RESEARCH ARTICLE

Influence of color and brightness on ontogenetic shelter preference by the prawn *Macrobrachium rosenbergii* (Decapoda: Palaemonidae)

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ABSTRACT. The giant river prawn, *Macrobrachium rosenbergii* (de Man, 1879), is a species of great commercial importance. It is farmed under different conditions that translate to a great range of light environments, which impact their behavior and productivity. We present the first study employing both visual modeling and behavioral data to evaluate the ontogenetic changes in color preferences of juveniles and adults of *M. rosenbergii*. We offered ten shelters of different colors to juveniles and adults and registered their preferences. Our results show that shelter preference changed with ontogeny: juveniles chose shelters based on chromaticity (preference for blue), while adults based their decisions on brightness (preference for dark grey). This preference adults show for dark colors is probably associated with light avoidance behavior. We recommend providing blue shelters for juveniles and dark shelters for adults.

KEY WORDS. Animal behavior, aquaculture, color vision, ontogeny, visual modeling, welfare.

INTRODUCTION

The giant river prawn *Macrobrachium rosenbergii* (de Man, 1879) is native to a region that encompasses Malaysia, East India, West Indonesia, Gulf of Bengal, and Gulf of Thailand (Holthuis and Ng 2010). In their natural environment, the larvae inhabit estuarine environments (Sandifer and Smith 1985), are planktonic (New 2002) and go through 11 larval stages (from Zoea I to Zoea XI) (Sandifer and Smith 1985). After a larval period of 20 to 50 days, the larvae undergo metamorphosis into post-larvae (Sandifer and Smith 1985), which are benthic and begin migration to freshwater environments, where they remain until adulthood (New 2002) and mate (Sandifer and Smith 1985). Then, the ovige-

rous female migrates to estuarine environments, where the larvae hatch from the eggs, restarting the cycle (Sandifer and Smith 1985).

Macrobrachium rosenbergii is a species of great commercial importance (Zeng et al. 2012, Engle et al. 2016) that, in 2018 alone, accounted for the production of 234,400 tons of food worldwide (FAO 2020). These prawns are farmed under various conditions (Coyle et al. 2010, Daniels et al. 2010, Valenti et al. 2010a, 2010b), which might translate to a great range of light environments, which have the potential to impact the biology and productivity of prawns. In fact, one study has already shown that the color of the environment can change the color of the prawns themselves, in order to favor camouflage (Borisov et al. 2022). Another study has

already shown that food color affects prawns' larvae feeding behavior (Yong et al. 2018). In different species, color preference has also been related to the selection of appropriate habitats (Strader et al. 2015, Gu et al. 2017, Havel and Fuiman 2017). For instance, changes in color preference throughout the ontogenetic development of some caridean shrimps (Lysmatidae) have been related to the physical properties of the environments occupied by them at different stages of development (Johnson and Rhyne 2015). Therefore, the study of color preference by species of economic interest might exert an important role in animal welfare and food productivity.

Morphologically, the eyes of *M. rosenbergii* change throughout ontogenetic development, since larvae have functionally apposition eyes, whereas adults have functionally reflecting superposition eyes (Nilsson 1983). The superposition eyes are more efficient for gathering light and can be advantageous in low light conditions, but the transformations necessary for the appearance of a superposition eye may not be complete in post-larvae, as seen in a caridean shrimp (Douglass and Forward 1989). Regarding the visual sensitivity of the species, it was found that dark-adapted individuals exhibit a light absorption peak at 563 nm, which corresponds to the yellow-red region of the spectrum (Matsuda and Wilder 2014), although the authors don't specify how many photoreceptor types would be accounting for the sensitivity curve. Still, in spite of the large number of experiments that have already been conducted with *M. rosenbergii* (Chong-Carrillo et al. 2016), only recently their visual system began to be studied through behavioral experiments (Kawamura et al. 2016, 2017, 2018, 2020).

Through visual modeling studies, a strategy that has currently gained popularity, it is possible to assess which spectral information available in the environment could be exerting an adaptive function. During visual modeling, we infer how the visual system of a given animal is stimulated by observing a particular object under a specific illuminant (Olsson et al. 2018). In other words, just by knowing how many kinds of photoreceptors (and their peak sensitivities) there are in the eye of an animal, the spectrum of ambient light, and the color of an object of interest, we can suppose how the object should be seen by that observer. Yet, although variations in the type and number of photoreceptors are usually related to the dimensionality of color vision, only behavioral tests can verify an animals' color perception (Jacobs 1996). So, it is important to couple visual modeling data with behavioral experiments that can validate them (Lind and Kelber 2009).

To our knowledge, the availability of chromatic and achromatic cues to *M. rosenbergii* has never been properly analyzed by means of visual modeling. The experiments already carried out either did not try to control the brightness of the stimuli or tried to do so without correctly taking into account the prawns' visual system. In color preference experiments, the choice of stimuli colors should consider the eye of the beholder (Hill 2002), not human vision. By using visual modeling, we can control the colors of the stimuli to be presented to prawns in a rigorous manner, as in studies with other animal species (Detto 2007, Siebeck et al. 2014, Olsson et al. 2015, Escobar-Camacho et al. 2019).

Therefore, here we developed the first color preference study on *M. rosenbergii* employing visual modeling, as a more rigorous control for stimuli brightness and chromaticity, according to the visual system of prawns. Our aim is to investigate whether their preference for different colors and brightness changes over their development. Since *M. rosenbergii* spontaneously occupies experimental shelters (Santos et al. 2015), we analyzed the preference that two benthic developmental stages (i.e. juveniles and adults) show for shelters of different chromaticities and brightness. Our hypothesis is that *M. rosenbergii* changes its color preference gradually throughout ontogeny, regardless of the farming conditions. This ontogenetic shift would be adaptive in natural populations because the spectral composition (i.e. color) of the surrounding natural photic environment changes as they start migrating from estuaries to freshwater ecosystems. Since this migration only begins when *M. rosenbergii* reaches its post-larvae developmental stage, we predict that adults will be more prone than juveniles to exhibit strong preferences for longer wavelengths, such as yellow and orange, which are colors associated with freshwater bodies (Stoffels 2013).

MATERIAL AND METHODS

Ethical statement

Our research was approved by the Ethics Committee on the Use of Animals of our institution (protocol 042/2018) and is in accordance with Brazilian law. It complies with ARRIVE guidelines and was carried out in accordance with the U.K. Animals (Scientific Procedures) Act 1986, and associated guidelines, EU Directive 2010/63/EU for animal experiments.

Animal maintenance

At the Sensory Ecology Laboratory of the Federal University of Rio Grande do Norte, we kept 39 juveniles of

M. rosenbergii. Animals were housed in a collective aquarium (100 x 50 cm, 40 cm water column), with transparent water, sandy substrate, and aeration. They were subjected to a 12-hour light/12-hour dark light cycle (light from 6:00 a.m. to 6:00 p.m.). Two fluorescent lamps provided a light intensity of approximately 320 lux (measured with an Extech Instruments HD 400 Light Meter), which should be sufficient for color discrimination (Kawamura et al. 2018).

We kept the physical-chemical parameters of the water at optimum levels for the prawns (pH: 7.0–7.5; ammonia: 0 mg/L; temperature: 26–28 °C) and fed the animals twice a day (morning and afternoon) with commercial food containing 42% crude protein. Twenty percent of the aquarium's water was changed twice a week.

Experimental apparatus

We also made available transparent water, sandy substrate, and aeration in two experimental aquaria, with aeration positioned, approximately, at the center of each aquarium. In each experimental aquarium, we arranged ten shelters, in two rows of five. We built the shelters with plastic-coated paper, folded in an appropriate way. Each aquarium had six grey shelters (PANTONE 19-1101 TPG, PANTONE P 172-15 C, PANTONE P 173-3 C, PANTONE P 179-3 C, PANTONE 10101 C, PANTONE P 179-1), each one with a different brightness, besides a blue (PANTONE 2728 C), a green (PANTONE 802 C), a yellow (PANTONE 397 C) and an orange (PANTONE 2012 C) shelter (Fig. 1).

Shelters' colors and brightness

For choosing our stimulus colors, we printed 101 different color patches that were coated with plastic and had their reflectance spectra measured by us with a spectrophotometer (USB4000 UV-VIS Fiber Optic Spectrometer, Ocean Optics, Inc.). We coupled the spectrometer to a bifurcated optical fiber (QR450-7-XSR, Ocean Optics, Inc.), also attached to a light source (DH-2000-BAL, Ocean Optics, Inc.). A white standard surface (WS-1-SL, Ocean Optics, Inc.), and the obstruction of the light source and optical fiber, were used as, respectively, the white and the black standards, for system calibration. We also measured the illuminant of the experimental room with the spectrometer coupled to an optical fiber (QP450-2-XSR, Ocean Optics, Inc.), attached to a cosine corrector (CC-3-UV-S, Ocean Optics, Inc.). We calibrated this spectrometric system with a calibration light source (LS-1-CAL, Ocean Optics, Inc.).

We run visual models, through pavo 2 (Maia et al. 2019), a package for R 3.4.1 (R Development Core Team
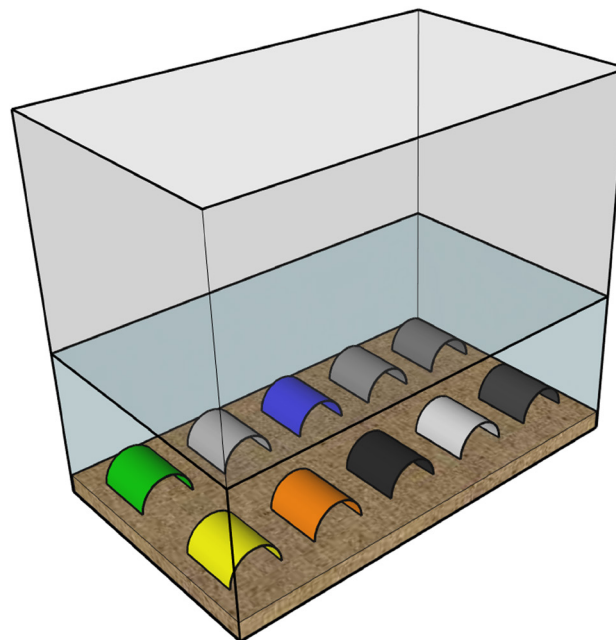

Figure 1. Schematic view of the arrangement of shelters in an experimental aquarium. The prawns were individually tested in aquaria with 10 colored shelters arranged in two rows of five.

2020), to infer how each color patch would be seen according to the visual system of the prawns. Our model computed the quantum catches absorbed by each type of photoreceptor described for prawns when the animals visualized each shelter (reflectance spectra in Fig. 2), that was illuminated by
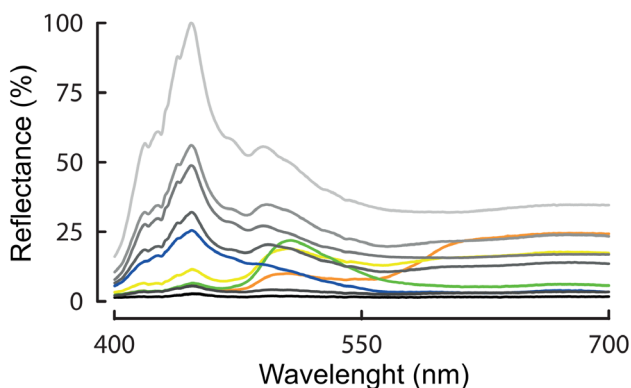

Figure 2. Reflectance spectra of experimental shelters. The reflectance of each curve is represented as a percentage, compared to the maximum reflectance of the most reflective curve. Each curve is represented approximately the same color as the respective shelter.

the fluorescent lamps of our experimental room (Fig. 3). The absorption peaks of the photoreceptors of another species, the ghost shrimp *Palaemon paludosus* (Gibbes, 1850) (380 nm and 555 nm) (Goldsmith and Fernandez 1968), were adopted in our model since data were not available for *M. rosenbergii*. *Palaemon paludosus* is the species most closely related to *M. rosenbergii* for which photoreceptors' absorption peaks have been established. Using photoreceptors' absorption peaks of related species is a viable alternative since small variations in estimated peaks do not carry a great influence on visual modeling results (Lind and Kelber 2009, Olsson et al. 2018).
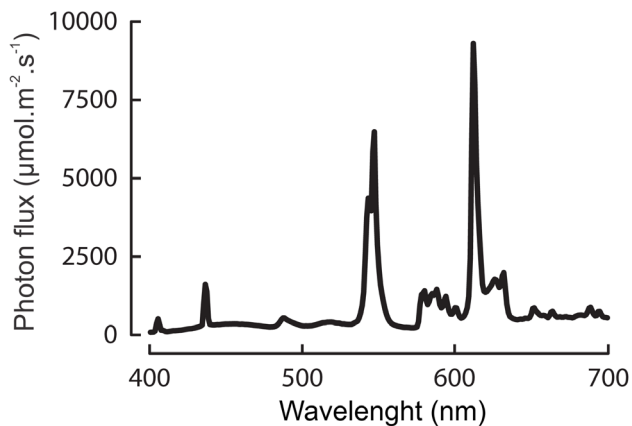

Figure 3. Illuminant spectrum of the experimental room. Illumination was provided by two fluorescent lamps.

In order to calculate the signal of each photoreceptor, we divided the amount of light reflected by a stimulus (shelter) and captured by a specific photoreceptor class (stimulus quantum catch), by the amount of light reflected by a perfectly white surface (white standard) and captured by the same photoreceptor class (maximum quantum catch). Following Detto (2007), we computed achromatic signals for each stimulus, as the sum of signals of short-wavelength (S signals) and long-wavelength (L signals) photoreceptors. For chromatic signals, we divided S signals by L signals (Siebeck et al. 2014). Chromatic and achromatic signals were plotted in a chromaticity-luminance diagram (Fig. 4) that shows how our stimuli varied with respect to color and brightness. We chose not to use the RNL model (Vorobyev and Osorio 1998) because it demands visual parameters (Olsson et al. 2018) that are still unknown for prawns.

Experimental design

In experiment 1, we individually tested 39 juveniles about two months after metamorphosis (body weight: 0.46 ± 0.13 g; total length: 3.89 ± 0.36 cm), two juveniles per day, each one in a smaller experimental aquarium (30 x 50 cm). The shelters, in experiment 1, measured 7 cm depth x 6 cm width x 3 cm height. The position of the different shelters for each animal was randomized. We completed this experiment in four weeks.

In experiment 2, we individually tested 24 of the 39 previously tested individuals, when they were already adults about seven months after metamorphosis (body weight: 6.4 ± 3.2 g; total length: 8.49 ± 1.84 cm), one adult prawn per day, in a larger experimental aquarium (50 x 100 cm). The shelters, in experiment 2, measured 7 cm depth x 9 cm width x 5 cm height. We completed this experiment in five weeks. Otherwise, the two experiments were identical. Differences in sample size between experiments 1 and 2 were due to animal mortality. We did not sex the prawns or record their morphotypes in our experiments.

In both experiments, we fed all prawns in the collective aquaria at 7:30 a.m., removed each prawn, that was about to be tested, from the collective aquarium and transferred it to the center of an experimental aquarium at 8:00 a.m. From 9:00 a.m. to 5:30 p.m., every 30 min, we recorded if the only animal was inside/on top of a shelter (shelter occupancy), or if it was away from any shelter (no choice), following Kawamura et al. (2017). This record was made directly, without the use of a video camera. After the experimental session, we removed the prawn from the experimental aquarium, recorded its weight and total length, and transferred it to another collective aquarium, in which individuals that had been already tested were kept. All animals were fed again at the end of the day.

Statistical analysis

We performed ten chi-square tests, one for each shelter, for unequal expected proportions, to verify if the occupancy of each shelter differed from the expected 10% of all cases. We employed the Bonferroni correction to account for multiple comparisons and set our α to 0.005. All tests were performed in BioEstat 5.3 (Ayres et al. 2007).

RESULTS

Visual modeling

Regarding our stimuli, the blue shelter generated a chromatic signal that stood out from the green, the yellow, and the orange shelters (Fig. 4), a strong indication that the blue shelter could be perceived, by the visual system of the prawns, as being of a different color. In contrast, these four
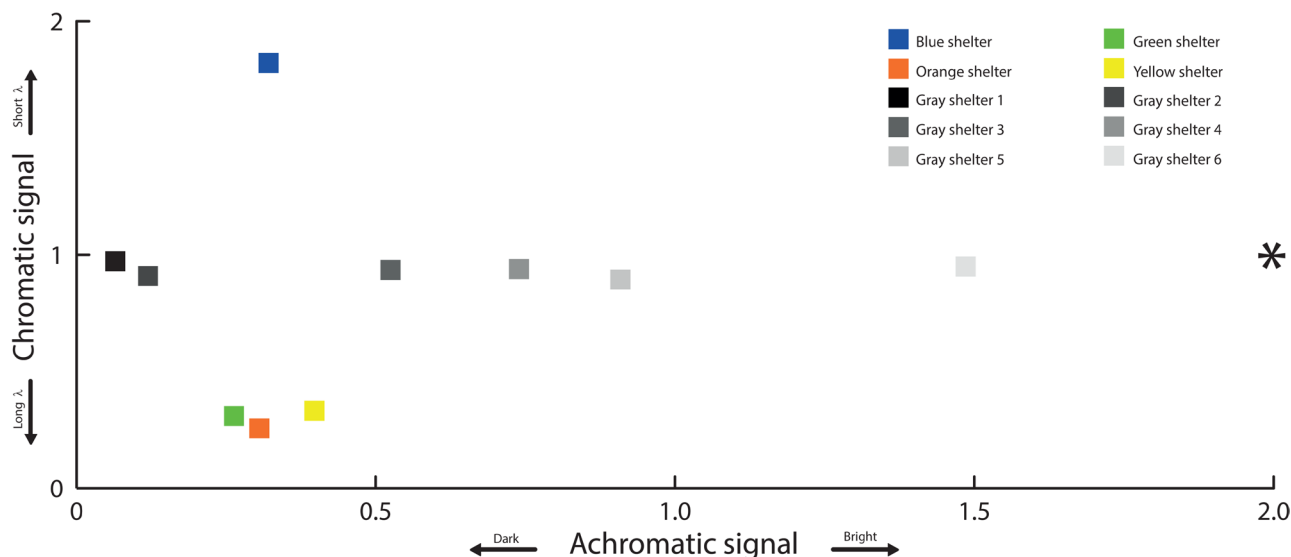
Figure 4. Chromaticity-luminance diagram for the visual system of prawns. Inferred chromatic and achromatic signals, determined for a perfectly white surface (asterisk depicted in the diagram) and for shelters employed in our experiments (squares), are represented. Distance between squares indicates color and brightness differences in chromatic and achromatic signal axes, respectively. Short λ = short wavelengths (e.g. blues), Long λ = long wavelengths (e.g. yellows).

colored stimuli (i.e. blue, green, yellow, and orange shelters) only showed discrete variations of achromatic signals, with the yellow shelter being slightly lighter than the others (Fig. 4). Moreover, all these colored stimuli, according to the visual system of the prawns, were of intermediate brightness when compared to grey shelters. That is, in the absence of chromatic information, animals should not be able to tell colored and grey shelters apart, and would have a great range of achromatic options, including darker (grey shelters), intermediate (grey and colored shelters), and brighter (grey shelters) stimuli, from which they could choose.

Shelter preference

The records of juveniles and adults occupying the shelters are shown in Fig. 5. Juveniles occupied the bluest available shelter (i.e. the one with the highest chromatic signal) significantly more than expected by chance ($p = 0.0034$), while occupied all the other available shelters (i.e. those with intermediate and low chromatic signals) at expectancy levels ($p \geq 0.009$). Adults, on the other hand, occupied two of the darkest available shelters (i.e. those with the lowest achromatic signals), grey 1 ($p < 0.0001$) and grey 2 ($p = 0.0001$), significantly more than expected by chance. They occupied the brightest available shelter (i.e. the one with the highest achromatic signal), grey 6 ($p = 0.0010$), significantly less than expected. Adults occupied all other shelters (i.e. those

with more intermediate achromatic signals) at expectancy levels ($p \geq 0.0435$).

DISCUSSION

Our study is the first to employ visual modeling to study color preference in *M. rosenbergii*. The computation of quantum catches, for the visual system of prawns, enabled us to choose blue, green, yellow, and orange stimuli that satisfied two criteria: 1) differed chromatically from the grey shelters, presenting a very high or a very low chromatic signal; and 2) exhibited intermediate brightness levels, when compared to grey stimuli. Our visual model showed that, for the prawns, the blue shelter presented a chromaticity very different from the chromaticity of the green, the yellow, and the orange shelters. On the other hand, the green, the yellow, and the orange shelters were very similar in chromaticity for the prawns, probably due to a dichromatic color vision maintained by the interaction of two different types of photoreceptors (Jacobs 1996). Nevertheless, we must emphasize that our results should be interpreted with caution since it is not already established if the visual system of *M. rosenbergii* works through chromatic opposition.

Our prediction that adult subjects would prefer longer wavelength colors (i.e. yellow or orange shelters) was not corroborated, since juveniles preferred the blue shelter, while
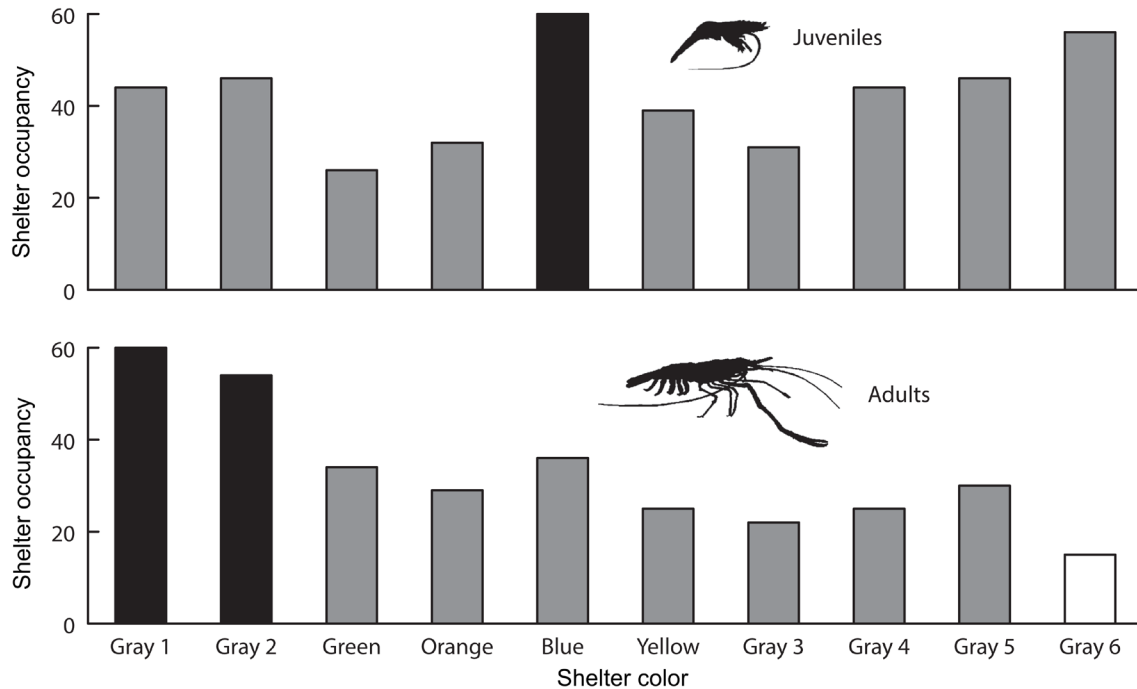
Figure 5. Preference for shelters of different colors by juvenile and adult prawns. The bars represent the number of records of occupancy for each shelter. Black bars represent shelters that were chosen significantly above the expectancy level. Grey bars represent shelters chosen at expected frequencies. The white bar represents a shelter chosen significantly below expectancy levels.

adults preferred the darkest ones. In our study, the stimulus that caught the attention of the juveniles (i.e. the blue shelter) was similar in brightness, and chromatically different, from other colored stimuli (i.e. the green, the yellow, and the orange shelters), which were disfavored. This is a strong indication that the preference for blue shown by juveniles was based on color alone, not brightness, which is the first indication of color vision in these animals. Adult preference, on the other hand, was probably based on brightness, since different neutral stimuli (grey shelters) were very similar in chromaticity and very different in brightness. Still, our results are not enough to determine whether adult giant river prawns enjoy color vision since there is a possibility that they prefer darker shelters despite a color vision sense. In fact, it has already been reported that adults favor the occupancy of shaded areas of the pond (Karplus and Harpaz 1990) and that the use of shelters by this species might be linked to light avoidance behavior (Costa and Arruda 2016). So, the preference for darker shelters by adults, in our study, may be explained by a tendency to avoid light expressed by the species, which should facilitate their escape from predators (Dabbagh and Kamrani 2011). This preference

for darker shelters has also been observed in other species of *Macrobrachium* (Mariappan and Balasundaram 2003, Balasundaram et al. 2004).

The ontogenetic changes in color preference exhibited by our animals, from blue to dark grey, are consistent with what has been found in less controlled experiments performed by other laboratories (Juarez et al. 1987, Kawamura et al. 2016, 2017, 2018, Yong et al. 2018), however, our data demonstrate that these shifts in color preference seem to occur later in life. Regarding the preference of juveniles, our findings are in line with what has been shown for the color preference of the larvae of *M. rosenbergii* in studies employing different colors of beads (Kawamura et al. 2016) and feed (Yong et al. 2018). Similarly, the preference for darker stimuli by our adult subjects is in line with what has been verified in previous studies that tested post-larvae of *M. rosenbergii* (Kawamura et al. 2017), which were shown to prefer black shelters over blue or green ones, and juveniles (Juarez et al. 1987), that preferred black over blue or white substrates. Kawamura et al. (2020), on the other hand, report that the yellow background was the most preferred by larvae and was avoided by post-larvae. The authors also claim that

larvae preferred brighter backgrounds, while post-larvae preferred darker ones. However, these authors were unable to satisfactorily consider the visual system of the animals, since nothing was done to assess the chromaticity of the different stimuli.

The discrepancies found between our results and previous studies might result from the lack of precise control over stimuli and also from methodological differences. For instance, Juarez et al. (1987) and Kawamura et al. (2017, 2020) tested *M. rosenbergii* in groups, while we adopted individual testing. We know these animals are aggressive from a young age (Silva and Arruda 2015), and since Kawamura et al. (2017) reported agonistic interactions among their experimental individuals, we can't rule out the possibility that their results were biased by hierarchy. For example, in a group context, it is plausible to imagine that a prawn might have avoided occupying a preferred spot that was already occupied by a more dominant individual, forcing it to opt for a suboptimal choice.

Hierarchy can even influence the expression of vision-related genes. Aziz et al. (2018) compared gene expression of the three morphotypes found in populations of *M. rosenbergii* and found higher expression levels of long-wavelength opsin genes in the eyestalk and hepatopancreas of small males, which are the most subordinate morphotype. Hence, they suggest that small males could present better color discrimination, which would help avoid dominant and subdominant morphotypes, which carry blue and orange claws, respectively. In addition, Santos et al. (2015) noticed a difference in color preference between sex, verifying that females preferred red and orange shelters, while males preferred black ones. Since we did not sex our prawns, and neither did Juarez et al. (1987) or Kawamura et al. (2017, 2020), we should not rule out sex bias as a possible explanation for the ontogenetic discrepancies found between studies. Additional behavioral studies should be encouraged, with careful control of stimuli's chromaticity and brightness, in order to study the development of a preference for chromatic and achromatic cues in males and females of *M. rosenbergii* and to elucidate whether adults have color vision.

The use of shelters can improve the welfare of animals used in aquaculture, for example, by preventing the appearance of body damage resulting, in part, from agonistic interactions (Gesto and Jokumsen 2022). A higher frequency of shelter use could reduce the occurrence of predation events and favor access to food (Santos et al. 2015). According to Huntingford et al. (2012), in aquaculture, animal welfare and production frequently go hand in hand. In fact, Santos

et al. (2015) propose that providing the shelters preferred by *M. rosenbergii* would favor the growth of the prawns and reduce production costs.

Our results strongly indicate that *M. rosenbergii* uses chromaticity alone to distinguish between stimuli. Juveniles show a higher preference for blue shelters, which is based on chromaticity, since, according to our visual model, other shelters with comparable brightness were not preferred by the animals in the same way. Later in life, prawns direct their preference to darker shelters and avoid brighter ones, which seems to be based, mostly, on brightness cues. We suggest that farmers should provide blue shelters for juveniles and dark shelters for adults, to favor shelter occupancy, which can improve productivity and animal welfare.

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FPC, MFA, KR, and DMAP designed the experiments; FPC conducted the experiments; FPC analyzed the data; FPC, MFA, KR, and DMAP wrote the paper.

Competing Interests

The authors have declared that no competing interests exist.

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