



Ecological differences in the facultative Caribbean cleaning goby *Elacatinus prochilos* do not predict learning performance in discriminatory two-choice tasks

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Abstract

The ecological approach to comparative cognition emphasizes that the ecological and social environment are important predictors of cognitive performance. We used this approach to test whether differences in habitat use and social behavior in the facultative Caribbean cleaning goby *Elacatinus prochilos* predict differences in learning performance in two discriminatory two-choice tasks. This species has two behavioral ecotypes: one that frequently engages in cleaning interactions and inhabits corals in male–female pairs (cleaning gobies) and another that rarely engages in cleaning interactions and inhabits barrel sponges in large groups (sponge-dwellers). We predicted that cleaning gobies would outperform sponge-dwellers in a pattern-cued task, which consisted of identifying the pattern on a plate that consistently provided food, while sponge-dwellers would outperform cleaning gobies in a spatial task, which consisted of identifying the location of the plate. Contrary to our predictions, there was no difference in performance between the two ecotypes. Most of the gobies performed poorly in the pattern-cued task and well in the spatial task. A possible explanation for these results is that the association of a pattern with positive and negative reinforcement may not be a pre-requisite for engaging in cleaning interactions, while spatial skills might be equally required in both ecotypes. Alternatively, the two ecotypes can flexibly adjust to new feeding conditions, which would explain their similar performance in the spatial task. Further research should investigate which aspects of *E. prochilos*' social and ecological environment might impose challenges that require spatial cognition and whether individuals can flexibly adjust to new habitats and feeding conditions.

Keywords Cleaning gobies · Cognition · *Elacatinus prochilos* · Social behavior · Cue use · Spatial task

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Introduction

The ecological approach to comparative cognition emphasizes that ecology may be a better predictor of cognitive performance than phylogenetic relatedness (Kamil 1987; Shettleworth 1993, 2010). It is based on the idea that individuals behaviors and brains are largely shaped by the challenges associated with the environment in which they live (Dukas 1998; Healy and Braithwaite 2000). This approach successfully explains why closely related species that face different ecological pressures diverge in cognitive performance as well as why distantly related species show similar cognitive performances when exposed to similar ecological challenges (Shettleworth 2010). For example, food-storing species of birds are better at processing and remembering spatial information than non-storing species (Balda and Kamil 1989; Olson et al. 1995). Similarly, rock-pool gobies learn to find a food reward faster in a spatial task than

sand-gobies from more homogeneous environments (White and Brown 2014a, b). On the other hand, species of distantly related groups such as corvids and apes use similar reasoning abilities to solve social and physical problems (Emery 2004; Emery and Clayton 2004a, b; cf. Seed et al. 2009). Most importantly, performance often appears to be tightly linked to specific ecological needs. For instance, seed-caching bird species that depend more on stored food supplies excelled less dependent species in a spatial non-matching-to-sample task but not in a non-spatial color non-matching-to-sample task (Olson et al. 1995). Likewise, black-capped chickadees from harsh environments outperform individuals from more stable environments only in ecologically relevant spatial tasks (Pravosudov and Clayton 2002). In fish, the cleaner wrasse *Labroides dimidiatus* outperforms other wrasses in tasks related to their cleaning interactions with client reef fishes, such as feeding against their preference or exploring novel objects, but do not in a non-ecologically relevant spatial discrimination task (Gingins and Bshary 2016). Furthermore, the cleaner wrasse may match or even outperform mammals and birds in tasks that capture the demands of their cleaning ecology (Pepperberg and Hartsfield 2014; Salwiczek et al. 2012; Zentall et al. 2016, 2018; Prétôt et al. 2016a, b). Therefore, the ecological approach encourages the comparison of closely related and distantly related species in a variety of tasks, so that each species is confronted with both ecologically relevant and irrelevant problems (Shettleworth 2010).

The logic of the ecological comparative approach has also been used to study intraspecific variation of performance in cognitive tasks. For example, a study on the cognitive performance of Australian magpies recently provided the first evidence that living in a larger group correlates with general intelligence parameters (Ashton et al. 2018), although the precise ecological pressures driving that correlation remain unknown. In Lake Tanganyika cichlids, early exposure to environmental enrichment enhances later cognitive performance (Kotrschal and Taborsky 2010). Another example is how strategic sophistication in the cleaner wrasse *L. dimidiatus* is specifically linked to its ecological needs (Wismer et al. 2014; Triki et al. 2018). Cleaner fishes remove ectoparasites from the body surface and cavities of other larger marine organisms referred to as clients (Côté 2000). Conflicts of interest between cleaners and clients can arise for various reasons. For instance, the cleaner wrasse prefers to eat client mucus, which constitutes cheating (Grutter and Bshary 2003). In addition, because they interact with about 2000 clients per day (Grutter 1996), clients may seek services simultaneously and thus compete over the priority of access. Consequently, both clients and cleaners show sophisticated strategic adaptations to these conflicts, such as image scoring, audience effects, and partner switching (Bshary and Schäffer 2002; Bshary and Grutter 2006; Pinto et al. 2011).

As an example, the cleaner wrasse prioritizes client species that can choose to interact with other cleaners over client species that cannot (Bshary and Grutter 2002). However, the use of sophisticated strategic adaptations seems to depend on the complexity of the social environment. Cleaner wrasse living in a socially simpler environment (characterised by low cleaner and client densities) failed to solve the same cognitive tests on audience effects and prioritization of ephemeral food sources that are solved by cleaners living in a more complex social environment (Wismer et al. 2014; Triki et al. 2018, 2019). Apparently, cleaners in socially simple environments do not use these abilities, because clients do not exert choice (Triki et al. 2018), possibly because partner switching is too costly when cleaner density is low.

While ecological variation in the cleaner wrasse system is rather subtle, the facultative Caribbean cleaning goby *Elacatinus prochilos* provides an ideal model for a comparative study aimed at investigating how social environment and habitat structure link to specific intraspecific differences in cognitive abilities in the context of cleaning interactions. In this species, habitat use is related to differences in social and feeding behavior (Whiteman and Côté 2002a, 2004a). *E. prochilos* gobies living on corals and other substrates are usually found in pairs or small groups that depend mostly on cleaning interactions for feeding (Whiteman and Côté 2002a, 2003, 2004a). In contrast, *E. prochilos* gobies inhabiting barrel sponges are organized into larger groups, with dominance hierarchies, that feed primarily on micro-organisms living inside the sponges' tissue and only rarely engage in cleaning interactions (Whiteman and Côté 2004b). We refer to the former as cleaning gobies and to the latter as sponge-dwelling gobies. It is still not fully understood whether the differences in habitat choice and feeding behavior in this species are a consequence of genetically determined mechanisms or of phenotypic plasticity. There is evidence that the two ecotypes belong to the same species (cytochrome b analysis, Mazzei 2019 unpublished data) but no evidence that individuals switch habitats and feeding modes during the adult stage (tagging and monitoring of a closely related species, *Elacatinus evelynae* (White et al. 2007); tagging and monitoring of *E. prochilos* (Mazzei 2019 unpublished data). Therefore, independent of the mechanisms causing the habitat-feeding mode differences between the two ecotypes, cleaning and sponge-dwelling gobies seem to experience very different social and ecological environments, at least in the adult stage (Whiteman and Côté 2002a, 2004b). This difference in experience provides a good opportunity to investigate how ecological and social factors link to intraspecific variation in cognitive performance.

Different ecological and behavioral studies have highlighted the differences in cleaning and social behavior between cleaning gobies and sponge-dwellers (Whiteman and Côté 2002a, 2004b; White et al. 2007). Here, we first

conducted field observations to confirm the patterns previously described. Second, we tested the gobies in laboratory in two discriminatory two-choice tasks that differed with respect to the relevant cues available to identify the correct choice. In the pattern-cued task, individuals had to identify the specific pattern of a plate that consistently provided food, while in the spatial task, they had to identify the location of a plate, where food was consistently provided. We predicted that the pattern-cued task would be more ecologically relevant for the cleaning gobies, because it mimics a situation in which the individual has to choose between two clients arriving simultaneously at the cleaning station. In the wild, when both a harmless and a predatory fish approach a cleaning station, the cleaning gobies give priority of service to the predatory fish (Soares et al. 2007), which indicates that they are able to discriminate between clients. Therefore, we expected that cleaning gobies would outperform sponge-dwellers in the pattern-cued task. Furthermore, because female cleaning gobies spent more time in cleaning interactions than male cleaning gobies (Whiteman and Côté 2002b; Soares et al. 2009), we predicted that the cleaning females would outperform the males in this task. On the other hand, we predicted that the spatial discrimination task would be more relevant to sponge-dwellers, because food in barrel sponges is patchily distributed and sponge-dwellers are known to be able to locate their home sponge from over 40 m away (Whiteman and Côté 2004b). By testing cleaning and sponge-dwelling gobies in the two tasks, we expect to understand how general individual cognitive performance is. If cognition is tightly linked to the ability to solve an ecologically relevant challenge, cleaning gobies and sponge-dwellers should outperform each other only in the ecologically relevant tasks.

Methods

Field observations

Behavioral observations were conducted from March to June 2016, on SCUBA, between 08:30 and 17:30 h, from a distance of 2 m, at the South Bellairs reef (13.191542° N, 59.641882° W), on the west coast of Barbados. We performed approximately 20 h of underwater observations in total, with individual observations on 27 cleaning gobies (10 h) and 25 sponge-dwellers (9 h 14 min) distributed in 23 cleaning stations (3.5–8.7 m deep) and 18 sponges (4.5–9.4 m deep). The sponges were distributed over three separated reef patches, while the cleaning stations were distributed over five spurs of the spurs and grooves zone. Observation duration for each individual varied from 15 to 30 min. We registered the frequency, duration, and species involved for all cleaning interactions that occurred.

Capture and housing

Laboratory experiments were conducted from March to July 2017. Sixty-four gobies were caught from 24 barrel sponges (sponge-dwellers) and 25 cleaning stations (cleaning gobies) from three fringing reefs on the west coast of Barbados (16 cleaning gobies and 16 sponge-dwellers from North and South Bellairs 13.191542° N, 59.641882° W; 8 cleaning gobies and 8 sponge-dwellers from Heron Bay 13.196817° N, 59.643521° W and 8 cleaning gobies and 8 sponge-dwellers from Greensleeves 13.225882° N, 59.644153° W). Sponge-dwellers were found on giant barrel sponges (*Xestospongia muta*) distributed over three separated reef patches (6–10 m). In contrast, cleaning gobies were found either solitary or in pairs, mainly associated with alive coral, but also with other substrates like coralline algae and dead coral distributed over five reef spurs (3–8 m). The gobies were captured using plastic bags and hand nets after sedating them with a spray mixture of 50 ml of clove oil and 200 ml of ethanol (1:4) diluted in approximately 700 ml of seawater. Fish were then transported to the lab inside zip lock bags. Individuals belonging to the same sponge or the same cleaning station were transported together in the same bag and were housed together either in a glass aquarium (60×40×39 cm) or mesh bags placed inside an aquarium (15 cm diameter), depending on the group size. Within 2 days after capture, each goby was sexed, sized, weighted and individually housed in a mesh bag. Individuals' size and weight ranged from 2.2 to 3.4 cm and 0.07 to 0.39 g. To determine the sex, we observed the shape of the urogenital papilla under a binocular microscope. The papilla is conical and long in males and short and truncated in females (Thresher 1984). Because the individuals had to be flipped over for the papilla observation, we sedated each goby before the procedure in a petri dish containing 100 ml of seawater and around 5 ml of clove oil mixture. Together, sexing, sizing, and weighting took less than 2 min per goby. The gobies were left to recover in another petri dish with seawater before being returned to their mesh bags. Another 2–3 days after this procedure, part of the gobies (48 out of 64 individuals) were injected with an elastomer implant. The implants were used for individual identification in a separate experiment that occurred prior to the learning tasks. The experiment consisted of forming groups of cleaning gobies or sponge-dwellers, each containing 6 individuals (one pair of dominants, one pair of subordinates and one pair of juveniles), and registering all interactions among individuals. After the group manipulations, cleaning gobies and sponge-dwellers were assigned to one of the two different learning tasks, based on their sizes and sex, in a counterbalanced manner. Individuals stayed in the lab for a maximum of 3–7 weeks before being sacrificed for a separate project on brain anatomy. Before starting the experiments, we lost

two fish as a consequence of the clove oil mixture manipulation and suffered one loss caused by the implant injection. All 64 individuals that started the learning tasks survived until the end of the study.

Experimental setup and acclimation

Learning process in fish can be investigated using Plexiglas plates offering food as proxies of real clients. The Caribbean cleaning gobies can learn to eat items off Plexiglas plates (Soares et al. 2010) and this experimental paradigm has been used extensively with cleaner wrasses (Bshary and Grutter 2002, 2006; Grutter and Bshary 2003; Wismer et al. 2014; Gingins and Bshary 2016; Triki et al. 2018; Gingins et al. 2018). This paradigm captures the essence of cleaning interactions as demonstrations of key results have been reproduced in experiments with real cleaner–client interactions (Pinto et al. 2011). The experimental setup (Fig. 1) consisted of a holding compartment (15 × 40 cm) and an experimental compartment (45 × 40 cm), separated by an opaque Plexiglas partition containing a small door (5 × 5 cm). Fish were given 1–2 days to get used to the experimental setup and to the feeding location. They were fed with mashed prawn spread on a rectangular white Plexiglas plate (5 × 8 cm) starting from the second day of arrival in the lab. After testing, fish would be kept in the experimental compartment, with the door closed and a PVC pipe provided as shelter. Every morning the gobies were directed to the holding compartment and kept there for acclimation with the door closed for 20 min. Meanwhile, the experimental compartment was cleaned. Fish that ate little during the experimental trials (because of many incorrect decisions or because some fish would not consume items after a correct choice in the beginning) were fed with some mashed prawn by the end of the day to reduce any potential variance in individual performance caused by differences in satiation levels.

Learning and reversal learning tests

In total, 64 gobies were assigned to one of the two different tasks: (i) pattern-cued task (16 cleaning gobies and 16 sponge-dwellers), in which the fish had to learn to eat on a plate with a pre-established correct pattern and (ii) spatial task (16 cleaning gobies and 16 sponge-dwellers), where the fish had to learn to eat on a plate positioned in a pre-established correct side of the aquarium (Fig. 1). In both tasks, two Plexiglas plates (5 × 8 cm) were placed on the side of the aquarium opposite to the door. In the pattern-cued task, the plates had two different patterns (two horizontal blue stripes or two vertical blue bands), while in the spatial task, both plates were white. We chose to use the blue color, because it is one of the most ubiquitous colorations in reef fish due to its conspicuousness against the reef background

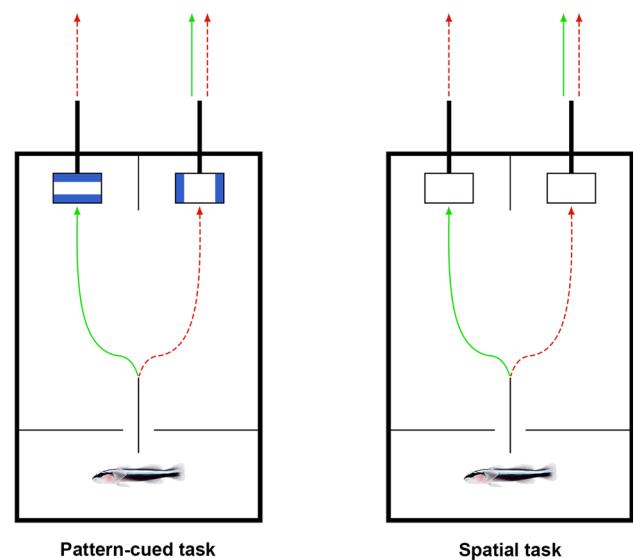


Fig. 1 Diagram of **a** pattern-cued task and **b** spatial task procedure as viewed from above. The goby is illustrated in the holding compartment and the plates are positioned in the experimental compartment. At the beginning of each trial, a small opaque barrier separating the two compartments was lifted. In both tasks, the gobies were presented with two plates separated by a small opaque partition. In the pattern-cued task (**a**), the plates had different patterns, whereas the plates were identical in the spatial task (**b**). Both plates contained a small piece of food reward located at the back of the plate. The solid and dashed lines illustrate what happened to the plates when a goby made a choice. When the goby made a correct choice (solid arrows), the plate with the incorrect pattern (**a**) or at the incorrect side (**b**) was removed and the goby was allowed to access the reward behind the correct plate. When a goby made an incorrect choice (dashed lines), both plates were removed and the goby had no access to a reward. The correct/incorrect pattern or side was determined according to the initial preference of each subject during the acclimation phase. Figure modified with the permission of Gingins et al. (2018)

(Marshall 2000). We first conducted 10 familiarization trials with each goby, during which the gobies were free to eat from both plates. Both plates had equal amounts of food on their backside, to ensure that choices were not based on olfactory cues. The less frequent choice made during the familiarization trials (horizontal × vertical or right × left) was determined as the correct pattern for the pattern-cued task and the correct side for the spatial task. This was done to ensure that successful performance was based on learning and not preference-bias. In case a goby showed no preference, we would determine the correct pattern/side based on the preferences of other individuals from the same habitat, to counterbalance the correct options within subjects from the same habitat as much as possible. The subject was considered to choose a plate when it touched it or passed behind it. Whenever the subject made the correct choice, the fish would be given a maximum of 1 min to eat on the plate. In case it chose the wrong plate, both plates were removed simultaneously and no food reward was available. The

left–right position of the plates was switched every trial. As soon as a trial ended, fish were gently directed back to the holding compartment with the handle of a hand net. After some trials, most of the fish had learned to swim back to the holding compartment by themselves at the end of the trial. One session consisted of ten trials. The fish was considered to learn a task if: (i) it solved 9/10 or 10/10 trials in one session; (ii) it solved 8/10 trials in two consecutive sessions; and (iii) it solved 7/10 trials in three consecutive sessions. We provided a maximum of 100 trials for each fish to solve the task. If a fish took more than 5 min to choose a plate, this was considered an incorrect choice (this happened in 1.97% of the trials). In the event that this occurred for a fish that was close to reaching the learning criteria (in a session in which individuals made 8 or 9 correct choices), the trial was repeated at the end of the session. The successful individuals immediately started the reversal test within the same or next day. In the reversal test, the correct pattern/side was reversed and the individuals were given another 100 trials to solve the task using the same procedure and learning criteria. The reversal procedure has been widely used in cognitive studies with fish (Kuroda et al. 2017; Petrazzini et al. 2017; Buechel et al. 2018; Triki et al. 2018; Gingsins et al. 2018). This procedure tests the cognitive flexibility of individuals, which is another aspect of learning thought to be more cognitively demanding than simple associative learning (Lai et al. 1995; Bonté et al. 2014). Experiments were performed from 8 am to 7 pm. Each individual was tested for a maximum of two sessions per day with a minimum interval of 15 min between trials. The 64 individuals were tested in four groups of 16 individuals and each group was tested during a maximum of 15 consecutive days (we performed a maximum of 320 trials per day or 2240 trials per week).

Data analysis

To analyze the behavioral data from field observations, we performed Mann–Whitney U tests using the function `wilcox.test` from the package `stats` (R Core Team 2017). We tested whether cleaning gobies and sponge-dwellers significantly differed in the following variables: number of individuals occupying the same cleaning station or sponge, frequency and average duration of cleaning interactions, and proportion of time spent in cleaning interactions. To test whether the proportion of interactions initiated by clients versus cleaners significantly differed between ecotypes, we ran a binomial generalized linear model, using the function `glm` and `anova` from package `stats` (R Core Team 2017). We considered that a client initiated the interaction whenever they entered the cleaning station or sponge territory and posed for the goby. Alternatively, we considered that the gobies initiated an interaction whenever they actively moved towards a client that did not pose beforehand. We corrected the p values

for the multiple behavioral comparisons by performing the Holm's p values adjustment (Holm 1979) with the function `p.adjust` from package `stats` (R Core Team 2017).

Regarding the laboratory experiments, we performed survival analyses to compare the performance of phenotypes and sexes in the spatial task using the function `Surv` from package `survival` (Therneau 2015). We only performed the analyses for the spatial task due to the small number of individuals that learned the pattern-cued task. The survival analysis was chosen, because the data are right censored, meaning that we do not know whether individuals that failed to solve the task within 100 trials could have learned if given more trials. The number of trials to solve the task was used as the response variable and a status variable was created to inform the function whether the observations were censored (individuals that did not solve the task after a 100 trials) or not (individuals that solved the task). The `Surv` function creates a survival object that compiles the response variable and censoring information. One survival object was created for each phase of the spatial task (learning and reversal tests) and used as a dependent variable in the survival regression models. Mixed-effects Cox's proportional hazards models were fitted using the function `coxme` from package `coxme` (Therneau 2018). Ecotype (cleaning goby or sponge-dweller, sex (male or female), body length, and their interactions were included as fixed factors in each model. The site of capture (Bellairs, Heron Bay, or Greensleeves) was included as a random factor. To investigate the role of contextual variables in the learning performance of individuals, we further included the following variables as fixed factors in both models: preference ratio, which refers to the number of trials in which an individual chose a certain pattern/side during the preference assessment; average time to enter the experimental compartment, which refers to the average time individuals took to pass through the door and enter the experimental area; average time to choose a plate, which refers to the average time individuals took to choose a plate after entering the experimental area, and proportion of feeding, which refers to the proportion of correct trials in which individuals ate the food reward. In addition, we used the function `lm` from package `stats` (R Core Team 2017) to test whether accuracy (percentage of correct trials) depended on the average decision-making time (average time to choose a plate). Ecotype, sex, body length, and their interactions were also included as fixed factors in this model. Finally, to test for possible effects of the previous separate experiment (group manipulation) on the learning ability of individuals, we performed a binomial linear model using the function `glm` (family = binomial) from package `stats` (R Core Team 2017). We added whether the individuals participated in the group manipulation (yes or not) and whether they were injected with elastomers (yes or not) as fixed factors. The significance of factors in all models was obtained with the

function Anova from package car (Fox and Weisberg 2011). We assessed the models' validity by visual inspection of residuals homogeneity and normality.

Results

Field observations

Cleaning stations were inhabited by significantly fewer gobies than barrel sponges (Fig. 2a, $W=2.5$, corrected p value <0.001). In terms of cleaning activity, cleaning gobies spent more time overall inspecting clients than sponge-dwellers (Fig. 2b, $W=507.5$, corrected p value $=0.001$). We registered a total of 149 cleaning interactions with cleaning gobies and only 13 interactions with sponge-dwellers. Cleaning gobies engaged in more cleaning per minute than sponge-dwellers (Fig. 2c, $W=506.5$, corrected p value $=0.001$), although the average duration of these interactions did not significantly differ between ecotypes (Fig. 2d, $W=50.5$, corrected p value $=0.17$). Finally, the proportion

of inspections initiated by clients versus cleaners did not significantly differ between ecotypes (z value $=1.4$, corrected p value $=0.2$). Clients initiated the interactions with cleaning gobies 94.8% of the time (129 out of 136 interactions for which initiators were registered) and in 84.6% of the cases with sponge-dwellers (11 out of 13 interactions).

Laboratory-learning experiments

Two out of the 16 sponge-dwellers solved the pattern-cued task, whereas none of the 16 cleaning gobies was able to solve it within 100 trials (Fig. 3a). Moreover, only one of the two sponge-dwellers solved the reversal test (Fig. 3b). The sponge-dweller individual that solved the learning test within 10 trials (9 trials correct out of 10) also solved the reversal test within 70 trials (46/70), while the individual that solved the learning test within 60 trials (39/60) did not solve the reversal test within 100 trials. In contrast, 10 out of the 16 cleaning gobies and 15 out of the 16 sponge-dwellers managed to succeed in the spatial task (Fig. 3c) and only two cleaning gobies and one sponge-dweller could not solve

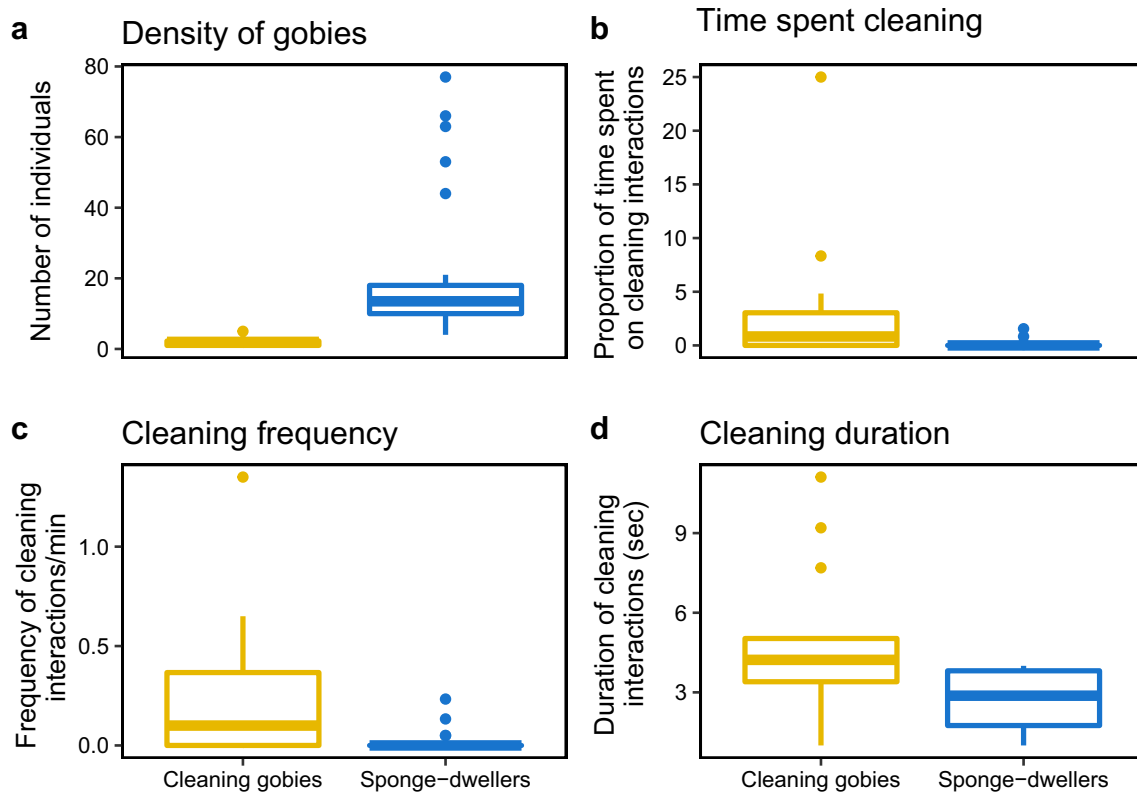


Fig. 2 Natural abundance and behavior of cleaning gobies and sponge-dwellers registered in the field: **a** abundance of cleaning gobies at cleaning stations ($n=23$) and of sponge-dwellers at barrel sponges ($n=18$); **b** proportion of time cleaning gobies ($n=27$) and sponge-dwellers ($n=25$) spent on cleaning interactions; **c** frequency of cleaning interactions per minute of observation of individual

cleaning gobies ($n=27$) and sponge-dwellers ($n=25$); **d** Average duration (s) of cleaning interactions registered for cleaning gobies ($n=149$) and sponge-dwellers ($n=13$). The central line in boxes, the boxes, and the whiskers indicate the median, Q1, Q3, and $1.5*QR$, consequently. Dots represent outlier values ($> \text{median} + 1.5*QR$)

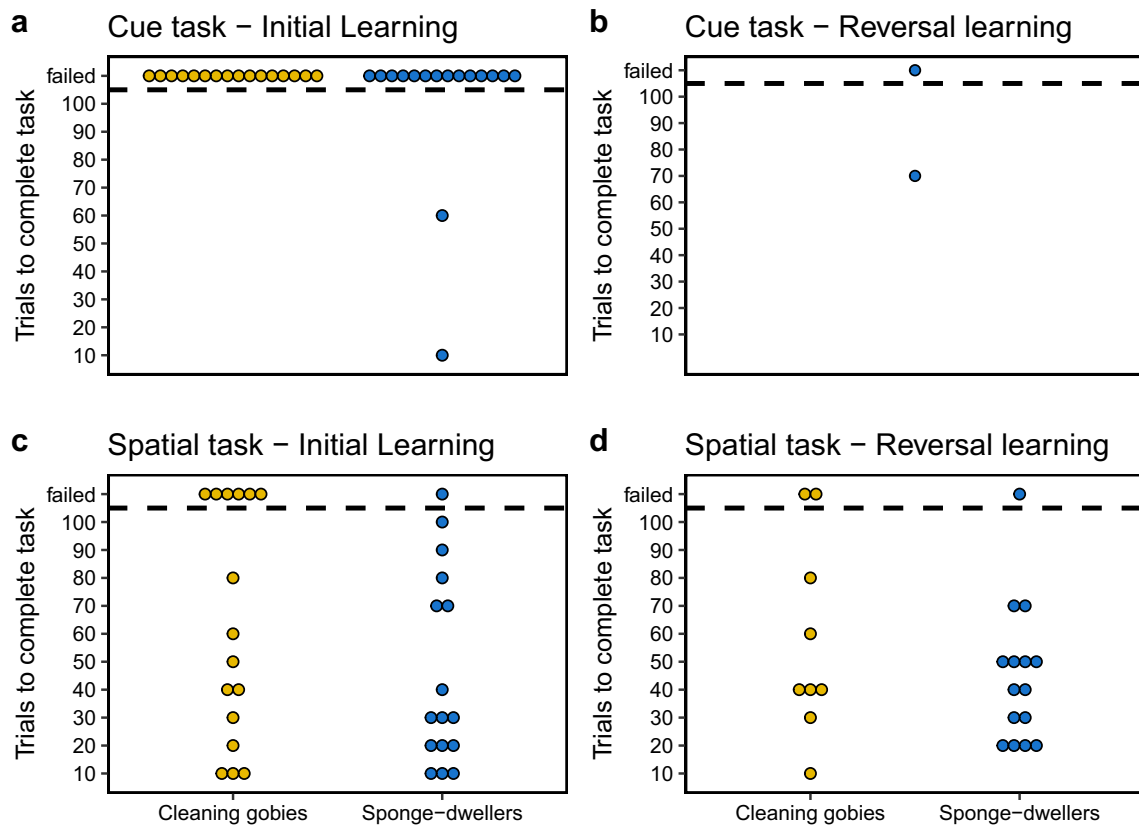


Fig. 3 Performance of cleaning gobies and sponge-dwellers on the two discriminatory two-choice tasks. The plots show the number of trials (individual dots) that the gobies needed to complete the learn-

ing (a, c) and reversal learning (b, d) of the pattern-cued and spatial learning tasks. The dots above the dashed line represent fish that failed to complete the task in the allotted number of trials

the reversal test (Fig. 3d). Concerning the performance of the gobies in the spatial task, we did not find significant differences between the two ecotypes, both in the learning (Fig. 3c, $\chi^2=0.66, p=0.41$) and reversal tests (Fig. 3d, $\chi^2=0.07, p=0.93$). In addition, the performance of males and females did not differ in the learning ($\chi^2=0.22, p=0.63$) and reversal ($\chi^2=0.15, p=0.69$) tests. We found a significant effect of body length ($\chi^2=4.49, p=0.03$) and a significant interaction between body length and sex in the initial learning test performance ($\chi^2=5.82, p=0.01$). Larger females solved the task faster and failed less often than smaller females (Fig. 4). There was no significant effect of body length in the reversal test performance ($\chi^2=2.36, p=0.12$). Concerning the contextual variables, we found that learning performance significantly decreased with the increase of the average time to enter the experimental area in the reversal test (Fig. S1d, $\chi^2=4.74, p=0.02$). All the other contextual variables tested had no effect on the gobies' performance in the learning or reversal learning tests [statistics (Tables S1 and S2) and figure (Fig. S1) in the electronic supplementary material]. In addition, there was no significant correlation between accuracy and decision-making time during the learning and reversal learning tests of the spatial task

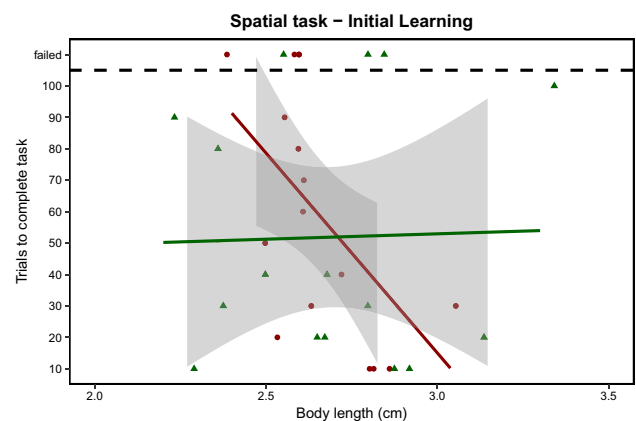


Fig. 4 Relationship between learning performance of female (red/dots) and male (green/triangles) gobies in the initial learning trials of the spatial task and gobies' body length (cm). The dots and triangles above the dashed line represent fish that failed to complete the task in the allotted number of trials. The jitter function was used to separate overlapping data points. The smoothed lines were produced with linear model functions for visual purposes. For the statistical analysis models, please see the data analysis section

(Tables S3 and S4). Finally, we did not find a significant effect of the group manipulation ($LR \chi^2 = 0.90, p = 0.34$) or the elastomer injections ($LR \chi^2 = 0.08, p = 0.76$) in the initial learning ability of the individuals.

Discussion

The aim of this study was to investigate how two different forms of sociality—pair living while largely relying on cleaning interactions versus living in larger groups with little to no cleaning interactions—may predict the performance of *E. prochilos* in two different learning tasks. We predicted that cleaning gobies would outperform sponge-dwellers in the pattern-cued task and that the opposite would be true in the spatial task. Contrary to our predictions, there was no difference in performance between the two ecotypes. Furthermore, the pattern-cued task was apparently very difficult, as only a small minority solved it within 100 trials, which is in stark contrast to the performance of cleaner wrasses (Cardoso et al. 2015; Messias et al. 2016; Soares et al. 2016). Below, we further discuss which factors could have influenced the performance of the gobies in the pattern-cued and spatial tasks and what factors are potentially associated with individual variation in performance within tasks.

Pattern-cued task

When animals cannot solve a certain cognitive task, it is always challenging to determine if the underlying causes are related to the species' ecology, social environment, cognitive abilities, the experimental procedure, or a combination of these factors (Shettleworth 2010; Prétôt et al. 2016b). It was surprising that almost none of the gobies could solve the pattern-cued task. We expected that cleaners would find this task relatively easy to solve, as they feed off a variety of client species that differ in pattern and parasite load (Soares et al. 2007; Dunkley et al. 2019). Indeed, cleaner wrasses can easily solve similar dichotomous choice tasks in less than 50 trials (Cardoso et al. 2015; Messias et al. 2016; Soares et al. 2016). However, here, we solely used plates with different patterns, while in the cleaner wrasse studies, plates had different patterns as well as different colors (Cardoso et al. 2015; Messias et al. 2016; Soares et al. 2016). It is possible that fish may perceive color cues as more salient than pattern cues, i.e., that they can more readily form associations between color cues and a reward (Ingle 1965). In the specific case of cleaning gobies, size variation might even be more relevant. Cleaning gobies preferentially clean client species that carry more ectoparasites (Soares et al. 2007) and ectoparasite infestation is positively related to body size (Grutter and Poulin 1998; Grutter 1999a; Poulin 2000; Coile and Sikkell 2013). Nonetheless, discriminating among

horizontal versus vertical patterns should not be such a difficult task for fishes. For instance, the Ambon damselfish *Pomacentrus amboinensis* are able to discriminate between different printed shapes (Siebeck et al. 2009) and between plates with distinct 2D images of the same color (Binning et al. 2018). Finally, strong lateralization is known to affect learning performance in fish (Sovrano et al. 2005; Bibost and Brown 2014). However, the general failure to solve the pattern-cued task in our study can only in part be attributed to gobies showing a strong side preference. Only 43% of the gobies that did not solve the pattern-cued task had a strong side bias (9 or 10 choices on the same side in one session) in the first 5 sessions and 52% in the last 5 sessions.

Alternatively, the differences in learning performance in the pattern-cued task between *E. prochilos* gobies and *L. dimidiatus* wrasses may be partially explained by the differences in cleaning interaction patterns between the two species. We observed that *E. prochilos* gobies spent much less time in cleaning interactions (2.47% for cleaners and 0.10% for sponge-dwellers) than cleaner wrasses usually do (26–35%, Grutter 1996, 1999b). They also interact with fewer client species (Bansemmer et al. 2002; Soares et al. 2007; Luiz et al. 2016) and are largely reactive, while cleaner wrasses are proactive [6% initiation of interactions versus 35% (this study, Oates et al. 2010)]. These differences alone indicate that *E. prochilos* gobies have fewer opportunities to learn and to choose clients than cleaner wrasses. In addition, although cleaning gobies can cheat (Cheney and Côté 2005; Soares et al. 2008a, b; Côté and Soares 2011) and adjust their service quality (proportion of cheating) when the competition for clients increase (Soares et al. 2008b), they prefer to eat ectoparasites over mucus (Soares et al. 2010). The frequency and costs of cheating seem to be reduced to gobies' clients, as they do not attempt to control cheating through partner switching, delayed revisiting of cleaning stations or aggressive chasing of gobies, as clients of *L. dimidiatus* do (Soares et al. 2008c, 2013). The apparent reduced conflict between the cleaning gobies and their clients may result in lower selective pressure on cleaning gobies for associating the pattern with positive and negative reinforcements. The same explanations apply to why we did not find differences between females and males, as we had expected. Even if females do interact more often with clients than males do, females spend less time cleaning than the cleaner wrasse does, resulting in lower pressure on learning to distinguish between clients of different quality.

Spatial task

Despite the differences in habitat and food acquisition between *E. prochilos* cleaning gobies and sponge-dwellers, the two ecotypes performed similarly in the spatial task. Previous studies with intertidal gobies have shown that species

from rocky platforms have better spatial memory abilities than species from sandy beaches (White and Brown 2014a, b). Here, we predicted that sponge-dwellers would outperform cleaning gobies in the spatial task, because food is patchily distributed in sponges, with specific locations consistently offering more food (Whiteman and Côté 2004b). The average performance of *E. prochilos* in the spatial task (~40 trials until reaching learning criterion) was similar to that of cleaner and non-cleaner wrasse species that were tested in the same paradigm (Gingins et al. 2013, 2018; Cardoso et al. 2015). There are three possible non-exclusive explanations for why we did not find differences between the two ecotypes: (i) sponge-dwellers do not need improved spatial skills for finding their territory/food; (ii) cleaning gobies do match the sponge-dwellers' spatial skills for other purposes; and (iii) cleaning gobies can flexibly adjust their feeding behavior. Although cleaning gobies may not need to locate their main source of food (clients carrying ectoparasites), they might still use spatial learning for shelters, potential mates or alternative food sources. Indeed, in places where ectoparasite availability is low, cleaning gobies have a more diverse diet, which indicates that they can present some flexibility in their feeding behavior (Cheney and Côté 2005; Côté and Soares 2011). Further research should investigate which aspects of *E. prochilos*' social and ecological environment might impose challenges that require spatial cognition and whether individuals can flexibly adjust to new conditions. Finally, the fact that larger females performed better in the spatial task than smaller females suggests that spatial skills might be improved with experience, at least in females.

Factors associated with individual performance

Although we found no differences in performance between *E. prochilos* ecotypes in the spatial task, there was large individual variation in performance within ecotype in this task. Some studies with fish have found that individual differences in learning performance correlate with measures of boldness and sociality (Trompf and Brown 2014; Mamuneas et al. 2015; Kareklas et al. 2017). There is currently a debate on whether there is a connection between behavioral types (e.g., in respect to boldness, aggressiveness, and exploration tendency) and cognitive speed–accuracy trade-offs (Sih and Del Giudice 2012). Some studies have found that individuals making faster decisions were less accurate (Burns and Rodd 2008; Wang et al. 2015), whereas others have found that some aspects of decision-making and learning are related to boldness and sociality, but independent of speed–accuracy trade-offs (Trompf and Brown 2014; Mamuneas et al. 2015; Kareklas et al. 2017). In our study, we found no evidence for the decision speed and decision accuracy trade-off, because the elapsed time for making a choice and choice accuracy

was not significantly correlated. We found that the individuals that took longer to enter the experimental compartment performed worse than the others did. The individuals that took longer to pass through the door were potentially more stressed, which might explain their lower performance. Alternatively, slower individuals could be less exploratory or bold behavioral types that were less prone to enter the experimental compartment. A study with *E. evelynae* found that cleaning gobies show consistent differences in activity, boldness and exploration levels, which correlate to the frequency of cleaning interactions and client visits/choice (Dunkley et al. 2019). The other contextual variables like average time taken to make a choice or initial side/pattern preference did not explain the observed differences in learning performance in the spatial task. Therefore, our additional analyses only partially explain the variance in goby learning performance within the spatial task.

Conclusion

The ecological differences between cleaning and sponge-dwelling populations of *E. prochilos* do not seem to cause differences in individual performance in the two learning tasks. While we lack information on whether habitat choices are linked to any innate preferences in a genetically diverging population or whether the choice is based on individual decisions linked to the current local distribution of conspecifics, the two social and environmental conditions appear to be so different that we expected genetic or ontogenetic divergence to have taken place. However, it seems that associating the choice of a pattern with positive or negative reinforcement is not important for engaging in cleaning interactions in gobies. Furthermore, it appears that spatial memory skills are equally present in a foraging context in both ecotypes. We hypothesize that the benefits of associative pattern learning may be lower for *E. prochilos* cleaning gobies than for *L. dimidiatus* cleaner wrasses, because (i) the gobies spent less time cleaning, (ii) interact with a lower diversity of client species, and (iii) have no conflict of interests with their clients. Further research should investigate which aspects of cleaning and sponge-dwelling gobies' ecological and social environment may require spatial learning.

The successful application of the ecological approach to comparative cognition may strongly depend on the proper identification of the challenges associated with living in a certain environment or adopting a certain life strategy. In the case of the cleaning gobies, it seems that differences in habitat use and feeding mode linked with a cleaning strategy do not require enhanced pattern association skills. It is also possible that the two ecotypes are not as different as predicted and that individuals can flexibly adjust to new feeding conditions, which translates into similar spatial cognitive

performance. Of particular interest would be to explicitly test the intraspecific social skills of the two ecotypes. Typically, living in pairs as cleaning gobies do, should require different social skills than living in large groups with a hierarchy, as sponge-dwelling gobies do. This intraspecific variation in social organization that can be observed within a single location offers great potential to study the ontogeny, physiology, cognition, and brain organization underlying social behavior.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval This study was carried out in accordance with the recommendations of the Coastal Zone Management Unit (CZMU) in Barbados. The protocol was approved by the Minister of Environment on behalf of the CZUM (permit reference number: CZ01/9/9).

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