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No evidence for general intelligence in a fish

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Abstract

The average mammal or bird has a roughly ten times larger brain relative to body size than the average ectotherm vertebrate. It has been surprisingly challenging to determine how this translates into increased cognitive performance. In particular, it is unclear whether the brain size differences translate into qualitative differences in specific cognitive abilities. Here, we provide a first exploratory study to examine the possibility that the larger brains of endotherms support a different organisation of information processing, rather than specific differences in cognitive processes. In mammals, individual performance across domain-general cognitive tasks is positively correlated, resulting in the psychometric factor g . The value of g is positively correlated with brain size. We tested wild-caught female cleaner fish *Labroides dimidiatus*, known for its highly sophisticated social behaviour, in four ecologically nonrelevant cognitive tasks that have been used to varying degrees to assess g in mammals. Cleaner fish solved three of these four tasks, flexibility (reversal learning), self-control (detour around an obstacle) and numerical competence (simultaneous two-choice task), while also providing enough interindividual variation to test for g . They did not perform above chance levels in the fourth task, which tested for object permanence. For the three retained tasks, individual performance did not load positively on one principal component. Furthermore, all pairwise correlation coefficients were close to zero. These negative results contradict a frequent criticism of g studies, which proposes that g is a default result of how brains are designed. Rather, the results provide a first indication that endotherm and ectotherm vertebrates may process cognitive tasks in fundamentally different ways due to differences in brain organisation. Our relatively low number of experiments compared to mammalian studies enhances this hypothesis, as the probability of finding a g factor by chance would have been higher.

KEYWORDS

brain evolution, cognition, ectotherm vertebrates, general intelligence, *Labroides dimidiatus*

1 | INTRODUCTION

Fish do many apparently smart things (Brown, 2015; Bshary et al., 2014; Salena et al., 2021; Vila Pouca & Brown, 2017), often based on cognitive processes that are considered to be more complex than

Pavlovian and operant conditioning. To give a few examples, fish use cognitive maps (Reese, 1989), payoff-based social learning rules (Brown & Laland, 2003; Kendal et al., 2009; Street & Laland, 2016; Truskanov et al., 2020; Vila Pouca et al., 2020), generalised rule learning (Wismer et al., 2016), or transitive inference (Hotta et al.,

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2020) and show evidence for mirror self-recognition (Kohda et al., 2019), some basic perspective-taking (McAuliffe et al., 2021), prosocial behaviour (Satoh et al., 2021), and counting abilities and the ability to delay gratification that match the performance of primates (Aellen et al., 2021; Triki & Bshary, 2017). Yet, being ectotherm vertebrates, they have on average ten times smaller brains corrected for body size compared to endotherm vertebrates (Jerison, 1973; Tsuboi et al., 2018). Size differences are even more pronounced if only the pallial part of the forebrain is considered, i.e. the part that is responsible for more complex cognitive functions (Finger et al., 2013; Karten, 2015). So what can mammals and birds do with big, physiologically expensive brains (Herculano-Houzel, 2012; Olkowitz et al., 2016) that fishes and other ectotherm vertebrates, i.e. reptiles and amphibians, cannot?

It is possible that many cognitive differences between endotherm and ectotherm vertebrates are quantitative in nature (Bshary et al., 2011). On a qualitative level, a possible hypothesis is that only endotherms have general intelligence. In humans, general intelligence in its broad definition involves the central integration of various domains of cognition, such as reasoning, planning, problem-solving and learning from experience. The domains are present in ectotherms. However, a central integration supposedly allows for more flexible behaviours as separate abilities can work together: a complex task may require for example a combination of working memory, self-control and counting (Gottfredson, 1997). If ectotherms were found to lack general intelligence, then a major aim for future cognitive studies would be to design experiments that combine several domains and compare performance across clades in such tasks.

A good indicator of the presence of general intelligence in humans is the psychometric factor g . g results from the positive manifold, i.e. the well-established finding that, in humans, individual performance across tasks testing different domains is correlated (Carroll, 1993; Deary et al., 2010; Jensen, 1999; Jensen & Weng, 1994; Nisbett et al., 2012; Spearman, 1904). Factor analyses of performance across such tasks will thus result in a first factor on which all tasks load positively, and this general factor is referred to as g . g has been demonstrated for a variety of mammals in controlled laboratory experiments, including average brained species, i.e. species with a brain size that lies on the brain-body regression line for mammals, such as mice (Burkart et al., 2017). Despite the general presence of g in mammals, reported values of g can differ considerably between species and are positively correlated with overall brain size (Deaner et al., 2006, 2007). Evidence for g is less clear in birds (Searcy & Nowicki, 2019) (but see Ashton et al., 2018) but those studies have been conducted on small numbers and/or in the field, potentially creating biased data as mostly motivated, and/or bold individuals will participate under these conditions (Searcy & Nowicki, 2019). Furthermore, it should be noted that the use of principal component analyses has been criticised for various reasons, including the apparent overestimation of effect sizes (Poirier et al., 2020). Nevertheless, bivariate correlations still yielded significantly positive results for 4/4 mammalian and 5/7 bird species (Poirier et al., 2020).

Using g as indicator of general intelligence in species other than humans has been criticised with the argument that the positive manifold might be a pure side-effect. For instance, the positive manifold may simply reflect variation in low-level biological properties, due to ontogenetic disturbances, or genetic load, i.e. the accumulation of deleterious, pleiotropic mutations, for example (Arslan et al., 2017; Penke et al., 2007). Individuals with less disturbances, or less genetic load, may more fully express their growth potential, which may also lead to better myelination of the nervous system, which ultimately will operate smoother and faster across domains (Matzel et al., 2006). Moreover, a positive manifold can be an artefact of how brains are generally organised. Thomson (Thomson, 1916) pointed out already in 1916 that a positive manifold can arise in the absence of general intelligence due to between-task neural overlap (see also Arslan et al., 2017; Bartholomew et al., 2009, 2013; Kovacs & Conway, 2016, 2019; Van Der Maas et al., 2006; Rabaglia et al., 2011)).

To the best of our knowledge, no attempts have so far been made to conduct a series of cognitive tests to assess the presence of g in an ectotherm vertebrate. Thus, our aim was to simultaneously test two closely linked hypotheses by using female cleaner fish *Labroides dimidiatus* as study species. We can easily distinguish between males and females in nature, as this species is protogynous the smallest individuals are females, whereas the biggest ones are males (Randall, 1958). First, do cleaner fish, as a representative of ectotherm vertebrates, express general intelligence as measured by a positive manifold, g , when tested for their performance on cognitive tasks from different cognitive domains? Second, does a g -factor mandatorily arise whenever a large random sample of animals is tested, i.e. more than 50 individuals based on the literature on mice? *L. dimidiatus* is a particularly suitable study species as there is plenty of evidence suggesting that its cognitive performance is rather outstanding for an ectotherm vertebrate. It engages in interactions with client fish that visit to have ectoparasites removed while cleaners prefer to eat client mucus (Grutter & Bshary, 2003). Most likely due to this conflict of interest, cleaners show high strategic sophistication in ecologically relevant tasks, even outperforming primates (Salwiczek et al., 2012). Also, cleaners are able of generalised rule learning (Wismer et al., 2016) and apparently even pass the mirror self-recognition test (Kohda et al., 2019). Furthermore, cleaners solve tasks that test for so-called 'executive functions', which are a family of general-purpose top-down mental processes that modulate the operation of various cognitive subprocesses (Burkart et al., 2017; Diamond, 2013; Miyake et al., 2000). Cleaners show various evidence for inhibitory control by detouring around barriers to reach a food source (Triki & Bshary, 2021), delaying gratification in order to receive a higher reward (Aellen et al., 2021) and being able to feed against preference (Bshary & Grutter, 2005). Also, cleaners perform very well in reversal learning tasks (Salwiczek et al., 2012; Triki & Bshary, 2021), which is the standard test for cognitive flexibility and where performance correlates with brain size in primates (Deaner et al., 2007). Working memory, the third important executive function, has not yet been tested in cleaners, but it has been shown that

cleaners have very good long-term memory (Triki & Bshary, 2019) and remember the 'where' and 'when' of interactions with clients (Salwiczek & Bshary, 2011).

A study on wild Australian magpies revealed that variation in intraspecific social complexity may affect performance in *g* tasks in birds (Ashton et al., 2018). For cleaner fish, it is well-established that fish densities affect cleaner fish expression of strategic sophistication in ecologically relevant social tasks (Binning et al., 2017; Triki et al., 2019; Wismer et al., 2019). We compared 80 individuals from two connected sites. The outside reef slope harbours high cleaner densities and the inside lagoon low densities (3.3 versus 0.4 cleaners/100m², see Figure S2), which correlate strongly with large client densities (Triki et al., 2019). Previous research has shown that different densities correlate with different ratios of the forebrain versus the rest of the brain (Triki et al., 2019), which in turn predict socially competent behaviour (Triki et al., 2020). If cleaners from the high-density site perform better also in *g* tasks, this would increase the likelihood that we would find a positive manifold. Taken together, according to current knowledge, we maximised the chance of finding *g* in an ectotherm vertebrate, which would support the notion that *g* is an artefact and refute the hypothesis that *g* requires large brains.

A major challenge in applying the *g* concept to fishes for the first time was to choose suitable experiments. We conducted four laboratory experiments (Figure 1). The choice was based on a screening of the experiments that had been conducted on mammals before (Burkart et al., 2017). The four experiments tested for different cognitive domains that we also considered relevant for cleaners in their daily life: flexibility (reversal learning; abbreviated 'RL'), self-control (detour task, abbreviated 'DT'), numerical competence (dot number task, abbreviated 'NC') and working memory (object permanence). All the experiments had loaded positively on the first principal component in at least one mammalian study (Burkart et al., 2017), though numerical competence has rarely been part of *g* studies (but see (Banerjee et al., 2009)). As tests for *g* have to warrant performance above chance without ceiling effects, we had to omit the object permanence task (presented in Figure S5) but could keep the other three tasks. Note that the reversal learning task in principle warrants another task, i.e. learning the initial association between a stimulus and a reward. However, such operant condition tasks are usually excluded in *g* studies (Arden & Adams, 2016; Banerjee et al., 2009; Damerius et al., 2018). Furthermore, we could not consider the inclusion of this task in our analysis as pretraining of the fish caused virtually no variation in the subjects' performance (64 out of 69 fish only needed a single session of ten trials to reach learning criterion). Crucially, the designs of the experiments were such that the problems were not presented in an ecologically relevant way in order to minimise the risk that variation in experience may cause variation in performance. We were nevertheless interested to what extent individual performance in *g* tasks would correlate with performance in similar tasks presented in ecologically relevant ways. We therefore conducted a fifth, ecologically relevant experiment, i.e. the individuals' ability to feed against preference in order to obtain more food. The ecological relevance is due to cleaners having

to eat less preferred parasites rather than mucus to prolong interactions with clients that would otherwise take evasive actions (Bshary, 2001; Grutter & Bshary, 2003). Like the detour task, the experiment measures self-control, allowing us to ask how performance in an ecological task relates to performance in an abstract task within a single domain.

2 | MATERIALS AND METHODS

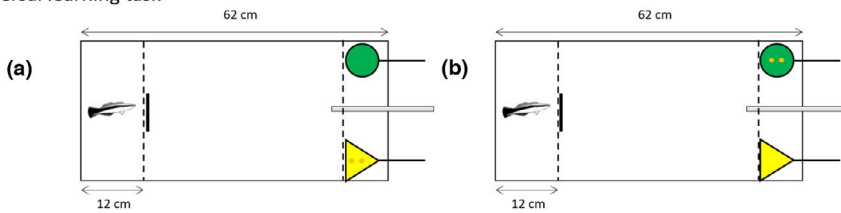
2.1 | Cleaner fish: *Labroides dimidiatus*

The cleaner wrasse, *Labroides dimidiatus*, is a protogynous fish and lives in a small territory called cleaning station (Côté, 2000). It lives in harems and males can have up to five females in their territory comprising several cleaning stations (one per female) (Robertson, 1972). The species is widespread in the Indopacific ocean and can also be found in the Red Sea (Randall, 1958). It feeds on the surface of other reef fish called clients by removing ectoparasites from them. Cleaner fish have around 2000 interactions per day (Grutter, 1996). As cleaner fish prefer to eat mucus over ectoparasites (Grutter & Bshary, 2003), this creates a conflict of interest between cleaner and client over what the cleaner should eat. As a consequence, cleaners need to eat against preference in order to cooperate and hence to avoid that clients respond to evasive actions like chasing the cleaner or switching to a different partner for their next interaction (Bshary & Grutter, 2002). Therefore, the experiment in which cleaners needed to feed against preference reflects high ecological relevance (Gingins et al., 2013).

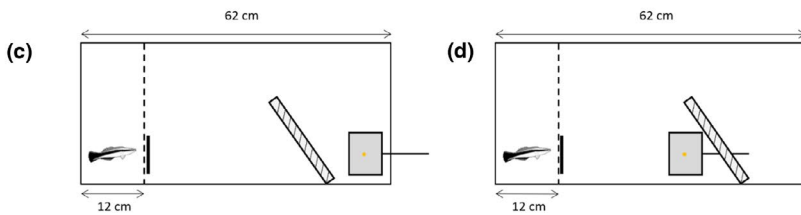
2.2 | Capture, individual housing and acclimation

Following recommendations by the STRANGE framework (Webster & Rutz, 2020), we repeatedly refer to the presence or absence of potential biases in our study in this section. The study was conducted at the Lizard Island Research Station, Great Barrier Reef, Australia in February – May 2018 and 2019. By finding pairs of cleaners and avoiding the larger individual, 80 female cleaner fish were caught with a barrier net (2 m long, 1.5 m high, mesh size 0.5 cm; 40 fish each year) and hand nets on nearby reefs. There was hence a sampling bias towards females, excluding males. The females, on the other hand, represent a random sample as the catching method is highly successful, i.e. individuals cannot avoid being caught unless the catcher makes a handling error. Forty individuals were from a high-density client fish area (Birds Islet crest; 20 each year; Figure S1) and another forty were from a low-density client fish area (Birds Islet lagoon; 20 each year; Figure S1). Thirty-metre-long transects covering a width of 5m (for detailed methods see (Wismer et al., 2014)) revealed that mean cleaner fish density, which is highly correlated with the density of large clients (Triki et al., 2019), differed by a factor 8 (3.3 versus 0.4 individuals/100m²; Wilcoxon test, $m = 6, n = 5; p = .012$; Figure S2). Mixing the ecological background

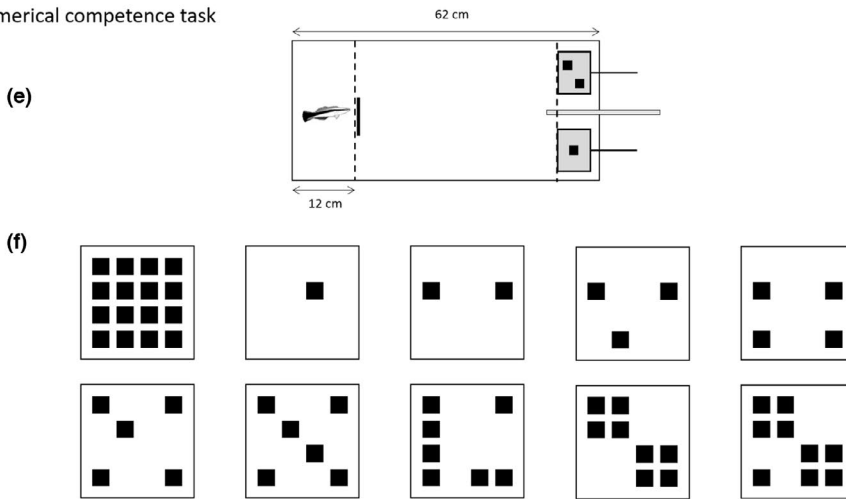
Reversal learning task



Detour task



Numerical competence task



Feeding against preference task

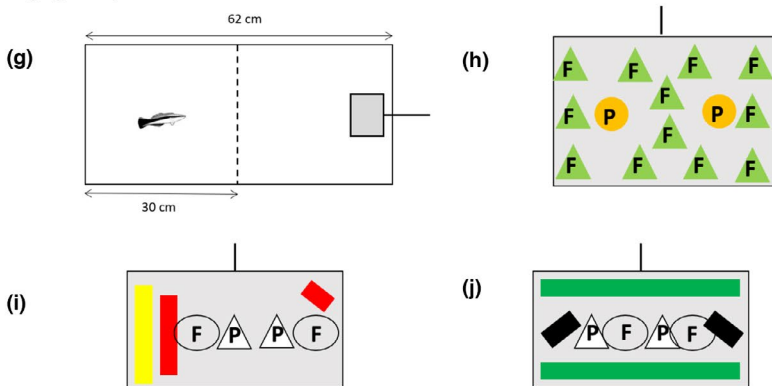


FIGURE 1 Spatially explicit experimental setups of the three *g* tasks (a–f), and experimental setup of the ecologically relevant task, the ability to feed against preference in order to increase food intake (g–j). Dashed lines: the transparent barrier that separated the holding compartment from the experimental compartment (with the short black line indicating the door through which fish could cross). Thicker grey and hatched structures represent opaque and transparent barriers. Orange dots on the plates show the location of food rewards (mashed prawn items). Panel a. shows the initial associative learning task, and upon its completion, we started the reversal learning task by changing the role of the two plates (panel b.). Panels c. and d. show the positions of the reward plate in the detour task, where only trials with the reward plate behind the barrier were analysed. Panel e. shows the experimental setup for the numerical competence task. In panel f., the plate to the upper left indicates the 16 possible positions for the back squares, while the other plates give examples for plates displaying 1–9 squares. g. General setup. The dashed line shows the see-through barrier that kept fish in the holding compartment while the experimenter placed a plate with food items in the experimental compartment. h. The plate used to train fish that eating flake items is allowed while eating a prawn item leads to the immediate removal of the plate. F: Flake item. P: Prawn item. i. and j. The two plates used alternately in the actual experiment, offering 2 flake and 2 prawn items. We used coloured tapes (green, red, yellow and black) to make the two plates look different

of the subjects was an explicit part of the experimental design, following results by Ashton et al. (2018) that group size mattered in Australian magpies. Fish were housed individually in glass aquaria (62 × 27 × 38 cm). Each year, the forty individuals were caught at the beginning of the field trip and split into two experimental cohorts of 20 individuals each, which were tested simultaneously. Cleaner fish were acclimatised for at least twelve days before being subjected to five different experiments (experimental cohorts 1 and 3) or for at least 44 days (experimental cohorts 2 and 4). Previous research on cleaner fish has revealed that this delay is sufficient for subjects

to participate in experiments. During the twelve days, cleaner fish were first acclimated to feed on Plexiglas plates, mimicking client fish in the captive environment. We provided mashed prawn as food that we smeared on the Plexiglas plate. When fish were well accustomed to their feeding plate (which took two to three days), they were trained to eat small pieces of mashed prawn placed on dots drawn on a new feeding plate. Once fish were eating invariably well on the feeding plate with and without dots, they were habituated to the different plates and barriers that we used during all the different experiments (Figure 1). Most notably, fish were exposed to a

barrier that divided the aquarium into the holding compartment and the experimental compartment. A door (dimension 7 × 18 cm) in the barrier could be opened, so that the cleaner fish could swim through. Cleaners thus had to be habituated to swimming through the door, which invariably happened within a day.

2.3 | General experimental procedures

All individuals were tested in the same order, i.e. first in reversal learning, then in the detour task, then in the (failed) object permanence task, then in the numbering task and finally in the feeding against preference task. We considered that keeping the order of tasks constant would induce less bias in performance than varying the order in a counterbalanced way between subjects. Task experience can be controlled for in this way, while the personal reward history would vary between subjects if task order was randomised. During all experiments, subjects were guided into the holding compartment before each trial. This allowed the experimenter to subsequently set up the trial, i.e. plates with or without food, partitions, barriers, without the fish intervening. Once a trial was properly set up (which took 10–30 s, depending on the task), the door was opened so that the cleaner fish could swim through and make its choices. During simultaneous choice tasks (reversal learning and numerical competence tasks), an opaque separation (10 cm wide) between the two plates helped to define a subject's choice: when the subject's head passed the imagined line perpendicular to the start of the opaque separation (Figure 1a,b,e), we scored that the subject had chosen the plate inside the compartment. If the choice was wrong, the experimenter removed the correct plate immediately. If the choice was correct, we allowed subjects to still inspect the wrong plate after having finished eating the reward before removing both plates simultaneously.

In all tasks, the experimenter tested each fish once before moving on to the next fish. Once each fish had been exposed to one trial, the next round of trials began, leading to an intertrial interval of about 30 min. Twenty trials could be completed within a day, starting at 6:00 and finishing at 17:00. This matched natural activity patterns of the cleaners cleaning their clients in the wild, i.e. from briefly after sunrise until shortly before sunset.

Fish conducted the experiments in their home aquarium. All experiments were video recorded with a GoPro mounted on the forehead of the experimenter. All fish from 2018 and 18 fish from 2019 were released at their respective sites of capture after experiments had been completed. Another 22 fish were used in another project that included brain analyses. The project was approved by the Animal Ethics Committee of the Queensland government (DAFF; AEC Application Reference Number CA 2018/01/1155).

Before and in between the experiments, the fish were fed *ad libitum* every day, introducing the feeding plate in the morning and removing it at the end of the day. During experimental days, fish had to obtain food from making the correct choices as long as trials were conducted. They were fed *ad libitum* at the end of

the day after the trials had been completed. One day off was kept between each experiment.

2.4 | Specific experimental protocols

2.4.1 | Reversal learning task (RL): learning – flexibility

(Figure 1a,b) In reversal learning tasks, subjects first learn to associate one of two stimuli with a reward. After this initial association learning, the contingencies are reversed and the other stimulus is rewarded. This task thus measures how flexibly individuals can adjust to the new reward contingencies. For this task, we offered two plates simultaneously: a yellow triangle shape Plexiglas plate (8 cm wide and 7.5 cm height) was placed on the left side of the aquarium with two pieces of prawn located on the back such that subjects could only see them once they swam behind. We did not add inaccessible food items to the nonrewarding plate as previous experiments on cleaners never yielded any indication that olfaction could be important in these experiments (Bshary, 2001). On the other side, a green round shape Plexiglas plate (8 cm wide and 7.5 cm height) without food was positioned. The positions of the two plates remained constant during a first training phase, testing for initial learning and during the reversal learning phase. For each trial, fish were first placed behind a transparent grid barrier with a transparent door on one side of the aquarium, 12 cm from the aquarium wall to form the waiting area. The plates were then introduced on the other side (with the handle leaning against the aquarium wall providing stability), and only then, the door was lifted, and the fish could make its choice by approaching one of the 2 plates.

To facilitate learning the initial association, we put two pieces of prawn on the back of the rewarding plate and left both plates in the aquarium. Initially, individuals differed with respect to how fast they would approach both plates. We hence varied the duration of first trials such that all individuals would inspect both plates and eat the food, yielding trial durations between five and 30 min. Within two days, trial durations were down for 30–60 s. Such time intervals allowed the fish to eat the two items and to confirm that the other plate did not offer any food. This training phase consisted of two exposures per day over ten consecutive days. We then tested the fish for a significant preference for the rewarding plate, offering only one item per trial, conducting 2 sessions of ten trials each per day. The criteria for success were either 10/10 or 9/10 correct choices in a session, twice 8/10 in two consecutive sessions or at least 7/10 in three consecutive sessions. Once an individual had reached criteria for the initial preference, we reversed the role of the two plates. Thus, two pieces of mashed prawn were now placed behind the green round shape Plexiglas plate on the right side of the aquarium. Each fish performed 20 trials per day and was tested the same way according to the same learning criteria as described for the initial learning. We initially ran trials for up to five days. If a subject had not succeeded yet

within these 100 trials, we conducted an extra five trials in which we prevented subjects to swim to the yellow plate by inserting a see-through barrier in front of it. These extra trials either ensured that the individuals were exposed to feeding off the green round plate, or they showed that some individuals simply refused to approach that plate. We considered that these latter individuals were rather afraid of the plate, and hence, their performance could not be interpreted as a failure to learn. We therefore removed them from the data set. In contrast, we exposed the subjects that had eaten off the green round plate to another 20 trials on the 6th day to see whether after these extra five trials, they could reach the criterion or not. The number of trials needed to reach learning criterion in this reversal learning task was used as measure of behavioural flexibility for the statistical analysis.

2.4.2 | Detour task (DT): inhibitory control

(Figure 1c,d) We tested whether cleaners were able to swim around an obstacle to get a food reward. This task permitted to measure inhibitory control as well as spatial problem-solving. On the day prior to the first test, we familiarised subjects with the anthracite Plexiglas plate (10 cm × 5 cm) that offered a visible piece of mashed prawn on its front side. We also acclimated the fish to the obstacle by inserting it in the aquarium for 45 min twice during the day (once on the right-hand side and once on the left-hand side). Given that cleaners had never been tested in a detour task, we did not know what level of performance we could expect. We therefore decided a priori to start with a simple task and to increase difficulty on consecutive days as long as subjects readily managed to access the food reward. On the first day, we placed a transparent obstacle in form of a plate and made visible by drawing a grid of black lines (1–1.5 cm apart) onto it, in front of a food plate. The obstacle was placed perpendicular to the aquarium sidewall. It was 19 cm wide, leaving subjects 5 cm to swim around it to get to the food plate 15 cm behind the obstacle during test trials. In 50% of trials, the reward plate was placed in front of the obstacle. During the total of 10 morning trials, the plate, obstacle and door were always on the right side from the cleaners' perspective. In the 10 afternoon trials, all equipment was moved to the left side from the cleaners' perspective. As cleaners accessed the food plate without any problems, we counterbalanced the position of equipment within sessions on the second day, conducting no more than two consecutive trials on any side. As subjects continued to perform well, we tested all subjects with the obstacle at a 45-degree angle (Figure 1c,d) on day 3, further increasing the inhibition requirement because fish had to swim away from the food in order to access it. We only used data from day 3 for our analyses. Subjects had a maximum of 60 s to reach the reward plate. While we measured time to complete a trial, that measure may not well reflect cognitive performance as it is influenced by swimming speed, which may vary

according to body size and/or motivation. Many studies use the percentage of trials in which subjects did not touch the barrier as criterion (MacLean et al., 2014). In our case, using this criterion would have meant that 20/69 individuals would have scored 0/10 correct trials. As *g* analyses rely on continuous measures of individual performance (Burkart et al., 2017), we therefore recorded the mean number of head bumps against the obstacle in each trial as a quantitative measure of a cleaner's ability of self-control. Only trials in which the plate was behind the obstacle were analysed; trials in which the plate was in front of the obstacle only served to prevent the development of route routines. A total of 20 trials (10 experimental and 10 controls) were conducted, with an intertrial interval of about 30 min.

2.4.3 | Numerical competence task (NC): quantitative reasoning

(Figure 1e,f) This task was conducted after the failed object permanence task (see Supporting Information). It tested quantitative reasoning in fish in a general form. It builds on previous research on cleaner fish, which has shown that this species has numerical competence, being able to learn to prefer one plate over another one based on the number of black squares (rather than spread or total black surface area) (Triki & Bshary, 2017). In each trial, subjects were presented two white plates (7.4 cm × 7.4 cm) with differing numbers of black squares on them (Figure 1e). Each square was 11 mm² in size, and the number of squares on a plate varied between 1 and 9. On the day prior to the experiment, we acclimated the fish to the plate first by smearing mashed prawn on a version displaying 10 squares. We later conducted two presentations where we placed 2 prawn items on the back of the plate. During experiments, we used in total 20 different combinations of square numbers: 5:1, 6:3, 6:2, 6:4, 4:3, 3:2, 2:1, 4:1, 5:2, 3:1, 5:3, 7:3, 7:4, 7:2, 9:3, 8:3, 8:4, 8:5, 9:4 and 9:5. Each combination was presented once per day, over a total of 8 days (yielding 160 trials in total), with the order of presentation randomised between days. There were in total 16 potential positions for a square on a plate (Figure 1f). We randomised the positions of squares for each number, removing any configurational cues for cleaners to make choices. Across the 8 days, the position (left or right) of the two plates in each combination was counterbalanced. The plate with the greater number of squares invariably offered two food items on its back, while the other plate contained inaccessible food on its back. Thus, some plates (those with 2–6 squares) sometimes yielded food and sometimes they did not, depending on which plate they were paired with. As a consequence, only the learning of a general rule based on numeric competencies would yield performance above chance levels ('always choose the plate that shows more squares'). We scored individual performance as the number of correct trials in the last 80 trials, i.e. in the second half of the experiment.

2.4.4 | Feeding against preference task (FAP): inhibitory control (ecologically relevant task)

(Figure 1g–j) The first three tasks presented cognitive challenges in abstract experimental setups, testing for cognitive skills in the absence of ecologically relevant contexts. In contrast, the ability of feeding against preference (hereafter FAP) is of high ecological relevance. In natural interactions with client fish, cleaners need to largely feed on less preferred ectoparasites (gnathiid isopods) instead of preferred client mucus, so that it pays clients to visit cleaners (Grutter & Bshary, 2003). Our task mimicked natural interactions, replacing clients, parasites and mucus with a plate, preferred prawn items and less preferred flake items. There were three flake and three prawn items on the plate. A trial continued as long as cleaners ate items, while the experimenter removed the plate as soon as a cleaner ate a preferred prawn item. The food-maximising strategy was hence to eat against preference. Therefore, the feeding against preference task is conceptually linked to the detour task as it measures inhibitory control. We included the task to test whether there was any correlation between ecological and nonecological tasks within a single cognitive domain.

In order to prepare the fish for the experiment, we first gave them fish flakes (a mixture of 20% fish flakes and 80% mashed prawn to make the food stick to plates) on feeding plates instead of pure mashed prawn to familiarise subjects with the new type of food. In the next step, we conducted six training trials using a 15 × 10 cm plate with 14 items displayed on it (12 flake and 2 prawn items (Bshary & Grutter, 2005); Figure 1h). During a single trial, the plate was removed for 30 s as soon as the cleaner ate the first prawn item, and then reintroduced to allow the cleaner a second feeding bout until it ate the second prawn item. With this design, all subjects ate flake items and could hence potentially learn that feeding on a prawn item leads to the removal of the plate, while eating a flake item has no negative consequences. The intertrial interval was of one hour.

The next day, we conducted the experiment. We exposed cleaners 12 times to a single plate (10 cm × 6 cm) with two flake and two prawn items (Figure 1i,j). For a different study on reputation management, we also conducted trials involving the simultaneous presentation of two plates, but those data were not relevant for the current analyses. We took the mean number of flake items eaten over the 12 trials as a measure of inhibitory control for the analysis.

2.5 | Data analysis and supplementary results

In each experiment, we ranked each fish by its performance according to the criteria specified in each section above (Table S1). From the eighty fish caught for this study, we were able to run the analysis with 69 individuals. A total of four individuals died before completing all tasks, while seven failed to participate in at least one task. It is unclear whether the loss of these individuals may have introduced any bias in the data. Of the 69 individuals, 36 were from the high-density

site (Birds Islet crest), and 33 were from the low-density site (Birds Islet lagoon). By focussing on females as subjects, we avoided one additional factor we would have had to control for otherwise.

We first examined whether there was sufficient interindividual variation in the performance of the cleaners in each task using descriptive statistics (mean values with standard deviation, and maximum–minimum values; Table S1). For the NC task, we also verified that cleaners as a group performed above chance using a non-parametrical Wilcoxon signed-rank test (Wilcoxon test, $p < .001$). In all three *g* tasks, we found substantial variation in performance and neither floor nor ceiling effects, so that the three data sets were included in a principal component analysis (PCA; using the packages FactoMineR and missMDA). The key question was whether individual performance in each task was loading positively on the first PC factor. In a second step, we calculated correlations in individual performance across all possible pairs of the three tasks, using Spearman-Rho correlations as presented in the main text.

In order to check the robustness of our results, we investigated whether noncognitive variables such as the site of capture, the year, the experimental set and body length could have had an effect on the variation found in the PCA using a linear model (package 'lme4') (Bates et al., 2015). Moreover, we analysed the individuals from the different capture sites separately.

To test the extent to which abstract and ecological tests yield similar performances, we correlated individual performances in the detour task and the feeding against preference task, using a Spearman-Rho correlation. Thus, we calculated in total four correlations with our data. As a consequence, we used Bonferroni correction to calculate a new $\alpha' = 0.0125$ ($\alpha/\text{number of tasks} = 0.05/4$) to control for finding a spurious result. Finally, we used the Wilcoxon tests to evaluate whether performance in any one test differed systematically as a function of site of capture. Again, we used Bonferroni correction to control for multiple testing, which resulted in an $\alpha' = 0.0125$ ($\alpha/\text{number of tasks} = 0.05/4$). The Spearman-Rho correlation test, the PCA, the linear models and the Wilcoxon test were carried out in R Rstudio © (R Version 1.3.1093, © 2009–2019 RStudio, PBC).

3 | RESULTS

Of the 80 subjects, we had to remove eleven individuals because they did not participate in at least one task. With the remaining 69 individuals, we used a principal component analysis to test for the presence of a positive manifold (Figure 2). Dimension 1 explained 38.5% of the variance in performance, with an eigenvalue of 1.16. Two tasks loaded positively (RL and DT), whereas the other one loaded negatively (NC). Dimensions 2 and 3 explained rather similar amounts of variance (32.8% and 28.7%; eigenvalues 0.98 and 0.86). The results thus revealed no evidence of a psychometric *g* in *L. dimidiatus*. Indeed, pairwise correlations of individual performance across tasks support the view that the performances in the three tasks are independent of each other (Spearman-Rank correlations,

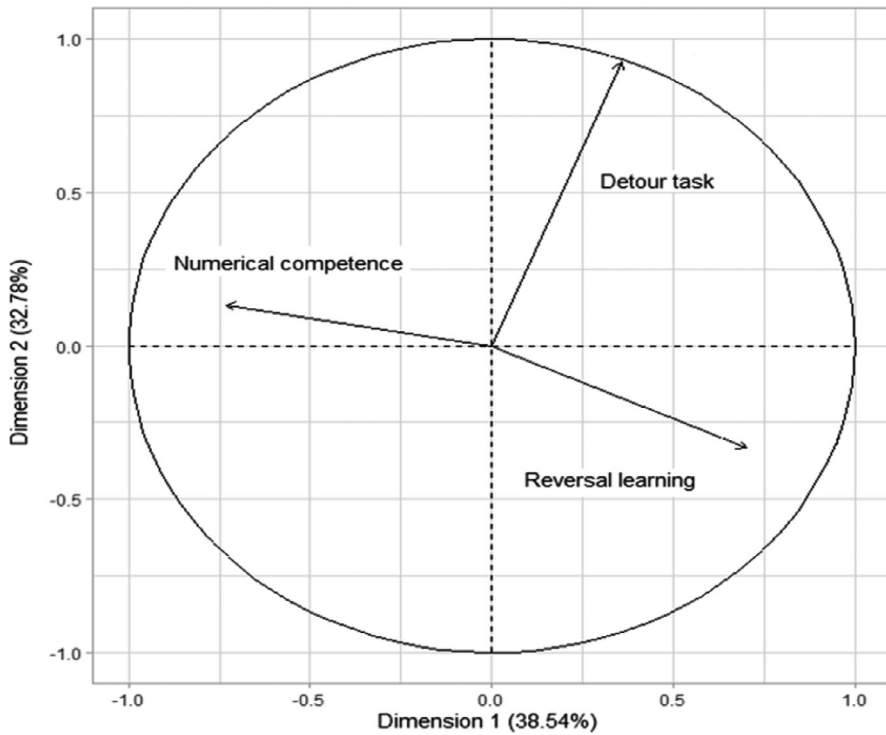


FIGURE 2 No evidence for *g* in a fish. Principal component analysis (PCA) of the three cognitive tasks. Dimension 1 (explaining 38.54% of the variance in performance) and dimension 2 (explaining 32.78% of the variance) are represented. The results for each task are represented as vectors

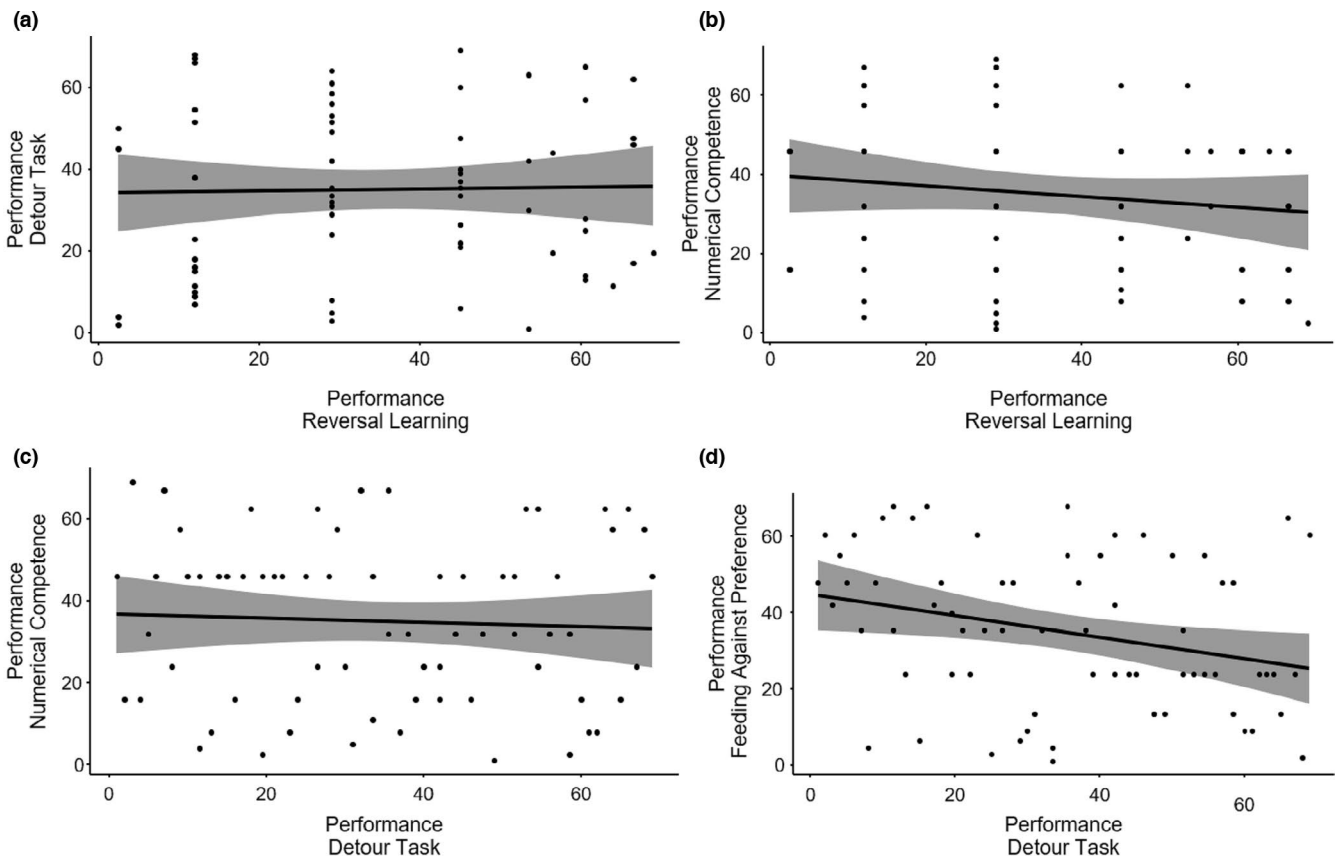


FIGURE 3 Lack of positive correlations across cognitive tasks. Pairwise correlations between the ranks of individual performances in four different cognitive tasks (rank 1 being highest performance and rank 69 being lowest performance). Individual performances did not significantly correlate between any two of the three *g* tasks (a) RL – DT, Spearman-Rho $r = .026$, $p = .8$; (b) RL – NC, Spearman-Rho $r = -.137$, $p = .3$; (c) DT – NC, Spearman-Rho $r = -.051$, $p = .7$). The only significant correlation was negative rather than positive and found between DT and FAP; (d) Spearman-Rho $r = -.283$, $p = .02$ ($p = .03$ with Bonferroni correction), a *g* task and an ecologically relevant task that are both testing for inhibition

all $n = 69$, RL-DT: $r = .026$; RL-NC: $r = -.137$; DT-NC: $r = -.051$; all NS, Figure 3a–c).

Finally, we correlated individual performance in the two tasks testing for inhibitory control. We found that DT was negatively correlated with the ability to feed against preference (abbreviated FAP) (Spearman-Rho $r = -.283$, $p = .018$, Figure 3d). While not expected, the result suggests that positive correlations in performance may even be absent within domains.

Comparisons of cleaners from high- and low-density sites revealed no consistent differences in the performance in each task separately (Figure 4). Differences were far from being significant for all tasks (RL (panel a), DT (panel b), NC (panel c) and FAP (panel d) (Wilcoxon tests, all $p > .13$).

For the separate analyses of the two different capture sites, the PCA analysis with the individuals from the high-density site explained 41.1% of the variance in the performance in dimension 1, with an eigenvalue of 1.23. Two tasks loaded positively (RL and DT), whereas NC loaded negatively. No significant correlations were found between the three different tasks (Spearman-Rank correlations, $n = 36$, RL-DT: $r = .179$; RL-NC: $r = -.086$; DT-NC: $r = -.072$; Figure S3a). In the PCA analysis with the individuals from the low-density site, dimension 1 explained 41.12% of the variance in performance with an eigenvalue of 1.23. Two tasks loaded positively (DT and NC), whereas RL loaded negatively. The correlations of individual performance across tasks were invariable slightly negative and nonsignificant (Spearman-Rank correlations, $n = 33$, RL-DT: $r = -.095$; RL-NC: $r = -.217$; DT-NC: $r = -.010$; Figure S3b). No difference was found in the body length between the high and the low-density captures sites (Wilcoxon test, $p = .12$; Figure S4), suggesting no systematic differences in age that could potentially have confounded the results.

4 | DISCUSSION

We had asked how female cleaner fish perform in cognitive tasks that test for abilities relevant for the assessment of general intelligence in mammals and birds. With the exception of the object permanence task (see Supporting Information), cleaners performed well. However, an individual's performance in any task did not predict its performance in the other tasks. The lack of correlated performance, and thus, g in this fish species has potentially far-reaching implications. First, given that we tested a large random sample of cleaner fish under controlled laboratory conditions, we provide the strongest evidence as yet that a positive manifold does not emerge as a default of how brains are organised. The few number of experiments compared to mammalian studies enhances this conclusion, as this meant a higher probability to detect a positive manifold by chance. Therefore, a positive manifold and/or overall significantly positive bivariate correlations appear to be the result of some centralised cognitive unit(s). Although preliminary, our results support the notion that a major consequence of the differences in brain size between mammals and fish is that mammals have some system-level

cognitive abilities that can be used across tasks tapping into different cognitive domains, while the fish brain is organised in a more modular way.

Our study should be considered preliminary for several reasons. One important issue is that a bivariate correlational approach to mammalian data sets suggests that the g factor may be much weaker in mammals than what had been suggested by principal component analyses (Poirier et al., 2020). If g factors are weak in mammals, the question arises whether such weak effects warrant a much larger brain compared with ectotherm vertebrates. Second, it is always problematic to support a hypothesis with negative results. Nevertheless, we obtained correlation coefficients close to zero and partly negative, despite having a larger than average sample size. The results hence suggest that at least cleaner fish show less evidence for g than endotherms. Third, one should always wonder with negative results whether the tasks actually captured variation in cognitive abilities. They apparently do in mammals because of the cross-correlations in performance. For fishes, a next step would be to present different versions of tests for each domain. Fourth, we only tested one ectotherm vertebrate species. More species from different clades will need to be tested in order to obtain a more general picture on whether the presence/absence of g provides a major divide between endotherm and ectotherm vertebrates. Finally, the lack of cleaners performing in the object permanence task means that we only had data from three tasks for our analyses. Within these three tasks, we would have preferred higher performance levels in the numerical competence task. Furthermore, there is discussion whether or not numerical competence is a part of g . In a study on humans, tapping into the more basic vertebrate nonverbal number acuity skills did not yield correlations with g (Halberda et al., 2008). In contrast, numerical competence loaded positively on the first principal component in tamarins (Banerjee et al., 2009). Our main motivations for including the task were that (i) numerical competence is domain-general in the sense that it can clearly be used in both social and environmental contexts, and (ii) previous research on cleaners has already shown that cleaners can solve such tasks, and that they do so by using the number of squares to rather than overall black surface area or the density of squares (Triki & Bshary, 2017).

The negative correlation in individual performance in the two self-control tasks reinforces the results from the g tasks. We have no explanation why the correlation was significantly negative. As the feeding against preference task has clear ecological relevance while swimming around a Plexiglas barrier does not, we might have expected no correlation at all. Alternatively, if self-control involves a central unit in the brain and has a learning component, sufficient exposure to the need to feed against preference should have helped in the detour task and hence yielded a positive correlation. Thus, while we cannot explain the negative correlation, the result clearly argues against the presence of a g factor in cleaners even within a single domain like self-control.

It is important to note that a more modular organisation of the brain does apparently not prevent the emergence of complex cognitive processes like transitive inference, generalised rule learning

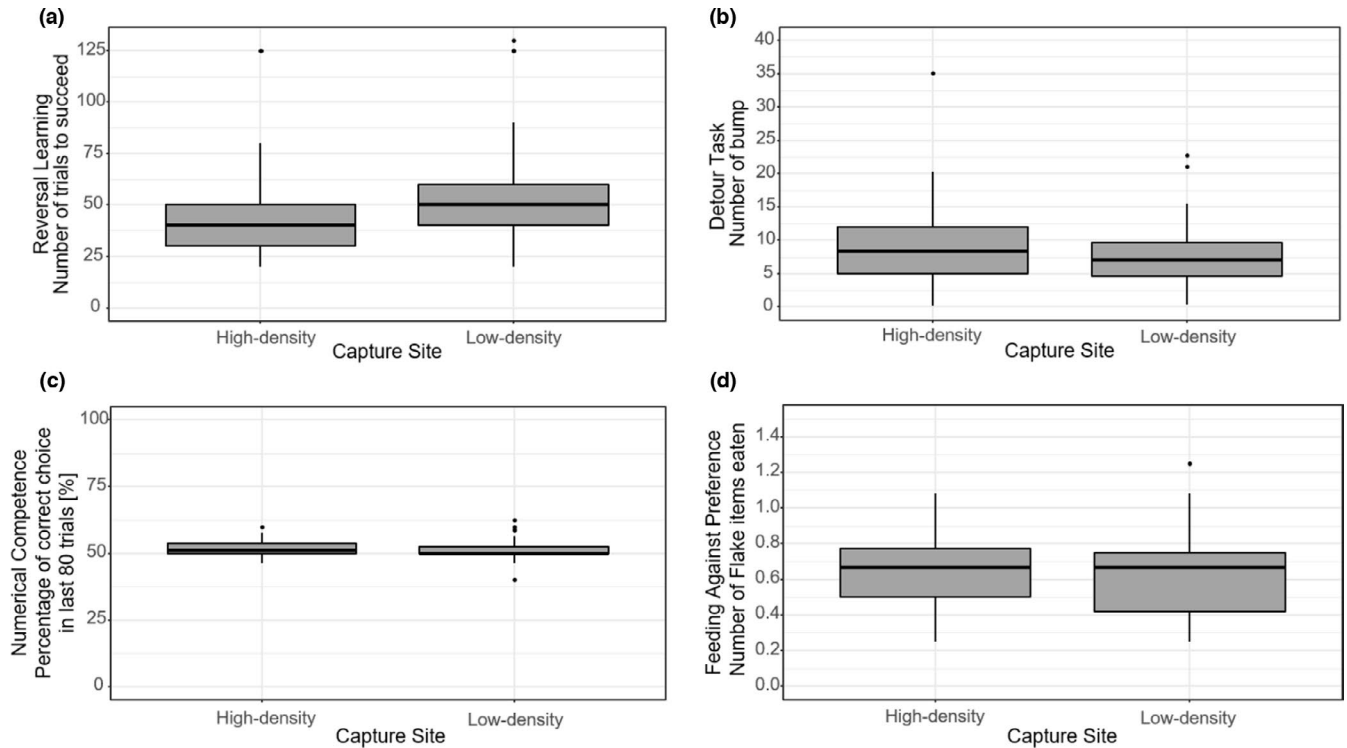


FIGURE 4 Fish densities do not affect performance. Box plots showing median, interquartiles and 95% range of individual performances split by site of capture (high-density and low-density site). a: number of trials to complete reversal learning task; b: mean number of head bumps into Plexiglas separation in the detour task; c: % correct choices in the numerical competence task; d: mean number of flakes eaten before a prawn item (i.e. highly preferred food) in the feeding against preference task

and even mirror self-recognition (Grosenick et al., 2007; Hotta et al., 2020; Kohda et al., 2019; Wismer et al., 2016), i.e. processes that go beyond conditioning. Also, there is evidence that various fishes match mammals with respect to numerical competence (Agrillo et al., 2008, 2009; Bshary et al., 2014; Dadda et al., 2009; Feigenson et al., 2004; Messina et al., 2020; Piffer et al., 2012; Stancher et al., 2013). Thus, a presence/absence of these cognitive processes cannot explain the ten-fold difference in relative brain size and the even larger difference with respect to the pallial brain part (Finger et al., 2013; Karten, 2015) between endotherm and ectotherm vertebrate clades. The complete failure of cleaners in the object permanence task came as a surprise to us, as cleaners perform well in memory tasks, regarding both events that took place a few minutes ago (Salwiczek & Bshary, 2011) or almost a year ago (Triki & Bshary, 2019). However, other fish species apparently show high levels of object permanence, like groupers waiting more than 20 min for unsuccessfully chased prey to leave the crevice where it is hiding (Vail et al., 2013). Taken together, these results suggest that single cognitive tasks used to test for general intelligence are not per se too difficult for ectotherms. In contrast, the transition from a modular organisation to more general-purpose intelligence may have required a massive increase in brain size.

A second major insight from our results is that environmental complexity, as indicated by cleaner and other fish densities, largely fails to affect performance of cleaner fish in *g* tasks, in contrast to results from Australian magpies (Ashton et al., 2018). Therefore, it

appears that previously documented differences in strategic sophistication in ecologically relevant tasks between cleaner fish individuals from high-density and low-density sites (Triki et al., 2019; Wismer et al., 2019) are due to specific experience effects, in this case most likely the frequency and probability of visitor clients swimming off if not serviced immediately (Prat et al., 2021; Quiñones et al., 2020; Triki et al., 2020) rather than cognitive abilities per se. More studies on wild populations or on wild-caught individuals will be needed to test whether the reported differences reflect systematic differences in the importance of ontogeny between birds and fishes and/or endotherm versus ectotherm vertebrates. Another potential future extension would be to compare males and females. We focussed on females because of their higher abundance and to strengthen the power of our analyses by avoiding to add another factor to the analyses. However, we know that cleaner fish males outperform females in the reversal learning task, while females outperform males in the detour task (Triki & Bshary, 2021). Therefore, we predict that adding males would not change the outcome.

Currently, most discussions on brain evolution focus on the relative importance of social versus environmental complexity. This discussion remains key to explain variation in size and structure within clades. However, recent analyses show that endotherm vertebrate brain development and organisation are fundamentally different from ectotherm vertebrates. For example, the early exponential growth phase of brains is much prolonged in endotherms (Tsuboi et al., 2018), and the intraspecific slopes between body

size and brain size are systematically larger in ectotherms than in endotherms (van Schaik et al., 2021; Triki et al., 2021; Tsuboi et al., 2018). Data on sexually dimorph primate species and on cleaner fish suggest that despite the different intraspecific slopes, cognitive performance is uncorrelated with body size (van Schaik et al., 2021; Triki et al., 2021). Thus, the slopes seem to indicate equivalence in cognitive performance. Our current results indicate that the higher slopes in ectotherm vertebrates might be due to a more modular structure, while endotherms may have more general-purpose units. The hypothesis that the fundamental divide between endotherm and ectotherm vertebrates brain sizes may be largely driven by brains being more general-purpose machines in the former versus specialised learning machines in the latter clearly deserves more experimental research, using large random samples to test a variety of bird and ectotherm vertebrate species.

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CONFLICT OF INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

All authors conceived the project and designed the experiments. M. A. collected the data (with the help of Yasmin Emery; see acknowledgements). M. A. performed the analyses, and all authors analysed the results. All authors wrote the manuscript and revised it.

DATA AVAILABILITY STATEMENT

All data, meta-data and the R codes can be found on [10.6084/m9.figshare.13215434](https://doi.org/10.6084/m9.figshare.13215434).

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