Title: Relative brain size and cognitive equivalence in fishes

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ABSTRACT

There are two well-established facts about vertebrate brains: brains are physiologically costly organs, and both absolute and relative brain size varies greatly between and within the major vertebrate clades. While the costs are relatively clear, scientists struggle to establish how larger brains translate into higher cognitive performance. Part of the challenge is that intuitively larger brains are needed to control larger bodies without any changes in cognitive performance. Therefore, body size needs to be controlled for in order to establish the slope of cognitive equivalence between animals of different sizes. Potentially, intraspecific slopes provide the best available estimate of how an increase in body size translates into an increase in brain size without changes in cognitive performance. Here, we provide slope estimates for brain-body sizes and for cognition-body in wild-caught "cleaner" fish *Labroides dimidiatus*. The cleaners' cognitive performance was estimated from four different cognitive tasks that tested for learning, numerical, and inhibitory control abilities. The cognitive performance was found to be rather independent of body size, while brain-body slopes from two datasets gave the values of 0.58 (MRI scans data) and 0.47 (dissection data). These values can hence represent estimates of intraspecific cognitive equivalence for this species. Furthermore, another dataset of brain-body slopes estimated from 14 different fish species, gave a mean slope of 0.5, and hence rather similar to that of cleaners. This slope is very similar to the encephalisation quotients for ectotherm higher taxa, i.e. teleost fishes, amphibians and reptiles (~ 0.5). The slope is much higher than what has been found in endotherm vertebrate species (~ 0.3). Together, it suggests that endo- and ectotherm brain organisations and resulting cognitive performances are fundamentally different.

Keywords: encephalization quotient; cognitive equivalence; intelligence; brain size; body size: slopes; cognitive performance; cleaner fish

Introduction

While brain tissue is costly [Herculano-Houzel, 2011], various studies reveal that larger brain size may yield benefits by positively affecting cognitive performance [Deaner et al., 2007; Reader et al., 2011; Rumbaugh et al., 1996]. Specific cognitive abilities are best linked to the specific brain parts known to be involved [Dunbar, 1998]. For a more global appreciation of a species' overall intelligence, total brain sizes currently provide the most accessible information. While brain size is potentially confounded by systematic differences in neuronal densities between orders, this problem apparently does not arise within orders [Herculano-Houzel, 2012].

When attempting to link brain size and cognitive performance, it has long been appreciated that total brain size must be corrected for body size [Gould, 1975; Schmidt-Nielsen, 1984; Smith, 1984]. As a consequence, there has been a long-standing interest in estimating overall cognitive abilities from brain size or cranial capacity by statistically removing the effect of body size. A highly influential proposal was by Jerison [1973], who developed the encephalisation quotient or EQ (the ratio of expected-to-predicted brain size for given body size). The empirical regression slope of log-brain mass on log-body mass has been used as the expected average, based on the argument that it reflects a fundamental physiological regularity, linking brain size to the body's surface area and need for proprioceptive inputs [Jerison, 1973] or metabolic turnover [Armstrong, 1983; Martin, 1981]. Species above the regression slope are supposed to be more intelligent than average, while species below the

line are less intelligent than average. However, the slope varies between lineages [Martin, and Harvey, 1985; Tsuboi et al., 2018], and at least cognitive abilities of birds and mammals, when estimated, do not scale with body size as predicted by EQ. Instead, larger-bodied species generally outperform smaller-bodied species [Deaner et al., 2007; Rensch, 1973]. As a consequence, we need to control for body size differently in order to calculate the slope that predicts cognitive equivalence (the line connecting species of equal cognitive abilities) that should allow us to produce a new estimate of cognitive brain size to replace the EQ.

Intriguingly, the brain-body slope varies by taxonomic level, becoming steeper as one includes higher taxonomic units. This is called the taxon-level effect, which, if true, indicates that larger-bodied lineages (which tend to have evolved more recently: [Jerison, 1973; Rowe et al., 2011]) generally have larger brains for their body size than smaller-bodied ones. Largely based on detailed data on mammals, it has been suggested this taxon-level effect is mostly an artefact of errors due to measurement error or developmental noise. This reduces estimated slopes because individuals within a species and closely related species are all of similar body size [Pagel, and Harvey, 1988]. However, a recent paper by Tsuboi et al. [2018] challenged this suggestion. The authors aimed at explaining why the endotherm lineages (mammals and birds) have evolved relatively larger brains that are also more variable in size corrected for body size compared to ectotherm jawed vertebrates (fishes, amphibians and reptiles). Based on information on 20’213 specimens across 4’587 species of jawed vertebrates, the authors reported two important results that relate to our aim to determine slopes of cognitive equivalence. Although they replicated the taxon-level effect in mammals as well as in birds (henceforth: endotherms), they showed it was much smaller or even absent in the ectotherm vertebrates they sampled (fishes, reptiles and presumably amphibians). Furthermore, Tsuboi et al. [2018] calculated reliability ratios to assess the potential

importance of variation in adult body size, which should be smaller in ectotherms due to the greater abundance of indeterminate growth [Froese, and Froese, 2019]. Tsuboi et al. concluded that unrealistically large errors are required to explain the full extent of the taxon-level effect in endotherms, suggesting there are fundamental differences in brain-body relationships between endotherms and ectotherms. However, it remains possible that errors can explain some part of why the taxon-level effect is prominent in endotherms but not in ectotherms. For this, we also must have an estimate of the error effect in ectotherms.

A suitable alternative to predict cognitive equivalence [see van Schaik et al., in prep] is provided by the within-species brain-body slope. The logic is that as long as the cognitive performance of an individual is not related to its body size (derived from the cognition-body slope), the intraspecific brain-body relationship should inform us about the necessary brain tissue needed to control a given body size (sensory information, complex motor control, etc.). That is, an increase in body size will be accompanied by an increase in brain size without the individual becoming smarter. To test for this, we explored the intraspecific relationship between body size and cognitive performance, and between body size and brain size, in a fish species.

We provide an explicit analysis that combines both cognitive performance and brain size as a function of body size in the cleaner fish *Labroides dimidiatus* (hereafter “cleaner”). Cleaners engage in iterative mutualistic interaction with a variety of coral reef fish (hereafter “client”) to remove their ectoparasites and dead tissue in exchange for food [Losey, 1979], a behaviour that is mutually beneficial for both cleaners [Grutter, 1999] and clients [Demairé et al., 2020; Ros et al., 2020; Clague et al., 2011]. Cleaner fish show a highly sophisticated strategic

behaviour that includes reputation management [Bshary, and Grutter, 2002; Binning et al., 2017], social tool use [Bshary et al., 2002], reconciliation [Bshary, and Würth, 2001], and social competence [Triki et al., 2020a]. Cleaners may outperform primates in some learning tasks [Salwiczek et al., 2012] that go beyond conditioning [Quiñones AE et al., 2020]. They also show evidence for generalised rule learning [Wismer et al., 2016], numerical discrimination [Triki, and Bshary, 2018], long-term memory [Triki, and Bshary, 2019], and mirror self-recognition [Kohda et al., 2018]. On the other hand, the brain size relative to body size is rather average for a *Labridae* [Chojnacka D et al., 2015].

Here, we used published data on brain size [Triki et al., 2019a; Triki et al., 2020a] and cognitive performance in cleaner fish [Aellen et al., 2021 Preprint] to explore the relationship between body size, brain size and cognitive performance. The resulting brain-body and cognition-body slopes provide a first test to what extent intraspecific brain-body slopes in fishes may reflect cognitive equivalence. In addition, we identified 14 fish species for which sample sizes of wild specimens were large enough (> 10 data points) to calculate brain-body slopes. In the absence of information on the relationship between body size and cognitive performance from the literature, we asked to what extent the brain-body slopes from these fish species are similar to the cleaners' slope and those slopes shown by Tsuboi et al. [2018]. Importantly, the compiled dataset allowed us to test whether the range in adult body sizes may explain the steepness of intraspecific slopes. Suppose slopes correlate positively with variation in adult body size (i.e., estimated as the ratio of the largest to the smallest individual in a species dataset). In that case, that means errors in measurements play an important role in estimating and interpreting the brain-body slope in animals. It is noteworthy to mention that using fishes have indeterminate growth and thus have a much larger range of body sizes than

birds or even mammals [Froese, and Froese, 2019]. Therefore, fishes are more suitable than mammals or birds to address these issues.

Material and Methods

Brain size, body size and cognitive performance data in Labroides dimidiatus:

1. Brain size data

For brain and body size data, we compiled datasets from published studies by Triki et al. [2019a; 2020b]. These two studies were conducted on wild-caught female cleaner fish. We used these data to calculate the slope of brain size as a function of body size. The two studies differ with respect to the method used to quantify brain size: Triki et al. [2019a] used magnetic resonance image (MRI) technic to estimate brain volume of 15 female cleaners, while Triki et al. [2020a] manually dissected and weighed the brains of 18 female cleaners (for further details, please refer to the original studies by Triki et al. [2019a; Triki et al., 2020a]). We run Linear models LMs in the open-source statistical software R [R Core Team, 2019] to estimate the regression slopes of log-transformed brain size on log-transformed body size.

2. Cognitive performance data

For the cognitive performance and body size data, we compiled data from the study by Aellen et al. [2021 Preprint]. The dataset comprises cognitive performance of 69 wild-caught female cleaner fish tested in four laboratory tasks (For further details, please refer to the original study by Aellen et al. [2021 Preprint]). Here, we used these data to explore the relationship

between body size and cognitive performance. Aellen et al. used Plexiglas plates with food as surrogates for client fish.

2.1. Reversal learning task

Aellen et al. [2021 Preprint] tested fish learning and flexibility abilities in a reversal learning task. The experiment was based on a simultaneous two-choice task with colour and shape cued Plexiglas plates, i.e., yellow triangle vs green round plates. Fish had to learn first the association between the yellow triangle and food. As soon as fish learned this association, reward contingency was reversed, and the previously non-rewarding green plate became the one with the food reward. At this stage, fish were offered a maximum of 100 trials (i.e., ten sessions of ten trials each over five consecutive days) to learn the reversal association.

For data analyses, we ran a Generalised Linear Model (GLM) to estimate the regression slope of learning performance (i.e., individual performance as a rank with respect to the performance of all tested fish, rank from 1 to 69, with 1 being the highest rank) on log-transformed body weight.

2.2. Detour task:

This task aimed at estimating fish inhibitory control abilities. In this task, a novel Plexiglas plate with a food reward was placed behind a transparent barrier. To access to the food reward, fish had to detour the barrier and swim around it to reach for the Plexiglas plate. Fish were tested in ten trials. The performance was estimated as the average number of fish head

bumps on the barrier before detouring. To estimate the cognition-body slope of this task, we ran an LM regression of square root transformed average of head bumps on log-transformed body weight.

2.3. Numerical discrimination task:

To test for fish numerical abilities, Aellen et al. [2021 Preprint] used Plexiglas plates with various numerical quantities in the form of black squares depicted on a white background. There were nine quantities ranging between one to nine black squares. The task consisted of presenting two Plexiglas plates at a time with two different quantities of black squares. In total, there were 20 different combinations of the nine quantities. The general rule was that, in every combination, the plate depicting the largest quantity of black squares was always the rewarding plate. The performance consisted of the proportion of correct choices from 160 test trials over eight days. A linear regression of log-transformed success proportion on log-transformed bodyweight generated the cognition-body slope from this cognitive task.

2.4. Feeding against the preferences task:

During the cleaner-client cleaning interaction, cleaners often prefer to bite client mucus instead of cooperating and eating ectoparasites [Grutter, and Bshary, 2003]. Such event can be reproduced in laboratory conditions with Plexiglas plates as surrogates for clients, and fish flakes and mashed prawn as surrogates for client ectoparasite and mucus, respectively [Bshary, and Grutter, 2006]. Aellen et al. [2021 Preprint] used similar laboratory set-up to test whether cleaner fish can inhibit their preferences for prawn and feed on fish flakes. During test trials, a Plexiglas plate with two fish flakes items and two prawn items was

presented to the fish. As long as fish fed on flakes items, the plate remained in the aquarium. Upon eating a prawn item, however, the plate withdrew from the aquarium. The optimal feeding strategy to maximise food intake is to feed first on the less preferred food (flakes) before eating one highly preferred food item (prawn). The performance was estimated as a feeding against the preferences ratio: calculated as the total number of fish flakes eaten divided by the total of prawn items consumed over 12 test trials. For the cognition-body slope from this data, we fitted a linear regression model of feeding ratio on log-transformed body weight.

Brain and body size data from other fish species

We compiled fish brain and body size data from wild-caught individuals from the database FishBase [Froese, and Pauly, 2019]. We selected only adult individuals based on the adult body size for the species. Species were only included when at least ten individual measurements of body and brain size were reported. Overall, we had 14 species with sample size ranging from 11 to 42 individuals. The regression slope within each of these species was estimated from Linear models (LMs). We also calculated the body size range by dividing the body size of the largest individual by the body size of the smallest individual in a species dataset. In our analysis, we corrected for the effects of phylogenetic relatedness between species by running phylogenetic generalised least-squares regression (PGLS) models.

To test the relationship of the brain-body slopes and body size ratios within a species, we ran a PGLS model, with sample size (i.e., number of individuals per species) added to the model as a covariate to test for the potential effect of sample size on variation in the estimated slopes. Normal distribution and homogeneity of variance of the residuals were tested for the

statistical models (LMs and PGLS). Pagel's λ (lambda) as the phylogenetic signal in PGLS models was estimated from a likelihood function for each model separately (see Code for further details). For all the statistical models ran in the present study, model assumptions were checked and met when applicable. Code for detailed step-by-step analyses is provided as a script file that runs in the open-source statistical software R [R Core Team, 2019] (see Data and code accessibility statement).

Ethics note

There is no ethics for this present study because all data were compiled from published studies by Triki et al. [2019a; 2020b; 2020a] and Aellen et al. [2021 Preprint], and from FishBase [Froese, and Pauly, 2019].

Results

Cleaner fish slopes

Our two datasets used to calculate the slope for the relationship between log brain size and log body size yielded values of 0.58 (MRI scans, LM, N = 15, t-value= 6.133, $p < 0.001$, 95% CI [0.38, 0.79], Fig. 1a) and 0.47 (dissection data, LM, N=18, t-value= 3.593, $p = 0.002$, 95% CI [0.19, 0.75], Fig. 1b), respectively.

For the cognition-body slopes, there was no significant relationship between body size and performance from either of the four cognitive tasks: reversal learning (GLM: N=69, t-value=1.473, p=0.145, 95% CI [-0.13, 0.94], Fig. 2a), detour task (LM: N=69, t-value=0.158,

p=0.875, 95% CI [-0.91, 1.07], Fig. 2b), numerical discrimination task (LM: N=69, t-value=1.025, *p*=0.309, 95% CI [-0.03, 0.09], Fig. 2c), and feeding against the preferences task (LM: N=69, t-value=1.150, *p*=0.254, 95% CI [-0.09, 0.34], Fig. 2d).

In two tasks, namely, reversal learning and detour, the cognition-body slopes (0.4 and 0.08, respectively) should better be considered as negative slopes because higher values on the y-axes indicate lower performance (Fig. 2 a & b). In the other two tasks, numerical discrimination and feeding against preference, the cognition-body slopes (0.032 and 0.12, respectively) are indeed positive given that higher values on the y-axes indicate high performance (Fig. 2 c & d). To generate an overall cognition-body slope, we averaged these four slopes coefficients, and we got a slightly negative overall slope (- 0.082) of the relationship between cognitive performance and body size.

The intraspecific brain-body slope in other fish species

We calculated intraspecific slopes in wild-caught individuals from 14 fish species (Fig. 3a). We found a mean slope within species of 0.49 (slopes range from 0.27 to 0.64, Fig. 3b). As expected, sample size (the number of individual data points per species) did not significantly affect the brain-body slopes estimates (GLS: N =14, t-value= -1.687, p = 0.117, 95% CI [-0.01, 0.00], λ = 0.15). Most importantly, we found no effect of the range of adult body size within a species on the slope of the brain on body size (GLS: N =14, t-value= -1.638, p = 0.127, 95% CI [-0.09, 0.01], λ = 0.51, Fig. 3b). If anything, the Pagel's λ of 0.51 indicated that the phylogenetic signal was relatively important in this analysis; that is, the relationship between brain slopes and the range of adult body size is sensitive to the phylogenetic relatedness between the studied species.

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Discussion

We had asked whether intraspecific slopes of the relationship between body and brain measures may provide a useful hypothesis regarding cognitive equivalence within as well as between species. Our key result on cleaner fish *L. dimidiatus* was that individual performance in the four cognitive tasks was independent of body size (Fig. 2). As a consequence, the observed brain-body slopes (Fig. 1) of *L. dimidiatus* correctly reflect how much brain size must be increased when the body grows to deal with somatic maintenance processes without affecting cognitive performance. To values of these slopes were in the same range as those we found in the other fish species (Fig. 3), as well as to those reported by Tsuboi et al. [2018] in species from higher taxonomic levels within the Actinopterygii class. Below we discuss how these findings can have major implications for our understanding of the evolution of cognitive performance within vertebrates.

Three of the four cognitive tasks for *L. dimidiatus* involved classic experimental paradigms with abstract cues aimed at testing for aspects of general intelligence, such as flexibility in the reversal learning task, self-control in the detour task and numbering skills in numerical discrimination task [Burkart et al., 2017; Aellen et al., 2021 Preprint]. Cleaner fish grow larger as they grow older [Hubble, 2003], which means that any systematic variation in performance as a function of body size could reflect experience or intelligence. By using these abstract tests, not linked to any ecological problems, we could exclude the role of experience. The ability to feed against preference in the fourth task also tested for self-control but in a context of high ecological relevance [Grutter, and Bshary, 2003]. Cleaners do face this challenge during every interaction with clients, i.e., eating less preferred ectoparasites vs biting highly preferred client mucus. One would expect that experience in this task may

matter. Nevertheless, all tested cleaners must have had abundant experience with feeding inhibition and that biting client mucus can yield clients to either punish the cleaner by chasing or by terminating the interaction [Grutter, and Bshary, 2003]. All tested cleaners were adult females, indicating that the youngest ones were at least one year old, and given an estimated number of 800-3000 cleaning interaction per day [Grutter, 1995; Wismer et al., 2014; Triki et al., 2018; Triki et al., 2019b], they would all have already had a few hundred thousand cleaning interactions from which to gain experience. Therefore, it is unlikely that having more experience would make a difference in favour of older and hence larger individuals, which is indicated by a shallow performance-body slope of 0.12. Given that the overall cognition-body slope is close to zero (-0.082), the brain-body slope for *L. dimidiatus* indeed reflects the slope of cognitive equivalence.

Similar studies on other fish species are thus needed to test to what extent our findings can be generalised to other species. From our study and that by Tsuboi et al. [2018], the intraspecific brain-body slopes in Actinopterygii are around 0.5. This provides evidence that any measurement errors would have at best minor negative effects on slope estimations. This conclusion is further supported by the absence of taxon effect on slopes in Actinopterygii. According to Tsuboi et al. [2018], the brain-body slopes for class, order, family, genus and species are 0.50 ± 0.01, 0.51 ± 0.03, 0.49 ± 0.02, 0.50 ± 0.03, and 0.44 ± 0.02 (mean ± se), respectively. The mean value 0.5 for the species level entirely removes the taxon effect. Therefore, if other fish species also show no relationship between body size and cognitive performance, especially in general intelligence tasks (like in *L. dimidiatus*), the brain-body slope of 0.5 emerges as a predictor for cognitive equivalence. So, brain-body slopes can be used as a proxy for cognitive equivalence for any comparison of Actinopterygii, independently of the taxonomic level. In other words, the predictions for species differences

in cognitive performance based on EQ are likely to hold for Actinopterygii. By extension, the results from Tsuboi et al. [2018] suggest that EQ also works reasonably well for the other major ectotherm vertebrate clades. In those data sets, Chondrichthyes showed no taxon-level effect (0.5 for species, 0.41 for class), while there was a weak taxon-level effect in amphibians (0.36 for species, 0.46 for class) and a somewhat stronger one in non-avian reptiles (0.41 for species, 0.56 for the class).

The results presented here clearly differ from a recent study on primates, which has taken extra care to reduce the effects of any measurement errors, and found that intraspecific cognitive equivalence is achieved with a brain-body slope of 0.25 to 0.30 [van Schaik et al., in prep]. It thus confirms a major taxon effect for mammals, where the brain-body slope is 0.65 on the class level [Tsuboi et al., 2018]. Presumably, the same taxon level effect also exists in birds [Tsuboi et al., 2018], and hence in endotherm vertebrates in general. It thus appears that EQ may work well as estimates of overall cognitive performance in ectotherm but not endotherm vertebrates. Crocodilians may be of particular interest for testing the endotherm-ectotherm divide as they are phylogenetically closer to birds than to other reptiles, though still being ectotherms. An interesting prediction immediately follows. Among both endotherms and ectotherms, cognitive performance should be unrelated to body size within species, even though the brain-body slope in mammals is around 0.25 and in fishes is around 0.5. If the intraspecific slope of cognitive equivalence in cleaner fish had been like in mammals, there should have been a significant positive correlation between body size and performance. In conclusion, fishes and mammals, and presumably ectotherms and endotherms in general, have a pronounced difference in their slope of cognitive equivalence. This points at fundamental differences in brain organisation, which warrant more detailed examination.

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Data and code accessibility

Data and code for statistical analysis and figures are accessible at the public repository Figshare. DOI: 10.6084/m9.figshare.8867660

Authors' contributions

CvS conceived the cognitive equivalence idea. ZT compiled the data from the different sources, analysed the data and generated the figures. ZT collected the cleaner fish brain size data. MA collected the cognitive performance data. ZT, CvS and RB wrote the manuscript. All authors approved the final version of the manuscript.

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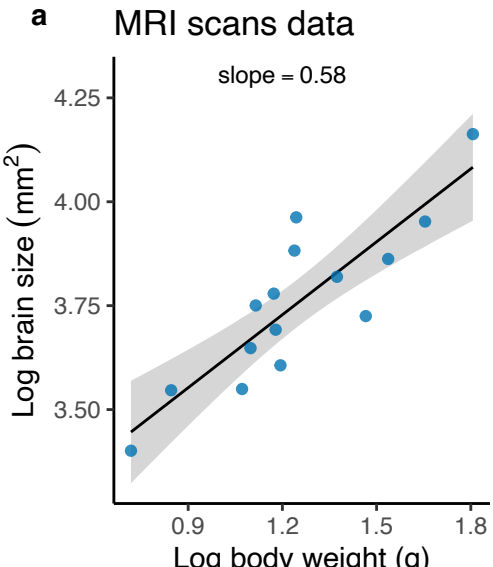
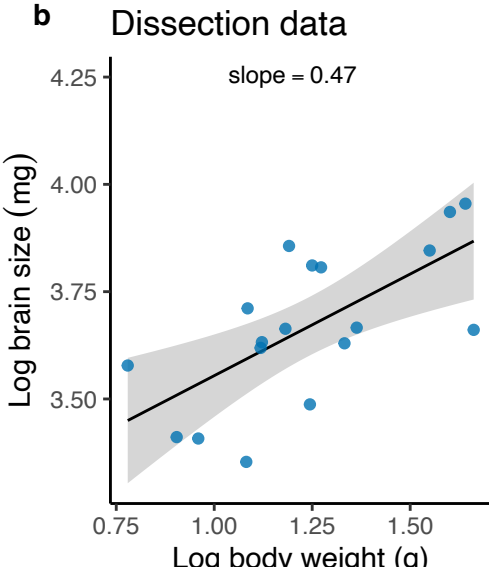
Figures legend:

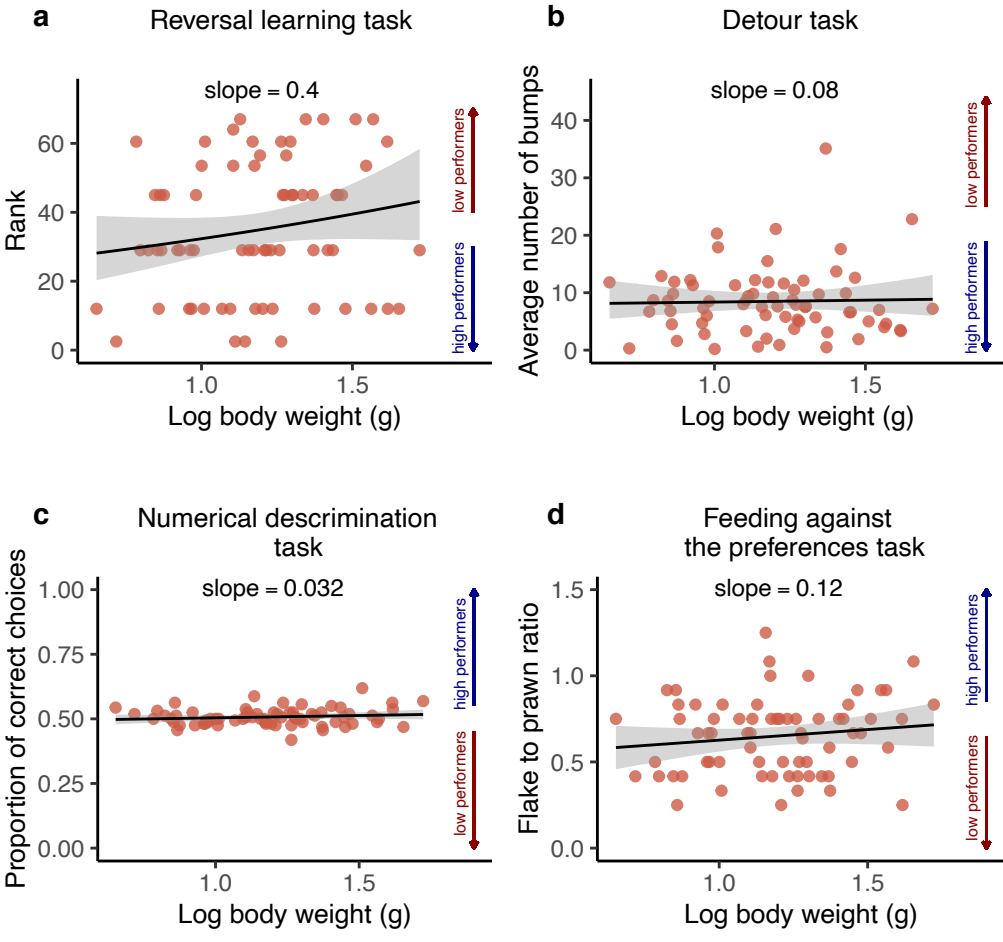
Figure 1. *Relationship between log-transformed brain size and log-transformed body weight (g) in cleaner fish (data from Triki et al. [2019a; Triki et al., 2020a]).* ***(a)*** *Data on brain volume (mm^2) estimated from magnetic resonance imagery (MRI) scans;* ***(b)*** *data on brain weight (mg) from manual dissection and weighing. In both panels P < 0.05. Shaded areas around the regression lines represent the 95% CI.*

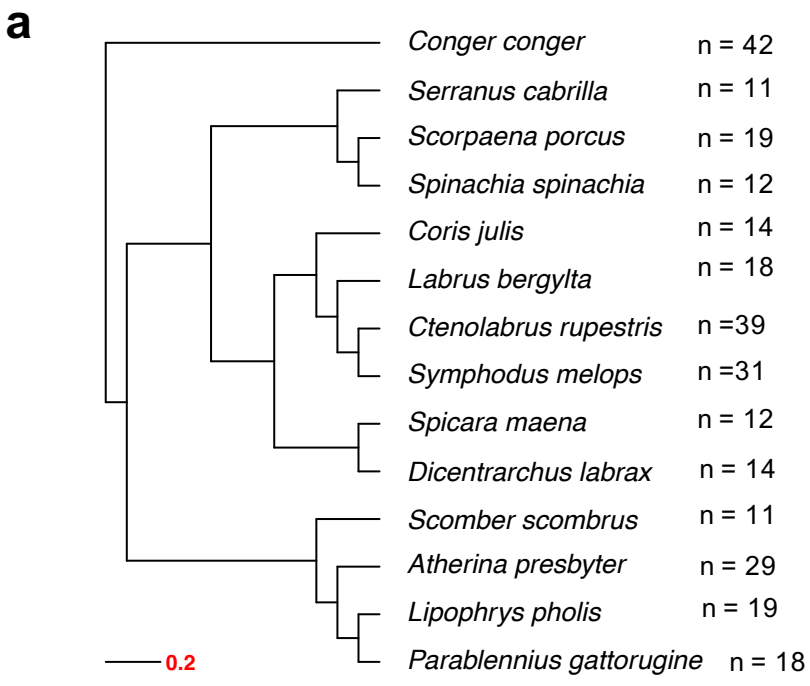
Figure 2. *Relationship between cognitive performance and log-transformed body size (g) in cleaner fish (Data from Aellen et al. [2021 Preprint]). Regression slope and 95% CI (grey shading) of log-transformed body weight and* ***(a)*** *learning abilities in a reversal learning task;* ***(b)*** *inhibitory 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. Arrows on the right side of panels indicate the direction of performance (better or worse) depending on the task. In all four panels P > 0.05. Shaded areas around the regression lines represent the 95% CI.*

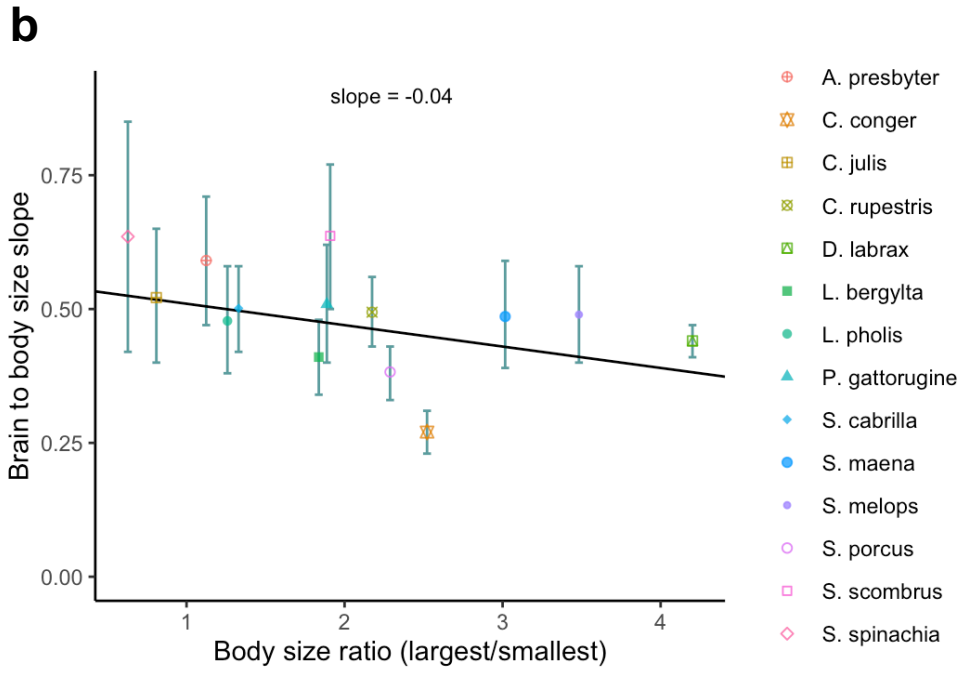
Figure 3. ***(a)*** *Phylogenetic tree of the 14 fish species with a scale indicating tree distance, and the exact number of individuals used to calculate the brain-body slope estimate per species.* ***(b)*** *Relationship of brain-body slope and body size ratio (i.e., a ratio calculated by dividing the body size – body weight in g – of the largest individual by the body size of the smallest individual in a species dataset). The plot shows the log brain-log body slope estimate with 95% CI for each species. Brain and body data compiled from the fish database FishBase [Froese, and Pauly, 2019]. P > 0.05.*


a
MRI scans data
slope = 0.58
Log brain size (mm^2)
4.25
4.00
3.75
3.50
0.9
1.2
1.5
1.8
Log body weight (g)


b
Dissection data
slope = 0.47
Log brain size (mg)
4.25
4.00
3.75
3.50
0.75
1.00
1.25
1.50
Log body weight (g)


a
Reversal learning task
slope = 0.4
Rank
Log body weight (g)
low performers
high performers
b
Detour task
slope = 0.08
Average number of bumps
Log body weight (g)
low performers
high performers
c
Numerical descrimination task
slope = 0.032
Proportion of correct choices
Log body weight (g)
high performers
low performers
d
Feeding against the preferences task
slope = 0.12
Flake to prawn ratio
Log body weight (g)
high performers
low performers


a
Conger conger
n = 42
Serranus cabrilla
n = 11
Scorpaena porcus
n = 19
Spinachia spinachia
n = 12
Coris julis
n = 14
Labrus bergylta
n = 18
Ctenolabrus rupestris
n =39
Symphodus melops
n =31
Spicara maena
n = 12
Dicentrarchus labrax
n = 14
Scomber scombrus
n = 11
Atherina presbyter
n = 29
Lipophrys pholis
n = 19
Parablennius gattorugine
n = 18
0.2


b
slope = -0.04
Brain to body size slope
0.75
0.50
0.25
0.00
1
2
3
4
Body size ratio (largest/smallest)
A. presbyter
C. conger
C. julis
C. rupestris
D. labrax
L. bergylta
L. pholis
P. gattorugine
S. cabrilla
S. maena
S. melops
S. porcus
S. scombrus
S. spinachia