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Group size allometry in humans, primates, and mammals

# 1 Unique allometry of group size and 2 collective brain mass in humans and 3 primates relative to other mammals 4

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11

## 12 **Abstract**

13 Group living is common in mammals, particularly in primates and humans. Across species,  
14 groups are social networks where co-residing members exchange information and balance  
15 trade-offs between competition and cooperation for space, resources, and reproductive  
16 opportunities. From a macroecological perspective, species-specific group sizes are ultimately  
17 constrained by body size, population density, and the environmental supply rate of home  
18 ranges. Here, we derive an allometric null model for group size in mammals based on individual  
19 energy demands and ecological constraints. Using Bayesian phylogenetic mixed models we  
20 show that primates exhibit unique allometries relative to other mammals. Moreover, as large-  
21 bodied primates, human hunter-gatherers have among the largest social groups of any  
22 mammal. We then explore the consequences of this unique social allometry by considering how  
23 mammalian brain size scales up in social groups that differ in size across mammals. We show  
24 similarly unique allometries in what we term the collective brain mass of social groups in  
25 primates relative to all other mammals. These results show that for a given body size primates  
26 have both larger brains and larger social networks than other mammals. Consequently,  
27 proportionally larger primate brains interact in proportionally larger social networks with  
28 important consequences for group cognition. We suggest that the size, scale, and complexity of  
29 human social networks in the 21<sup>st</sup> century have deep evolutionary roots in primate ecology and  
30 mammalian brain allometry.

31

32 **Keywords:** brain; social network; group size; hunter-gatherers; mammals; macroecology

## Group size allometry in humans, primates, and mammals

### 33 1. Introduction

34 Two of the most conspicuous features of the human species are large brains and intense  
35 sociality. How the two interact to influence cognition has become the focus of research across  
36 many disciplines (Clark and Chalmers, 1998; Dunbar, 1998; Richerson and Boyd, 2005; Dunbar  
37 and Shultz, 2007; Krubitzer, 2009; Woolley et al., 2010; Whiten and Erdal, 2012; Hutchins, 2014;  
38 Dennett, 2017; Everett, 2017; Graziano, 2017; Muthukrishna et al., 2018). Human brains are  
39 large, complex, and metabolically expensive, constituting ~25% of the basal metabolic budget  
40 but only ~2% of the body size. However, the computational returns on metabolic investment  
41 have been considerable. The initial doubling of hominin brain size to ~800 cm<sup>3</sup> in *Homo erectus*  
42 (*sensu lato*) ~2 MYA correlated with the expansion of the geographic range throughout Africa  
43 and southern Eurasia. The next major increase in brain size to ~1,350 cm<sup>3</sup> ~300 KYA saw  
44 another expansion where modern humans replaced other hominins wherever they existed,  
45 eventually extending the human geographic range to include the majority of the planet's  
46 terrestrial habitats. Humans began to genetically reengineer the biosphere ~12 KYA by  
47 redirecting flows of environmental net primary production to net agricultural production, and  
48 ~0.2 KYA humans leveraged thermodynamic principles to engineer machines to convert heat  
49 into work using fossilized biomass (Smil, 2008, 2019). Currently, the human species numbers  
50 about 7.7 billion, most of whom are connected by global communication networks, and now,  
51 through various technologies, have near-instant access to the majority of cultural knowledge  
52 accumulated over the last several thousand years. Humans now actively explore the solar  
53 system, are capable of manipulating matter at the smallest scales and gathering information at  
54 the largest. These innovations were facilitated not only by an initial increase in brain size and  
55 function, but by the intensity of social interactions.

56 The story of this evolutionary sequence is told, however incompletely, by the  
57 paleoanthropological, archaeological, and historical records (Christian, 2011). Explaining how  
58 and why humans are capable of such innovations is less clear. While the human brain is large  
59 for a mammal of our body size (~7 times the predicted size of a mammal, and ~3 times that of a  
60 primate), human cognition is not just a function of brain size, but brain specialization, where  
61 increasing size facilitates increasing diversity of function (Fuster, 1999; Elston et al., 2006;  
62 Striedter, 2006; Passingham, 2008; Barton, 2012; Bullmore and Sporns, 2012; Herculano-  
63 Houzel, 2012, 2016; Passingham and Wise, 2012; Roth and Dicke, 2012; Schneider, 2014;  
64 Wittmann et al., 2018). While the number of neurons in the mammalian brain increases with  
65 size, in primates an increasing proportion are located in the cerebral cortex (Herculano-Houzel,  
66 2012). As the human brain is largely a linearly scaled-up primate brain, as large-bodied  
67 primates, humans have particularly neuron-rich cerebral cortices compared to other mammals  
68 (Herculano-Houzel, 2009, 2012). Consequently, in contrast to other primates, humans can  
69 mentalize at high orders, engaging in both self-reflection and on the mental state of others  
70 (Frith and Frith, 2006; Passingham, 2008; Tomasello, 2009). Humans can place themselves in  
71 alternative circumstances, set goals, plan ahead and monitor progress, weigh alternatives,  
72 engage in mental time travel, use schema to simulate outcomes, or use theories to predict

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73 probabilities, communicate directly with each other using language, learn complex tasks  
74 quickly, and use past events to inform actions in the present or future (Fuster, 1999;  
75 Passingham, 2008; Graziano, 2013; Tomasello, 2014; Everett, 2017). However, the intelligence  
76 of an individual human brain is a necessary, but not sufficient condition for human innovation;  
77 adaptation, innovation, and creativity results not from individuals *per se*, but from networks of  
78 interacting individuals (Hutchins, 1995, 2014; Richerson and Boyd, 2005; Whiten and Erdal,  
79 2012; Bettencourt, 2013).

80 In this paper we take a macroecological approach to understanding the allometry of group size  
81 and brain size across mammals by combining principles of metabolic ecology (Brown et al.,  
82 2004) with Bayesian phylogenetic mixed models (Bürkner, 2017). We first derive and test an  
83 allometric null model of group size across mammals. Next, we consider the allometry of brain  
84 size scaling in social groups across mammals; we term this quantity *collective brain mass*. We  
85 do not assume the size of a social group necessarily equates to the degree of social complexity  
86 (Silk, 2007); the size of the network is the number of nodes (i.e., individuals), whereas the  
87 complexity would be the statistics of the network structure (i.e., connectomics). Here, we use  
88 the size of a network to quantify the collective brain mass within a group to which an individual  
89 brain contributes and interacts. Clearly, the nature of interactions varies widely within  
90 mammalian social groups, from prairie dog warning vocalizations to elephant infrasonic  
91 rumbling to human story-telling traditions. However, by definition, social species co-reside in  
92 groups of conspecifics who benefit, in one way or another, from living with others who share  
93 similar cognitive abilities and who use information received from others, intentional or not, to  
94 modify their behavior.

95

## 96 **2. Theory and results**

### 97 **a) Scaling relations for group size and collective brain mass.**

#### 98 **i) Data**

99 We compiled a large database of mammalian ecology from published sources, including body  
100 size, basal metabolic rate, group size, home range, population density, and brain size (see  
101 *Electronic Supplementary Material (ESM)* for details). To quantify the scaling behavior, we use  
102 ordinary least squares regression models and Bayesian phylogenetic mixed models (BPMM)  
103 (Bürkner, 2017). In the BPMMs the dependent variable is weighted by the variance-covariance  
104 matrix of evolutionary relationships between all species, thus controlling for phylogenetically-  
105 structured residuals. Intercepts and slopes of the dependent variable are allowed to vary using  
106 mammalian order as the random factor. This modeling technique allows us to isolate scaling  
107 behavior within different mammal orders while controlling for their phylogenetic history. All  
108 data and code used in this paper are available as *Electronic Supplementary Material* attached to  
109 this paper.

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## 110 ii) Theoretical development

111 Allometric relations are captured by power functions that take the general form

112

$$113 \quad y = y_0 x^\beta \quad (1)$$

114

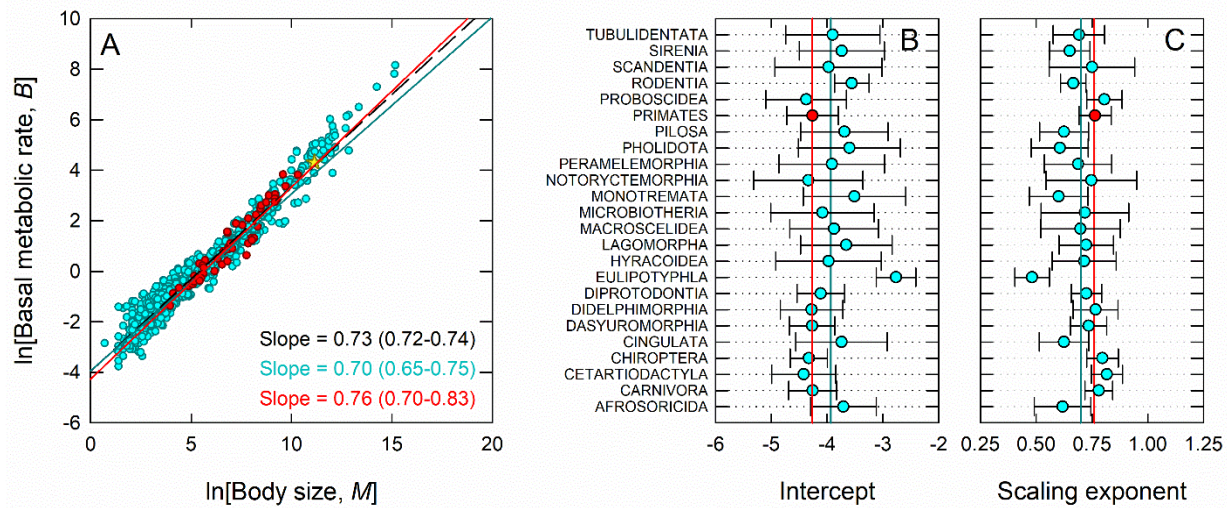
115 where  $y$  is a dependent variable, such as basal metabolic rate, brain size, group size, or home  
116 range size;  $x$  is an independent variable, commonly body size in allometry;  $\beta$  is the scaling  
117 exponent, an elasticity ( $d \ln y / d \ln x$ ) capturing the proportional response of a change in  $y$  to  
118 a change in  $x$ ; and  $y_0$  is a normalization constant. In biological systems when the independent  
119 variable is body size and the dependent variable is some measure of life history or physiology,  
120  $\beta$  is commonly less than 1 (i.e., sublinear). As such, there is an inherent economy of scale in  
121 biological systems as mass-specific efficiency increases with size. In human social systems,  
122 properties relating to energy and infrastructure show similar economies of scale for similar  
123 reasons (Bettencourt et al., 2007; Hamilton et al., 2007a; Brown et al., 2011). However, when  
124 the independent variable is group size or population size and the dependent variable is a  
125 measure of collective productivity, such as wealth, innovation, crime, or incidence of disease,  
126  $\beta$  is often greater than 1 (i.e., superlinear) (Bettencourt et al., 2007). This is because  
127 socioeconomic outputs are not the result of the number of people in a social network, but their  
128 interaction (Bettencourt, 2013); in a fully-connected unweighted social network the number of  
129 interactions,  $c$ , increases with network size,  $n$ , as  $c \sim n^2$  and so connectivity increases  
130 multiplicatively with size. As such, social networks achieve increasing returns to scale from  
131 intensified rates of interaction as they grow in size. This paper combines these approaches to  
132 understand how collective social phenomena scale with body size across mammals.

## 133 b) Basal metabolic rate.

134 Group living begins with the metabolic energy required to support individual organisms. The  
135 basal metabolic rate is a fundamental rate in biology setting the energy demand of all biological  
136 functions (Brown et al., 2004). Across mammals, the relationship between the basal metabolic  
137 rate,  $B$ , and body size,  $M$ , is described by a power function  $B = B_0 M^{3/4}$ , where  $B_0$  is a mass-  
138 specific normalization constant; in our data the empirical scaling across all mammals from OLS  
139 is  $B \propto M^{0.73}$  (Figure 1A; Table 1). The BPMM shows no statistical difference in the metabolic  
140 scaling of primates to any other mammalian order (see Figure 1 A-C and *ESM*). The human  
141 basal metabolic rate of  $\sim 75$  watts (the yellow star in figure 1A) is much as expected for a  
142 mammal of our body size ( $\sim 60,000$  g, or 60 kg).

143

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144

145 Figure 1. Basal metabolic rate and brain size allometries in mammals, primates and humans.  
 146 Red data points, lines, and text are non-human primates, blue are non-primate mammals, and  
 147 yellow diamonds are human. The red and blue lines are the scaling estimates from Bayesian  
 148 phylogenetic mixed models and the dashed black line and text is the OLS model estimate of the  
 149 slope. A) Scaling of basal metabolic rate in watts and body size in grams; B) Intercepts from the  
 150 phylogenetic mixed model by order; C) Scaling exponents from the Bayesian phylogenetic  
 151 mixed model by order.

152

Figure	OLS Model	Constant	95% CI	Slope	95% CI	d.f.	P-value	r <sup>2</sup>
1A	$B \propto M$	-3.94	-3.88, -4.00	0.73	0.72, 0.74	793	<0.001	0.95
1D	$W \propto M$	-2.78	-2.72, -2.84	0.73	0.72, 0.74	1366	<0.001	0.96
1G	$W \propto B$	-1.09	1.22, 1.14	0.98	0.96, 1.00	585	<0.001	0.93
3A	$D \propto M$	8.63	8.35, 8.92	-0.69	-0.73, -0.65	1117	<0.001	0.53
4A	$H \propto M$	-9.82	-10.19, -9.45	1.01	0.97, 1.06	950	<0.001	0.64
4D	$H' \propto M$	-9.32	-9.78, -8.86	0.81	0.75, 0.87	785	<0.001	0.49
5A	$N \propto M$	-0.35	-0.29, -0.51	0.17	0.15, 0.19	1205	<0.001	0.21
6A	$G \propto M$	-2.79	-2.49, -3.09	0.87	0.85, 0.89	716	<0.001	0.77

153

154 Table 1. Summary of OLS regression models and parameter estimates. For full details of ANOVA  
 155 tables and results see the *Supplementary Information*.

156

157 **c) Group size, population density, and home range.**

158 At all body sizes some species live solitarily, but many live in social groups. Living in groups may  
 159 help individuals maximize fitness by reducing predation risk, increasing foraging success,  
 160 providing opportunities for alloparental care, increasing mating opportunities, or reducing

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161 mortality risk, for example (Krause et al., 2002; Silk, 2007; Beauchamp, 2013). On the other  
162 hand, group living may increase competition for space, resources, and mates, increase disease  
163 loads and the risk of free-riders. Ultimately the calculus of group size reduces to whether the  
164 net benefits of group living outweigh the costs (see Silk, 2007).

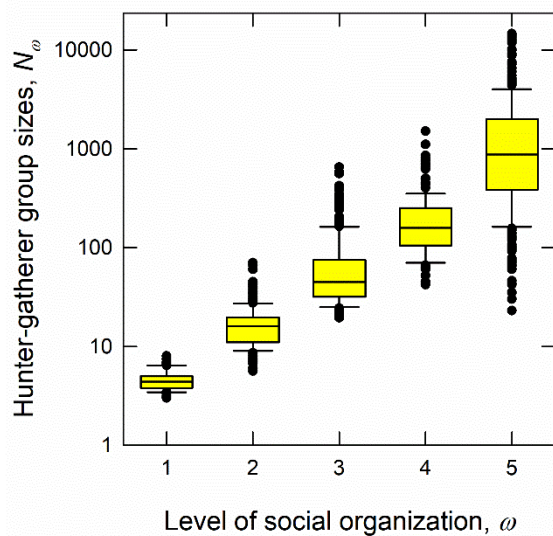
165 Human hunter-gatherer societies are organized into a complex hierarchy of social groups that  
166 form metapopulations (Figure 2) (Binford, 2001; Hamilton et al., 2007b; Bird et al., 2019).  
167 Interactions at all levels occur through fission-fusion dynamics that operate at different time-  
168 scales, from days to years (Hill et al., 2011, 2014). Using data from Binford (2001) we consider  
169 the five levels of hunter-gatherer social groups in Table 2.

170

171 Table 2. The five levels of hunter-gatherer social group sizes.

Level	Group	Geometric mean	95% CI	Sample
1	Families	4.48	4.31-4.67	116
2	Dispersed bands	15.60	14.68-16.58	228
3	Aggregated bands	53.66	49.86-58.29	298
4	Regional populations	165.32	152.25-181.00	214
5	Ethnolinguistic metapopulations	839.19	736.36-954.03	340

172



173

174 Figure 2. Boxplots of hunter-gatherer group sizes across five levels of social organization. The  
175 horizontal bars in the box bodies are medians, the height of the box is the middle 50% of the  
176 data, and the whiskers are  $\pm 25\%$ . At all scales of social organization hunter-gatherer group  
177 size are approximately normally distributed on the log scale, and so lognormally distributed on  
178 the linear scale. 1 = families, 2 = dispersed bands, 3 = aggregated bands, 4 = regional  
179 populations, and 5 = ethnolinguistic metapopulations (see Table 2 for details).

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180

181 In mammals social group size,  $N$ , is defined as the number of individuals that co-reside within  
182 a shared home range,  $H$ , and is usually measured in the field as the average number of  
183 individuals with whom a set of focal individuals interact over a 24-hour time period (Jones et  
184 al., 2009). The allometry of group size is inherently noisy as there are solitary species at all body  
185 sizes and so there is no simple correlation between group size and body size that holds for all  
186 mammal species. In other words, while average group size may increase with body size, the  
187 variance will also increase as group size is bounded at  $N = 1$  for all body sizes.

188 We derive a simple allometric null model for group size from the definitions of home range and  
189 population density. Let us assume the daily encounter rate of conspecifics,  $\lambda$ , is a function of  
190 the population density of conspecifics within a home range, and so the number of individuals  
191 encountered during a day,  $N$ , will be the product of the encounter rate,  $\lambda$ , and the home  
192 range size,  $H$ , both of which scale allometrically. Mammal population density,  $D$ , scales with  
193 body size as the inverse of metabolic rate;  $D = N / A \propto M^{-3/4}$ , where  $A$  is a sampled area in  
194  $\text{km}^2$ . This allometric relationship is known as Damuth's Law in ecology (Damuth, 1981). We see  
195 this scaling empirically in Figure 3A and Table 1. Note that primate population densities are  
196 shallower than the mammalian average (Figure 3C). In mammals, home range size scales  
197 linearly with body size;  $H \propto M^1$ , (Peters, 1986; Kelt and Van Vuren, 2001; Jetz et al., 2004). We  
198 see this empirically in Figure 4A and Table 1. Figures 4B and C show the remarkable consistency  
199 of home range scaling across mammalian orders, where only Rodentia deviate from all other  
200 mammals. Combining these two results we have a null allometric expectation for group size,  $N$   
201 :

202

$$203 \quad N \propto \lambda H \propto M^{-3/4} M^1 \propto M^{1/4} \quad (2)$$

204

205 We first test this model using an approach developed by Jetz et al. (2004). The size of a home  
206 range,  $H$ , is the space required by a mammal to meet their metabolic demand,  $B$ , the  
207 resource supply rate from the local environment,  $R$ , and the spatial overlap with conspecifics;  
208 thus  $H = B / \alpha R$ , where  $\alpha$  is the proportion of the environmental resource supply rate used  
209 exclusively by an individual (Jetz et al., 2004). Therefore, the home range used by an individual  
210 in a group is estimated by dividing the home range,  $H$ , by group size,  $N$ . The group size-  
211 corrected home range is then defined as  $H' = H / N$ . Following equation 2 and the allometry of  
212 home range the expected scaling of the group size-corrected home range is then

213

$$214 \quad H' \propto H / N \propto M^1 M^{-1/4} \propto M^{3/4} \quad (3)$$

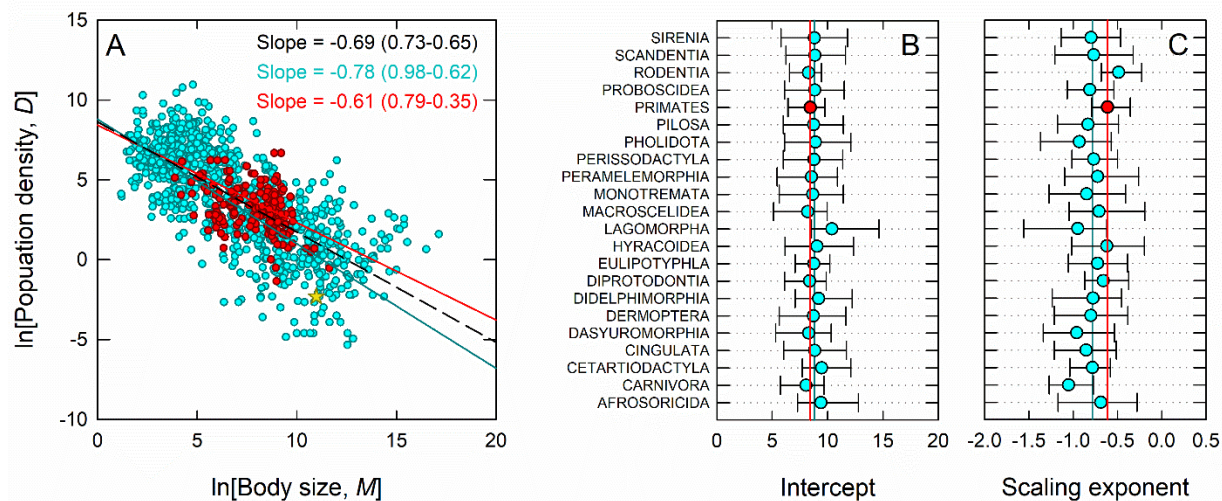
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216 We find support for this predicted scaling in Figures 4D-F, where the scaling estimates are  
 217 consistent this prediction. It is important to make two observation here. First, note that the  
 218 group size-corrected home range,  $H' = H / N$  (Figure 4D), is the inverse of population density,  
 219  $D = N / A$  (Figure 3A), and so Jetz et al.'s model directly links home range scaling with  
 220 Damuth's Law. Consequently, group size-corrected home ranges in primates deviate from the  
 221 overall mammal scaling (Figures 4D and F) in the same way that we see in primate population  
 222 densities (Figures 3A and C). Thus, for their body size primate species tend to be denser on the  
 223 landscape than most other mammals because individuals overlap in space with conspecifics  
 224 within their home ranges more so than other mammals. In other words, primate species in  
 225 general sustain larger group sizes per unit area than other mammals with the exception of  
 226 Rodentia and Eulipotyphla (shrews, moles, and hedgehogs) (Figure 4F). Interestingly, most  
 227 species in the orders Primates, Rodentia, and Eulipotyphla are either arboreal or fossorial. As  
 228 such, their home ranges include an additional vertical dimension that could explain the higher  
 229 observed population densities.

230



231

232 Figure 3. Population density allometries in mammals. A) The scaling of population density and  
 233 body size; B) Intercepts for each order from the phylogenetic mixed model; and C) Slopes for  
 234 each order.

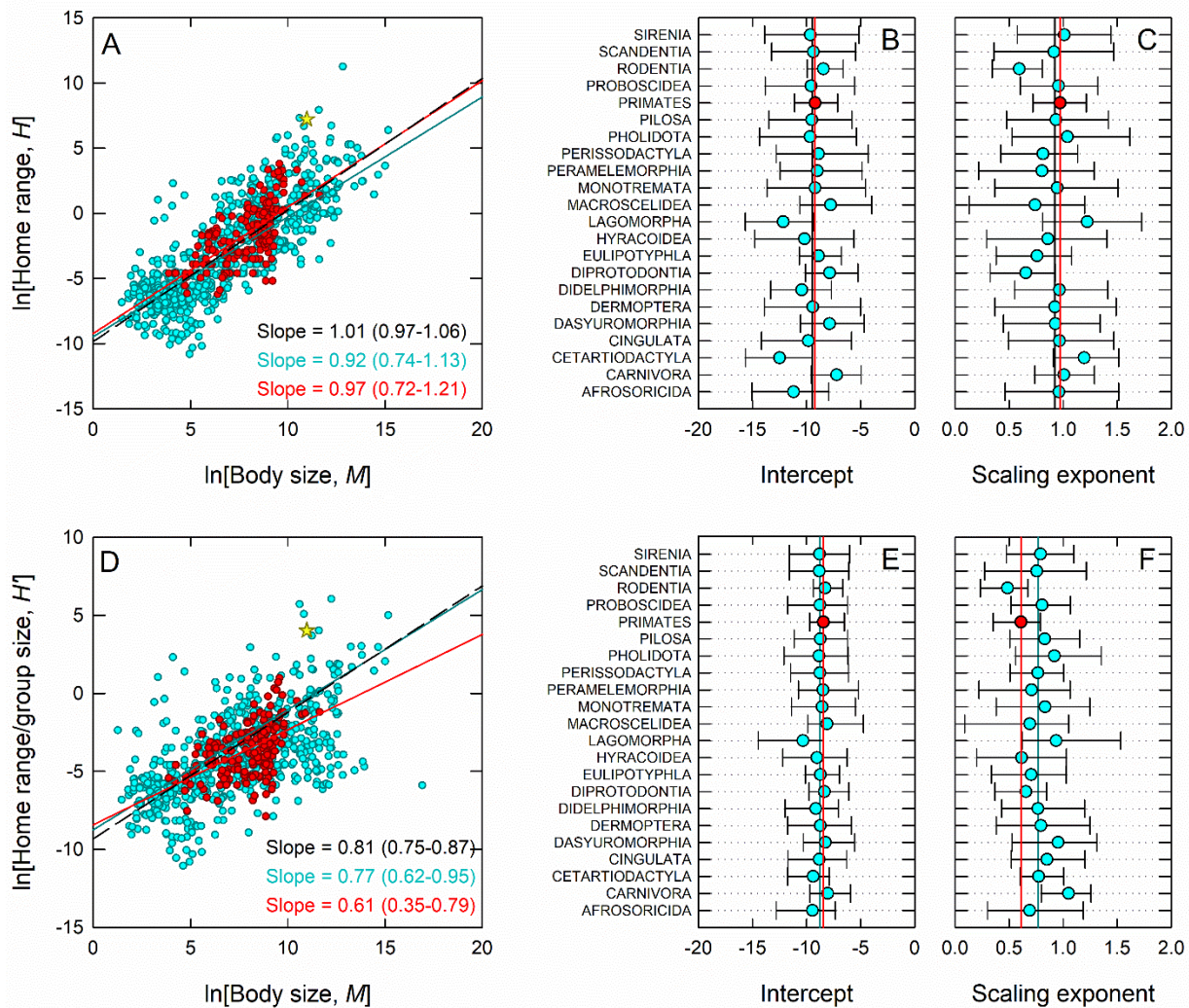
235

236 In Figure 3A, the hunter-gatherer average population density (yellow star) was estimated from  
 237 the geometric mean of total population sizes divided by the geometric mean of territory sizes  
 238 using data from Binford (2001) (see *ESM* for data). Hunter-gatherers have relatively low  
 239 population densities for mammals of their body size and have the lowest average population  
 240 densities of any primate. In Figure 4A, hunter-gatherer home ranges are residential patch sizes  
 241 estimated from mobility data in Binford (2001). The geometric mean distance of the average

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242 length of a residential move from the centroid of one patch to the centroid of an adjacent patch  
 243 is  $d$  (see Hamilton et al., 2016). Assuming patch sizes are circular the patch size (i.e., home  
 244 range),  $H$ , is estimated as  $H = \pi(d/2)^2$ . To estimate the group size-corrected home range we  
 245 then divide this quantity by the average size of dispersed bands (level 2 in Table 2), as this is the  
 246 number of individuals with which a hunter-gatherer will spend most of the year co-residing  
 247 (Binford, 2001; Hill et al., 2011). Figures 4A and D show that hunter-gatherers have particularly  
 248 large home ranges for mammals of their body size, and by far the largest of any primate (both  
 249 absolutely and relatively).

250



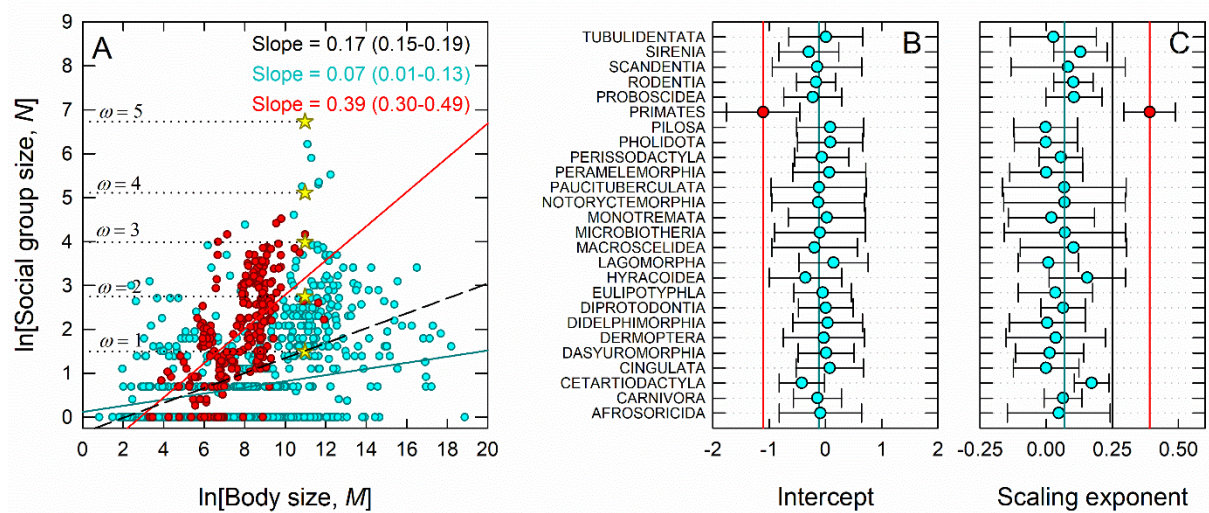
251

252 Figure 4. Home range allometries in mammals, primates and humans. A) The scaling of home  
 253 range size and body size; B) Intercepts for each order from the phylogenetic mixed model ; C)  
 254 Slopes for each order; D-F) The scaling of individual home range size and body size, and  
 255 phylogenetic mixed models results; G-I) the scaling of social group size and body size, and  
 256 mixed effect model results.

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257  
 258 Figure 5A shows that across mammals there is a noisy but statistically significant positive scaling  
 259 relationship between group size and body size,  $N \propto M^{0.17}$  (Table 1), though shallower than the  
 260 null expectation of  $N \propto M^{1/4}$ . Figure 5C shows that primate group sizes increase with body size  
 261 significantly faster than all other mammal orders, where  $N \propto M^{0.39}$ , and significantly faster  
 262 than the null prediction (the vertical black like in Figure 5C). As this scaling is steeper than the  
 263 allometric null model, this means that in primate species individuals form groups that are larger  
 264 than simply the average density of individuals encountered in their home range over a 24 hour  
 265 period. In other words, this is strongly indicative of prosocial behavior as there must be  
 266 additional behaviors that aggregate individuals into cooperative groups than simply shared  
 267 space and random encounters. On the other hand, in all other mammalian orders, the scaling  
 268 slope is less than 1/4 and so individuals form social groups at rates slower than the null model.  
 269 Group formation is much more limited and constrained in most other mammalian orders than  
 270 in primates. Figure 5A shows that largest group sizes of hunter-gatherers (levels 4 and 5;  
 271 regional and ethnolinguistic populations) are among the largest social groups of all mammals  
 272 and primates. The only other mammals in Figure 5A with similar body sizes and social groups  
 273 are all marine mammals, including seven species of Delphinidae (*Stenella attenuata*; *Delphinus*  
 274 *delphis*; *D. capensis*; *Peponocephala electra*; *Lissodelphis peronii*; *L. borealis*; and *S. longirostris*).  
 275 Interestingly, the human body size of ~60 kg place them near the empirical apex of maximum  
 276 group sizes observed at any body size suggesting the human ability to form large social groups  
 277 is partially a serendipitous function of having a body size near the midpoint of mammal body  
 278 sizes, above which maximum group size declines rapidly. We discuss this further below.

279



280  
 281 Figure 5. Group size allometries in mammals, primates and humans. A) Group size and body  
 282 size. B) Intercepts by order from the phylogenetic mixed model. C) Scaling exponents by order

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283 from the Bayesian phylogenetic mixed model. The vertical solid black line is the expectation  
284 from the null model, equation 2.

285

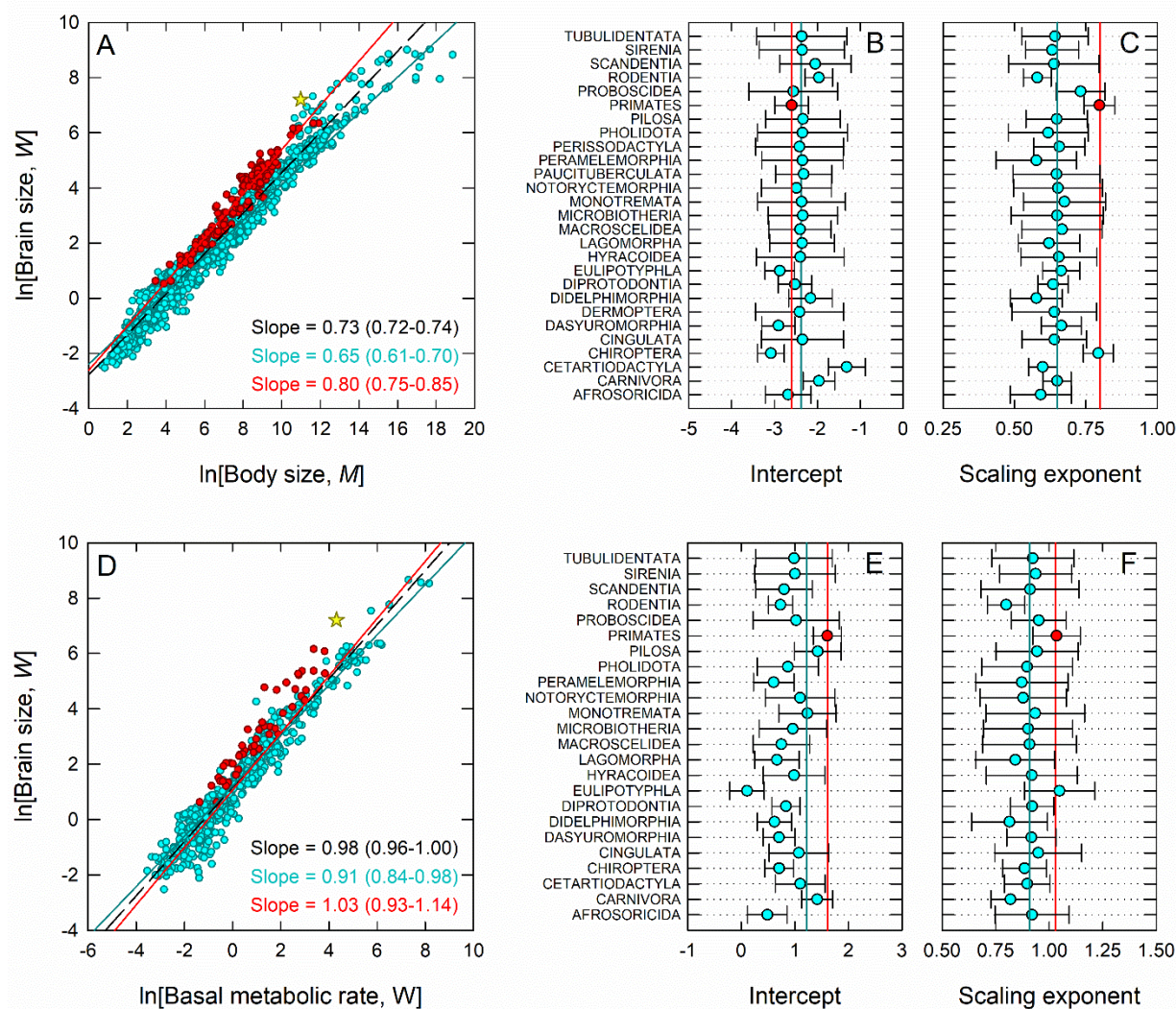
286 **d) Brain size and social networks of brains.**

287 A central aspect of group living is cooperation and the increased potential for information  
288 sharing among group members. One of the potential cognitive benefits of group living is the  
289 ability to interact with more brains. In mammals brain size,  $W$ , scales with body size as  
290  $W \propto M^{3/4}$  (Burger et al., 2019). We see this empirically in figure 6A, where  $W \propto M^{0.73}$  (see  
291 Table 1). In Figure 6C the BPMM shows that primate brain size (red data point and vertical line)  
292 increases with body size significantly faster than other mammals (vertical blue line) (see *ESM*  
293 for full results). Therefore, in primates, brains constitute an increasing proportion of body size  
294 as body size increases, with the notable exception of Chiropterans (see Smaers et al., 2012).  
295 Although the human brain is large for a mammal of 60,000 g at ~1,350 g, there are several  
296 large-bodied mammalian species that have brains absolutely larger than humans, including 26  
297 marine species of Cetartiodactyla (whales and dolphins) and both extant species of  
298 Proboscidea; *Loxodonta Africana* and *Elephas maximus*.

299 Consequently mammalian brain size increases linearly with basal metabolic rate,  $W \propto B^1$  as  
300 shown in Figure 6D and Table 1; the faster the metabolic rate the larger the brain. Figure 6E  
301 shows that primate brains are significantly more expensive to support per gram than other  
302 mammal brains, and Figure 6F shows that primate brain size increases significantly faster with  
303 basal metabolic rate than other mammals (see *ESM* for full results). Metabolically expensive  
304 primate brains thus become increasingly expensive with size. Figure 6A shows that while  
305 human brains are particularly metabolically expensive, so are those of several larger-bodied  
306 primates, including *Pongo pygmaeus*, *Papio Anubis*, *P. hamadryas*, *P. papio*, *Cercocebus*  
307 *torquatus*, *Erythrocebus patas*, and *Hylobates lar*.

308

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309  
 310 Figure 6. Brain size allometries in mammals, primates and humans. Red data points, lines, and  
 311 text are non-human primates, blue are non-primate mammals, and yellow diamonds are  
 312 human. The red and blue lines are the scaling estimates from Bayesian phylogenetic mixed  
 313 models and the dashed black line and text is the OLS model estimate of the slope. A) Scaling of  
 314 basal metabolic rate in watts and body size in grams; B) Intercepts from the phylogenetic mixed  
 315 model by order; C) Scaling exponents from the Bayesian phylogenetic mixed model by order; D-  
 316 F) Scaling of brain size in grams and body size, and Bayesian phylogenetic mixed model results;  
 317 G-l) Scaling of brain size and basal metabolic rate, and Bayesian phylogenetic mixed model  
 318 results.

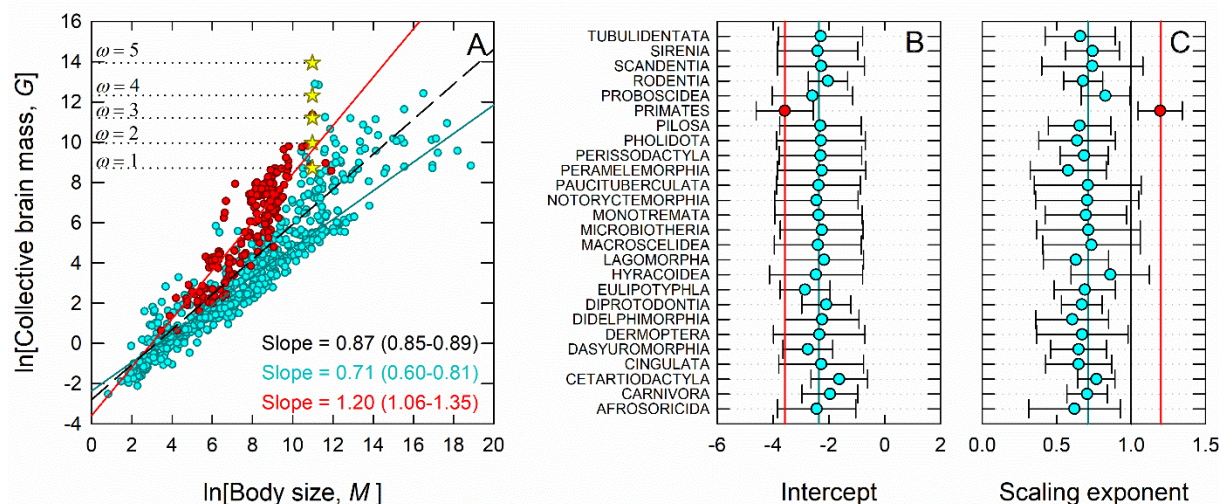
319  
 320 To consider how brain allometry scales up in social groups we combine the allometric scaling of  
 321 brain size,  $W$ , and social group size,  $N$ , to define the collective brain mass of a social group as  
 322  $G = NW$ . An allometric null model for collective brain mass is then

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323  
324 
$$G = NW = \lambda HW \propto M^{-3/4} M^1 M^{3/4} \propto M^1 \quad (3)$$

325  
326 Thus, the null model predicts collective brain mass within species-specific social groups  
327 increases linearly with body size. If so, this would have important consequences for group  
328 cognition as average brain size increases sublinearly with body size. Therefore, as body size  
329 increases brains would be connected within larger social networks, allowing for greater  
330 connectivity. However, Figure 7A shows that the scaling of collective brain mass across  
331 mammals is sublinear and significantly less than 1 (see Figure 7C), both in the OLS model  
332  $G \propto M^{0.87}$  and the BPMM,  $G \propto M^{0.72}$ . However, for primates the scaling is superlinear,  
333  $G \propto M^{1.20}$ , and significantly greater than 1 (the vertical black line in Figure 7C) (see *ESM* for full  
334 details). Primate collective brain mass increases with body size much faster than other  
335 mammals (~1.7-fold). In addition, primates are the only mammalian order to scale significantly  
336 differently than all other mammalian orders (Figure 7C). Hunter-gatherers exhibit among the  
337 largest collective brain masses of any mammal or primate (Figure 7A). As with social group size,  
338 the only other mammals with similar-sized collective brain masses are species of the  
339 Delphinidae family. The phylogeny of collective brain mass across mammals is shown in Figure  
340 8.

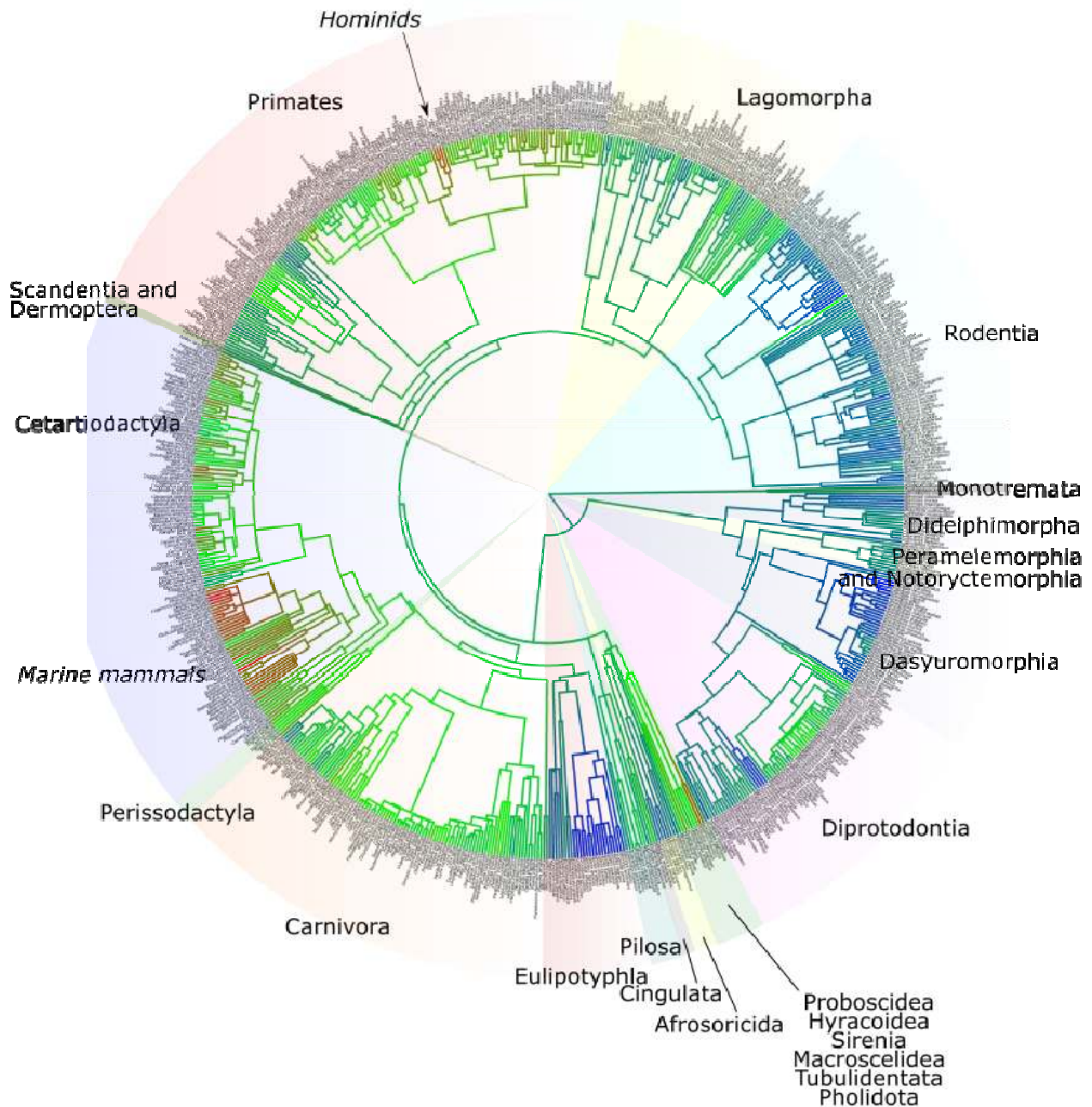
341



342  
343 Figure 7. Collective brain size allometries in mammals, primates and humans. A) Collective brain  
344 size and body size. B) Intercepts by order from the phylogenetic mixed model. C) Scaling  
345 exponents by order from the Bayesian phylogenetic mixed model. The vertical solid black line is  
346 the expectation from the null model, equation 3.

347

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348

349 Figure 8. The phylogeny of group brain networks in mammals using continuous character  
350 mapping. Colored sectors denote mammal orders.

351

### 352 3. Discussion

353 Primate species form social groups that are among the largest for their body size among  
354 mammals. The allometric scaling of primate group size is unique among mammals and the data  
355 show that group size increases with body size almost twice as fast than in other mammals

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356 (Figures 6A and C). The data show that this occurs because primates support greater densities  
357 of individuals than most other mammals (Figures 3A and 4D). The analysis of the null model we  
358 derive in this paper from ecological theory shows that primates form groups faster than would  
359 be expected from the random encounter rates of individuals within shared home ranges. As  
360 species in all other mammal orders tend to form groups slower than the null expectation, the  
361 results we report here show a strong statistical signature of a generalized primate prosociality  
362 not found in other mammals and which results in the unique allometry of social group scaling in  
363 primates.

364 Hunter-gatherers have a wide range of social group sizes (Figure 5A), including some of the  
365 largest observed in all mammals. The most common residential group sizes used during the  
366 course of a year are the dispersed and aggregated bands (levels 2 and 3 in Table 2 and Figure  
367 5A) that reflect the seasonal fission-fusion cycle of families as they aggregate into different  
368 group sizes over the course of a year (Binford, 2001). Figure 5A shows the sizes of these groups  
369 are much as expected for a primate of ~60 kg. However, because individual hunter-gatherer  
370 bands are embedded within larger social networks commonly of hundreds to thousands of  
371 people, all of which interact at various rates (Hill et al., 2014), these social group sizes are  
372 among the largest observed of any mammal species. While some mammal species aggregate  
373 into large collectives of many thousands of individuals, such as herds of artiodactyls or colonies  
374 of chiropterans in roosts, these aggregations are not social networks of co-residing individuals,  
375 but aggregations brought about by environmental conditions that are temporarily capable of  
376 supporting large focal densities of individuals. Analogous aggregations in human societies may  
377 be large-scale ritual events held over a number of days, or sporting events that aggregate tens  
378 of thousands for short periods of time. Of course, the largest human social groups in the 21<sup>st</sup>  
379 century connect billions of individuals through social media, cell phone networks, religious  
380 identities, languages, or the politics of nation states.

381 The self-organization of hunter-gatherer meta-populations into a fluid arrangement where  
382 families aggregate into different sizes of social groups at multiple levels results in a highly  
383 flexible social organization. On the one hand, the number of co-residing families in a band is  
384 often no more than 3-6 (Hamilton et al., 2007b, 2018), perhaps 10-20 individuals (Hill et al.,  
385 2011), a size which may optimize group return rates while minimizing competition for finite  
386 resources and the risk of free-riders, for example. On the other hand, by maintaining a fluid  
387 structure of fission and fusion among meta-populations composed of hundreds of people with  
388 some form of shared identity, information flows at much larger scales, often including multiple  
389 neighboring metapopulations (see Bird et al., 2019). Thus individuals living in small social  
390 groups on a daily basis receive the long-term benefit of being embedded within a much larger  
391 social network.

392 A consequence of the unique allometric scaling of primate group sizes is the similarly unique  
393 scaling of collective brain masses in social groups of primates (Figure 6A). This is because both  
394 social group size and brain size scale faster in primates than in all other mammals (Figure 6C)



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395 and so collective brain mass in primates diverges from all other mammals as body size  
396 increases. Therefore, at all body sizes, primates have both larger brains and larger social  
397 networks for that brain to interact with than other mammals. Importantly, the rate of  
398 allometric increase of collective brain mass in primates is superlinear (i.e., slope  $> 1$ ). This  
399 means that in primate species increasingly larger brains are embedded within even larger social  
400 groups. Because group connectivity increases multiplicatively with size (i.e.,  $c \sim n^2$ ) then larger  
401 brains have a multiplicatively greater potential for interaction than smaller brains. Across all  
402 other mammal orders the collective brain mass within social groups increases sublinearly with  
403 body size (Figures 6A and C), because larger brains occur in social group sizes that increase with  
404 body size only very shallowly (if at all) (Figure 6A and C).

405 Because the number of neurons scales positively with brain size in mammals (Herculano-  
406 Houzel, 2012; Herculano-Houzel et al., 2015), a social group with a larger collective brain mass  
407 can potentially recruit more brains with more neurons to perform a collective behavior, and so  
408 it reasonable to hypothesize that larger social networks will have a greater potential for group  
409 cognition and collective computation. If so, primates would be predicted to exhibit a greater  
410 potential for group cognition than non-primate mammals. It is perhaps not surprising then that  
411 the most evidence we have for advanced group cognition and collective computation in  
412 mammals comes from one of the largest-bodied primates.

413 Intriguingly, Figure 5A suggests that the ability of humans to form large social groups may be  
414 partially a function of its position on the mammal body size spectrum. The only other mammals  
415 with similar-sized social groups are several species of Delphinidae, all of whom have similar-  
416 sized bodies to humans. From the smallest terrestrial mammal, *Suncus etruscus*, the Etruscan  
417 shrew at  $\sim 2$  g, maximum social group size increases steadily up to the human body size of  
418  $\sim 60,000$  g, but thereafter declines rapidly. This suggests that while average group size may well  
419 be a function of body size and ecology (as described in our model), as body size increases there  
420 are shifting trade-offs in the ability of ecosystems to support the largest aggregations of larger-  
421 bodied mammals: above a certain body size (apparently near the midpoint of the body size  
422 spectrum) large groups are increasingly difficult to maintain and maximum group sizes decrease  
423 monotonically. This may be because about half of the mammal species with body sizes larger than  
424 humans are marine mammals (data not shown), which have different ecological constraints to  
425 maintaining aggregations than terrestrial mammals.

426 The estimated clade age of primates is on the order of  $\sim 53$ -88 MYA (Springer et al., 2012;  
427 O'Leary et al., 2013), and so the distinctive evolutionary trajectory of primates was a pathway  
428 that emerged early in the post-Cretaceous mammalian radiation. The hominin branch emerged  
429  $\sim 6$ -7 million years ago within the primate tree. Among other traits, the hominin clade saw not  
430 only increasing brain size but increasing neuroanatomical specialization (Lieberman, 2011) that  
431 ultimately allowed for self-expression (Berwick and Chomsky, 2016; Tattersall, 2019) and the  
432 transfer of social information among individuals through gestures, symbols, and language  
433 (Tomasello, 2010; Clark and Toribio, 2012; Everett, 2017). Some researchers suggest that

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434 modern human-like social complexity may have emerged with the first major expansion in  
435 hominin brain size  $\sim 2$  MYA with *Homo erectus (sensu lato)* (Deacon, 1998; Wrangham, 2009;  
436 Herculano-Houzel, 2016; Everett, 2017). However, the point at which complex social networks  
437 of the form we see in ethnohistoric hunter-gatherers first appear in the archaeological record is  
438 unclear.

439 It has been argued that the complexity, diversity, and specialization of the primate brain  
440 evolved in response to the selective pressures of living in complex 3-dimensional, arboreal  
441 environments (Passingham and Wise, 2012). Complex ecological environments are also  
442 complex social environments as the successful exploitation of ecological niches necessarily  
443 involves the successful negotiation of conspecifics (Passingham, 2008; Passingham and Wise,  
444 2012; Wittmann et al., 2018). Recent research in neuroscience suggests that the ability of  
445 brains to restrict attention to a subset of stimuli in complex environments resulted in the  
446 capacity for self-awareness of mental state, which in turn became awareness of the mental  
447 state of others (Frith and Frith, 2006; Graziano, 2017). If this is an accurate mechanistic model,  
448 the results we show here suggest that the evolutionary consequences of these dynamics led to  
449 feedbacks between group size and brain size that resulted in the unique allometries of group  
450 size and collective brain mass in primate species.

451

## 452 **4. Conclusion**

453 The unique allometric scaling of group sizes in primates leads to the superlinear scaling of  
454 collective brain masses. This superlinearity results from the faster allometric scaling of both  
455 brain size and group size in primates than other mammals. Thus primates have both larger  
456 brains and larger social networks than other mammals of a similar body size. Consequently, as  
457 large-bodied primates, human hunter-gatherers have the largest extended brain networks of  
458 any mammal. These networks have grown in size, scale, and complexity over human  
459 evolutionary history, particularly the last few thousand years to the extent that the majority of  
460 the human species is now connected globally by various overlapping social networks.  
461 Ultimately, the scale of these networks have deep evolutionary roots in mammalian allometry,  
462 primate ecology, and the serendipity of human body size.

463

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