1   **Title: Relative brain size and cognitive equivalence in fishes**

2   **Running title: Cognitive equivalence in fishes**

3   **Authors:** Zegni Triki[1,2#], Mélisande Aellen[1], Carel van Schaik[3*], Redouan Bshary[1*]

4

5   **Authors' affiliation:**

6   [1] Behavioural Ecology Laboratory, Faculty of Science, University of Neuchâtel, Emile-

7   Argand 11, 2000 Neuchâtel, Switzerland

8   [2] Institute of Zoology, Stockholm University, Svante, Arrheniusväg 18 B, SE-106 91

9   Stockholm, Sweden

10   [3] Department of Anthropology & Anthropological Museum, University of Zurich,

11   Winterthurerstrasse 190, 8057 Zurich, Switzerland

12   [#] Corresponding author: Zegni Triki, email: zegni.triki@gmail.com, phone number:

13   0046736465340

14   * authors contributed equally

15

16   **ABSTRACT**

17   There are two well-established facts about vertebrate brains: brains are physiologically costly

18   organs, and both absolute and relative brain size varies greatly between and within the major

19   vertebrate clades. While the costs are relatively clear, scientists struggle to establish how larger

20   brains translate into higher cognitive performance. Part of the challenge is that intuitively larger

21   brains are needed to control larger bodies without any changes in cognitive performance.

22   Therefore, body size needs to be controlled to establish the slope of cognitive equivalence

23   between animals of different sizes. Potentially, intraspecific slopes provide the best available

24   estimate of how an increase in body size translates into an increase in brain size without changes

25   in cognitive performance. Here, we provide the first evaluation of this hypothesis for fishes.

26   First, a dataset of 51 species that included only samples of ≥ ten wild-caught individuals yielded

27   a mean brain-body slope of 0.46 (albeit with a large range of 0.26 to 0.79). This mean slope is

28   similar to the encephalisation quotients for ectotherm higher taxa, i.e. teleost fishes, amphibians

29   and reptiles (~ 0.5). However, the slope is much higher than what has been found in endotherm

30   vertebrate species (~ 0.3). Second, we provide slope estimates for brain-body sizes and for

31   cognition-body sizes in wild-caught cleaner fish *Labroides dimidiatus* as a case study. Brain-

32   body slopes from two datasets gave the values of 0.58 (MRI scans data) and 0.47 (dissection

33   data). Furthermore, we have cognitive performance data from 69 individuals tested in four

34   different cognitive tasks that estimated learning, numerical, and inhibitory control abilities. In

35   all four tasks, the cognitive performance did not correlate significantly with body size. These

36   results suggest that the brain-body slopes represent estimates of intraspecific cognitive

37   equivalence for this species. While subject to further studies on various species, our results

38   suggest that endo- and ectotherm brain organisations and resulting cognitive performances are

39   fundamentally different.

40

41   **Keywords**: encephalization quotient; cognitive equivalence; intelligence; brain size; body size:

42   slopes; cognitive performance; cleaner fish

43

Introduction

45   Scholars have long sought regularities in the relationship between brain size and body size.

46   These analyses, largely focussing on mammals, showed an unexpected pattern: the slope of

47   (log-transformed) brain size on (log-transformed) body size is often lower within than between

48   species [Pilbeam, and Gould, 1974; Tsuboi et al., 2018; Pagel, and Harvey, 1988]. Two

49   different explanations for this phenomenon, called the taxon-level effect, have been proposed.

50   The first attributes the higher slope at higher taxonomic levels to the combined effect of two

51   parallel macroevolutionary processes: Cope's rule [Alroy, 1998], the tendency for more

52   recently evolved lineages to have larger bodies than their forebears, and Lartet-Marsh rule

53   [Jerison, 1973; Halley, and Deacon, 2017], the tendency for more recently evolved lineages to

54   have larger brains at a given body than their forebears. The combined effect of the two processes

55   would be to artificially inflate the regression slope through the total sample of all species

56   relative to those within a given species.

57   A second explanation is based on statistical logic: the estimated slope is reduced when the error

58   in body size measures is greater than that for brain size [see detailed discussion in van Schaik

59   et al., 2021]. This effect is strongly affected by body size range in the sample and thus far greater

60   within species than between them. This phenomenon has been argued to explain why estimates

61   for within-species slopes show extensive variation [Pilbeam, and Gould, 1974], even among

62   different mammalian lineages [Martin, and Harvey, 1985].

63   While the two explications for the taxon effect should in principle apply to all taxa, Tsuboi et

64   al. [2018] showed that there is a clear pattern in this variation: ectothermic vertebrates (fishes,

3

amphibians and reptiles) have far steeper intra-specific slopes (in their sample ca 0.50) than the endothermic birds and mammals (0.15-0.20). Because the majority of ectotherms show indeterminate growth and thus a far greater range of adult body sizes, the error problem might, in principle, explain this difference. However, Tsuboi et al. [2018] showed that the error problem was unlikely to explain this difference fully. Indeed, a recent analysis focused on sexually dimorphic primates to calculate intraspecific slopes using mean values for males and females, and so minimize the error problem, obtained only slightly larger slopes of 0.25-0.3 [van Schaik et al., 2021]. Nevertheless, it remains unclear what value we should expect for the ectotherms for two reasons. First, the full data set used by Tsuboi et al. [2018] contained both wild and captive fishes, but hatchery-reared fish have smaller brains compared to fish of the same species in the wild [see review by Huntingford, 2004]. Second, they did not analyse how much the range of body sizes in a species' sample affected the value of the slope. This is important because fishes have a much larger range of body sizes, due to their indeterminate growth, than birds or mammals [Froese, and Froese, 2019]. This feature makes fishes more suitable than birds or mammals to address these statistical issues. Therefore, the first aim of this paper is to refine the findings of Tsuboi et al. [2018] by estimating intra-specific slopes using only wild-caught individuals and assessing the effect of intraspecific variation in adult body size on the estimate. To do so, we identified 51 fish species for which sample sizes of wild specimens were large enough ($\geq$ 10 data points) to calculate brain-body slopes.

Suppose the analyses corroborate the difference between endothermic and ectothermic vertebrates in the slope of the brain-body relationship. In that case, this raises the important question of how the different slopes translate into cognitive performance. We follow Shetlleworth, who defined cognition as the ability to acquire, process, retain information and act on it [Shettleworth, 2010]. This broad definition of cognition may justify analyses on total brain size, while specific areas should be studied when their function is known, like the

90   hippocampus and spatial memory [Krebs et al., 1989]. Regarding total brain size analyses,

91   Jerison [1973] had proposed the encephalization quotient (called EQ), the ratio of a species'

92   actual brain size to its predicted brain size based on its clade-specific brain-body regression

93   line, to capture its cognitive performance relative to other species within the same clade. The

94   use of EQ as a predictor for relative cognitive performance across species has been criticised

95   largely because of the taxon-level effects reported for endothermic vertebrates, and intraspecific

96   slopes have been proposed as an alternative [van Schaik et al., 2021]. The key idea of this

97   alternative approach is that the intraspecific slope reflects the extra amount of brain tissue

98   required to sustain the additional somatic functions in larger individuals because there are no

99   changes in bauplan and sensory-motor abilities. Therefore, this slope would serve to identify

100   the line of so-called 'cognitive equivalence' [van Schaik et al., 2021]. The critical assumption

101   thus is that the cognitive performance of adult individuals within a species is independent of

102   their body size. This assumption can be argued to hold for humans: one good estimate of overall

103   cognitive performance, IQ, shows only a very modest effect of the sex difference in body size

104   [Irwing, and Lynn, 2005]. In addition, cognitive test batteries applied to various species find no

105   effects of body size, including sex differences among dimorphic species [reviewed in

106   van Schaik et al., 2021; see also Bohn et al., 2021]. The markedly higher value of the

107   intraspecific slope in ectotherms than endotherms, therefore, raises the question of whether

108   adult ectotherms of different sizes also show cognitive equivalence or whether larger and hence

109   older individuals outperform smaller ones.

110   Therefore, the second aim of this study is to provide a first test of the prediction that cognitive

111   performance of adult individuals within a fish species is not correlated with body size (which

112   is also a proxy of age in ectotherms). Although we know little about domain-general

113   intelligence in ectotherms [Aellen et al., 2021, preprint; Poirier et al., 2020], unlike in

114   endotherms [Burkart et al., 2017], we can examine whether a variety of cognitive tests show a

115   body size effect on performance. If they all yield similar results, we can conclude cognitive

116   equivalence in our study species, amenable to further testing in other fish species.

117   We examined cognitive performance in the cleaner fish *Labroides dimidiatus*, a species for

118   which we also provide the slope of the brain-body relationship. Cleaner fish engage in iterative

119   mutualistic interaction with a variety of coral reef fish species (hereafter "clients"). Cleaners

120   remove client's ectoparasites and dead tissue in exchange for food [Losey, 1979], a behaviour

121   that is mutually beneficial for both cleaner [Grutter, 1999] and client [Demairé et al., 2020; Ros

122   et al., 2020; Clague et al., 2011; Waldie et al., 2011]. Cleaner fish show a highly sophisticated

123   strategic behaviour that includes reputation management [Bshary, and Grutter, 2002; Binning

124   et al., 2017], social tool use [Bshary et al., 2002], reconciliation [Bshary, and Würth, 2001],

125   and social competence [Triki et al., 2020a]. Cleaner fish may outperform primates in some

126   learning tasks [Salwiczek et al., 2012] that go beyond conditioning [Quiñones AE et al., 2020].

127   They also show evidence for generalised rule learning [Wismer et al., 2016], numerical

128   discrimination [Triki, and Bshary, 2018], long-term memory [Triki, and Bshary, 2019], and

129   mirror self-recognition [Kohda et al., 2018].

130   We used published data on cleaner fish cognitive performance in four different cognitive tasks

131   [Aellen et al., 2021 Preprint] to explore the relationship between body size and cognitive

132   performance. These results were then combined with estimates of the brain-body slope in this

133   species using published data from two studies on brain size [Triki et al., 2019a; Triki et al.,

134   2020a]. These data sets also contain information regarding the size of five major brain areas,

135   i.e. telencephalon, diencephalon, midbrain, cerebellum and brainstem. As these areas differ in

136   their relative importance to subparts of cognitive performance (e.g., perception versus decision-

137   making versus execution of actions [Striedter, 2005]), we also explored the regression slopes

138   of the five main brain region sizes on body size in cleaner fish. The brain data and the cognitive

139   performance data were not collected from the same individuals, and thus these datasets are

6

140 independent. Nevertheless, the results show to what extent intraspecific brain-body slopes in

141 fishes may reflect cognitive equivalence.

142

Material and Methods

144 *Brain and body size data from other fish species*

145 We compiled fish brain and body size data from the database FishBase [Froese, and Pauly,

146 2019] and the published study by Tsuboi et al. [2018]. We selected only confirmed wild-caught

147 individuals and discarded every dataset from lab-reared fish or fish obtained through aquaria

148 trade. Furthermore, we selected only adult individuals based on the adult body size for the

149 species [Tsuboi et al., 2018; Froese, and Pauly, 2019]. Finally, species were included when at

150 least ten individual measurements of body and brain size were reported. Using these rigorous

151 selection criteria, we could include 52 species, with sample sizes ranging from 10 to 60

152 individuals (the exact sample size per species is reported in Table 1).

153 To estimate the log brain-log body regression slope of every species from the fishes dataset, we

154 fitted a set of Linear models (LMs with Ordinary Least Squares approach OLS). We validate

155 these LMs by checking model assumptions like the normal distribution and homogeneity of

156 variance of the residuals. Furthermore, we estimated the range of body sizes in a given species'

157 dataset for each of the 51 species by simply calculating the body size (as body mass in g) ratio

158 of the largest (i.e., heaviest) to the smallest (i.e., lightest) individual. We then tested whether

159 there is an effect of body size ratio on these species brain-body slopes. To do so, we fitted a

160 phylogenetic generalised least-squares regression (PGLS) of log brain-log body slope (i.e.,

161 response variable) on log-transformed body size ratio (i.e., continuous predictor). We also

162 explored whether sample size (log-transformed number of individuals per species) affected the

163 estimated brain-body slopes by fitting a PGLS. The PGLS approach considers the phylogenetic

7

164   relationships to produce an estimate of expected covariance in cross-species data. For this, we

165   estimated Pagel's λ (lambda) as the phylogenetic signal in PGLS models. Pagel's λ is an

166   estimate of the extent to which correlations in given traits reflect their shared evolutionary

167   history cross-species. To calculate Pagel's λ, we ran a maximum likelihood function for each

168   PGLS model separately (see code for further details). For the PGLS models to meet the

169   assumptions of normal distribution and homogeneity of variance, we had to exclude one species

170   (*Neolamprologus multifasciatus*) from the analyses because it had a studentized residuals larger

171   than three [Jones, and Purvis, 1997], bringing thus our sample size to 51 fish species.

172   We ran a phylogenetic signal analysis to test whether the Pagel's λ of the body-brain slope is

173   significantly different from zero (the null hypothesis). A significant $\lambda > 0$ ($p \leq 0.05$) would

174   mean that phylogeny affects the value of the estimated body-brain slopes. Furthermore, we ran

175   a multiple comparisons analysis on the 51 fish slopes by fitting a global model for brain-body

176   size with species as a factor. *Post hoc* tests with the Tukey correction method helped in

177   comparing brain-body slopes between all these fish species. A detailed step-by-step code is

178   provided as a script file that runs in the open-source statistical software R [R Core Team, 2020]

179   (see Data and code accessibility statement).

180

181   *Case study: Brain size, body size and cognitive performance data in Labroides dimidiatus*

182   We used published data on *Labroides dimidiatus* as a case study to test the link between brain

183   size and body size, on the one hand, and cognitive performance and body size, on the other

184   hand. There were no data on brain size and cognitive performance available at the individual

185   level. All the data we use here is from fish collected on the reef around Lizard Island, Great

186   Barrier Reef, Australia, between 2016 and 2019. Cleaner fish have a lifespan of about five years

187   [Eckert, 1987]. They undergo a pelagic larvae phase before settling on a coral reef [Victor,

188 1986]. Therefore, all fish sampled in these datasets belong to the same population [see Triki et

189 al., 2018].

190

191 *1. Brain size data*

192 We compiled datasets from published studies by Triki et al. [2019a; 2020b] for brain and body

193 size data. These two studies were conducted on wild-caught female cleaner fish *L. dimidiatus*

194 at Lizard Island. Both studies collected fish body size as body weight to the nearest 0.01 g but

195 differed with respect to the method used to quantify brain size: Triki et al. [2019a] used the

196 magnetic resonance image (MRI) technic to estimate brain volume (in mm^3) of N = 15 female

197 cleaner fish, while Triki et al. [2020a] manually dissected and weighed the brains of N = 18

198 female cleaner fish to the nearest 0.1 mg (for further details, please refer to the original studies

199 by Triki et al. [2019a; Triki et al., 2020a]). These data sets also had the volume/mass of the five

200 major regions of fish brains, i.e., telencephalon, diencephalon, midbrain, cerebellum, and brain

201 stem.

202

203 *2. Cognitive performance data*

204 We compiled data from the study by Aellen et al. [2021 Preprint] for the cognitive performance

205 and body size data. The dataset comprises cognitive performance of N = 69 wild-caught female

206 cleaner fish tested in four different laboratory tasks at Lizard Island, Great Barrier Reef, in

207 Australia. Here, we used these data to explore the relationship between body size and cognitive

208 performance. We provide below brief descriptions for each cognitive task, but for more details,

209 please refer to the original study by Aellen et al. [2021 Preprint]. Note that given the nature of

210 cleaner fish feeding behaviour (i.e., removing ectoparasites off the skin of client fish),

211   researchers often feed them in captivity with a paste of mashed prawn or a mixture of fish flakes

212   and mashed prawn smeared as a thin layer on Plexiglas plates. Such plates with smeared food

213   paste can be viewed as surrogates for client fish skin with ectoparasites in laboratory settings.

214

215   ## 2.1. Reversal learning task

216   Aellen et al. [2021 Preprint] tested fish learning and flexibility abilities in a reversal learning

217   task. The experiment was based on a simultaneous two-choice task with Plexiglas plates with

218   colour and shape cues, i.e., yellow triangular vs green round plates. Fish first had to learn the

219   association between the yellow triangle and a food reward. As soon as fish had learned this

220   association, the reward contingency was reversed, and the previously non-rewarding green plate

221   became the one with the food reward. At this stage, fish were offered a maximum of 100 trials

222   (i.e., ten sessions of ten trials each over five consecutive days) to learn the reversal association.

223   The learning criterion set for this task is that each individual has to significantly ($p \leq 0.05$) learn

224   the rewarding colour above chance level (50%). That is, successful fish were those that scored

225   either seven correct choices out of ten in three consecutive test sessions (i.e., 21/30), eight

226   correct choices out of ten in two consecutive sessions (i.e., 16/20), or at least nine correct

227   choices out of ten in a single session (i.e., 9/10).

228

229   ## 2.2. Detour task

230   The detour task aimed at estimating fish inhibitory control abilities. Here, a novel Plexiglas

231   plate with a food reward was placed behind a transparent barrier. To access the food reward,

232   fish had to inhibit their impulses to go straight to the visible food and instead swim around the

233   barrier to reach the food. Bumping into the barrier, however, shows that the subject is impatient

234 to get the food. Therefore, this measure (i.e., number of head bumps) provides an estimate of

235 inhibitory control abilities, where fewer head bumps indicate better abilities. In total, Aellen et

236 al. tested fish inhibitory control abilities in ten detour trials. The estimated performance was in

237 the form of the average number of fish head bumps on the barrier until reaching the food.

238

239   2.3. Numerical discrimination task

240 To test for fish numerical abilities, Aellen et al. [2021 Preprint] used Plexiglas plates with

241 various numerical quantities as black squares against a white background. The number of black

242 squares ranged from one to nine. The task consisted of presenting two Plexiglas plates at a time

243 with two different quantities of black squares. In total, there were 20 different combinations of

244 the nine quantities. The general rule was that, in every combination, the plate depicting the

245 largest quantity of black squares was always the rewarding plate with food items. The

246 performance consisted of the proportion of correct choices from 160 test trials over eight days.

247

248   2.4. Feeding against preferences task

249 During the cleaner-client cleaning interaction, cleaner fish often prefer to bite client mucus

250 instead of cooperating and eating ectoparasites [Grutter, and Bshary, 2003]. Such events can be

251 reproduced in laboratory conditions with Plexiglas plates as surrogates for clients, and fish

252 flakes and mashed prawn as surrogates for client ectoparasite and mucus, respectively [Bshary,

253 and Grutter, 2006]. Aellen et al. [2021 Preprint] used a similar laboratory set-up to test whether

254 cleaner fish can inhibit their food preferences for prawn and feed on fish flakes instead. A

255 Plexiglas plate with two fish flakes items and two prawn items was presented to the fish during

256 test trials. The plate remained in the aquarium as long as fish fed on flakes items (i.e., a less

257   preferred food as an indicator of inhibition of preferences). Upon eating a prawn item (i.e., a

258   highly preferred food as an indicator of non-inhibition of preferences), however, the plate

259   withdrew from the aquarium. Thus, the optimal feeding strategy to maximise food intake is to

260   feed first on the less preferred food (flakes) before eating one highly preferred food item

261   (prawn). We then estimated fish performance in this task as a ratio reflecting the degree of

262   feeding against preference. To do so, we divided the total number of fish flakes items by the

263   total of prawn items consumed throughout the 12 test trials. Next, we fitted a linear regression

264   model of feeding ratio on log-transformed body weight for the cognition-body slope from this

265   data.

266

267   *Data analyses for the cleaner fish brain data*

268   We used the cleaner fish brain data to calculate the slope of brain size (either as volume or

269   mass) as a function of body size and the regression slope of every brain part on body size. To

270   do so, we fitted Linear regression models LMs (with OLS) in the open-source statistical

271   software R [R Core Team, 2020] of log-transformed brain measurement on log-transformed

272   body mass. We had two separate sets of linear models, given that brain morphology was

273   estimated once as a volume and once as a mass via MRI and manual dissection methods,

274   respectively. We validated all these LMs by checking model assumptions like the normal

275   distribution and homogeneity of variance of the residuals.

276   For data analyses linked to the cognitive tasks, we ran a Generalised Linear Model (GLM) with

277   quasipoisson distribution error to estimate the regression slope of cognitive performance on

278   log-transformed body weight (g). We ranked individual performance with respect to the

279   performance of all tested fish. In all tasks, we ranked fish in a way that higher rank values

280   corresponded to better performance. We used rank data as cognitive performance (i.e., response

281   variable) in the fitted GLMs, where log-body size was the continuous predictor. We fitted

282   GLMs with quasipoisson to solve an overdispersion issue with the Poisson distribution error.

283

Results

285   *The intraspecific brain-body slope in fishes*

286   We calculated intraspecific slopes in wild-caught individuals from 51 fish species (Fig. 1a).

287   These slopes ranged from from 0.26 to 0.79 (Table 1), with a mean value of 0.46, and a median

288   also of 0.46. Sample size (the number of individual data points per species) did negatively affect

289   the brain-body slope estimates, though the effect size was relatively small (PGLS: N =51, β =

290   -0.105, t-value= -2.846, p = 0.006, 95% CI -0.18, -0.03], R^2= 0.13, λ = 0.55, Fig. 1b). Most

291   importantly, we found no effect of body size ratio on the brain-body slope estimates (PGLS: N

292   =51, β = -0.013, t-value= -0.682, p = 0.498, 95% CI -0.05, 0.03], λ = 0.47, Fig. 1c). Further

293   analyses showed that there was no significant phylogenetic signal in the brain-body slopes (p-

294   value of the likelihood ratio test = 0.16). Nevertheless, the multiple comparisons analysis of

295   fish slopes indicated that some fish species had significantly different brain-body slopes from

296   each other (Fig. 2).

297

298   *Cleaner fish slopes*

299   Our two datasets used to calculate the slope for the relationship between log brain size and log

300   body size yielded values of 0.58 (MRI scans, LM: N = 15, β = 0.585, t-value= 6.133, $p <$

301   0.001, 95% CI [0.38, 0.79], Fig. 3a) and 0.47 (dissection data, LM: N=18, β = 0.473, t-value=

302   3.593, p = 0.002, 95% CI [0.19, 0.75], Fig. 4a), respectively. Furthermore, the regression slopes

303   of every major brain part (i.e., telencephalon, diencephalon, midbrain, cerebellum and brain

13

304   stem) on body size are reported in Table 2 and Fig. 3 & 4. The goodness of fit seems to be

305   sensitive to the method used in estimating the size of these regions, wherein the MRI methods

306   yielded the best estimates with a narrower 95% CI compared to the values from the manual

307   dissection data (Figs. 3&4). Overall, brain part slopes showed some variation but were not

308   fundamentally different from the total brain slopes. For example, the telencephalon to body size

309   slopes of 0.54 with MRI and 0.49 with manual dissection are similar to the total brain's slopes

310   (Fig. 3b & 4b).

311

312   For the cognition-body slopes, there was no significant relationship between body size and

313   performance in any of the four cognitive tasks, nor did the four slopes yield the same (positive

314   or negative) sign: reversal learning (GLM: N=69, β = -0.400, t-value= -1.456, p=0.15, 95% CI

315   [-0.94, 0.14], Fig. 5a), detour task (GLM: N=69, β = 0.180, t-value= 0.642, p=0.523, 95% CI [-

316   0.37, 0.73], Fig. 5b), numerical discrimination task (GLM: N=69, β = 0.208, t-value= 0.745,

317   p= 0.459, 95% CI [-0.34, 0.76], Fig. 5c), and feeding against the preferences task (GLM: N=69,

318   β = 0.327, t-value= 1.181, p= 0.242, 95% CI [-0.22, 0.87], Fig. 5d).

Discussion

We had first asked to what extent intraspecific slopes of the relationship between body and brain measures are higher in fishes than in mammals and to what extent variation in adult body size contributes to the differences. Because the results obtained by Tsuboi et al. [2018] might have been biased, we repeated their analysis with a restrictive data set. This exercise closely replicated their findings and revealed no apparent effect of adult body size variation in fishes. We then asked whether intraspecific slopes provide a useful hypothesis regarding cognitive equivalence within a fish species, potentially between fish species as well. The key result in a case study on cleaner fish *L. dimidiatus* was that individual performance in four cognitive tasks was independent of body size. Consequently, the observed brain-body slopes (Fig. 3&4) of *L. dimidiatus* – which are rather average for a fish species – apparently reflect correctly how much brain size must be increased when the body grows to deal with somatic maintenance processes without affecting cognitive performance in this species. Below we discuss how these findings can have major implications for our understanding of the evolution of cognitive performance within vertebrates.

Brain-body slopes in fishes

Restricting data to species that included only wild-caught specimens and a minimal sample size of ten individuals, we found an average intraspecific brain-body slope of 0.46 for Actinopterygii, compared to 0.44 in Tsuboi et al. [2018]. The small negative effect of sample size on the reported slope is difficult to interpret as there is no obvious publication bias in our data: body and brain weight data are not published as a function of brain-body slopes. Importantly for us, the effect is small and hence does not affect the general conclusions presented above. Furthermore, the absence of an effect of adult size variation on the slope

15

343   estimate indicates that there is at most a minor effect of measurement error on slope estimates.

344   Thus, our reevaluation of intraspecific brain-body slopes in fishes revealed the robustness of

345   the slope estimates presented by Tsuboi et al. [2018] based on their much larger but less

346   conservative data set. This finding, therefore, corroborates that fish brain-body slopes (and

347   probably those of other ectotherms, too) are far steeper than those of birds and mammals [see

348   also van Schaik et al. 2021]. There was an important variation of slope estimates among fish

349   species, with minor effects of phylogenetic proximity. This suggests that targeted studies on

350   specific fish species need to measure the slope for the species in question to generate predictions

351   regarding the cognitive performance of individuals of this species. In our view, the average

352   slope estimate of 0.46 is useful only for big comparative questions regarding vertebrate brains.

353   Therefore, a major question arising is whether intraspecific slopes in fishes represent the slope

354   of cognitive equivalence, as they do in mammals.

355   Our study also confirms the absence of a taxon-level effect in Actinopterygii reported by Tsuboi

356   et al. [2018], with the brain-body slopes for class, order, family, genus and species being 0.50

357    $\pm$ 0.01, 0.51 $\pm$ 0.03, 0.49 $\pm$ 0.02, 0.50 $\pm$ 0.03, and 0.44 $\pm$ 0.02 (mean $\pm$ SE), respectively. This

358   confirmation for fishes contrasts with the taxon-level effect in mammals found by Tsuobi et al.

359   [2018] and recently confirmed for primates [van Schaik et al., 2021]. This finding, too, raises a

360   major question concerning the use of EQs in fishes. We will discuss these two major questions

361   in turn.

362

363   *A case study on brain-body slopes and cognitive performance in cleaner fish*

364   We used existing data sets on *L. dimidiatus* to obtain the first preliminary results on the

365   correlations between adult body size and cognitive performance and between adult body size

366   and brain (region) size. Even though the two brain slope data sets available for *L. dimidiatus*

16

367   yielded much higher values than birds and mammals, we did not find any systematic

368   relationships between an individual's body size and its performance in four different cognitive

369   tasks. The tasks we used here tested various important cognitive domains, such as flexibility in

370   the reversal learning task, self-control in the detour task and numbering skills in the numerical

371   discrimination task [Burkart et al., 2017; Aellen et al., 2021 Preprint]. The fourth task – the

372   ability to feed against preference – is of such high ecological relevance for cleaner fish in their

373   interactions with client fish [Grutter, and Bshary, 2003] that tested cleaner fish must have had

374   abundant prior knowledge about the consequences of eating highly preferred food (i.e., such as

375   biting off client's mucus). More precisely, with an estimated number of cleaning interactions

376   for a single cleaner ranging between 800 and 3,000 per day [Grutter, 1995; Wismer et al., 2014;

377   Triki et al., 2018; Triki et al., 2019b], all cleaner fish subjects must have had experienced in

378   hundreds of thousands of interactions that eating parasites off clients has no negative effects

379   while eating client mucus often leads to the client terminating the interaction [Bshary, and

380   Grutter, 2002]. Thus, performance in our tasks was unlikely to be affected by experience. As

381   the tasks did not address particular challenges in perception and execution of decisions but

382   learning and decision-making, total brain size in the analyses could have been misleading.

383   However, our analyses on the slopes of major brain regions revealed strong positive correlations

384   between all slopes, especially with a more measurement technic like MRI. Thus, our

385   conclusions regarding the slope of cognitive equivalence do not change much whether we take

386   the total brain or the telencephalon, for example.

387   As we do not have brain data and performance data from the same fish, we could not evaluate

388   whether individuals with a brain size above/below the slope perform above/below average.

389   However, other studies reported that brain size or telencephalon size indeed predicts positively

390   cognitive abilities in guppies in a reversal learning and a detour task [Buechel et al., 2018]

391   [Triki et al., 2021b]. Thus, taken together, while we concede that our data set is preliminary,

17

392 the current evidence conforms with the hypothesis that the brain-body slope also represents the

393 slope yielding cognitive equivalence in cleaner fish.

394

395 *Implications for ectotherm-endotherm differences*

396 In combination with a recent study on brain-body slopes in primates [van Schaik et al., 2021],

397 the results presented here have fundamental implications for predictions on the relationship

398 between absolute brain size, brain size relative to body size and cognitive abilities across major

399 vertebrate lineages. The primate study, which has taken extra care to reduce the effects of any

400 measurement errors, found that intraspecific cognitive equivalence is achieved with a brain-

401 body slope of 0.25 to 0.30 [van Schaik et al., 2021]. This means that if the results for cleaner

402 fish are representative for Actinopterygii, bony fishes need, on average, an increase in (log)

403 brain size with increasing (log) body size that is almost twice as steep to maintain cognitive

404 equivalence than primates do. By extension, we hypothesise that ectotherm vertebrates

405 systematically need steeper brain-body slopes than endotherm vertebrates do to achieve

406 cognitive equivalence. This is because a strong taxon-level effect has been shown for mammals

407 (0.25-0.3 for species according to our estimates, 0.59 for class) and birds (ca 0.15 for species,

408 which is not corrected for measurement error and thus too low, 0.57 for class) [Tsuboi et al.,

409 2018], while it is absent or considerably smaller in the major ectotherm vertebrate lineages

410 (Chondrichthyes: 0.5 for species, 0.41 for class; amphibians: 0.36 for species, 0.46 for class;

411 non-avian reptiles: 0.41 for species, 0.56 for the class). In conclusion, our preliminary tests

412 suggest that among both ectotherms [this study] and endotherms [van Schaik et al., 2021]

413 cognitive performance is unrelated to body size within species, even though the brain-body

414 slope in mammals is around 0.25 [van Schaik et al., 2021] and in fishes is around 0.5. If further

415 intraspecific tests validate this assumption, this points at fundamental differences with respect

416   to how brain organisation translates into cognitive performance between mammals and fishes,

417   which warrant a more detailed examination.

418

419   The use of EQ as a predictor for cognitive equivalence across species has been criticised for

420   various reasons. Some authors have proposed that absolute brain size is a better predictor than

421   relative brain size [Rensch, 1973; Deaner et al., 2006]. Others have pointed out that some brain

422   areas affect cognitive performance much more strongly than others [Dunbar, 1992; Healy, and

423   Rowe, 2007; Sherry et al., 1989; Lefebvre et al., 1998]. In addition, more recent analyses show

424   that neuron cell densities may differ between major vertebrate clades like birds and mammals

425   and between major mammalian lineages [Herculano-Houzel, 2017], which may impose

426   important limitations on the value of gross comparisons of brain size between more distantly

427   related species. These problems have led to the proposal that a bottom-up approach, which

428   focuses on comparisons between closely related species, should complement the dominating

429   literature on large-scale comparisons [Logan et al., 2018]. Finally, van Schaik et al. [2021] had

430   criticised the EQ concept largely because of the taxon-level effects reported for endothermic

431   vertebrates. Indeed, the more we will eventually know about the various features of brain

432   morphology, the better we will link them to variation in cognitive abilities. Our statistical testing

433   of slope values also revealed significant variation among fish species, and a future challenge

434   will be to search for potential ecological correlates of that variation. Consequently, the use of

435   the mean intraspecific slope as a predictor for cognitive equivalence in between-species

436   comparisons may be the best predictor we currently have, even if it will introduce large amounts

437   of unexplained variance. Nevertheless, based on the preliminary results presented in our study,

438   it currently appears that EQ may work far better well as a gross estimate of overall cognitive

439   performance in ectothermic vertebrates than in endothermic vertebrates, for which its use

440   should be discouraged [van Schaik et al. 2021]. At least the cleaner fish data suggest that large-

441 scale interspecific comparisons may be meaningful using EQ, i.e. without more detailed

442 knowledge on brain (part) neuron densities.

443

444 **Ethics note**

445 There is no ethics for this present study because all data were compiled from published studies

446 by Triki et al. [2019a; 2020b; 2020a] and Aellen et al. [2021 Preprint], and from FishBase

447 [Froese, and Pauly, 2019].

453 **Conflict of interest:** Authors declare that they have no conflict of interest.

454 **Data and code accessibility**

455 Data and code for statistical analysis and figures are accessible at the public repository Figshare.

456 DOI: 10.6084/m9.figshare.8867660

457 **Authors' contributions**

458 CvS conceived the cognitive equivalence idea. ZT compiled the data from the different sources,

459 analysed the data and generated the figures. ZT collected the cleaner fish brain size data. MA

460 collected the cognitive performance data. ZT, CvS and RB wrote the manuscript. All authors

461 approved the final version of the manuscript. A preprint version of this article is available on

462 bioRxiv [Triki et al., 2021a, preprint].

463

464 **References:**

465 Aellen M, Burkart JM, Bshary R (2021): No evidence for general intelligence in a fish
466   [Internet]. Preprint. DOI: 10.1101/2021.01.08.425841

467 Alroy J (1998): Cope's rule and the dynamics of body mass evolution in North American
468   fossil mammalsScience 280:731–734.

469 Binning SA, Rey O, Wismer S, Triki Z, Glauser G, Soares MC, et al. (2017): Reputation
470   management promotes strategic adjustment of service quality in cleaner wrasseSci
471   Rep 7:8425.

472 Bohn M, Eckert J, Hanus D, Haun DBM (2021): A Longitudinal Study of Great Ape
473   Cognition: Stability, Reliability and the Influence of Individual Characteristics
474   [Internet] DOI: 10.31234/osf.io/pdt5w

475 Bshary R, Grutter AS (2002): Experimental evidence that partner choice is a driving force in
476   the payoff distribution among cooperators or mutualists: the cleaner fish caseEcol Lett
477   5:130–136.

478 Bshary R, Grutter AS (2006): Image scoring and cooperation in a cleaner fish
479   mutualismNature 441:975–978.

480 Bshary R, Wickler W, Fricke H (2002): Fish cognition: a primate's eye viewAnim Cogn 5:1–
481   13.

482 Bshary R, Würth M (2001): Cleaner fish Labroides dimidiatus manipulate client reef fish by
483   providing tactile stimulationProc R Soc Lond B Biol Sci 268:1495–1501.

484 Buechel SD, Boussard A, Kotrschal A, van der Bijl W, Kolm N (2018): Brain size affects
485   performance in a reversal-learning testProc R Soc B Biol Sci 285:20172031.

486 Burkart JM, Schubiger MN, Schaik CP van (2017): The evolution of general
487   intelligenceBehav Brain Sci 40. DOI: 10.1017/S0140525X16000959

488 Clague GE, Cheney KL, Goldizen AW, McCormick MI, Waldie PA, Grutter AS (2011):
489   Long-term cleaner fish presence affects growth of a coral reef fishBiol Lett 7:863–
490   865.

491 Deaner RO, van Schaik CP, Johnson V (2006): Do Some Taxa Have Better Domain-General
492   Cognition than others? A Meta-Analysis of Nonhuman Primate StudiesEvol Psychol
493   4:147470490600400.

494 Demairé C, Triki Z, Binning SA, Glauser G, Roche DG, Bshary R (2020): Reduced access to
495   cleaner fish negatively impacts the physiological state of two resident reef fishesMar
496   Biol 167:48.

497 Dunbar RIM (1992): Neocortex size as a constraint on group size in primatesJ Hum Evol
498   22:469–493.

499 Eckert GJ (1987): Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef,
500   Great Barrier ReefMar Biol 95:167–171.

501 Froese R, Pauly D (2019): Editors. 2019. FishBase. World Wide Web electronic publication.
502   www.fishbase.org, version (02/2019).

503 Froese T, Froese R (2019): Comparisons of static brain–body allometries across vertebrates
504   must distinguish between indeterminate and determinate growthNat Ecol Evol DOI:
505   10.1038/s41559-019-0984-1

506 Grutter (1995): Relationship between cleaning rates and ectoparasite loads in coral reef
507   fishesMar Ecol Prog Ser 118:51–58.

508 Grutter (1999): Cleaner fish really do cleanNature 398:672–673.

509 Grutter AS, Bshary R (2003): Cleaner wrasse prefer client mucus: support for partner control
510   mechanisms in cleaning interactionsProc R Soc Lond B Biol Sci 270:S242–S244.

511 Halley AC, Deacon TW (2017): The developmental basis of evolutionary trends in primate
512   encephalization

513 Healy SD, Rowe C (2007): A critique of comparative studies of brain sizeProc R Soc B Biol
514   Sci 274:453–464.

515 Herculano-Houzel S (2017): Numbers of neurons as biological correlates of cognitive
516   capabilityCurr Opin Behav Sci 16:1–7.

517 Huntingford FA (2004): Implications of domestication and rearing conditions for the
518   behaviour of cultivated fishesJ Fish Biol 65:122–142.

519 Irwing P, Lynn R (2005): Sex differences in means and variability on the progressive matrices
520   in university students: A meta-analysisBr J Psychol 96:505–524.

521 Jerison H (1973): Evolution of the Brain and Intelligence. New York: Academic PressN Y
522   Acad Press

523 Jones KE, Purvis A (1997): An optimum body size for mammals? Comparative evidence
524   from batsFunct Ecol 11:751–756.

525 Kohda M, Takashi H, Takeyama T, Awata S, Tanaka H, Asai J, et al. (2018): Cleaner wrasse
526   pass the mark test. What are the implications for consciousness and self-awareness
527   testing in animals?bioRxiv :397067.

528 Krebs JR, Sherry DF, Healy SD, Perry VH, Vaccarino AL (1989): Hippocampal
529   specialization of food-storing birdsProc Natl Acad Sci 86:1388–1392.

530 Lefebvre L, Gaxiola A, Dawson S, Timmermans S, Rosza L, Kabai P (1998): Feeding
531   Innovations and Forebrain Size in Australasian BirdsBehaviour 135:1077–1097.

532 Logan CJ, Avin S, Boogert N, Buskell A, Cross FR, Currie A, et al. (2018): Beyond Brain
533   Size: Uncovering the Neural Correlates of Behavioral and Cognitive

534   SpecializationComp Cogn Behav Rev [cited 2018 Dec 20]; 13. Available from:
535   http://comparative-cognition-and-behavior-reviews.org/2018/vol13_logan_et-al/

536   Losey GS (1979): Fish cleaning symbiosis: proximate causes of host behaviourAnim Behav
537   27:669–685.

538   Martin RD, Harvey PH (1985): Brain Size Allometry Ontogeny and Phylogeny [Internet]; in
539   Jungers WL (ed): Size and Scaling in Primate Biology. Boston, MA, Springer US, pp
540   147–173.

541   Pagel MD, Harvey PH (1988): The Taxon-Level Problem in the Evolution of Mammalian
542   Brain Size: Facts and ArtifactsAm Nat 132:344–359.

543   Pilbeam D, Gould SJ (1974): Size and scaling in human evolutionScience 186:892–901.

544   Poirier M-A, Kozlovsky DY, Morand-Ferron J, Careau V (2020): How general is cognitive
545   ability in non-human animals? A meta-analytical and multi-level reanalysis
546   approachProc R Soc B 287:20201853.

547   Quiñones AE, Leimar O, Lotem A, Bshary R (2020): Reinforcement Learning Theory
548   Reveals the Cognitive Requirements for Solving the Cleaner Fish Market Task.Am
549   Nat DOI: 10.1086/707519

550   R Core Team (2020): A language and environment for statistical   computing [Internet].
551   Vienna, Austria, R Foundation for Statistical Computing.Available from: URL
552   https://www.R-project.org/

553   Rensch B (1973): Gedächtnis, Begriffsbildung und Planhandlungen bei Tieren. Parey.

554   Ros AFH, Nusbaumer D, Triki Z, Grutter AS, Bshary R (2020): The impact of long-term
555   reduced access to cleaner fish on health indicators of resident client fishJ Exp Biol
556   DOI: 10.1242/jeb.231613

557   Salwiczek LH, Prétôt L, Demarta L, Proctor D, Essler J, Pinto AI, et al. (2012): Adult Cleaner
558   Wrasse Outperform Capuchin Monkeys, Chimpanzees and Orang-utans in a Complex
559   Foraging Task Derived from Cleaner – Client Reef Fish CooperationPLoS ONE
560   7:e49068.

561   Sherry DF, Vaccarino AL, Buckenham K, Herz RS (1989): The hippocampal complex of
562   food-storing birdsBrain Behav Evol 34:308–317.

563   Shettleworth SJ (2010): Cognition, evolution, and behavior. 2nd ed. Oxford ; New York,
564   Oxford University Press.

565   Striedter GF (2005): Principles of brain evolution. USA, Sinauer Associates.

566   Triki Z, Aellen M, Schaik CV, Bshary R (2021a): Relative brain size and cognitive
567   equivalence in fishesPrepr BioRxiv :2021.02.09.430417.

568   Triki Z, Bshary R (2018): Cleaner fish <i>Labroides dimidiatus<i> discriminate numbers but
569   fail a mental number line testAnim Cogn 21:99–107.

Triki Z, Bshary R (2019): Long-term memory retention in a wild fish species *Labroides dimidiatus* eleven months after an aversive eventEthology DOI: 10.1111/eth.12978

Triki Z, Emery Y, Teles MC, Oliveira RF, Bshary R (2020a): Brain morphology predicts social intelligence in wild cleaner fishNat Commun 11:6423.

Triki Z, Emery Y, Teles MC, Oliveira RF, Bshary R (2020b): Data from: Brain morphology predicts social intelligence in wild cleaner fishFigshare DOI: 10.6084/m9.figshare.7415576

Triki Z, Fong S, Amcoff M, Kolm N (2021b): Artificial mosaic brain evolution of relative telencephalon size improves cognitive performance in the guppy (Poecilia reticulata)bioRxiv :2021.04.03.438307.

Triki Z, Levorato E, McNeely W, Marshall J, Bshary R (2019a): Population densities predict forebrain size variation in the cleaner fish *Labroides dimidiatus*Proc R Soc B Biol Sci 286:20192108.

Triki Z, Wismer S, Levorato E, Bshary R (2018): A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbationsGlob Change Biol 24:481–489.

Triki Z, Wismer S, Rey O, Ann Binning S, Levorato E, Bshary R (2019b): Biological market effects predict cleaner fish strategic sophisticationBehav Ecol 30:1548–1557.

Tsuboi M, Bijl W van der, Kopperud BT, Erritzøe J, Voje KL, Kotrschal A, et al. (2018): Breakdown of brain–body allometry and the encephalization of birds and mammalsNat Ecol Evol 2:1492–1500.

van Schaik CP, Triki Z, Bshary R, Heldstab SA (2021): A Farewell to the Encephalization Quotient: A New Brain Size Measure for Comparative Primate CognitionBrain Behav Evol :1–12.

Victor BC (1986): Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae)Mar Biol 90:317–326.

Waldie PA, Blomberg SP, Cheney KL, Goldizen AW, Grutter AS (2011): Long-term effects of the cleaner fish *Labroides dimidiatus* on coral reef fish communitiesPLOS ONE 6:e21201.

Wismer S, Grutter A, Bshary R (2016): Generalized rule application in bluestreak cleaner wrasse (Labroides dimidiatus): using predator species as social tools to reduce punishmentAnim Cogn 19:769–778.

Wismer S, Pinto AI, Vail AL, Grutter AS, Bshary R (2014): Variation in Cleaner Wrasse Cooperation and Cognition: Influence of the Developmental Environment?Ethology 120:519–531.

24

Table 1. Brain-body slope estimate of the 51 fish species with 95% Confidence interval.

Species	N	β	CI_lower	CI_upper	Species	N	β	CI_lower	CI_upper
Altolamprologus compressiceps	15	0.43	0.39	0.47	*Neolamprologus modestus*	10	0.29	-0.02	0.61
Atherina presbyter	29	0.59	0.47	0.71	*Neolamprologus pulcher*	24	0.26	0.12	0.41
Bathybates fasciatus	11	0.46	0.4	0.52	*Neolamprologus savoryi*	10	0.44	-0.21	1.09
Benthochromis tricoti	12	0.50	0.13	0.86	*Neolamprologus tetracanthus*	24	0.34	0.19	0.49
Chalinochromis brichardi	12	0.36	0.26	0.45	*Ophthalmotilapia nasuta*	17	0.28	0.12	0.45
Conger conger	42	0.27	0.23	0.31	*Ophthalmotilapia ventralis*	11	0.32	-0.07	0.71
Coris julis	14	0.52	0.4	0.65	*Parablennius gattorugine*	18	0.51	0.4	0.62
Ctenochromis horei	14	0.46	0.37	0.56	*Perissodus microlepis*	10	0.37	-0.01	0.75
Ctenolabrus rupestris	39	0.49	0.43	0.56	*Petrochromis famula*	12	0.42	0.25	0.59
Cyathopharynx furcifer	11	0.30	0.2	0.41	*Petrochromis orthognathus*	14	0.49	0.32	0.66
Cyprichromis leptosoma	12	0.55	0.36	0.74	*Pseudosimochromis curvifrons*	12	0.57	0.43	0.7
Dicentrarchus labrax	14	0.44	0.41	0.47	*Scomber scombrus*	11	0.64	0.5	0.77
Ectodus descampsii	14	0.47	0.17	0.76	*Scorpaena porcus*	19	0.38	0.33	0.43
Eretmodus cyanostictus	12	0.36	0.19	0.53	*Serranus cabrilla*	11	0.50	0.42	0.58
Gnathochromis pfefferi	11	0.71	0.54	0.88	*Simochromis diagramma*	13	0.45	0.35	0.55
Haplotaxodon microlepis	12	0.46	0.36	0.57	*Spicara maena*	12	0.49	0.39	0.59
Hippichthys cyanospilos	19	0.69	0.52	0.85	*Spinachia spinachia*	12	0.64	0.42	0.85
Hippocampus spinosissimus	16	0.47	0.26	0.69	*Symphodus melops*	31	0.49	0.4	0.58
Hippocampus trimaculatus	28	0.55	0.48	0.62	*Syngnathoides biaculeatus*	10	0.79	0.13	1.45
Julidochromis ornatus	23	0.35	0.21	0.49	*Syngnathus schlegeli*	60	0.29	0.19	0.4
Labrus bergylta	18	0.41	0.34	0.48	*Telmatochromis temporalis*	24	0.48	0.41	0.55
Lepidiolamprologus elongatus	15	0.41	0.35	0.47	*Trematocara unimaculatum*	10	0.47	0.23	0.71
Lepidiolamprologus profundicola	14	0.48	0.41	0.55	*Tropheus moorii*	15	0.39	0.12	0.66
Limnochromis staneri	10	0.41	0	0.82	*Tylochromis polylepis*	14	0.57	0.36	0.79
Lipophrys pholis	19	0.48	0.38	0.58	*Xenotilapia melanogenys*	15	0.46	0.23	0.7
Lobochilotes labiatus	14	0.44	0.39	0.48					

609 **Table 2. Brain-body slope estimate and brain part-body slope in the cleaner fish *L. dimidiatus* with 95% Confidence interval.**

Methods	Brain measure	N	β	CI_lower	CI_upper
MRI (volume in mm³)	Total brain size	15	0.58	0.38	0.79
	Telencephalon	15	0.54	0.23	0.85
	Diencephalon	15	0.65	0.41	0.88
	Midbrain	15	0.5	0.33	0.67
	Cerebellum	15	0.64	0.38	0.89
	Brain stem	15	0.62	0.39	0.85
Manual dissection (mass in mg)	Total brain size	18	0.47	0.19	0.75
	Telencephalon	18	0.49	-0.16	1.14
	Diencephalon	18	0.62	0.19	1.05
	Midbrain	18	0.48	0.23	0.74
	Cerebellum	18	0.28	-0.24	0.8
	Brain stem	18	0.31	-0.43	1.04

610

Figures legend:
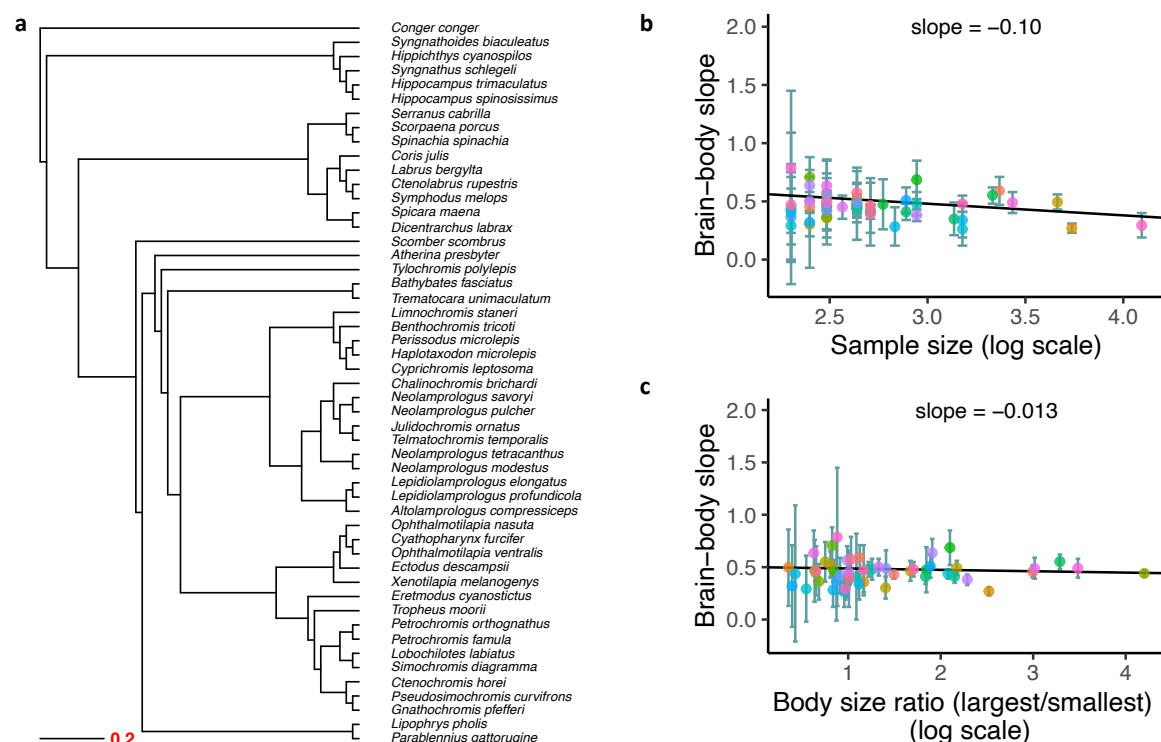
Figure 1. (**a**) Phylogenetic tree of the 51 fish species with a scale indicating tree distance. Relationship of brain-body slope and either (**b**) sample size used to estimate the brain-body slope, or (**c**) body size ratio. The plots show the brain-body slope estimate with 95% CI as error bars for each species. Brain and body data were compiled from the fish database FishBase [Froese, and Pauly, 2019] and from Tsuboi et al. [2018].
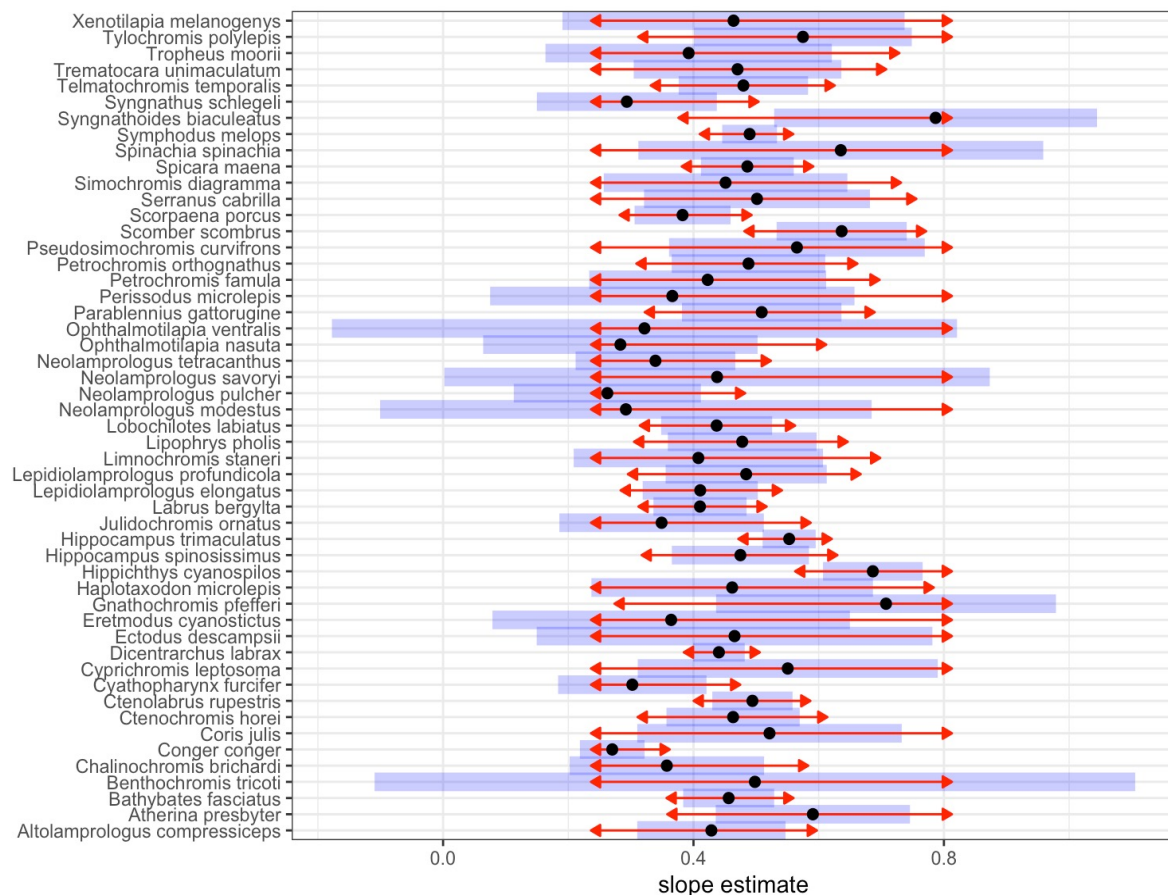
619

620
621
622 **Figure 2**. Comparison of the 51 fish slopes. Black dots are the slope estimate of log-transformed

623 brain size on log-transformed body size. Blue bars are the 95% CI estimated from the multiple

624 comparisons. The red arrows are indicators for the statical comparisons. If an arrow from one

625 slope estimate overlaps with an arrow from another species, the difference is not statistically

626 significant. We used Tukey methods to adjust for multiple comparisons with an alpha set at

627 0.05.

628

629

630

631
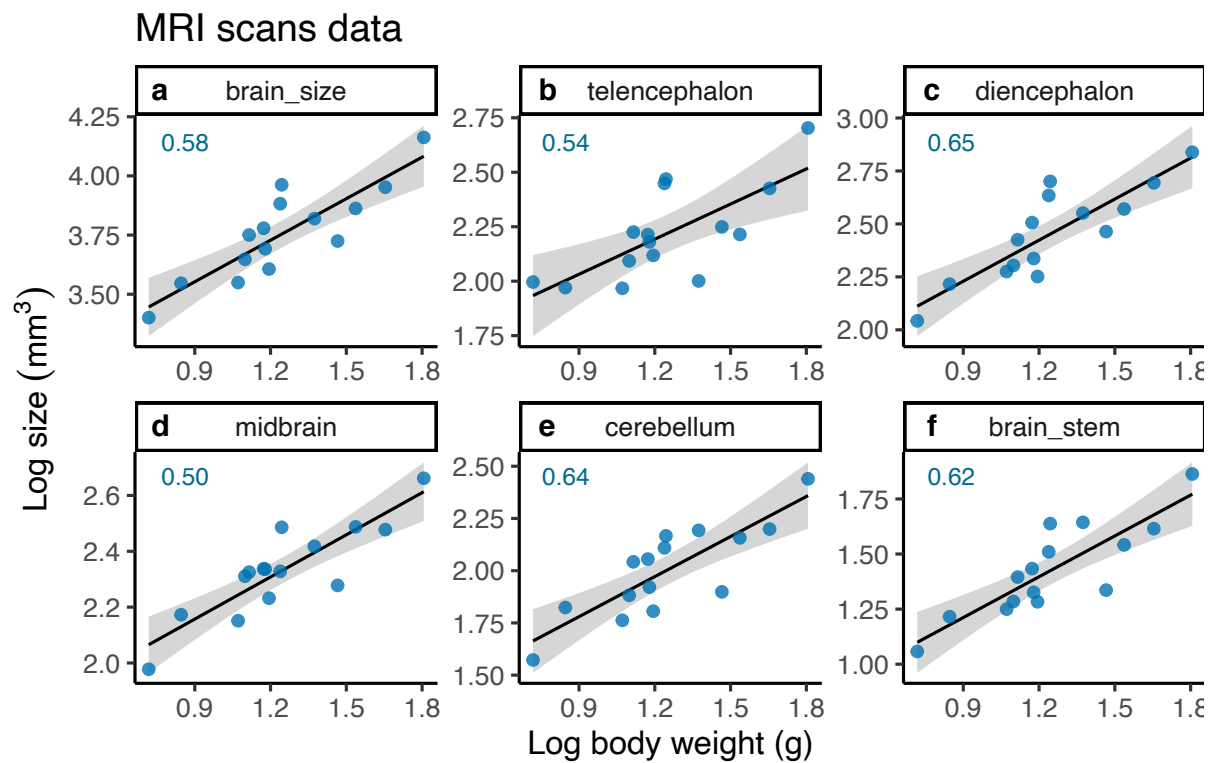
Figure 3. Regression relationship between (**a**) log-transformed total brain size, and (**b-f**) log-transformed major brain part sizes, and log-transformed body weight (g) in cleaner fish. Total brain and brain parts volume (mm^3) were estimated from magnetic resonance imagery (MRI) scans (data from Triki et al. [2019a]). The shaded area around the regression lines refers to the 95% CI. Slope estimates are also depicted in the different figure panels.

639
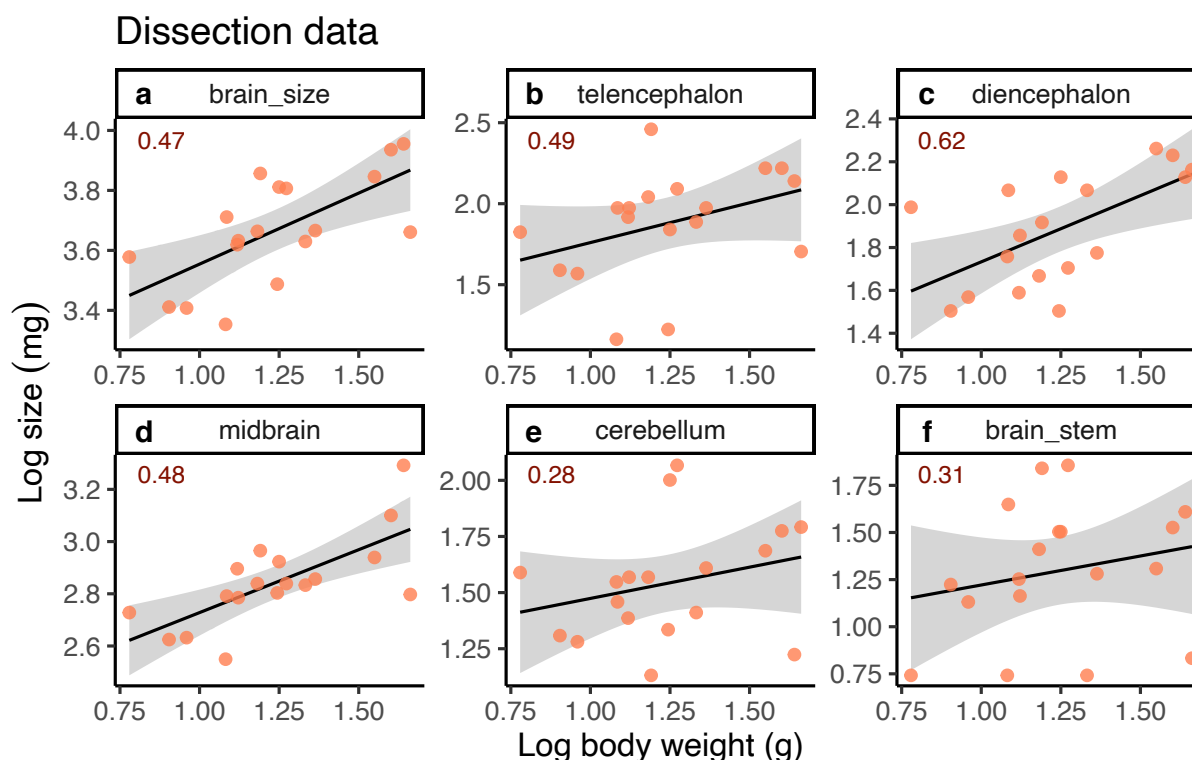
Figure 4. Regression relationship between (**a**) log-transformed total brain size, and (**b-f**) log-transformed major brain part size, and log-transformed body weight (g) in cleaner fish. Total brain and brain parts mass (mg) were estimated from manual dissection and weighing. The shaded area around the regression lines refers to the 95% CI. Slope estimates are also depicted in the different figure panels.
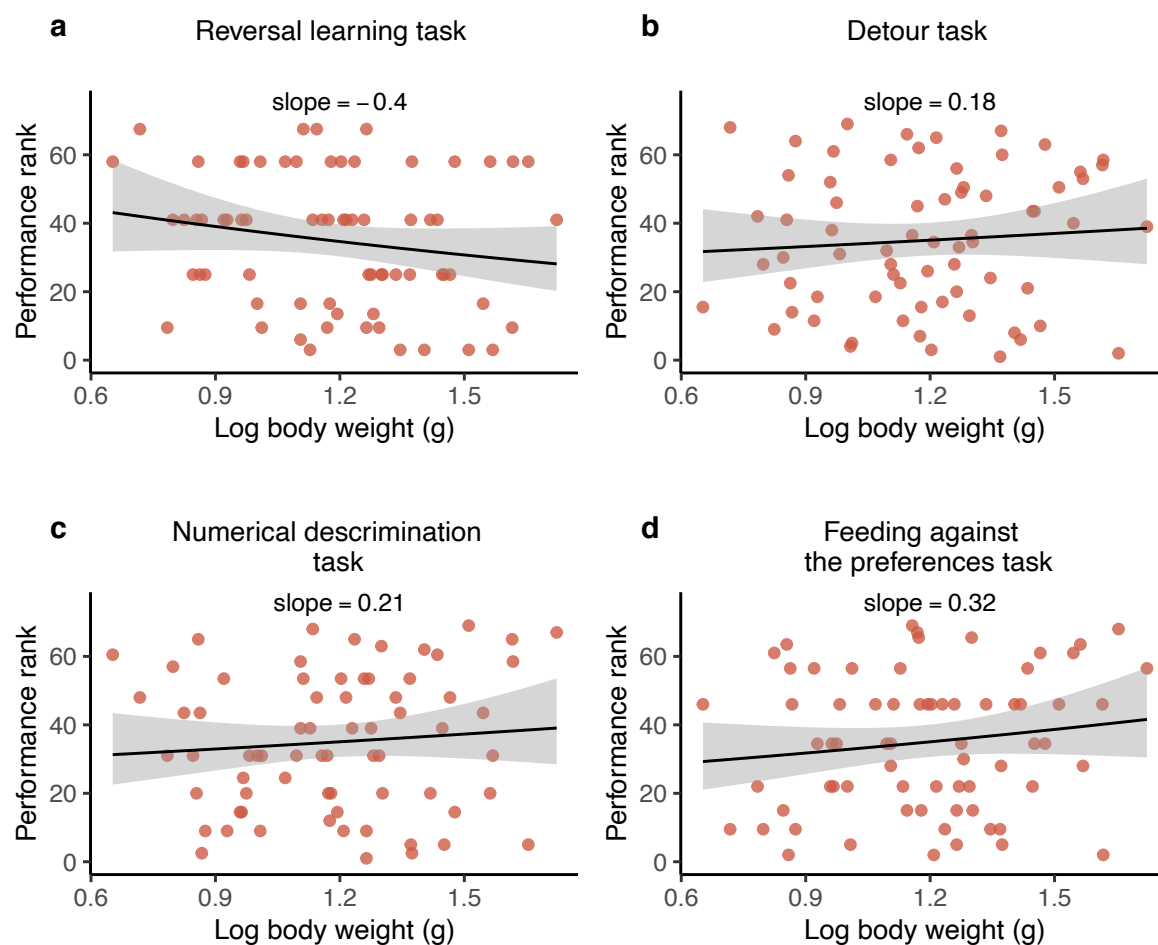
Figure 5. Relationship between cognitive performance and log-transformed body size (g) in cleaner fish (Data from Aellen et al. [2021 Preprint]). Regression slope and 95% CI (grey shading) of log-transformed body weight and (**a**) learning abilities in a reversal learning task; (**b**) inhibitory control abilities in a detour task; (**c**) numerical abilities in a numerical quantity discrimination task; and (**d**) inhibitory control abilities in a feeding against the preferences task. All y-axes represent performance as rank, where high values on the y-axes refer to higher performance. In all four panels, *P-values* > 0.05 were estimated from GLMs.