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

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5 Orlin S. Todorov[1], Vera Weisbecker[1], Emmanuel Gilissen[2], Karl Zilles[3], and Alexandra A. de

6 Sousa[4]

7 [1] School of Biological Sciences, The University of Queensland, St. Lucia, QLD,

8 4072, Australia

9 [2] Department of African Zoology, Royal Museum for Central Africa, Leuvensesteenweg,

10 3080 Tervuren, Belgium and Laboratory of Histology and Neuropathology, Université Libre

11 de Bruxelles, Brussels, Belgium

12 [3] Research Centre Ju☐lich, Institute of Neuroscience and Medicine (INM-1), Ju☐lich,

13 Germany,

14 [4] Psychology, Culture and Environment, Bath Spa University, Bath, BA2 9BN, UK

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26   hippocampus, social group, spatial cognition, primates

27

28   **Abstract**

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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 theses 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

663   **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 (

and parasubiculum were not included in Frahm and Zilles (1994) as part of the hippocampus volumes and were not examined here. In Ste

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

Shown are 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	<0.00

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	<0.00
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
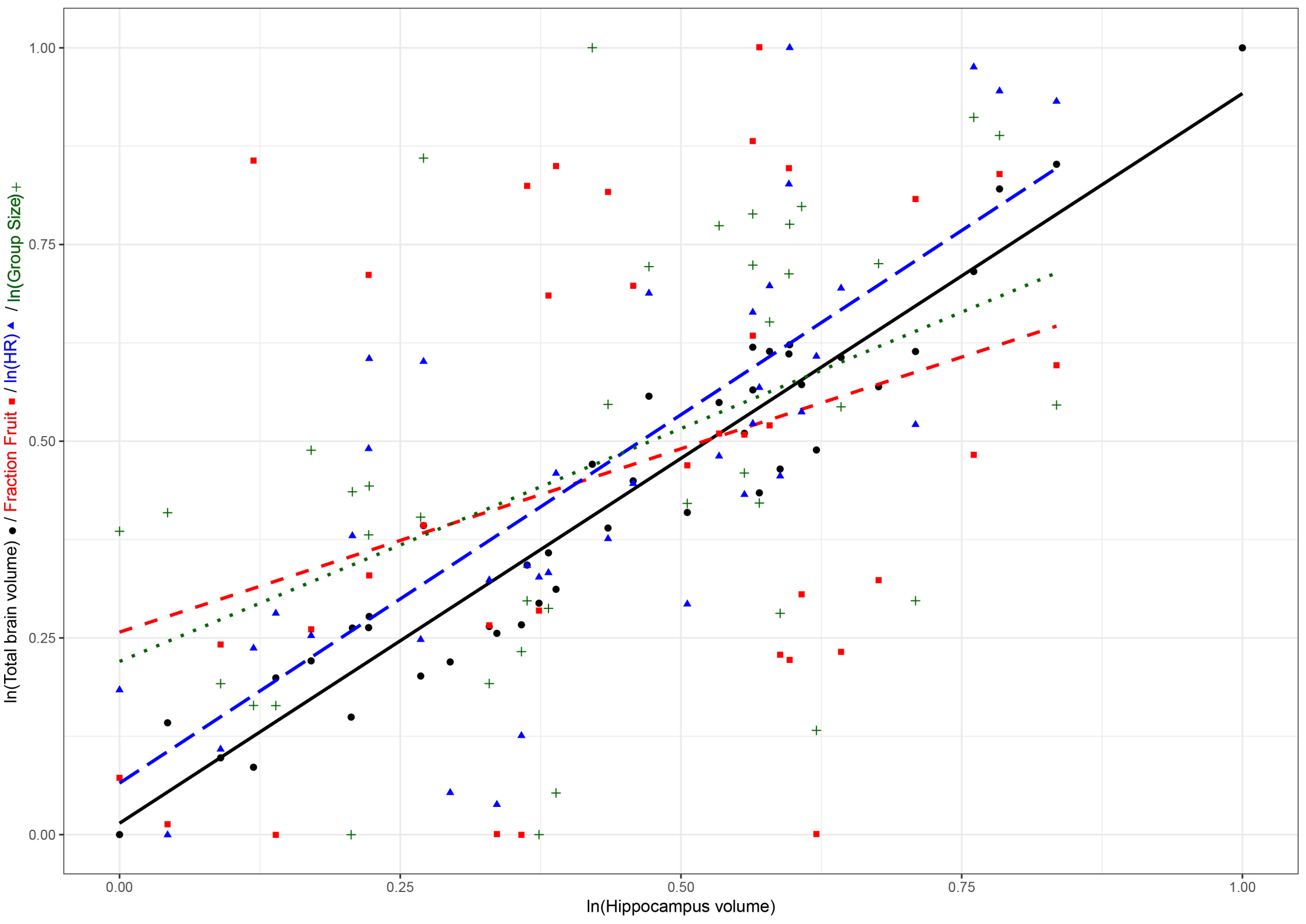
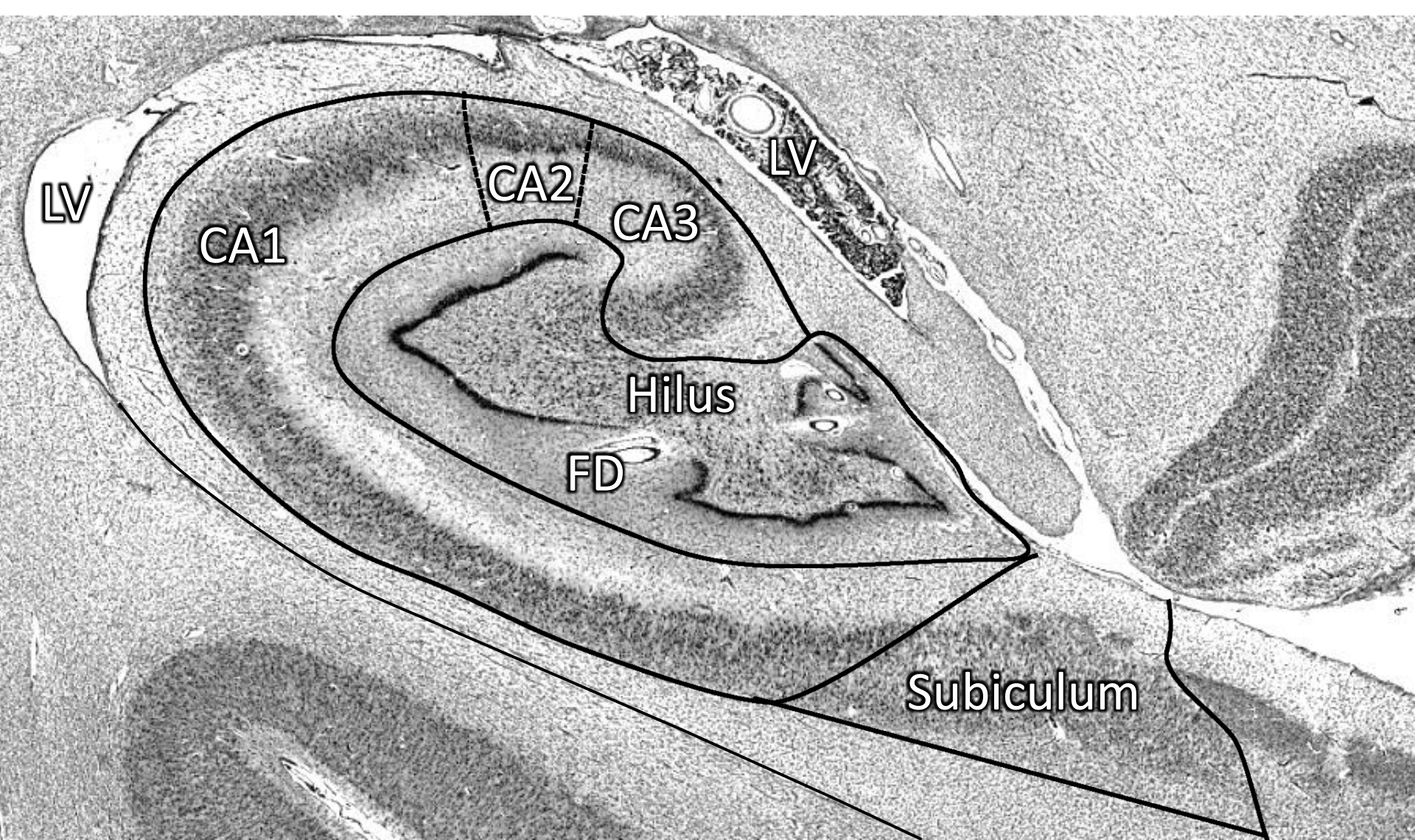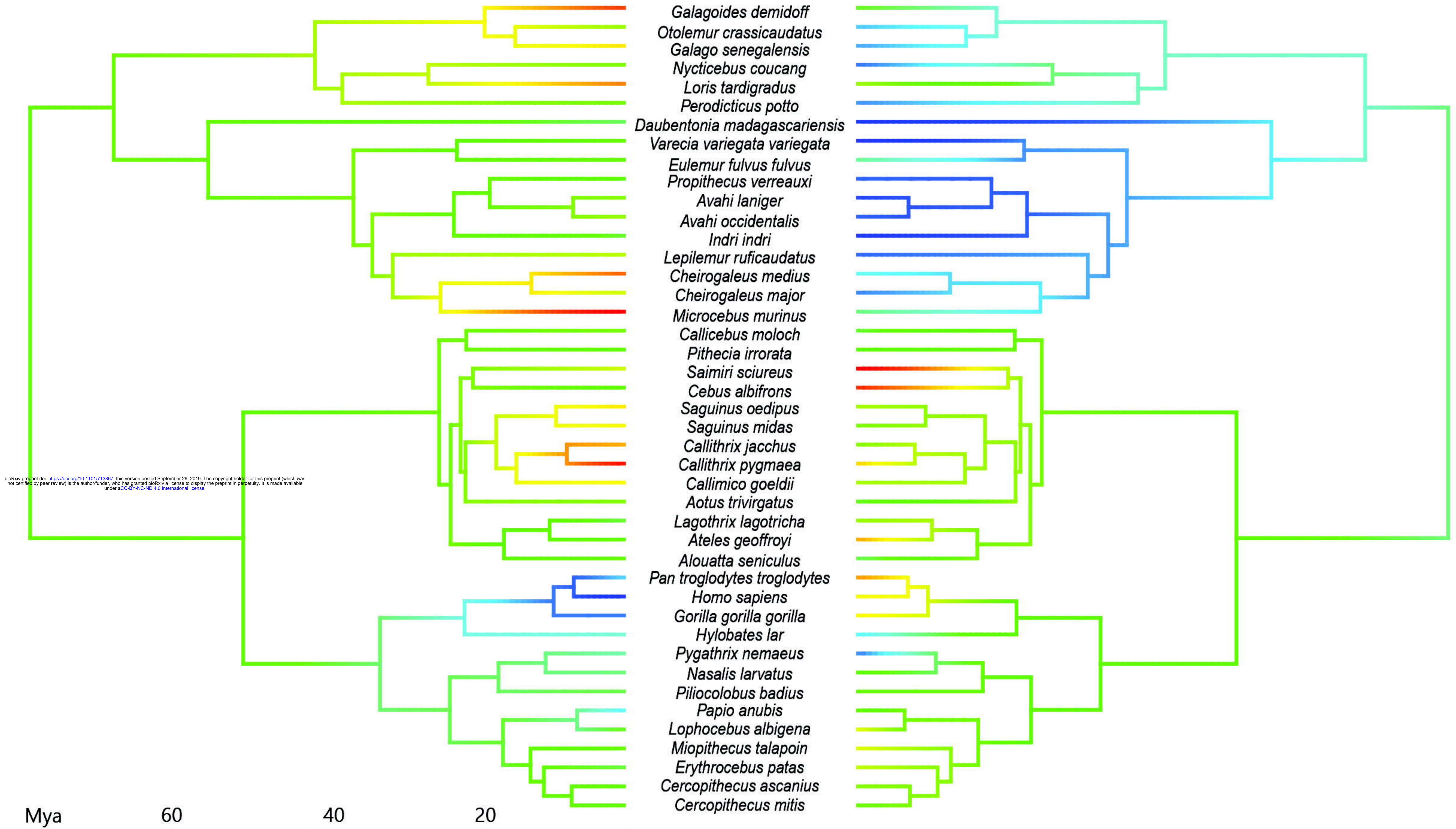675   volume relative to the whole brain.

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.

LV

CA1

CA2

CA3

LV

Hilus

FD

Subiculum

Galagoides demidoff
Otolemur crassicaudatus
Galago senegalensis
Nycticebus coucang
Loris tardigradus
Perodicticus potto
Daubentonia madagascariensis
Varecia variegata variegata
Eulemur fulvus fulvus
Propithecus verreauxi
Avahi laniger
Avahi occidentalis
Indri indri
Lepilemur ruficaudatus
Cheirogaleus medius
Cheirogaleus major
Microcebus murinus
Callicebus moloch
Pithecia irrorata
Saimiri sciureus
Cebus albifrons
Saguinus oedipus
Saguinus midas
Callithrix jacchus
Callithrix pygmaea
Callimico goeldii
Aotus trivirgatus
Lagothrix lagotricha
Ateles geoffroyi
Alouatta seniculus
Pan troglodytes troglodytes
Homo sapiens
Gorilla gorilla gorilla
Hylobates lar
Pygathrix nemaeus
Nasalis larvatus
Piliocolobus badius
Papio anubis
Lophocebus albigena
Miopithecus talapoin
Erythrocebus patas
Cercopithecus ascanius
Cercopithecus mitis

Mya   60   40   20

Total hippocampus volume

Relative hippocampus volume

trait value

decrease   increase