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Not so monochromatic: Size-dependency of both sex and color in the cleaner wrasse *Labroides dimidiatus*

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In marine interspecific cleaning mutualisms, small fish known as “cleaners” inspect the surface, gills and sometimes the mouth of “client” reef fish, eating ectoparasites, mucus, scales and dead or infected tissue. These cleaner fish species share similar vivid coloration that makes them recognizable by clients. To gain insight on additional communication roles of cleaner fish color, we tested if differences in color among cleaner wrasse *Labroides dimidiatus* individuals captured from the wild are explained by sex, body size or parasite loads. We found that males were larger, heavier and tended to have more saturated blue tails than females. We also found blue color saturation to be positively correlated with size, and that this size-dependence explains the trend for the sexes to differ in color. Parasite loads did not predict individual differences in color, but fish in our sample were not heavily parasitized. Other color traits (including yellow color saturation and black color brightness) did not differ between the sexes and were associated with morphological differences. Size-dependence of blue color may thus suggest that it is a condition-dependent signal that could be used in various types of inter- and intraspecific social interactions.

KEYWORDS

cleaner fish, mutualism, coloration, communication, parasites

1. Introduction

The Indo-Pacific cleaner wrasse, *Labroides dimidiatus*, is one of the most studied cleaner fish species and has been a model system for work on the evolution of among-species cooperation (Soares, 2017). This cleaner has a lateral black stripe on a conspicuously vivid blue background, together with some yellow in the front, resembling the coloration of several other cleaner species in the same family (Arnal et al., 2006). These color patterns are used by client fishes to identify cleaners (Stummer et al., 2004; Cheney et al., 2009), and their blue color within the pattern attracts more client fish to cleaning stations (Cheney et al., 2009). Moreover, at least in juvenile *L. dimidiatus*, their color pattern appears to deter predation (Cheney, 2013). Therefore, the vivid colors of cleaner fish are an interspecific communication signal of cleaning for prospective clients (Vaughan et al., 2017).

In non-cleaner species, vivid colors often signal among-individual differences in some aspects of quality. For example, colorful signals are often sexually dichromatic and used in mate choice and may indicate aspects of individual health or condition such as parasite infection level (Johnstone, 1996; Maan et al., 2008; Megía-Palma et al., 2016). In aposematic species, differences in color can also indicate differences in toxicity among individuals (reviewed in Summers et al., 2015). Similarly to sexual and aposematic color signals, among-individual differences in the vivid colors of cleaner fish might also provide cues to aspects of individual quality that are useful for either conspecifics or to interspecific clients. For example, clients use this blue color to distinguish cleaner fish from non-cleaning species (Cheney et al., 2009), and recent laboratory experiments suggested that blue color saturation in *L. dimidiatus* is condition-dependent, thus providing cues on the quality of individuals or the quality of the cleaning service they provide (Trigo et al., 2020). These cues could inform clients decisions when evaluating individual cleaners, which in nature would allow choosing a better cleaning service. But natural variation in color within a wild population has never been studied for any cleaner fish species. Therefore, there is a lack of insight from the wild on which individual traits color differences may signal.

In order to gain further understanding on the communication role of cleaner fish color variation, specifically their blue color saturation, here we asked if among-individual differences in coloration are explained by sex, body size or degree of parasitism in *L. dimidiatus*. This cleaner species is protogynous hermaphrodite, first breeding as females and some eventually changing sex to become male harem owners (Robertson, 1972, 1974). As in other members of the genus *Labroides*, males are on average larger than females (Robertson, 1972) but, although detailed studies of sex differences in color are lacking, the species is described as sexually monochromatic, that is, females can display the same color patterns as males (Pandian, 2010). Since sex and size are correlated in this protogynous hermaphrodite species, we measured color in males and females, tested for sex differences in color, and whether those differences could be a consequence of, or independent from, body size. Additionally, these cleaner fish also naturally carry ecto and endoparasites (Narvaez et al., 2021), which they obtain from their environment or are transmitted from their clients (e.g., Jones et al., 2004; Narvaez et al., 2022). Because parasite load can be a major challenge to the condition of cleaner fish we also asked if this is reflected in their color signal variation.

2. Methods

2.1. Cleaner collection and measurements

All work carried was in accordance with the James Cook University Animal Ethics guidelines (JCU Animal Ethics approvals A2558). We collected cleaner fish *Labroides dimidiatus* ($n = 30$) on the Great Barrier Reef (GBR) at Lizard Island (14° 40'S, 154° 24'E) during November 2018 by SCUBA divers with barrier- and hand-nets at different sites around the island (for a detailed description of locations see Narvaez et al., 2021). Larval settlement of *L. dimidiatus* at these reefs mostly occurs in November and December (larvae settle about 3 weeks after hatching, Brothers et al., 1983). This indicates that cleaner spawning occurs between October and December (Waldie et al., 2011; Grutter, 2012), when we conducted

our work, making it easier to distinguish the sexes. Fish were transferred to individual hermetic plastic bag filled with water to keep them alive and minimize the loss of ectoparasites. At the Research Station (Lizard Island Research Station), we euthanized each fish using an ice slurry. We then measured size (total length, in centimeters), mass (weighted wet, in grams), and photographed (see below) each fish, within the following 3 min, to minimize color loss due to death. We calculated size-corrected mass using residuals from a regression of mass on size for all the individuals, as this is a robust method to obtain indices of body condition (Schulte-Hostedde et al., 2005). Male and female data fitted well the same regression line (Supplementary Figure S1), and therefore we computed the index of body condition together for both sexes. The final sample size was 21 females and 8 males (one individual could not be sexed and was excluded from analyses). Cleaner sex was determined by visually analyzing the gonads. Because our field collection occurred within the spawning season, fish were easily sex based on gonad morphology as female gonads were larger and often contained eggs.

2.2. Determination of cleaner parasite load

To determine the parasite community of the cleaner fish, fish were examined fresh for ecto- and endo-parasites (see Narvaez et al., 2021 for detailed methods). For ecto-parasites, the external surface, fins, gills and oral cavity were visually inspected under a low-power dissection microscope, and a skin scrape was done. Gills were removed and placed on a microscope slide for further analysis of smaller parasites (e.g., protozoan parasites). Fish were then placed into a Petri dish with physiological saline during 10 min to remove any potential external parasites. After all the external evaluation procedures, the fish were dissected for examination of endoparasites. All organs were superficially inspected under a low-power dissection microscope. Smears and squashes of body muscle and internal organs (gall bladder/bile, brain, kidney, spleen, and liver tissue) were produced and inspected for the presence of protozoan and myxozoan infection. Ectoparasite load included isopod crustaceans in the family Gnathiidae and parasitic species in the subclass Copepoda, and endoparasite load included trematode worms in the digestive tract.

We calculated the prevalence (number of fish infected/number of fish examined) and the abundance of parasites (mean \pm standard error), for all the individuals.

2.3. Cleaner skin coloration

We measured fish skin colors based on digital photographs taken in same light conditions (two artificial white led lights placed 25 cm above the fish and on each side of the fish). Photographs were taken with a Nikon COOLPIX W300 camera, with a fish placed laterally in a petri dish above a squared sheet of paper (Supplementary Figure S2). We used the software GIMP (Gimp 2.8.20) to quantified the mean RGB (red, green, blue) values in four circles with diameter of 2.5 mm, located at: (a) the dark blue patch at the base of the tail; (b) the blue/yellow patch midway in the fish body (i.e., above the end of the pelvic fin and at the center of the blue/yellow stripe); (c) the yellow patch, measured at the center of the stripe above the beginning of the pelvic fin; and (d) the black stripe, measured at the center of the stripe above

the beginning of the anal fin (Supplementary Figure S2). We then converted RGB values into HSB (hue, saturation, and brightness) with the R function `rgb2hsv` which converts the red, green, and blue values of an RGB image to hue, saturation, and value (HSV) values of an HSV image. Each cleaner was photographed twice, and we averaged the HSB color measurements so as to obtain a single color hue, saturation and brightness per fish per body part. Measurements from with the two photographs on the same individual had high repeatability on tail blue saturation ($R=0.81$) and mid-body hue ($R=1.0$), and medium repeatability for yellow saturation ($R=0.48$) and black brightness ($R=0.33$). Therefore, we perform analyses for all the color variables, but results for yellow saturation and black brightness should be interpreted with caution.

These measurements were used to quantify different aspects of the fish coloration. For the blue and yellow patches (measurements in patches a and c, respectively), we used the measurement of color saturation, since this relates to the conspicuousness of color, and color saturation is related to individual quality in several animal species (Weiss, 2006; Simons et al., 2012; Trigo and Mota, 2015). For the black stripe (measurements in patch d) we measured brightness as a means to quantify the purity of black color (as indicated by low brightness). And we used the hue measured midway the blue/yellow stripe (patch b) as an index for the extent of blue: the lower (i.e., the bluer) the hue in the middle of this stripe, the larger is the extent of blue coloration. We thus obtained four color variables: (a) tail blue saturation; (b) mid-body hue, to evaluate individual differences in the extent of blue coloration; (c) yellow saturation, and (d) black brightness.

We standardized all measurements by reference to the background yellow and brown colors in the same squared paper below each fish. For this, we selected a square of the squared paper immediately below the beginning of the anal fin, and measured the RGB values of paper yellow (“py”) using a 2.5 mm circle as before, and of paper brown (“pb”) using a circle small enough to be inside the brown line. We used these measurements to standardize each color measurement following Hill et al. (2009). We first calculated, separately for each fish measurement (“sample”) $(\text{sample} - \text{py})/(\text{pb} - \text{py})$, which rescales the sample measurement (either H, S or B) to a scale from 0 to 1 where 0 and 1 correspond to the “pb” and “py” values in that same photograph. We then multiplied these rescaled measurements (either H, S, or B) by the mean difference between “py” and “pb” values across the photographs of all fish, and added the mean value of “py” across the photographs of all fish, in order to approximate the original scale of either H, S or B values.

2.4. Statistics

Mass (in grams), size (in cm), size-corrected mass, blue and yellow saturation and mid-body hue followed approximately normal distributions. Black brightness was log-transformed ($\log_{10} x + 1$) in order to approximate a normal distribution. Ecto and endo-parasite loads were strongly non-normal and, therefore, we analyzed them using non-parametric tests. We verified that there was homogeneity of variance between sexes, for all color variables.

To test for sex differences in body measurements and color variables we ran independent sample *t*-tests. For sex differences in parasite loads we instead ran non-parametric Mann–Whitney tests. To test for associations between color and morphological traits (size and size-corrected mass) or parasite loads we first used simple Pearson correlations, or non-parametric Spearman’s correlations in the case of

parasite loads. Then, to test for these associations with color while controlling for covariates, we ran general linear models (GLM) with a color trait as dependent variable, sex as fixed factor, and size, size-corrected mass and parasite loads as covariates. In these GLMs we chose to include size and not weight because these two variables are highly correlated (Pearson correlation = 0.96, $p < 0.001$). We checked that residuals in these GLMs approached normality. Analyses were performed in IBM SPSS Statistics.

3. Results

3.1. Sex differences

Ectoparasite prevalence was 33% for females (i.e., seven females) and 50% for males (i.e., four males). For endoparasites, prevalence in females and males were 29 and 38%, respectively. The complete description of the parasites in these individuals (irrespective of sex) can be found in Narvaez et al. (2021) (Supplementary Table S1).

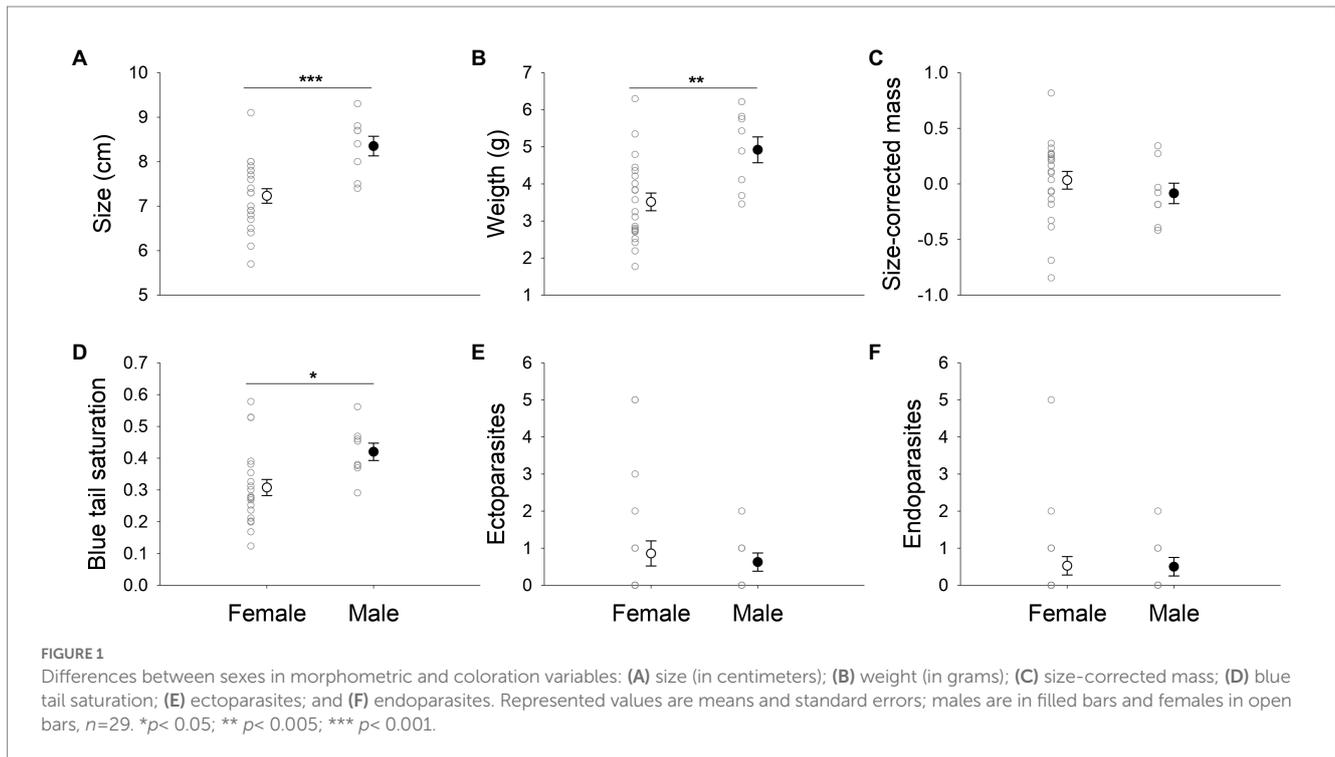
Males were on average heavier and longer than females (Independent sample *t*-test, weight: $t = 3.06$, $p = 0.005$; size: $t = 3.63$, $p = 0.001$; Figures 1A,B), and size-corrected mass did not differ between the sexes (Independent sample *t*-test, $t = -0.81$, $p = 0.43$; Figure 1C). Males show a non-significant tendency to have higher tail blue saturation values than females (Independent sample *t*-test, $t = 1.97$, $p = 0.06$; Figure 1D). Males and females did not differ significantly in ectoparasite (Mann–Whitney test, $U = 76.0$, $p = 0.65$; Figure 1E) or endoparasite loads (Mann–Whitney test, $U = 77.0$, $p = 0.68$; Figure 1F), nor in the remaining color variables (Independent sample *t*-test, yellow skin saturation: $t = 1.20$, $p = 0.24$, mid-body hue: $t = 0.84$, $p = 0.41$, black brightness: $t = 0.78$, $p = 0.44$).

3.2. Color, body measures, and parasites

Tail blue saturation was positively correlated with size (Pearson correlation, $r_p = 0.50$, $p = 0.006$, $N = 29$; Figure 2A), but not with size-corrected mass (Pearson correlation, $r_p = -0.14$, $p = 0.48$, $N = 29$; Figure 2B), ectoparasite (Spearman’s correlation, $r_s = 0.22$, $p = 0.24$, $N = 29$; Figure 2C) or endoparasite loads (Spearman’s correlation, $r_s = -0.07$, $p = 0.71$, $N = 29$; Figure 2D). All remaining color variables did not have significant correlations with any of the body or parasite variables (Pearson correlation, all $|r| < 0.32$, all $p > 0.09$, $N = 29$; Supplementary Table S2).

When controlling for covariates, however, the association between size and tail blue saturation was slightly weaker ($\beta_{st} = 0.39$) and no longer statistically significant with our sample size (General linear model, $F_{1,29} = 2.95$, $p = 0.10$), and a sex difference in blue color saturation was no longer suggested (General linear model, $\beta_{st} = -0.15$, $F_{1,29} = 0.34$, $p = 0.57$; Table 1). Other body color variables were not predicted by any of the predictors (General linear model, all $|\beta_{st}| < 0.27$, all $p > 0.36$; Supplementary Table S3).

Because differences in size were associated both with sex and blue color saturation, we repeated the General linear model for blue saturation, now also including the interaction terms between sex and the other predictors. These interaction terms were not significant (interaction sex * size: $F_{1,29} = 1.84$, $p = 0.19$; other results in Supplementary Table S4), indicating that the relation between size and color did not differ between males and females (Figure 2A).



4. Discussion

We found that male cleaner wrasses (*L. dimidiatus*) are heavier, longer and had a non-significant tendency to show more saturated blue color than females. Endo- and ectoparasite loads did not predict blue color saturation. The saturation of blue color was positively correlated with size but, when using a model with multiple predictors (sex, size, size-corrected mass, parasite loads) to control for the effects of covariates, the trend for sex differences in color was no longer detected, and the association of color with size was also slightly weakened. Therefore, sex differences in color may appear in the cleaner wrasse as a consequence of sex differences in size and an association between size and blue color saturation. The remaining color traits studied here did not differ between the sexes nor were associated with morphology or parasite loads. These latter results should be interpreted with caution, because repeatability was not strong for some of those other color measurements (namely for yellow saturation and brightness of black).

Finding an association between blue color saturation and body size or mass suggests that the conspicuous blue color of *L. dimidiatus* could signal for physical condition. This agrees with previous experimental results, showing that an oxidative stress treatment was able to reduce blue color saturation and the quality of the cleaning service in these species (Trigo et al., 2020). Such a condition-dependent signal could be used both in intra- and inter-specific contexts. In an inter-specific context, this condition-dependent signal could be used by potential clients when choosing cleaners. In fact, clients are known to exert choice between alternative individual cleaners and cleaning stations (Bshary and Schäffer, 2002). Furthermore, cleaners also advertise their cleaning stations to clients with “dances” (Potts, 1973) in which they swim in an oscillating manner (Youngbluth, 1967; Losey, 1971), with their conspicuous black stripe and strikingly prominent blue tail during these dances. Stummer et al. (2004) used models of *L. dimidiatus* to show that, in

models of normal body size, a larger black stripe increased the number of clients approaching, but not their interest at close distance. They concluded that the black stripe attracts clients at distance, but at close range, the client interest may be based on other cues such as behavioral (e.g., cheating behavior) or sensorial (e.g., chemical cues). Another example of choice exerted by clients, occurs when these eavesdrop on cleaners’ interaction with other clients in order to choose whether to wait and visit that cleaner or search for another (Pinto et al., 2011). Clients benefit from choosing among individual cleaners, because cleaning service can differ significantly: cleaners may attend to clients rapidly or make them wait, they may or may not provide tactile stimulation, and they can also cheat by feeding on healthy body tissue instead of ectoparasites (Bshary, 2002; Bshary and Côté, 2008). Whether or not clients evaluate among-individual differences in blue color saturation to help with their choice remains to be studied. If the color of the blue tail indicates aspects of quality, then clients may use this information when making their choices.

In an intra-specific context, condition-dependent color may perhaps help to assess dominant status among cleaners, which is important for their social behavior. For instance, dominant cleaner males are generally older individuals that live and clean in pairs, choosing for this the largest female of their harem, but patrolling all other females regularly (Robertson, 1972). When the male disappears, usually the largest (and more dominant) female of that harem, or from a nearby territory, changes sex and takes over the harem (Sakai et al., 2001). We can assume that cleaner wrasses compete to increase social status and hence to gain access to better territories. In the case of males also to gain access to female harems, and in the case females also to clean with the dominant male as a pair (since pairs usually inspect larger clients; Bshary et al., 2008) and eventually to gain priority in transitioning sex to a harem-holding male. Since dominance increases with size (Sakai et al.,

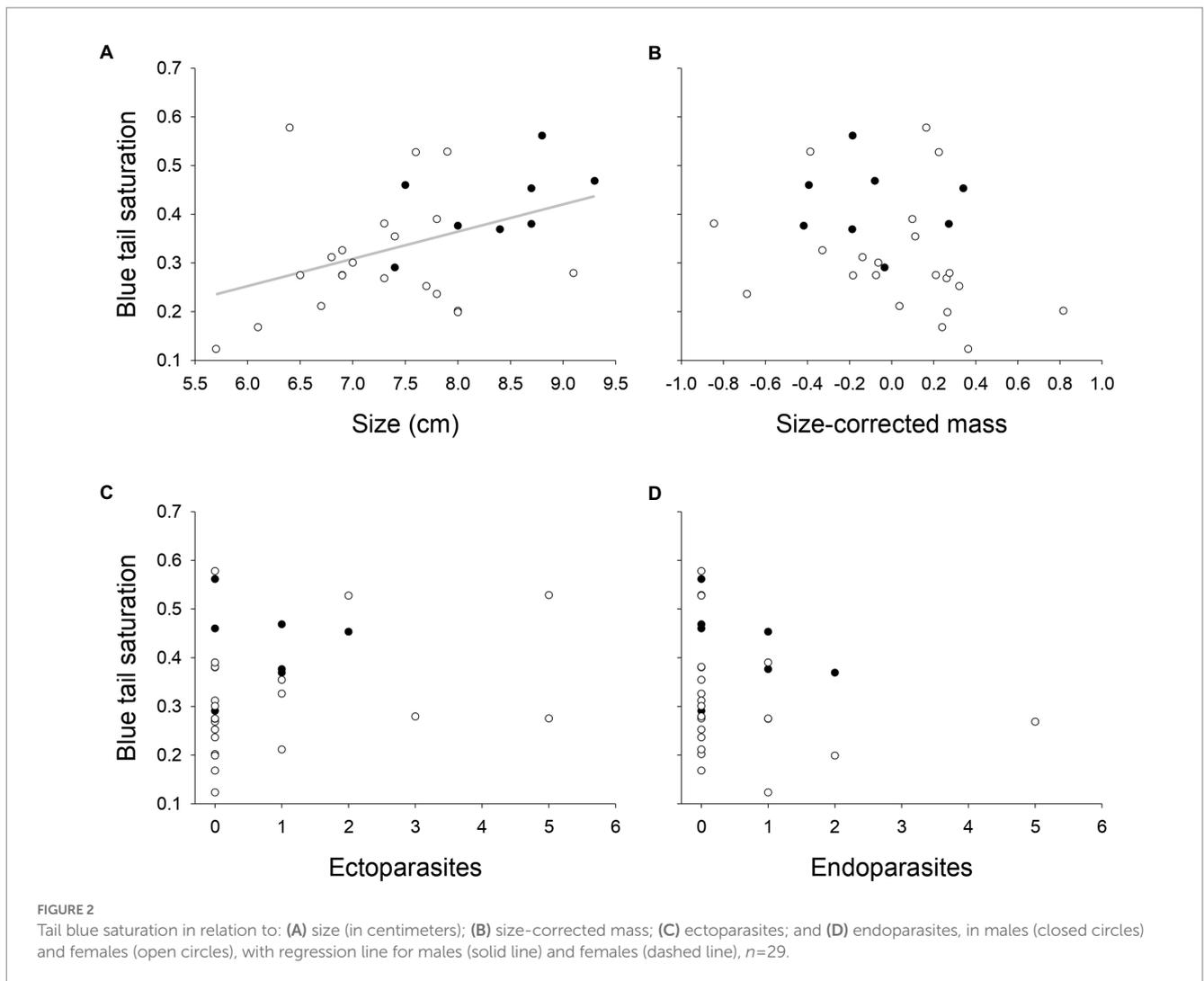


TABLE 1 GLM for tail blue saturation.

	β_{st}	F (P)
Sex	-0.15	0.34 (0.57)
Size	0.39	2.95 (0.10)
Size-corrected mass	-0.11	0.37 (0.55)
Ectoparasites	0.17	0.88 (0.36)
Endoparasites	-0.06	0.12 (0.73)

Represented are the standardized regression coefficients (β_{st}), test value (F) and respective significance (P), sample size is 29.

2001), and having found that blue color saturation covaries with size, we hypothesize that cleaner wrasses may use the blue color of conspecifics to help evaluate social dominance during these various types of social interactions. This too, however, remains to be studied.

The absence of sex or size differences regarding other colors (yellow or black) is not surprising considering the importance of blue guild coloration to distinguish cleaner fish species from non-cleaners (Cheney et al., 2009). While cleaners are more likely to have a combination of blue and yellow colors and there is evolutionary correlation between displaying black stripes and cleaning behavior (Arnal et al., 2006), blue color is still the source of highest chromatic

contrast against most microhabitat backgrounds, as evaluated by the visual systems of most client species (Lettieri et al., 2009). Finally, we expected higher parasitism levels affected coloration, since some studies in other fish species have reported negative associations between parasite infection and aspects of individual quality (e.g., size of sand bowers in *Copadichromis* spp., Taylor et al., 1998, or territory size and red coloration in a diverse lineage of Lake Victoria cichlids, *Pundamilia nyererei*, Maan et al., 2008). However, we did not find associations between parasite infestation and cleaners, which could be due to parasite loads in the wild being low to affect coloration, while cleaners not being exempted from parasite infection (Narvaez et al., 2021, 2022), or to these parasites not being detrimental.

In this study we found that, unlike commonly assumed, the cleaner wrasse *L. dimidiatus* may not be entirely sexually monochromatic (Pandian, 2010) but show size-dependency in both their sex and their blue color. Since the cleaner wrasse is able to change sex bidirectionally, depending on sex-ratio and social-environmental factors, perhaps the association between blue color saturation and size makes the blue color a useful signal of sex, or even a sexually-selected trait. Simultaneously, since blue color saturation indicates size, it can be a more general signal of individual quality or condition, useful also for interspecific (cleaning) interactions with clients. Such a condition-dependent

signal of quality might be used in various types of inter- and intraspecific interactions, including choice of cleaning stations, competition for resources or individual dominance within harems, thus suggesting several hypotheses for future research.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

PN performed the material preparation and data collection. ST performed the analysis and wrote the first draft of the manuscript. All authors commented on previous versions of the manuscript, read and approved the final manuscript, and contributed to the study conception and design.

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Conflict of interest

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1110079/full#supplementary-material>

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