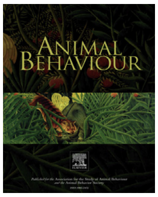
Animal Behaviour 206 (2023) 29–38

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Dominance is associated with reduced cleaning activity in group-living *Elacatinus prochilos* gobies

Renata Mazzei [a, *, 1], Yasmin Emery [a, 1], Marta C. Soares [b], Redouan Bshary [a]

[a] Eco-Ethology, Institute of Biology, University of Neuchâtel, Switzerland
[b] CIBIO/InBIO, Research Center in Biodiversity and Genetic Resources, University of Porto, Portugal

ARTICLE INFO

Article history:
Received 16 January 2022
Initial acceptance 23 May 2022
Final acceptance 20 July 2023
Available online 13 October 2023
MS. number: 22-00024R

Keywords:
behavioural flexibility
cleaning interaction
decision making
dominance
social behaviour

Animals living in complex social environments are often able to flexibly adjust their behaviour to different social contexts. Yet, flexible responses require time and energy and can be constrained by a variety of mechanisms. Here we asked whether the socio ecological environment experienced by the facultative cleaning goby *Elacatinus prochilos* influenced their interest in cleaning interactions. *Elacatinus prochilos* can be found in two socio ecological contexts: inhabiting cleaning stations, where they live in pairs and feed by removing ectoparasites from larger marine organisms (cleaners), or barrel sponges, where they live in dominance hierarchies and rarely engage in cleaning interactions (sponge-dwellers). We tested individuals used in a previous experiment with controlled social structures (small groups with dominance hierarchies) and feeding conditions (better access to food to dominants) to better understand which factors influence cleaning activity in facultative species. We found that dominance significantly decreased cleaning activity in male (and potentially female) sponge-dwellers. We hypothesize that long-term hormone-mediated or time allocation constraints may explain reduced cleaning activity in dominant male sponge-dwellers. While previous studies showed that *E. prochilos* can be socially flexible, here we showed that feeding flexibility might be restricted for dominant sponge-dwellers. This highlights the importance of testing the flexibility of individuals in different social contexts to better understand the evolutionary importance of adaptive behavioural flexibility.

Animals living in biodiverse environments are often presented with multiple social interaction opportunities that require decision making. For example, they may have to decide whether to avoid, approach, cooperate with or compete with conspecifics and heterospecifics. The resulting behaviour depends on the individual's ability to perceive and evaluate the social and ecological environment and respond appropriately (Taborsky & Oliveira, 2012). Such an ability to regulate the expression of social behaviour in order to optimize social relationships often requires high levels of behavioural and cognitive flexibility (Varela et al., 2020). This may be achieved by multiple mechanisms, for instance, by evolving different neural circuits and behaviours to respond to different social contexts, or, alternatively, by using the same behaviour and neural circuit to serve different functions depending on the context (Varela et al., 2020). Regardless of the mechanism, it is expected that natural selection will favour adaptive flexible behavioural responses. However, individuals are typically constrained by the amount of time and energy that they can direct to different stimuli.

The level of flexibility of individuals is largely influenced by the social and ecological environment experienced early in life but also by environmental cues they are exposed to during multiple life stages (Cardoso et al., 2015). How frequently individuals collect and process information, and how much, before making decisions may depend on their internal state (e.g. level of hunger or fear), cognitive ability, and the predictability of the environment (Fawcett et al., 2014). The more stable the environment is, the less advantageous it should be to evolve mechanisms to keep collecting further information (Fawcett & Frankenhuis, 2015; Frankenhuis & Panchanathan, 2011; Stamps & Krishnan, 2014; Taborsky, 2017). Flexible decision rules of adults including many ‘if, then…’ rules may be under positive selection if the social environment is highly variable, but such flexibility might be constrained by limited genetic variation, phylogenetic history (e.g. the vertebrate highly conserved social decision-making network, O'Connell & Hofmann, 2011, 2012) or hormone-mediated constraints (McGlothlin & Ketterson, 2008). Further , learning plays an important part in the development of behaviour, and different reinforcement regimes

---

* Corresponding author.
E-mail address: renata.mazzei@gmail.com (R. Mazzei).

[1] Shared co-first authorship.

https://doi.org/10.1016/j.anbehav.2023.09.001
0003-3472/

and/or different exposures during early life stages may lead to consistent behavioural differences (Farine et al., 2015; Fischer et al., 2017; Honarmand et al., 2015).

Marine cleaning interactions provide a unique framework for investigating how restricted animals are in making flexible decisions when exposed to multiple social possibilities. Cleaners remove ectoparasites and other material from larger organisms (i.e. clients) and adjust their service to a client's species, size, behaviour and ectoparasitic infestation (Roche et al., 2021; Soares et al., 2007; Triki et al., 2019). Here we aimed to investigate whether the social and ecological environments experienced by the facultative cleaning goby *Elacatinus prochilos* influence how they interact with clients. In this species, habitat use is related to differences in social and feeding behaviour. Individuals living on corals and other substrates (cleaners) are usually found in pairs or small groups that depend mostly on cleaning interactions for feeding (Whiteman & Côté, 2002, 2003). In contrast, individuals inhabiting barrel sponges (sponge-dwellers) are organized into larger groups, with dominance hierarchies, feeding primarily on micro-organisms living inside the sponges' tissue and only rarely engaging in cleaning interactions (Mazzei et al., 2019; Whiteman & Côté, 2004).

The reason why sponge-dwellers only rarely engage in cleaning interactions is still unknown. It could be because environmental differences reduce the access of clients to barrel sponges or because sponge-dwellers, living in size-based dominance hierarchies, and having to dispute and constantly defend another type of food source, lose their ability or interest in engaging in cleaning interactions. To answer this, we used *E. prochilos* cleaners and sponge-dwellers exposed to similar social and feeding conditions in the laboratory (groups of four adult individuals where larger individuals, i.e. dominants, had more access to food than smaller individuals, i.e. subordinates, Mazzei et al., 2021), and exposed them to different clients in a controlled laboratory setting. Our study provides the first attempt to disentangle the different causes of intraspecific behavioural variation in *E. prochilos* and shed some light on the factors influencing flexibility in decision making in species that live in variable social contexts.

METHODS

Capture and Housing

Cleaning and sponge-dwelling *E. prochilos* were collected from North and South Bellairs' fringing reefs (13°11′30″N, 59°38′31″W) in Holetown, Barbados from March to April 2018. Sponge-dwelling gobies were caught from groups in giant barrel sponges, *Xestospongia muta*, in the patch reef zone (6–10 m). Cleaning gobies were caught from cleaning stations (mostly in pairs) in substrates such as coralline algae, coral or dead coral in the spurs and grooves zone (3–8 m). Individuals were first sedated using a 1:4 clove oil and ethanol (70%) solution, captured with hand nets, and transported to the laboratory of the Bellairs Research Institute in plastic bags within 1 h of capture. 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 cm and 39 cm high) or mesh bags (made of mosquito screens) placed inside an aquarium (15 cm diameter), depending on the number of individuals captured. Each aquarium was individually connected to a flow-through water system. Also, each aquarium/bag contained one or multiple cylindrical PVC shelters for refuge. The gobies were fed with mashed prawn paste smeared on a rectangular, white, Plexiglas plate (5 × 8 cm) starting from the second day of arrival in the laboratory.

Within 2 days after capture, each goby was sexed, sized and individually housed in a mesh bag. Sex was determined based on the shape of the urogenital papilla. The papillae on *E. prochilos* are ventrally located flaps of tissue distinguished by a 'V' shape in males and a cylindrical and truncate shape in females (Thresher, 1984). Because 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 sea water and around 5 ml of clove oil mixture. Together, sexing and sizing took less than 2 min per goby. Gobies were left to recover in another petri dish with sea water before being returned to their mesh bags. Another 2–3 days after sexing and sizing, the gobies were sedated again, using the same clove oil mixture, before being injected with visual elastomer implants (VIE, Northwest Marine Technology Inc., Anacortes, WA, U.S.A.). VIE tags are biocompatible colourful liquids that cure as a solid and are safe and used widely in fish identification including small-bodied fish (Hoey & McCormick, 2006; Jungwirth et al., 2019). The implants were used to identify each individual in a standardized laboratory experiment performed in a previous study aiming to understand how flexible cleaners and sponge-dwellers were in terms of social organization and social structure (social flexibility study; Mazzei et al., 2021). In this previous study, we created experimental groups by placing unfamiliar individuals captured from the same type of habitat together, i.e. either cleaning stations ($N = 13$ groups) or sponges ($N = 15$ groups). We first sorted individuals by size and sex to ensure that each group had the same composition: one larger female, one larger male, one smaller female, one smaller male, and one or two immature juveniles. Each aquarium had the same habitat structure (one larger compartment with two shelters and one smaller compartment without shelter), and the same feeding conditions (a Plexiglas plate with food introduced once a day in the larger compartment). The goal of this previous study was to determine how individuals would behave and organize themselves once natural differences in habitat structure and feeding conditions, which occur naturally in the wild, were controlled. We did not set a priori which individuals would be dominants or subordinates. We let individuals organize themselves freely to form either pairs or dominance hierarchies. After observing the groups for 5 days, we found that in all groups (independently of the habitat of origin), individuals organized themselves in a similar manner: one dominant pair (always the larger male and female) that showed affiliative behaviours towards each other and were equally aggressive towards the smaller individuals (always the smaller male and female, which never formed a pair and showed no affiliative behaviours). For more details, see Mazzei et al. (2021).

The client exposure experiment (this paper) started 17–21 days after the end of the social flexibility study, except for eight gobies, which were tested 1 day after. This difference happened because we initially struggled to capture clients for the experiments (due to lack of experience), so most groups had to wait until the clients were fully acclimated before being exposed to them, except for two groups (four cleaners and four sponge-dwellers), which were tested later on, when clients were already acclimated and therefore could be tested immediately after the previous experiment. During this waiting period, gobies remained in their original experimental groups and were fed once a day with the Plexiglas plate. The client fish species selected for the client exposure are known clients of cleaning gobies (Whiteman & Côté, 2002) and have been previously used in a similar study with the obligatory cleaning goby *E lacatinus evelynae* (Soares et al., 2012): Graysby groupers, *Cephalopholis cruentata* ($N = 3$) and French grunts, *Haemulon flavolineatum* ($N = 2$). Both species were captured using fish traps or barrier nets and brought to the laboratory in buckets. Clients were placed individually in glass aquaria (60 × 40 cm and 39 cm high), where they acclimated for at least 12 days before experimentation and fed pieces of prawn until satiation each morning during acclimation and experimental days. The experimental trials took place in the same aquaria in which the clients had been acclimated, to minimize client stress.

Client Exposure Procedure

We exposed 48 gobies to both client species: 24 cleaners (mean ± SD: length = 2.6 ± 0.26 cm; 12 per sex, six per social status) and 24 sponge-dwellers (length = 2.79 ± 0.25 cm; 12 per sex, six per social status). Experiments took place in client tanks to avoid the movement of clients and to ensure they remained calm. Client tanks were divided into three sections (Fig. 1): the acclimation section A (30 × 40 cm) was separated by a piece of opaque Plexiglas from experimental sections B and C (both measuring 15 × 40 cm). Sections B and C were separated from one another by a net with holes large enough for gobies to pass through, but that prevented clients from crossing, ensuring that all interactions were initiated by gobies. Prior to experimentation, clients were confined in section C and given 30 min to acclimate. Gobies were transferred to section A with small hand nets where they remained visually isolated from clients for 15 min, to acclimate before the experiment began. Once all fish appeared at ease with the experimental set-up, the opaque partition was lifted, and the trial began once gobies passed into section B. Immediately after exposure to the first client, each goby was transferred to the aquaria of the second client and allowed to acclimate for another 15 min before the second exposure. All individuals belonging to the same group were exposed to both treatments on the same day and period (morning or afternoon). Individuals would be rotated around the different clients available (three groupers and two grunts). The order in which gobies were exposed to each species, as well as the period of the day in which animals were tested were counterbalanced across gobies' sex and social status (dominant or subordinate). The rationale for exposing the gobies to the clients for 40 min was based on a pilot study performed in the previous field season showing that of the gobies that interacted with clients, it took on average 9 min after barriers were lifted to do so, and in some instances up to 15 min. Because cleaners and clients did not appear to be affected by the experimental set-up, we decided to give individuals extra time to interact with the client. GoPro Hero 3+ cameras were secured to the right side of experimentation tanks with adjustable arm clamps, and trials were recorded for 40 min. We used the BORIS software (Behavioural Observation Research Interactive Software v. 2.981), to extract the latency to interact (time until the first interaction began) and the proportion of time spent interacting with a client. We considered interaction when the goby was in direct contact (touching) with the client, even if no clear mouth movements could be observed. Videos were analysed blindly with regard to gobies' phenotype, sex and social status, but not client treatment.

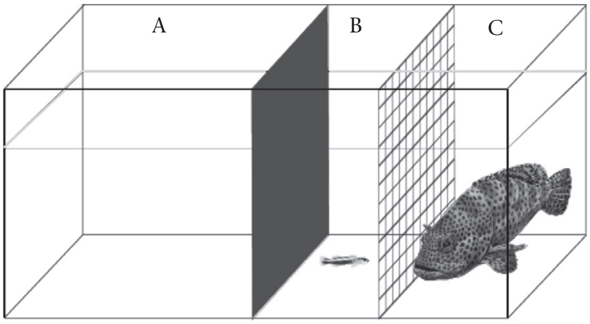


Figure 1. Schematic representation of the experimental set-up. Section A (30 × 40 cm and 35 cm high) was separated by a piece of opaque Plexiglas from sections B and C (each measuring 15 × 40 cm and 35 cm high). Gobies acclimated in section A for 15 min and subsequently passed into section B. Sections B and C were separated by a net with holes big enough for gobies but not clients to pass through. Recordings lasted approximately 40 min.

Ethical Note

This work was subject to ethics review by the Coastal Zone Management Unit (CZMU) of Barbados (permit reference number: CZ01/9/9). The permit covered both authorizations for specimens and samples collected from marine-protected environments, as well as ethical assessments of animal welfare for laboratory experiments. Animals brought to the laboratory were kept in aquaria connected to a flow-through water system that continuously pumped fresh sea water from the lagoon directly facing the research station into each aquarium. Each aquarium/bag contained one or multiple cylindrical PVC shelters for refuge. The lights in the aquaria room were turned on at 0700 and off at 1900 hours, mimicking the light cycle in Barbados between March and April, and experiments took place between 0800 and 1700 hours. The gobies were fed ad libitum with mashed prawn spread in a rectangular white Plexiglas plate (5 × 8 cm) starting from the second day of arrival in the laboratory and every day thereafter. On days when experiments took place, individuals were fed ad libitum following the experimental period, typically between 1700 and 1900 hours, and in the mornings of days when no experiments took place. No gobies were eaten by predators and were all in good health following the experiment. The gobies from this study were ultimately humanely killed as part of another study examining the brain structure differences between cleaning and sponge-dwelling gobies. Clients were released at their original reefs at the end of the experiments. Two clients died of unknown causes a few days after the end of the experiment. Gobies were euthanized with a clove oil mix overdose (50 ml of clove oil and 200 ml of ethanol (1:4) diluted in approximately 100 ml of sea water). The individuals were left in the clove oil solution for a minimum of 5 min or until the heartbeat was no longer visible under a binocular microscope.

Data Analysis

All analyses were performed using R version 4.0.0 (R Core Team, 2021). We initially aimed to test the effects of phenotype (cleaners versus sponge-dwellers), sex, social status (dominant versus subordinate) and client species on the proportion of time individuals spent cleaning and the latency to clean (amount of time (s) it took gobies to come in contact with a client). However, more thorough analyses of the data indicated that client identity had a significant effect on the behaviour of the gobies (generalized linear mixed model, function glmmTMB, $\chi^2_4 = 12.13$, $P = 0.016$; Fig. A1) and that the number of clients of each species used in our experiment (three groupers and two grunts) was not large enough to test for the effect of species on cleaning behaviour. However, differences across clients were consistent across the gobies' groups and experimental days (Figs A1, A2), and an a posteriori power analysis indicated that our design was powerful enough (85.30%, calculated using the function powerSim, Kumle et al., 2021) to test for the effects of phenotype, sex, social status and interactions. We included sex as a variable of interest because it has been found that obligatory cleaning females spend more time cleaning than males (Whiteman & Côté, 2002). To test how these factors influenced the proportion of time spent cleaning, we used a generalized linear mixed model (GLMM) using the function glmmTMB (Brooks et al., 2017). Phenotype, sex, social status and all interactions were included as fixed factors, while goby identity, client identity, and group identity were included as random factors, to account for the repeated measurement design as well as group and client identity effects. Considering the nature of our data (proportions and excess of zeros) we specified a beta family and a zero-inflated formula for the model.

To test how these same factors affected the latency to clean, we performed a survival analysis. We chose this type of model because our data were right-censored, meaning that it is unknown whether individuals that did not interact with a client would have refrained from doing so were they given more time. Using mixed-effects Cox proportional hazard models from the coxme package (Therneau, 2018), we fitted a model with latency to interact (s) as our dependent variable, and the same independent and random terms as used in the GLMM analysis above. The significance of factors of both models was determined using the function Anova (Type II test) from the car package (Fox & Weisberg, 2019). We assessed the validity of models by visually inspecting the homogeneity and normality of residuals. Post hoc pairwise comparisons of estimated marginal means were performed using the emmeans R package (Lenth, 2021).

RESULTS

The proportion of time cleaners and sponge-dwellers spent with clients varied according to the phenotype, social status and sex of individuals (see Fig. 2 and Tables A1–A3 for full model statistics, ANOVA results and effect size statistics of pairwise comparisons). Dominant male sponge-dwellers spent significantly less time interacting with clients than cleaners and subordinates (three-way interaction between phenotype, social status and sex, Table A2; for raw data see Fig. 2 and for the marginal effects plot see Fig. A3). Although dominant female sponge-dwellers seemed to spend less time interacting with clients than cleaners and subordinates (Fig. 2), our model was limited in capturing this effect because only one dominant female sponge-dweller interacted with the clients, and therefore the uncertainty for the effect estimate in the non zero part of the model was very high (see Table A3 and for the marginal effect Fig. A3). In contrast, for the latency to first interact with clients, we found no significant effect of phenotype, social status or sex (Fig. 3; see Tables A4 and A5 for full model statistics and ANOVA results).

DISCUSSION

We asked how cleaning and sponge-dwelling gobies would react to and interact with clients after being artificially kept in the same social organization (dominance hierarchy) and feeding regimes. The goal was to find whether differences in cleaning rates observed in the wild are a consequence of ecological and social differences inherent to the different habitats (e.g. more clients showing at cleaning stations than at barrel sponges) or a lack of interest/ability to clean in sponge-dwellers. Although we also originally aimed to test whether cleaning behaviour was influenced by the potential risk imposed by the client species (predatory versus harmless species), a posteriori analysis indicated that our design was not powerful enough to detect such differences. We, therefore, limit our conclusions to the effect of the phenotypes and social status on the observed behaviours. We found that subordinate sponge-dwellers kept their interest in cleaning and spent almost as much time cleaning as cleaners. In contrast, only a few dominant sponge-dwellers interacted with clients (four of 24) and male dominant sponge-dwellers (and potentially females) spent significantly less time interacting with clients. Although cleaning gobies also assumed dominant and subordinate roles before being exposed to clients, dominance was not associated with a decrease in cleaning rates in cleaning gobies. Together, our results indicate that the differences in cleaning rates observed in the wild between cleaners and sponge-dwellers are not a consequence of genetic differentiation (because subordinate sponge-dwellers can clean). Rather, they indicate that dominant sponge- dwellers lose their interest or ability to clean. Importantly, the effect of dominance in

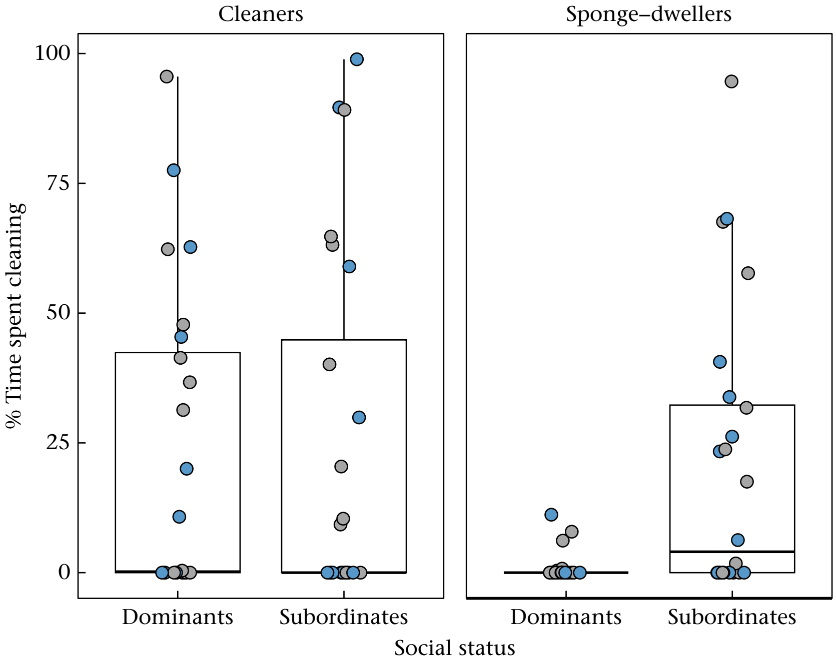


Figure 2. Percentage of time spent cleaning by gobies of different phenotypes (cleaners or sponge-dwellers) and social status (dominants or subordinates). Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes) and outermost values within the range of 1.5 times the respective quartiles (whiskers). Blue (females) and grey (males) dots indicate individual observations.

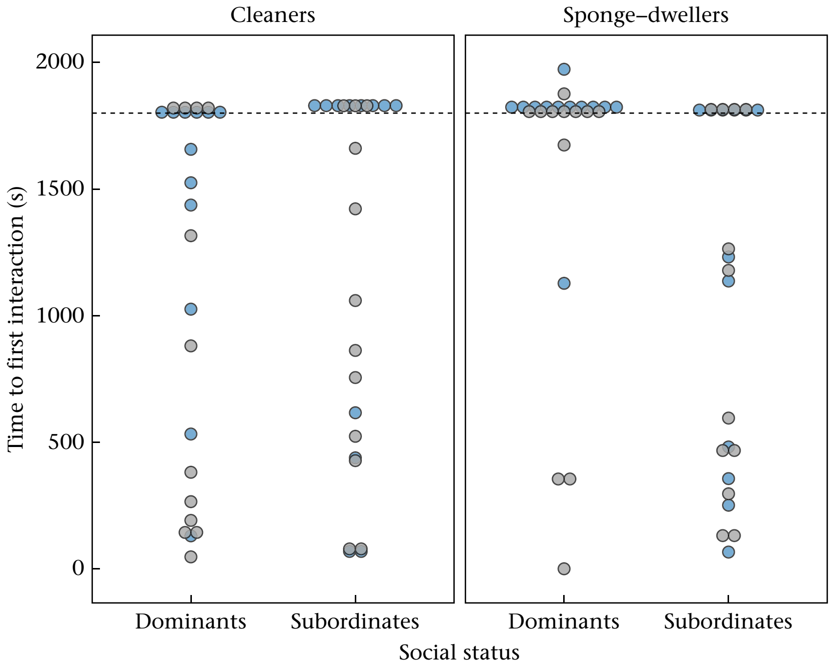


Figure 3. Latency (s) to first interact with clients by gobies of different phenotypes (cleaners or sponge-dwellers) and social status (dominants or subordinates). Blue (females) and grey (males) dots indicate individual observations. Dots above the dashed line represent individuals that had not interacted with the client by the end of the experiment.

our study cannot be exclusively explained by body size (see Fig. A4). Although dominant sponge-dwellers were on average larger than dominant cleaners (sponge-dwellers: 2.9 cm; cleaners: 2.8 cm), the size of dominant individuals largely varied across groups within the same phenotype (sponge-dwellers: 2.6–3.4 cm; cleaners: 2.4–3.1 cm).

The reduced cleaning activity of dominant sponge-dwellers could be related to a trade-off in the expression of conflicting behaviours (dominance versus cleaning) and/or a lack of practice of cleaning resulting from a long-term trade-off in time allocation. Hormone-mediated trade-offs between aggression and prosocial behaviours are well known for several species. For example, bluegill, *Lepomis macrochirus* , treated with androgen implants increased aggression and reduced nurturing while prolactin treatment caused the opposite effect (Cunha et al., 2019). In meerkats, *Suricata suricatta*, individuals treated with androgen blockers initiated less and received more high-intensity aggression, and engaged in more prosocial behaviour (delBarco-Trillo et al., 2016). Most relevant to our study, testosterone-treated cleaner wrasse, *Labroides dimidiatus*, females interacted less with clients and showed more aggression towards smaller females (Soares et al., 2019). A similar hormone-mediated trade-off could explain why dominant sponge-dwellers, which are very aggressive towards subordinates (Mazzei et al., 2021; Whiteman & Côté, 2004), did not clean. Other hormones and neuromodulators could be implicated in such trade-offs. Different compounds such as cortisol, arginine vasotocin, serotonin and dopamine can promote, inhibit or modulate cleaning interactions in different contexts (reviewed in Soares et al., 2018). Alternatively, or in addition , a time allocation trade-off between cleaning and territorial defence/foraging inside the sponge could lead to a lack of practice or interest in cleaning interactions by dominant sponge-dwellers, which we captured in our experiment.

No matter the mechanism, the loss of cleaning performance must be due to long-term effects, as subjects from both habitats had been kept in social groups before the experiment, and dominant cleaners had shown similar levels of territoriality and aggressiveness (Mazzei et al., 2021). Thus, short-term exposure to dominance hierarchies is not enough to constrain cleaning behaviour. Long-term displays of aggression and territoriality in dominant sponge-dwellers might lead to more permanent and irreversible social phenotypes that are incompatible with cleaning activity. Likewise, cleaners may be more strongly wired to react to and interact with a client after being exposed to cleaning interactions long term in the wild. Because we were not able to quantify feeding rates per individual, we cannot completely exclude the possibility that dominant sponge-dwellers ate more than dominant cleaners, potentially reducing their interest in cleaning. However, dominant cleaners and sponge-dwellers were equally defensive of their plates and feeding areas against subordinate individuals (Mazzei et al., 2021) so if feeding differences had played a strong role in reducing cleaning activity, we should have seen at least a small difference in cleaning rates between dominant and subordinate cleaners, which was not the case. Finally, although our results provide evidence that dominance plays a role in reducing cleaning activity, further studies should focus on reversing the social status of individuals and repeating client exposure to confirm that social status is indeed the main causal factor.

Conclusions

Our previous study with *E. prochilos* showed that they were flexible in terms of social organization and structure, being able to adjust their social behaviour to short-term exposure to a new social context (Mazzei et al., 2021). In contrast, here we found that sponge- dwellers are less flexible in their ability/willingness to interact with clients and that long-term exposure to a cleaning/non cleaning lifestyle seems to have an impact on individuals' social decisions. Together, these studies indicate that *E. prochilos* can have variable levels of flexibility in different aspects of their social behaviour. Therefore, our study highlights the importance of testing individuals' social performance and flexibility across different social contexts, to get a better understanding of the evolutionary importance of adaptive behavioural plasticity.

Author Contributions

Renata Mazzei and Yasmin Emery: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing – Original draft, Writing–Review & editing. **Redouan Bshary and Marta Soares***:* Conceptualization, Methodology, Writing–Review & editing, Supervision.

Declaration of Interest

The authors declare no conflict of interest.

Data Availability

The data set for this paper is available at https://doi.org/10.6084/m9.figshare.21936378.v1.

Acknowledgments

We thank Hanaa Sarhan, Charlotte Henriksen, Holly Trew, Amy Cox, Nadeishini Paras, Shawn Simpson, and Jeniece Germain for the assistance in the field, the staff of the Bellairs Research Institute, Henri Vallès for the logistical support and Radu Slobodeanu for statistical advice. R.M. was supported by a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brazil (CNPq) (CNPQ/201522/2014-4). M.C.S. is currently supported by National Funds through Fundação para a Ciência e a Tecnologia (FCT) (DL57/2016/CP1440/CT0019). Funding for the project was provided by the CNPQ (grant to R.M.) and the Swiss National Science Foundation (SNSF) (grant to R.B.).

References

Brooks, M. E., Kristensen, K., Benthem, K., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal, 9*(2), 378. https://doi.org/10.32614/RJ-2017-066

Cardoso, S. D., Teles, M. C., & Oliveira, R. F. (2015). Neurogenomic mechanisms of social plasticity. *Journal of Experimental Biology, 218*(1), 140–149. https://doi.org/10.1242/jeb.106997

Cunha, A. A. P., Partridge, C. G., Knapp, R., & Neff, B. D. (2019). Androgen and prolactin manipulation induces changes in aggressive and nurturing behavior in a fish with male parental care. *Hormones and Behavior, 116*, Article 104582. https://doi.org/10.1016/j.yhbeh.2019.104582

delBarco-Trillo, J., Greene, L. K., Goncalves, I. B., Fenkes, M., Wisse, J. H., Drewe, J. A., Manser, M. B., Clutton-Brock, T., & Drea, C. M. (2016). Beyond aggression: Androgen-receptor blockade modulates social interaction in wild meerkats. *Hormones and Behavior, 78*, 95–106. https://doi.org/10.1016/j.yhbeh.2015.11.001

Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers Juvenile zebra finches to switch social learning strategies. *Current Biology, 25*(16), 2184–2188. https://doi.org/10.1016/j.cub.2015.06.071

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences, 18*(3), 153–161. https://doi.org/10.1016/j.tics.2013.12.012

Fawcett, T. W., & Frankenhuis, W. E. (2015). Adaptive explanations for sensitive windows in development. *Frontiers in Zoology, 12*, S3. https://doi.org/10.1186/1742-9994-12-S1-S3

Fischer, S., Bohn, L., Oberhummer, E., Nyman, C., & Taborsky, B. (2017). Divergence of developmental trajectories is triggered interactively by early social and ecological experience in a cooperative breeder. *Proceedings of the National Academy of Sciences of the United States of America, 114*(44), E9300–E9307.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Frankenhuis, W. E., & Panchanathan, K. (2011). Balancing sampling and specialization: An adaptationist model of incremental development. *Proceedings of the Royal Society B: Biological Sciences, 278*(1724), 3558–3565. https://doi.org/10.1098/rspb.2011.0055

Hoey, A. S., & McCormick, M. I. (2006). Effects of subcutaneous fluorescent tags on the growth and survival of a newly settled coral reef fish, *Pomacentrus amboinensis* (Pomacentridae). *Proceedings of the 10th International Coral Reefs Symposium, 2006*, 420–425.

Honarmand, M., Riebel, K., & Naguib, M. (2015). Nutrition and peer group composition in early adolescence: Impacts on male song and female preference in zebra finches. *Animal Behaviour, 107*, 147–158. https://doi.org/10.1016/j.anbehav.2015.06.017

Jungwirth, A., Balzarini, V., Zöttl, M., Salzmann, A., Taborsky, M., & Frommen, J. G. (2019). Long-term individual marking of small freshwater fish: The utility of Visual Implant Elastomer tags. *Behavioral Ecology and Sociobiology, 73*(4), 49. https://doi.org/10.1007/s00265-019-2659-y

Kumle, L., Võ, M. L.-H., & Draschkow, D. (2021). Estimating power in (generalized) linear mixed models: An open introduction and tutorial in R. *Behavior Research Methods, 53*(6), 2528–2543. https://doi.org/10.3758/s13428-021-01546-0

Lenth, R. V. (2021). *emmeans: Estimated marginal means, aka least-squares means*. R Package Version 1.5.4 https://CRAN.R-project.org/package=emmeans.

Mazzei, R., Lampe, M., Ohnesorge, A., Pajot, A., Soares, M. C., & Bshary, R. (2019). Ecological differences in the facultative Caribbean cleaning goby *Elacatinus prochilos* do not predict learning performance in discriminatory two-choice tasks. *Animal Cognition, 22*, 1039–1050. https://doi.org/10.1007/s10071-019-01295-w

Mazzei, R., Soares, M. C., & Bshary, R. (2021). Social organization variation and behavioural flexibility in the facultative cleaning goby *Elacatinus prochilos*. *Animal Behaviour, 174*, 187–195. https://doi.org/10.1016/j.anbehav.2021.01.020

McGlothlin, J. W., & Ketterson, E. D. (2008). Hormone-mediated suites as adaptations and evolutionary constraints. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1497), 1611–1620. https://doi.org/10.1098/rstb.2007.0002

O'Connell, L. A., & Hofmann, H. A. (2011). The vertebrate mesolimbic reward system and social behavior network: A comparative synthesis. *Journal of Comparative Neurology, 519*(18), 3599–3639. https://doi.org/10.1002/cne.22735

O'Connell, L. A., & Hofmann, H. A. (2012). Evolution of a vertebrate social decision-making network. *Science, 336*(6085), 1154–1157. https://doi.org/10.1126/science.1218889

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Roche, D. G., Jornod, M., Douet, V., Grutter, A. S., & Bshary, R. (2021). Client fish traits underlying variation in service quality in a marine cleaning mutualism. *Animal Behaviour, 175*, 137–151. https://doi.org/10.1016/j.anbehav.2021.03.005

Soares, M. C., Bshary, R., Cardoso, S. C., Côté, I. M., & Oliveira, R. F. (2012). Face your fears: Cleaning gobies inspect predators despite being stressed by them. *PLoS One, 7*(6), Article e39781. https://doi.org/10.1371/journal.pone.0039781

Soares, M. C., Cardoso, S. C., & Côté, I. M. (2007). Client preferences by Caribbean cleaning gobies: Food, safety or something else? *Behavioral Ecology and Sociobiology, 61*(7), 1015–1022. https://doi.org/10.1007/s00265-006-0334-6

Soares, M. C., Gerlai, R., & Maximino, C. (2018). The integration of sociality, monoamines and stress neuroendocrinology in fish models: Applications in the neurosciences. *Journal of Fish Biology, 93*(2), 170–191. https://doi.org/10.1111/jfb.13757

Soares, M. C., Mazzei, R., Cardoso, S. C., Ramos, C., & Bshary, R. (2019). Testosterone causes pleiotropic effects on cleanerfish behaviour. *Scientific Reports, 9*(1), Article 15829. https://doi.org/10.1038/s41598-019-51960-w

Stamps, J. A., & Krishnan, V. V. (2014). Combining information from ancestors and personal experiences to predict individual differences in developmental trajectories. *American Naturalist, 184*(5), 647–657. https://doi.org/10.1086/678116

Taborsky, B. (2017). Developmental plasticity. *Advances in the Study of Behavior, 49*, 49–99. https://doi.org/10.1016/bs.asb.2016.12.002

Taborsky, B., & Oliveira, R. (2012). Social competence: An evolutionary approach. *Trends in Ecology & Evolution, 27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003

Therneau, T. (2018). *Package 'coxme'. Mixed Effects Cox Models. R package version 2*. https://CRAN.R-project.org/package=coxme.

Thresher, R. E. (1984). *Reproduction in reef fishes*. T.F.H. Publications.

Triki, Z., Wismer, S., Rey, O., Ann Binning, S., Levorato, E., & Bshary, R. (2019). Biological market effects predict cleaner fish strategic sophistication. *Behavioral Ecology, 30*(6), 1548–1557. https://doi.org/10.1093/beheco/arz111

Varela, S. A. M., Teles, M. C., & Oliveira, R. F. (2020). The correlated evolution of social competence and social cognition. *Functional Ecology, 34*(2), 332–343. https://doi.org/10.1111/1365-2435.13416

Whiteman, E. A., & Côté, I. M. (2002). Sex differences in cleaning behaviour and diet of a Caribbean cleaning goby. *Journal of the Marine Biological Association of the United Kingdom, 82*(4), 655–664. https://doi.org/10.1017/S0025315402006021

Whiteman, E. A., & Côté, I. M. (2003). Social monogamy in the cleaning goby Elacatinus evelynae: Ecological constraints or net benefit? *Animal Behaviour, 66*(2), 281–291. https://doi.org/10.1006/anbe.2003.2200

Whiteman, E. A., & Côté, I. M. (2004). Dominance hierarchies in group-living cleaning gobies: Causes and foraging consequences. *Animal Behaviour, 67*(2), 239–247. https://doi.org/10.1016/j.anbehav.2003.04.006

Appendix

Table A1
Regression parameter estimates and P values for each investigated variable in the generalized linear mixed model predicting the proportion of time spent cleaning

	Estimate	SE	z	Pr(>|z|)
Conditional model				
Fixed coefficients				
(Intercept)	−0.10818	0.65315	−0.166	0.869
Phenotype Sponge-dwelling	0.02056	1.1275	0.018	0.986
Status Subordinate	1.48263	0.55106	2.691	**0.007**
Sex Male	−0.51779	0.46186	−1.121	0.262
Sponge-dwelling: Subordinate	−2.20062	1.271	−1.731	0.083
Sponge-dwelling: Male	−2.76285	1.28539	−2.149	**0.032**
Subordinate: Male	−1.27824	0.68227	−1.873	0.061
Sponge-dwelling: Subordinate:Male	4.6872	1.51953	3.085	**0.002**
Zero-inflation model				
Fixed coefficients				
(Intercept)	0.7995	0.4338	1.843	0.065
Phenotype Sponge-dwelling	0.3614	0.4265	0.847	0.397
Status Subordinate	−0.5392	0.427	−1.263	0.207
Sex Male	−0.882	0.4276	−2.063	**0.039**
Random effects				
Conditional model				
Groups	Variance	SD		
Goby id	1.370e-09	3.701e-05		
Client id	1.062e+00	1.030e+00		
Social experiment group	3.181e-01	5.640e-01		

Significant P values are highlighted in bold (alpha level: 0.05).

Table A2
Analysis of deviance table (Type II Wald chi-square tests) for models predicting the proportion of time spent cleaning

Predictors	χ^2	*df*	Pr(>χ^2)
Phenotype	7.6567	1	**0.006**
Status	11.4726	1	**0.001**
Sex	6.4505	1	**0.011**
Phenotype: Status	3.9846	1	**0.046**
Phenotype: Sex	1.4346	1	0.231
Status: Sex	0.115	1	0.735
Phenotype: Status: Sex	9.515	1	**0.002**

Significant P values are highlighted in bold (alpha level: 0.05).

Table A3
Effect sizes and confidence intervals of pairwise differences of estimates

Contrasts	Effect size	SE	*df*	Lower CL	Upper CL
Cleaning dominant F − Sponge-dwelling dominant F	−0.00284	0.1555	Inf	−0.3075	0.3019
Cleaning dominant F −Cleaning subordinate F	−0.20443	0.0777	Inf	−0.3567	−0.0522
Cleaning dominant F − Sponge-dwelling subordinate F	0.09616	0.084	Inf	−0.0685	0.2608
Cleaning dominant F −Cleaning dominant M	0.07139	0.0639	Inf	−0.0539	0.1967
Cleaning dominant F − Sponge-dwelling dominant M	0.44951	0.1104	Inf	0.2331	0.6659
Cleaning dominant F −Cleaning subordinate M	0.04321	0.0656	Inf	−0.0853	0.1717
Cleaning dominant F − Sponge-dwelling subordinate M	0.07847	0.078	Inf	−0.0744	0.2313
Sponge-dwelling dominant F −Cleaning subordinate F	−0.20159	0.1531	Inf	−0.5017	0.0985
Sponge-dwelling dominant F − Sponge-dwelling subordinate F	0.099	0.1505	Inf	−0.1961	0.394
Sponge-dwelling dominant F −Cleaning dominant M	0.07423	0.1517	Inf	−0.2231	0.3715
Sponge-dwelling dominant F − Sponge-dwelling dominant M	0.45234	0.1706	Inf	0.118	0.7867
Sponge-dwelling dominant F −Cleaning subordinate M	0.04605	0.1521	Inf	−0.2522	0.3443
Sponge-dwelling dominant F − Sponge-dwelling subordinate M	0.08131	0.1464	Inf	−0.2056	0.3682
Cleaning subordinate F − Sponge-dwelling subordinate F	0.30059	0.0945	Inf	0.1154	0.4858
Cleaning subordinate F −Cleaning dominant M	0.27582	0.0772	Inf	0.1245	0.4271
Cleaning subordinate F − Sponge-dwelling dominant M	0.65394	0.1261	Inf	0.4068	0.9011
Cleaning subordinate F −Cleaning subordinate M	0.24764	0.076	Inf	0.0988	0.3965
Cleaning subordinate F − Sponge-dwelling subordinate M	0.2829	0.0898	Inf	0.1069	0.4589
Sponge-dwelling subordinate F −Cleaning dominant M	−0.02477	0.0789	Inf	−0.1794	0.1298
Sponge-dwelling subordinate F − Sponge-dwelling dominant M	0.35334	0.0958	Inf	0.1656	0.5411
Sponge-dwelling subordinate F −Cleaning subordinate M	−0.05295	0.0819	Inf	−0.2134	0.1075
Sponge-dwelling subordinate F − Sponge-dwelling subordinate M	−0.01769	0.068	Inf	−0.151	0.1156
Cleaning dominant M − Sponge-dwelling dominant M	0.37811	0.1008	Inf	0.1806	0.5757
Cleaning dominant M −Cleaning subordinate M	−0.02818	0.0584	Inf	−0.1427	0.0863
Cleaning dominant M − Sponge-dwelling subordinate M	0.00708	0.074	Inf	−0.1379	0.1521
Sponge-dwelling dominant M −Cleaning subordinate M	−0.40629	0.1043	Inf	−0.6108	−0.2018
Sponge-dwelling dominant M − Sponge-dwelling subordinate M	−0.37104	0.0901	Inf	−0.5475	−0.1945
Cleaning subordinate M − Sponge-dwelling subordinate M	0.03526	0.076	Inf	−0.1137	0.1842

F: female; M: male; CL: confidence limit; Inf: infinite. Sigma used for effect sizes: 7.253. Confidence level used: 0.95.

Table A4

Regression parameter estimates and *P* values for each investigated variable in the survival analysis predicting the latency to interact with clients

	Coefficient	Exp(coefficient)	SE(coefficient)	*z*	*P*
Conditional model					
Fixed coefficients					
Phenotype Sponge-dwelling	−1.86734044	0.1545341	1.1814673	−1.58	0.11
Sex Male	0.90194416	2.4643896	0.5941476	1.52	0.13
Status Subordinate	−0.04846777	0.952688	0.6844669	−0.07	0.94
Sponge-dwelling: Male	0.86546145	2.3761023	1.2559731	0.69	0.49
Sponge-dwelling: Subordinate	2.59063999	13.3383053	1.2963541	2	0.05
Male: Subordinate	−0.0494864	0.9517181	0.8660059	−0.06	0.95
Sponge-dwelling:Male:Subordinate	−1.81419272	0.1629694	1.5149357	−1.2	0.23
Random effects:					
Groups	Variance	SD			
Goby id	0.000398507	0.019962645			
Client id	0.352386177	0.59362124			
Social experiment group	0.477156062	0.690764839			

Table A5

Analysis of deviance table (Type II Wald chi-square tests) for models predicting the latency to interact with clients

Model including:	*df*	χ^2	Pr(>χ^2)
Phenotype	1	0.4672	0.494
Sex	1	3.6314	0.057
Status	1	1.4332	0.231
Phenotype: Sex	1	0.2634	0.608
Phenotype: Status	1	3.4258	0.064
Sex: Status	1	0.8055	0.369
Phenotype: Sex: Status	1	1.4341	0.231

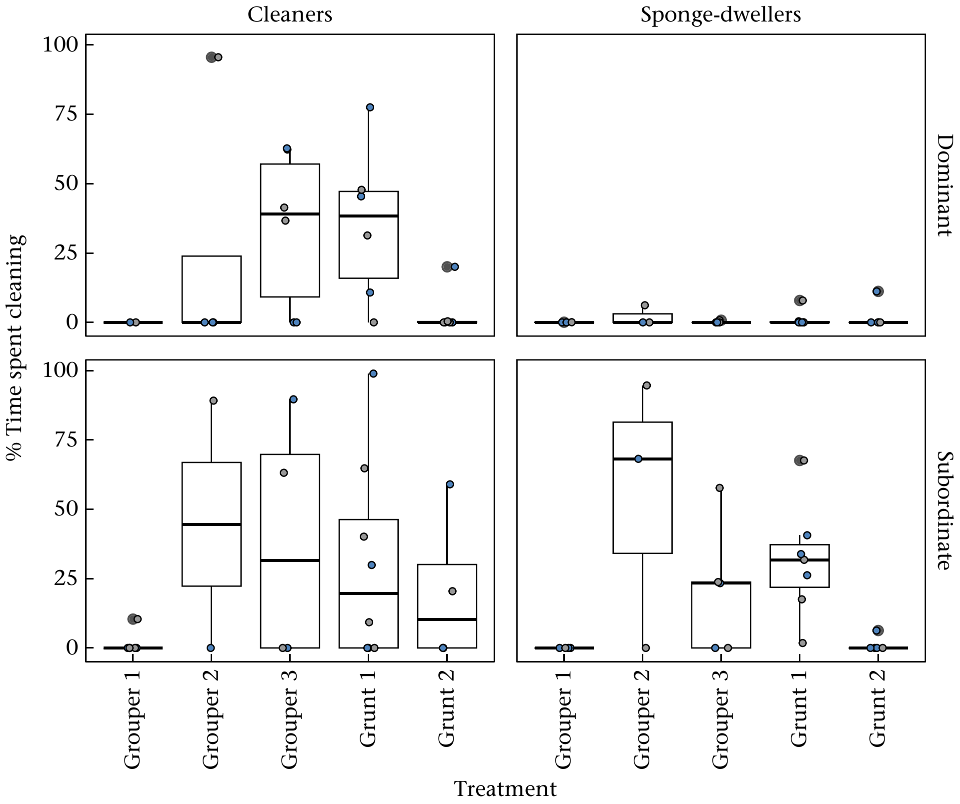


Figure A1. Percentage of time spent by gobies cleaning each client used in the experiment, according to phenotype (cleaners or sponge-dwellers), social status (dominants or subordinates) and sex (blue = females, grey = males).

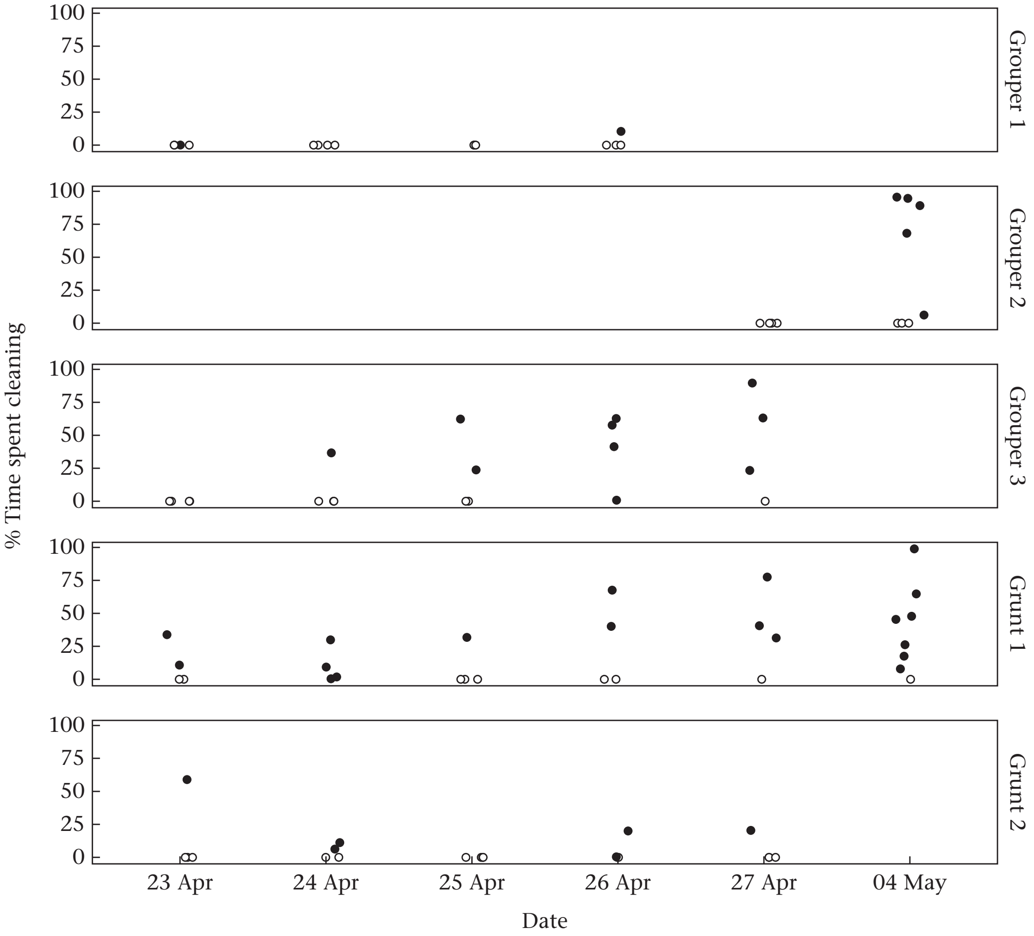


Figure A2. Percentage of time spent cleaning by experiment date (April–May 2018), separated by client. Black circles indicate no cleaning occurred and white circles represent individuals that spent time cleaning.

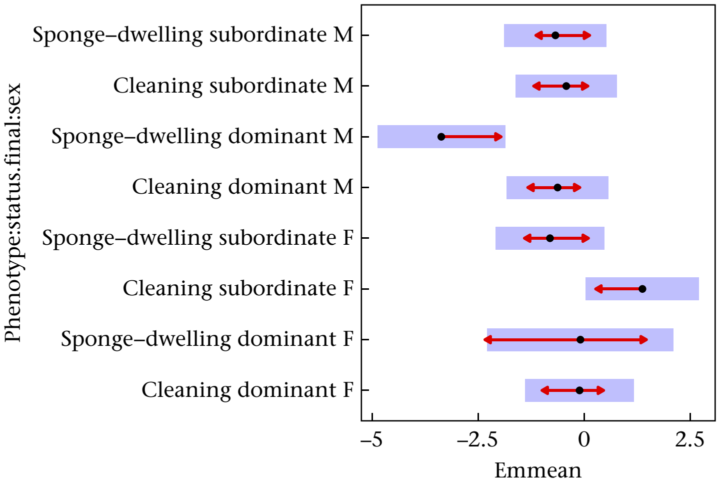


Figure A3. Pairwise comparison of estimated marginal means (EMMs) for levels of phenotype (cleaners or sponge-dwellers) versus social status (dominants or subordinates) versus sex (M = male, F = female) interactions in the glmm model (percentage of time cleaning). Blue bars show confidence intervals for the EMMs and red arrows indicate the comparisons among them. If an arrow from one mean overlaps an arrow from another group, the difference is not significant (Tukey test, alpha = 0.05).

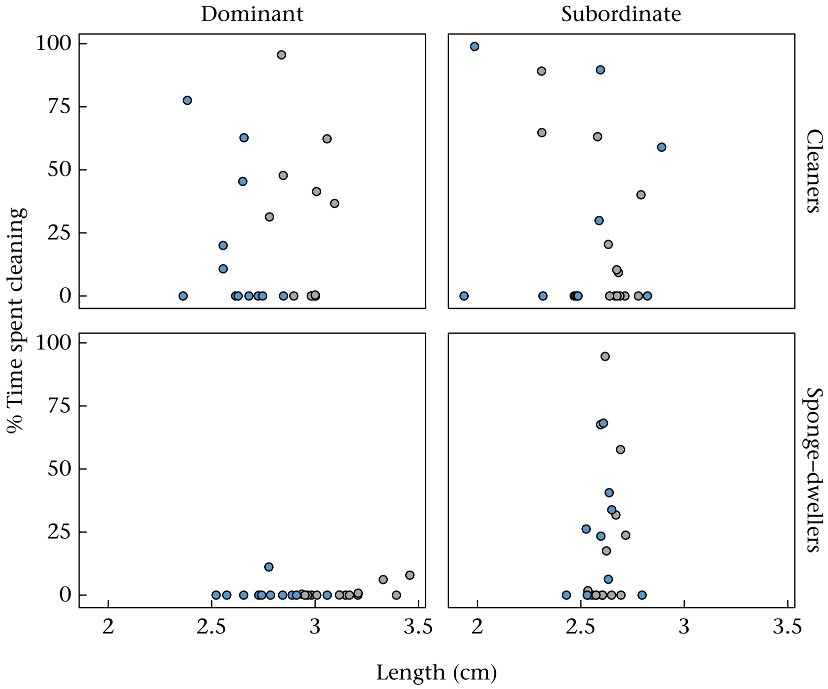


Figure A4. Percentage of time spent cleaning by phenotype (cleaners or sponge-dwellers), social status (dominants or subordinates), sex (blue = females, grey = males) and body size (total length, cm). Size range varied across groups, meaning that an individual of total length 2.9 cm could be a dominant in one group and a subordinate in another group.