardless of body mass (Fig. 3e). Given the tight scaling of the number of cortical neurons and brain mass in both mammals and primates (Fig. 1c), hunter-gatherer bands

then have the highest computational power of any mammal or primate social group. But more importantly, information is exchanged throughout metapopulations at scales far beyond the daily interactions of co-residing individuals: the information processing capacity of an entire hunter-gatherer metapopulation is clearly unique in the mammalian world. This metapopulation structure thus provides the benefits of a large social network (i.e., access to potential cooperators; allies; innovators; marriage partners; defenders; raiders; and economies of scale in general), but minimizes much of the ecological and computational costs of maintaining connectivity.

At the largest scale, hunter-gatherer metapopulations are decentralized networks where the optimizations of energy and information flow that constrain band size play out at local scales. The collective computation of hunter-gatherer societies is to achieve local optima by minimizing band sizes thus minimizing the costs of maintaining network connectivity in a much larger metapopulation. These trade-offs result in small-worlds. The macroecological solution is to maintain large metapopulations by distributing local subpopulations in space. In urban scaling theory, cities are sometimes referred to as *social reactors*^[16], a term capturing the hyper-productivity of dense nucleations of people and their interactions concentrated in space. In this spirit, we might then refer to hunter-gatherer societies as *social diffusers*, a term capturing the optimal, adaptive decentralized modularity of people and their interactions dispersed in space. The challenge now is to understand how the social diffusion that characterized the deep evolutionary history of human sociality eventually nucleated to form the social reactions of the Holocene.

5 Conclusion

In the introduction, we posed Tinbergen's four questions to help frame the phylogenetic, causative, adaptive, and ontogenetic roles of collective computation in hunter-gatherer macroecology. Here, we summarize the answers:

Phylogeny. Collective computation in humans has deep phylogenetic roots as the complex 3-dimensional environments of primate evolutionary history promoted large complex brains^[110]. The increasingly 2-dimensional niches of the hominin lineage required specialized diets of nutrient-dense resources to fuel the increasingly expensive hominin brain, which in turn required complex predictive models, collective

behaviors, and extensive cooperation^[38, 39, 111].

Causation. Macroscopic regularities are extracted from the environment and used to inform decision-making processes. Optimizations at the individual level scale up to form the collective behavior of social groups integrated into extensive social networks across landscapes to form hierarchically modular metapopulations. Thus, hunter-gatherer societies are not *small-scale* (sensu [112]), but *small-world*.

Function. Collective computation is the scale invariant processing of information at multiple spatial-temporal levels of hunter-gatherer social organization. Information is used to build models to make inferences about the world that resolve environmental uncertainty and therefore maximize fitness by optimizing energy budgets, time allocation strategies, reproductive decisions, and survival.

Ontogeny. Information processing at levels above the individual is deeply integrated into all aspects of the human life course, including the scheduling of life history events^[39], the social learning of culturally inherited information^[2], the mastery of complex skills^[113, 114], cooperation amongst non-kin^[90, 108], and the coordinated mobility of individuals in space^[23, 91].

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