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1 **Primate hippocampus size and organization are predicted by sociality but not diet**

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26 hippocampus, social group, spatial cognition, primates

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Abstract

29

30 The hippocampus is well known for its roles in spatial navigation and memory, but it is
31 organized into regions that have different connections and functional specializations. Notably,
32 the region CA2 has a role in social and not spatial cognition, as is the case for the regions
33 CA1 and CA3 that surround it. Here we investigated the evolution of the hippocampus in
34 terms of its size and organization in relation to the evolution of social and ecological variables
35 in primates, namely home range, diet and different measures of group size. We found that the
36 volumes within the whole cornu ammonis coevolve with group size, while only the volume of
37 CA1 and subiculum can also be predicted by home range. On the other hand, diet, expressed
38 as a shift from folivory toward frugivory, was shown to not be related to hippocampal
39 volume. Interestingly, CA2 was shown to exhibit phylogenetic signal only against certain
40 measures of group size but not with ecological factors. We also found that sex differences in
41 the hippocampus are related to body size sex dimorphism. This is in line with reports of sex
42 differences in hippocampal volume in non-primates that are related to social structure and sex
43 differences in behaviour. Our findings support the notion that in primates, the hippocampus is
44 a mosaic structure evolving in line with social pressures, where certain subsections evolve in
45 line with spatial ability too.

1. Introduction

46

47 The relationship between behaviour and brain size and proportions has been the topic of
48 intensive research for decades, with works on mammals focusing mainly on the question of
49 how the exceedingly large brains of primates, and particularly humans, could evolve.
50 However, while there is an emerging consensus on the energetic constraints on the evolution
51 of brain enlargement [1, 2], the search for behavioural correlates of relative brain size has a
52 long history of producing a frustrating diversity of results [3]. In primates, there's a long-
53 standing debate about the degree to which ecological challenges have been met either directly
54 through selection for individuals traits that are adaptations to those ecological challenges, or
55 indirectly through social solutions [4]. Models of primate social intelligence and brain size
56 emphasize social skills, including managing social complexity, theory of mind, social
57 learning, and culture [4, 5]. On the other hand, models of ecological intelligence demonstrate
58 an important impact of home range size and/or diet [6-9] on relative brain size. Evidence
59 about which of these (home range or diet) is the main determinant of brain size is ambiguous
60 [6][7], but both possibly relate to the memory demands of locating and identifying
61 unpredictable food sources or mates, or tool use and social behaviour [10-13].
62 An important caveat to studies of "intelligence" and brain morphology is the fact that most
63 analyses of brain morphology addressing social and ecological factors across primate
64 evolution only consider how they relate to brain size (absolute or relative). However, there is
65 increasing awareness that more specific aspects of brain organization may better relate to
66 more specific cognitive abilities [14], consistent with long-standing evidence that the brain is
67 a mosaic of different regions, which may respond differentially to selection for specific
68 behaviours [15-18]
69 The mammalian hippocampus is of particular interest in terms of dissecting the morphological
70 correlates of ecological and social behaviour. It is well known for its roles in both spatial

71 cognition [19] and memory [20], and also has an important role in behavioural inhibition [21]
72 in rodents and primates, including humans. The hippocampus' role in spatial cognition has
73 been the topic of several comparative analyses related to “ecological intelligence”, and has
74 benefitted from studies in rodents that have revealed a neurophysiological mechanism for
75 mapping spatial coordinates in navigation [19]. The hippocampus contains a population of
76 neurons (‘place cells’) that respond whenever an animal is in a specific location [22] and
77 these produce a dynamic ‘cognitive map’ of the environment by firing in a concerted fashion
78 [23]. Similarly, the entorhinal cortex, a structure neighbouring the hippocampus in the larger
79 "hippocampal complex", has a population of “grid cells”, which fire when an animal enters an
80 environment with geometrically patterned locations [24]. Another component of
81 hippocampus-related “ecological intelligence” is its essential function in declarative or
82 relational memory possibly through a spatial-based mechanism [25, 26]. The hippocampus
83 also has a role in behavioural inhibition [21] and olfactory memory [27].
84 While declarative memory is a very broadly relevant cognitive ability it is hard to relate to
85 ecological variables. On the other hand, the hippocampus' role in spatial cognition is often
86 related to the ecological variable home range, defined as "that part of an animal’s cognitive
87 map of its environment that it chooses to keep updated” [28]. Some studies have suggested a
88 direct link between species’ home range size and species’ hippocampal size . In desert
89 rodents, the bannertail kangaroo rat has relatively low spatial memory requirements and has a
90 small hippocampus, whereas Merriam's kangaroo rat uses spatial memory to relocate its
91 caches in scattered locations, and larger hippocampus [29]. The "avian hippocampus” in the
92 medial pallial zone is homologous to that in mammals and also functions in spatial memory
93 [30]. This is consistent with the fact that food-storing birds have relatively larger hippocampi
94 [31, 32].

95 The size and internal organization of the hippocampus is also subject to within-species
96 variation and individual plasticity. Volumetric reorganization of the hippocampus has been
97 related to the occupational specialization in humans [33]. In birds, hippocampal size and
98 structure is plastic, being affected by experience [34], and seasonality [35]. In arboreal
99 primates, a relationship was found between hippocampus size and home range size [36], but
100 overall, this relationship remains unclear [36] [37]. The possibility for a predictive function of
101 the hippocampus is particularly evident from studies of sexual dimorphism in hippocampal
102 size and spatial ability. Whereas male and female meadow voles are sexually dimorphic in
103 their performance on spatial tasks, hippocampus volume, and home range size, pine voles are
104 not [38]. Further, in two other polygamous rodent species the relative size of the hippocampus
105 is greater in males than in females [29], while males and females of the monogamous desert
106 kangaroo rat do not differ in home range nor in spatial ability [39]. Similarly, during breeding
107 season, deer mice are polygynous and males have larger home ranges, and outperform
108 females on spatial tasks [40]. Sex differences in spatial ability and home range size are also
109 related in two species of carnivores - males exhibit larger home ranges and superior spatial
110 ability compared to females in the promiscuous giant pandas, but not in the monogamous
111 Asian small clawed otter [41]. Consistent with the hypothesis that function drives anatomy,
112 the sex differences are reversed in wider ranging females. In a brood parasite bird species, the
113 brown-headed cowbirds, females which travel further than males have larger hippocampi [42]
114 and exhibit superior spatial memory [43].

115 As of recently, some light has been shed on the role of the hippocampus in social behaviour
116 and cognition. Hippocampal place cells are involved in processing the presence of
117 conspecifics in bats [44] and hippocampal volume has been related to social phobia as part of
118 adjacent circuits in humans [45]. Although the representation system of the hippocampal
119 complex is itself spatial, this coordinate system is capable of processing other spatially

120 representable information – such is the case of its role as a "memory map" for encoding
121 declarative memories [25], or social information [46]. In rats, support for the mechanism
122 comes from studies finding the hippocampus (specifically a substructure described below,
123 CA2) uses place fields to encode information about conspecifics [47]. Given these novel
124 insights into hippocampus function, in species where social behaviour plays an important role,
125 the involvement of the hippocampus in social information processing might be greater. This
126 also has implications for linking social and spatial cognition more generally, as they can be
127 represented in the same cognitive systems [48].

128

129 **Hippocampal regions**

130 All fields of the hippocampus formation (retrohippocampus, RH) receive inputs from the
131 entorhinal cortex (EC) along the perforant pathway [49]. Part of it, hippocampus proper,
132 refers to the cornu ammonis (CA) and the fascia dentata (FD); more commonly these same
133 regions are divided up into CA1-3 and the dentate gyrus (DG) (Table 1). DG has traditionally
134 been considered the gateway of the hippocampus because it blocks or filters excitatory
135 afferents from the EC [50]. Sensory and associative projections from the EC synapse in the
136 DG [51]. DG arranges sensory inputs to create a metric spatial representation and is involved
137 in episodic memory and spontaneous exploration of novel environments [52]. DG can be
138 further subdivided into the fascia dentata (FD) and the hilus (part of the CA). Adjacent to the
139 FD, the CA is comprised of four fields arranged in a loop, beginning with the hilus (i.e., CA4)
140 [53]. The hilus is situated along the mossy fiber pathway from the granular stratum of FD to
141 CA3 and is involved in spatial learning and memory retrieval [54]. It has a role in sequence
142 learning [55], and local lesions affect pattern separation, particularly for highly similar inputs
143 [56]. Next are the sequential CA regions in descending order - CA3, CA2, CA1. CA3 receives
144 connections from the mossy fibers of FD, which it projects to CA1 and back, bypassing CA2.

145 There are associational bilateral (ipsilateral and contralateral) connections to CA3 [57]. CA3
146 can be further divided into subregions: CA3a and CA3b encode spatial information into short-
147 term memory, while CA3c processes environmental geometry along with DG [58]. CA1
148 receives projections from CA3 and is involved in spatial memory [59]. The spatial properties
149 of CA1 and CA3 are due to these regions being the primary locations of ‘place cells’,
150 responding differentially according to the spatial location of the animal [60]. Adjacent to
151 CA3, the subiculum has inputs from EC and bilateral connections with perirhinal cortex and
152 CA1 [61]. It is a major output of the hippocampus with pronounced dorso-ventral segregation
153 of function: the dorsal component is involved in processing of spatial information and
154 information related to movement and memory, while the ventral is a type of interface between
155 the hippocampus and the hypothalamic–pituitary–adrenal axis, a feedback system that
156 regulates homeostasis and stress [61]. The subiculum receives projections mostly from CA1
157 and these are organized in a simple pattern - all sections of CA1 project to the subiculum and
158 all parts of the subiculum receive input from CA1 [62]. Moreover, subicular neurons exhibit
159 spatially-selective firing [61] with a robust location signal [63].

160

161 <<Figure 1 about here>>

162

163 CA2 has been suggested to act as an interface between emotion and cognition [64]. CA2
164 receives strong inhibitory inputs from EC, CA3, and DG, and has outputs to CA1 [65]. It is
165 also influenced by many neuromodulators, receiving unique input from hypothalamic nuclei
166 associated with social context, reward, and novelty [64] – supramammillary, paraventricular,
167 median raphe, septal, and the vertical and horizontal limbs of the nucleus of diagonal band of
168 Broca [65]. CA2 has outputs to septum and the supramammillary nucleus. Unlike CA1 and
169 CA3, lesions to CA2 do not affect spatial memory in Morris water maze test, nor impact

170 locomotor ability, anxiety or fear memory in rodents [66]. Rather, CA2 is involved in social
171 memory and recognition of conspecifics [66]. There are some indications its size may be
172 particularly adaptive to social and emotional experiences - decrease in CA2 neuron numbers
173 is associated with schizophrenia and bipolar disorder [67] and stress-related increases in the
174 density of brain-derived neurotrophic factor neurons are greater in CA2 than CA3 [68].

175

176 Here we investigate the evolution of hippocampal size and organization in primates, in
177 relation to social and ecological pressures. Given the importance of the hippocampus in
178 spatial cognition, and the subiculum, CA1, CA3, and FD in particular, we predict that these
179 will be related to variation in ecological variables: home range size and/or dietary complexity.
180 Additionally, we predict CA2 volume to be related to social memory, measured through
181 group size. We also expect that amongst brain areas, dimorphism in hippocampal size will be
182 the best predictor of dimorphism in body size.

183

184

2. Methods

185

186 (a) Anatomical data

187 The morphometric structure of the hippocampus was determined from previously published
188 volumetric data [69]. For measurements, the retrohippocampus (RH) has been divided into:
189 dentate gyrus (reported in [69] as *fascia dentata*, FD), *hilus* (HIL), CA3, CA2, CA1, and
190 *subiculum* (SUB). Volume measurements include the white matter comprising the rest of the
191 hippocampus [69, 70] measured together as *HP+HS+fibers*, that is the hippocampus
192 praecommissuralis (HP) plus the hippocampus supracommissuralis (HS) plus the fibers of the
193 fimbria/fornix complex. Volumes for whole *brain* were taken from the same source [69].

194 Volumes for *neocortex* (white and grey matter; NEO) were obtained from the same research
195 group [70].
196 Unpublished data on brain component volumes of males and females were used to determine
197 averages for each sex in a subsample of primates, and correspond to anatomical definitions in
198 [70]. The brain components include 7 telencephalic components: *bulbus olfactorius* + *bulbus*
199 *olfactorius accessorius* (bulbus olfactorius accessorius is absent in higher primates; BOL),
200 *lobus piriformis* (palaeocortex and amygdala; PAL), *septum* (septum pellucidum, septum
201 verum, Broca's diagonal band, bed nuclei of the anterior commissure and stria terminalis;
202 SEP), *striatum* (caudate nucleus, putamen, nucleus accumbens, and the parts of the capsula
203 interna running through the striatum; STR), *schizocortex* (ento- and perirhinal, pre- and
204 parasubicular cortices and the underlying white matter; SCH), *hippocampus* (including all
205 regions; HIP), *neocortex* (white and grey matter; NEO). Included were *diencephalon* (plus
206 globus pallidus without hypophysis; DIE), *mesencephalon* (without substantia reticularis;
207 MES), *cerebellum* (brachium and nuclei pontis, CER), and *medulla oblongata* (plus
208 substantia reticularis; MED). Body weight (BoW) data was available for the same individuals,
209 except for *Miopithecus talapoin* female body weight, which was taken from [71]. Sexual size
210 dimorphism was determined from BoW and calculated as the ratio of male BoW divided by
211 female BoW. Sexual dimorphism in each of the brain structures was calculated as the ratio of
212 the volume in males vs females.

213

214 **(b) Social and ecological data**

215 Data were collated from three different sources. Home range area in hectares “HR size
216 average” (HR) were from Powell et al. [7], frugivory “% fruit” were from DeCasien et al. [6],
217 “group size combined” were from [7]. Further, “social group size” data are from [6] and
218 “mean group size” and “mean number of females per group” are from Dunbar et al. [72].

219 These different studies use different methods for collating the datasets, where it is not always
220 clear whether group size indicates social or foraging group, or whether diet information has
221 been calculated uniformly and reliably.

222

223 **(c) Phylogeny**

224 The consensus phylogenetic tree of 43 species of apes and monkeys was obtained from 10k
225 Trees [73] and information about phylogenetic non-independence was incorporated in all
226 analysis. Changes in taxonomic nomenclature were considered for matching species names
227 from the brain dataset to the tree.

228

229 **(d) Statistical analysis**

230 All continuous variables were natural log transformed, except for % fruit. Bonferroni
231 correction was applied on the α level (“significance cut-off” of 0.05) on models tested
232 multiple times by dividing it by the number of comparisons with the same dependent variable
233 (4 models with different group size measures resulting in corrected α of 0.0125).

234 Analyses were run on R version 3.6.1 [74] using the packages phytools [75] and caper [76].

235 Using the fastanc function in phytools we estimated the ancestral states and painted them on
236 the tree using Fancytree. We used caper for all PGLS analyses. Phylogenetic signal (Pagel's λ)
237 was estimated using Maximum Likelihood and kappa (k) and delta (δ) were fixed to 1. We
238 tested four ‘full’ models including home range size, fraction fruit and each of four different
239 measures of group size against hippocampus and hippocampal region volumes.

240 Additionally, we explored the relationship between neocortex and brain volume with
241 hippocampus volume. Means square statistics were obtained via sequential sum of squares
242 ANOVA.

243 The volume of the region of interest was always used as the dependent variable in our models,
244 and brain volume was included as a covariate. All variables were shown to be normally
245 distributed, and variance inflation factors of each models were shown to be <3.5 meaning that
246 there was no problem with collinearity. Interactions between predictors were not included as
247 to avoid high cross-collinearity.

248 We also tested additional single variable models including either only home range, diet or
249 group sizes against hippocampal regional volumes, also correcting for total brain volume.

250 This was done because the ‘full’ model resulted in sample sizes between 20 and 30, while
251 running the separate models mostly utilised the full dataset of 43 species. For results of these
252 models see the Supplementary material.

253 Additionally, all four ‘full’ models were evaluated and ranked using AIC (Akaike Information
254 Criterion). [77].

255

256 All data (including anatomical, social and ecological variables), code, phylogenetic trees and
257 analysis outputs are included in the supplementary material.

258

259

260

3. Results

261

262 (a) Ancestral state estimation

263 An exploratory ancestral state estimation revealed that in species where relative hippocampal
264 volume has decreased (calculated as the residuals from the phylogenetic regression with total
265 brain volume) have nonetheless undergone an increase in absolute hippocampus volume (Fig.
266 2). We further tested this observation using PGLS and found that hippocampus volume
267 increased with a shallower slope compared to both brain and neocortex volumes i.e. species

268 that evolve towards greater neocorticalization have smaller relative hippocampi. (See
269 Neocortex section). An exception is the pygmy marmoset (*Callithrix pygmaea*), for which
270 both absolute and relative volume have decreased. This finding is unsurprising due to the
271 expected effects of dwarfism in this species and the limitation this exerts on brain size [78]. In
272 the case of the lar gibbon (*Hylobates lar*) the analysis revealed an increase in both volumes
273 from the ancestral state, possibly reflecting the complexity of its habitats and the subsequent
274 expansion of both hippocampus volume and brain volume.

275

276 <<Figure 2 about here>>

277

278 (b) PGLS

279 Testing the ‘full’ models with all four different group size measures separately yielded
280 comparable results. Shown in Table 2 are the results with the groups size measure resulting in
281 the largest sample size – group size from Dunbar [72]. Hippocampus and all regional volumes
282 besides subiculum and hilus could be predicted by group size, home range was shown to be a
283 significant predictor of subiculum and CA1, while fraction fruit was not significantly related
284 to any of the hippocampal structures. The results of the other three models are included in the
285 supplementary material.

286

287 Additionally, each of the four models using different group size measures were compared
288 using AIC (Table 3) and while female group size (from Dunbar [72]) was shown to produce
289 best fitting models in most cases, the sample size was the lowest (N=20) eliminating more
290 than half of the species included in the dataset. In order to utilise our full dataset of 43
291 species, we also ran separate models including only 1 class of predictors (ecological, social or

292 dietary). The results were concordant with the ‘full’ models and are included in the
293 supplementary material.

294

295 <<Tables 2 and 3 about here>>

296 <<Figure 3 here>>

297

298 **(d) Neocortex**

299 Following up on the observation that 1) both hippocampus and all its subcomponents were
300 positively related to brain volume, 2) many interactions between predictors and brain volume
301 were yielding negative slopes and 3) with increase in absolute hippocampal volume in some
302 species there was nonetheless a decrease in the relative hippocampal volume, we investigated
303 whether that relationship is driven by variation in neocortex volume as it comprises
304 significant proportion of the total brain volume. We found that hippocampal volume is
305 strongly negatively related to neocortex volume ($\lambda = 0$, slope = -3.81, $t = -8.11$, $p < 0.0001$, 3,
306 40 df) even after accounting for brain volume (see Supplementary results).

307

308 **(e) Sexual size dimorphism**

309 We further explored the relationship between somatic and brain structure sexual dimorphism
310 in a separate dataset of 12 primate species. Somatic sexual dimorphism was best predicted by
311 hippocampus volume dimorphism, ($\lambda = 0$, slope = 1.87, Std. error = 0.35, $t = 5.19$, $p = 0.0004$
312 on 1 and 10 df). Even though dimorphism in mesencephalon ($\lambda = 0$, slope = 1.35, Std. error =
313 0.45, $t = 2.96$, $p = 0.014$ on 1 and 10 df) and lobus piriformis ($\lambda = 0.78$, slope = 0.67, Std. error =
314 = 0.23, $t = 2.83$, $p = 0.018$ on 1 and 10 df) were also significant predictors of somatic sexual
315 dimorphism, these relationships didn’t stand after correction for multiple comparisons. The
316 new level of α for this batch of analysis was fixed to 0.0045 (dividing 0.05 by 11 structures)

317 and was sufficed by hippocampus volume alone. None of the other structure volumes (OBL,
318 CER, DIE, BOL, SCH, SEP, STR, NEO) showed a relationship with somatic sexual
319 dimorphism.

320

321

3. Discussion

322 We find that in primates, hippocampal volume and most of its subcomponents can be reliably

323 predicted by different measures of group size and home range to a certain extent, but not diet.

324 Moreover, we suggest that as brains get larger, the neocortex may take on functions shared

325 with the hippocampus and thus hippocampus size relative to the rest of the brain gets smaller.

326 Alternatively, the size of the hippocampus might be under strong developmental constraint.

327 Hippocampal structures crucial to spatial memory, CA1 and subiculum, evolve in line with

328 ecological (spatial) and social demands. CA2, CA3 and fascia dentata were shown to evolve

329 in line only with social demands, unlike the hilus, for which volume could not be predicted by

330 any of our models. No relationship between hippocampal volume and any of its

331 subcomponents was detected with increased fruit consumption in the primate's diet.

332 First, neocorticalization outpaces the enlargement of the hippocampus, as indicated in the

333 ancestral state estimation and the subsequent follow-up analysis. This is likely due to a

334 reallocation of functions such as memory, spatial cognition, and inhibition from the

335 hippocampus to the neocortex. With neocorticalization, parallel systems are thought to have

336 emerged, leading to an increased neocortex ratio [79] and allocation of functions to the

337 neocortex [80]. Whereas in smaller brained species the hippocampus is of utmost importance

338 in many cognitive abilities, as the neocortex expands there may be a greater proportion of

339 these functions allocated to it, or the neocortex might be taking up on an array of new social

340 functions that do not exist in smaller brained species. The neocortex, like the hippocampus,

341 provides mappings used in information acquisition, retention and use. Compared to rodents,

342 in highly neocorticalized humans, the hippocampus may not have as prominent a role in
343 spatial cognition (especially when compare to its well-known role in human memory) [81].
344 On the flip side, in primates, the neocortex may also have an increased role in spatial
345 processing. Parietal association areas of the neocortex are also crucial to spatial perception
346 and may provide navigational information and are the focus of spatial cognition studies [82].
347 The interplay between the parietal and hippocampal neural networks remains poorly
348 understood [83] although it has been suggested that both are involved in spatial navigation.
349 Parietal representations provide an egocentric frame of reference and may map movements
350 along a route according to route-centred positional information [84].

351 Second, of the hippocampal regions, both CA1 and CA3 residuals show phylogenetic signal
352 and coevolve with home range (CA1) and group size (CA1 and CA3) when we test single
353 variable models (see Supplement for data on phylogenetic signal within each separate model).
354 This is consistent with the notion that the hippocampus is involved in both social and
355 ecological behaviour [44, 47]. Compared to other brain component volumes, hippocampus
356 volume was found to be the best predictor for cognitive tasks measuring executive function in
357 primates [85]. This is the first study linking these specific hippocampal substructures to both
358 social and ecological factors across primates. This is in line with work in other taxa linking
359 species-specific requirements for spatial memory and hippocampus volume [29], but the
360 implication - which would benefit from future study - is that in primates the role of the
361 hippocampus may be even more influenced by social factors.

362 We found no relationship between the percentage fruit in diet and the size of the hippocampus
363 or any of its subcomponents. While fruit acquisition may play an important role in
364 intelligence [10, 86] and brain size [6], our findings suggest that the primary contribution of
365 diet to these features may be the generalized support of the brain's high metabolic costs [9]
366 rather than specifically influencing neural systems specialized for spatial ability. On the other

367 hand, non-dietary social-spatial memory factors, such as the ability to code for the locations
368 of conspecifics, may be linked to hippocampus size.

369 Third, CA2 volume residuals showed no phylogenetic signal, except for in a regression with
370 social and female group sizes in the single variable analysis (see Supplement for data on
371 phylogenetic signal within each separate model). Thus, CA2 seems not to be under
372 phylogenetic constraint related to home range or diet but is only shaped by social pressures.
373 This finding can be interpreted as an indicator of the relative functional decoupling of this
374 zone to the rest of the hippocampus. CA2 may show species-specific adaptations related to
375 behavioural niche which deviate from trends within a clade. Recent work on the function of
376 CA2 in mice found that it has a special role in social memory [66] and it has a different gene
377 expression profile from CA1 and CA3 [47]. On the other hand, the adaptability of CA2 might
378 come at a cost in terms of maintaining elementary functions shared across species - unlike
379 CA1 and CA3 it is a smaller region and is not involved in spatial tasks [66]. Additionally,
380 hilus was one of the structures that showed no relationship to social group size. It is important
381 in spatial and memory functions and may be less adaptable to changes in social structure.

382 We further investigated how hippocampus size is related to sexual dimorphism in primates
383 since sex differences in hippocampal anatomy, spatial cognition, and home range size seem to
384 be linked in some taxa [87]. We found that, of all brain structures examined, sexual
385 dimorphism in the hippocampus is most closely related to somatic sexual dimorphism. It
386 should be considered that spatial functions, like other brain functions, have become more
387 corticalized in taxonomic groups with larger palliums such as primates [80]. However, the
388 nature of the link is debated, for example, male superiority in spatial cognition may be a by-
389 product of sex hormones rather than driven by ecological demands [88]. This provides a
390 preliminary attempt to understand sex differences in the primate hippocampus.

391 Overall, we show that group size can predict the size of most hippocampus regions, while diet
392 seems to be unrelated to hippocampal size at all. Moreover, group size was the only predictor
393 that was related to total hippocampal size. Social group size is thought to be related to an
394 increase in neocortex size, but this is mainly because of its role in higher cognitive social
395 processes that are more demanding than simply remembering other individuals [89] [79].
396 Social memories seem to be structured within the spatial framework of the hippocampus too
397 [25]. In fact, social memory might in part be an exaptation that "reuses" neural circuitry of the
398 hippocampus for spatial maps in an ancestral mammal [90, 91]. In line with this, the role of
399 hippocampus in spatial cognition is pronounced in rodents, but less well understood in
400 primates; in humans, it is argued that the hippocampus appears to function in memory rather
401 than spatial cognition [81]. Given the importance of social skills in primates, it is possible that
402 in this order, social memory (overlain onto spatial maps originally for navigation) has
403 increased in dominance over spatial mapping. The importance of the increasing evidence that
404 social and spatial cognition rely on the same underlying representations in humans, such that
405 spatial maps provide a means for mapping social relations, is developing into applications
406 ranging from design considerations in the built environment to clinical implications [48].
407
408
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662

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Appendices

664

665

666 **Table 1. Hippocampal regions investigated**

Hippocampus total (=Hippocampal formation; HIP)

Retrocommissural hippocampus (= Retrohippocampus; HR)

Hippocampus proper

Cornu ammonis

CA1

CA2

CA3

CA4

"deep stratum multiforme of the dentate gyrus" | "Hilu

Fascia dentata (FD)

Prosubiculum | "Sub:

Subiculum

"HP+HS+fibers" or "fibers"

Hippocampus praecommissuralis (HP)

Hippocampus supracommissuralis (HS)

fimbria/fornix complex

Note. The subicular complex includes pro-, pre-, parasubiculum and subiculum. The region called "subiculum (SUB)" in Frahm and Zilles (2007) and parasubiculum were not included in Frahm and Zilles (1994) as part of the hippocampus volumes and were not examined here. In Striedter (2005) with entorhinum and perirhinum as the Schizocortex.

Table 2. ANOVA output from testing the full model (with Group size from Dunbar) versus hippocampal and regional volumes. On the diagonal are shown means squares from the sequential SS ANOVA, p-values and lambda values of the phylogenetic signal of the residuals.

	Hippocampus		HP+HS+ fibers		Retrohippocampus		Subiculum		Hilus		CA1	
	Mean sq	p	Mean sq	p	Mean sq	p	Mean sq	p	Mean sq	p	Mean sq	p
Total Brain	0.397	<0.001*	0.568	<0.001*	0.354	<0.001*	0.342	<0.001*	0.441	<0.001*	0.367	<0.001*

Home Range	0.002	0.074	0	0.58	0.005	0.02	0.014	0.007*	0.009	0.04	0.012	0.001
Group Size (Dunbar)	0.012	<0.001*	0.011	0.002*	0.013	<0.001*	0.008	0.04	0.007	0.06	0.013	<0.001
Fraction Fruit	0.001	0.25	0	0.94	0.001	0.27	0	0.74	0.002	0.38	0	0.34
Residuals	0		0.001		0		0.001		0.002		0	
λ	0.59		0.56		0.59		0.47		0.22		0.58	

Table 3. Model fit ranking of all four group size measures. Displayed are the AIC scores and all m are bolded.

	Group size (Powell)	Social group size (DeCasien)	Group size (Dunbar)	Female group (Dunbar)
Hippocampus	-3.7	-6.8	9.0	-6.7
HP+HS+ fibers	10.3	9.5	4.2	6.1
Retrohippocampus	0.2	-1.8	-2.2	-2.5
Subiculum	25.5	23.1	24.3	17.1
Hilus	33.9	34.9	34.1	12.6
CA1	4.3	2.5	1.5	5.4
CA2	4.9	2.1	1.4	2
CA3	-14	-4.9	-9.7	-7
FD	7.7	6.6	6.9	-4.2

667

668

Figures Captions

669

670 Figure 1. Hippocampus of *Miopithecus talapoin*. LV – Lateral ventricle, FD – Fascia dentata

671

672 Figure 2. Ancestral state estimations of absolute hippocampal volume (left), and the residuals

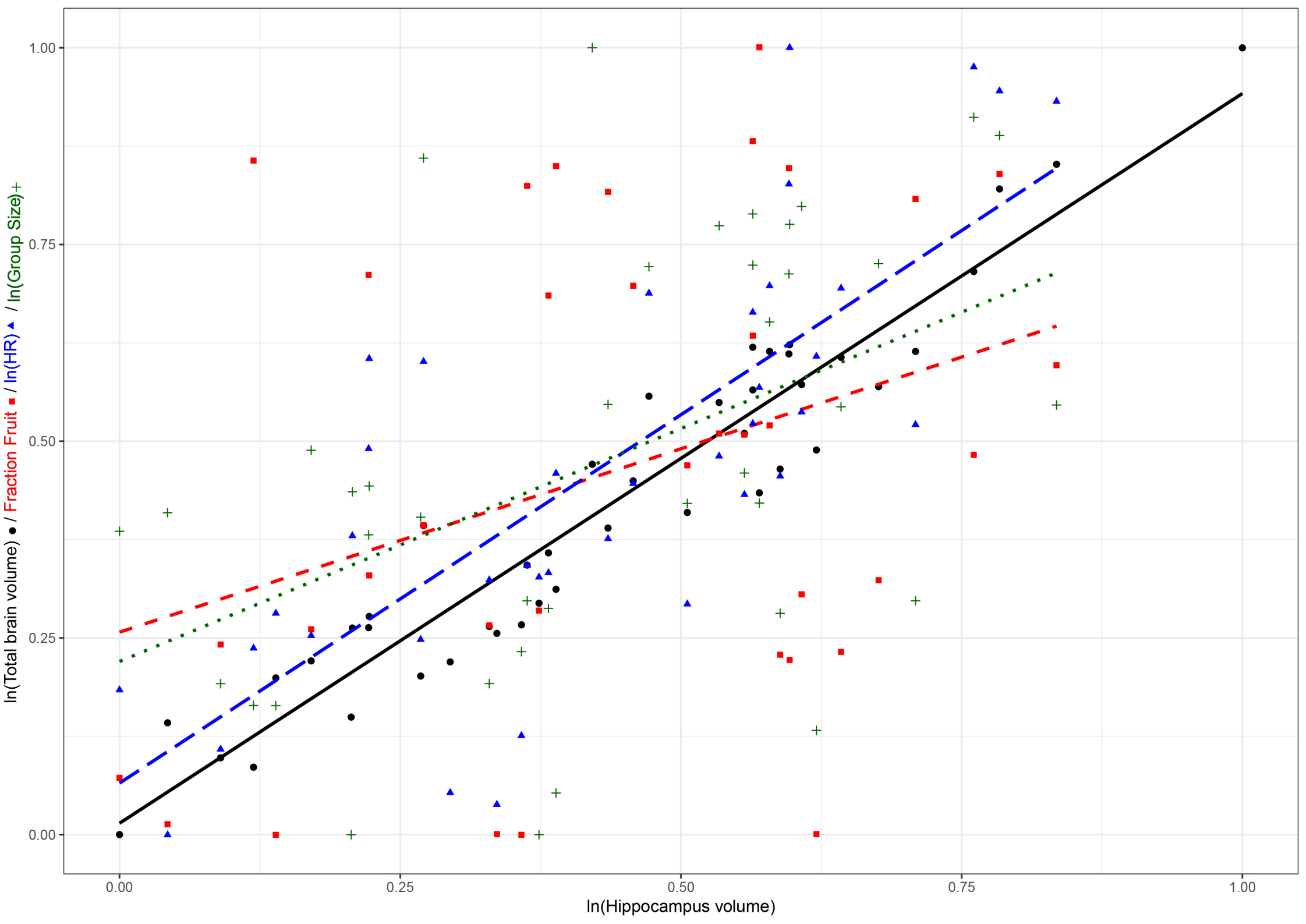
673 from the phylogenetic regression with total brain size (right). We observe that most species

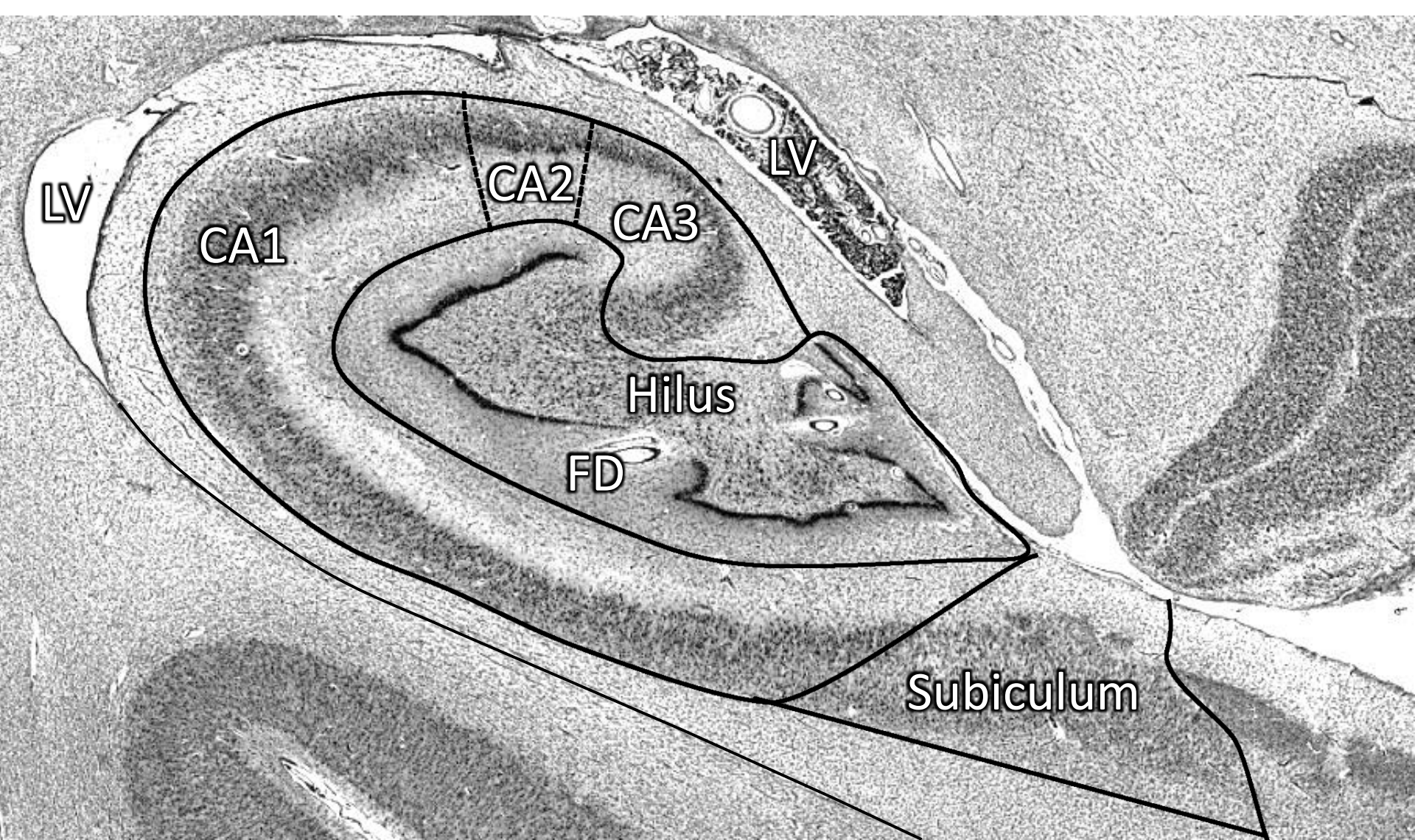
674 that had increase in absolute hippocampal volume had a reciprocal decrease in hippocampal

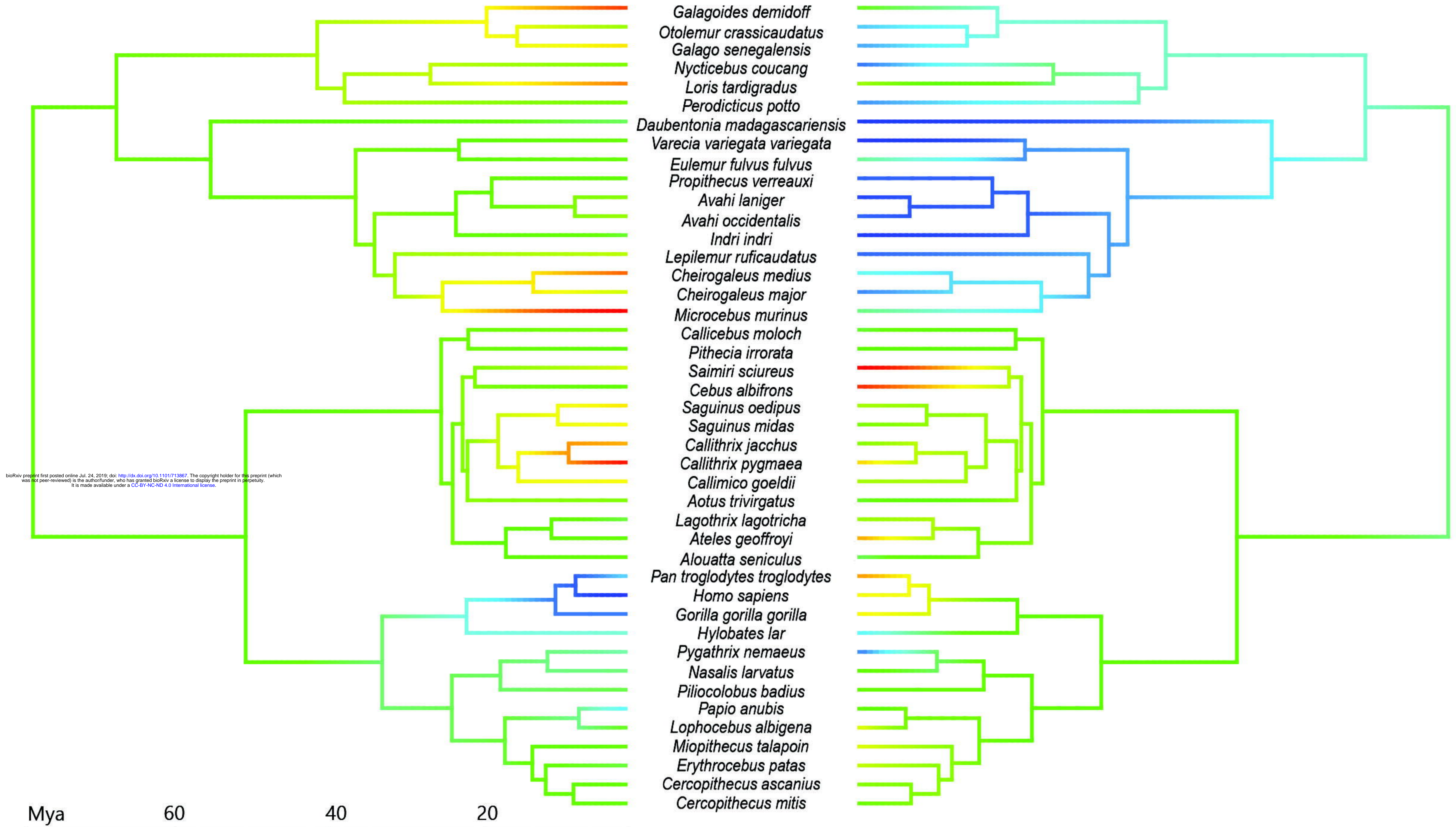
675 volume relative to the whole brain.

676

677 Figure 3. Plot of regression of total brain volume (black solid line and black circles), fraction
678 fruit (red small-dashed line and red squares) and home range (blue long-dashed line and blue
679 triangles), and group size (green dotted line and green pluses) against hippocampal volume.







Total hippocampus volume

Relative hippocampus volume

