Influence of color and brightness on ontogenetic shelter preference by prawns (*Macrobrachium rosenbergii*)

Felipe P. da Costa[a], Maria F. Arruda[b], Karina Ribeiro[c], Daniel M. A. Pessoa*[a]

[a] Laboratory of Sensory Ecology, Department of Physiology & Behavior, Biosciences Center, Federal University of Rio Grande do Norte, Natal-RN, Brazil

[b] Laboratory of Behavioral Biology, Department of Physiology & Behavior, Biosciences Center, Federal University of Rio Grande do Norte, Natal-RN, Brazil

[c] Agricultural School of Jundiai, Federal University of Rio Grande do Norte, Macaíba-RN, Brazil

Correspondence:

pernambucofelipe3@gmail.com

mariadefarruda@gmail.com

ribeiro_k@hotmail.com

* Corresponding author: Caixa Postal 1511, 59078-970 Natal, Brazil, Email: pessoadma@cb.ufrn.br

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Abstract

The giant river prawn (*Macrobrachium rosenbergii*), native to rivers and river mouths of different Asian countries, is a heavily widespread species that has been introduced around the world due to its great commercial importance. These prawns are farmed under many different conditions that might translate to a great range of light environments, which impact their behavior and productivity. Here, as a contribution for prawns' welfare and economical productivity, we present the first study employing both visual modeling and behavioral data to evaluate ontogenetic changes on color preference of juveniles and adults of *M. rosenbergii*. For this purpose, we offered ten shelters of different colors to juveniles and adults and registered their preference. Our results showed that the criterion for shelter preference changed with ontogeny, since juveniles chose shelters based on chromaticity (preference for blue), while adults based their decisions on brightness (preference for dark gray). This preference of adults for dark colors is probably associated with a light avoidance behavior. We recommend providing blue shelters for juveniles and dark shelters for adults.

1. 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 & Ng, 2010). In their natural environment, the larvae inhabit estuarine environments (Sandifer & Smith, 1985), are planktonic (New, 2002) and go through 11 larval stages (from Zoea I to Zoea XI) (Sandifer & Smith, 1985). After a larval life of 20 to 50 days, the larvae undergo metamorphosis into post-larvae (Sandifer & Smith, 1985), which are benthic and begin migration to freshwater environments, where they remain until adulthood (New, 2002) and mate (Sandifer & Smith, 1985). Then, the ovigerous female migrates to estuarine environments, where the larvae hatch from the eggs, restarting the cycle (Sandifer & Smith, 1985).

M. rosenbergii is a species of great commercial importance (Engle, Quagrainie, & Dey, 2016; Zeng, Cheng, Lucas, & Southgate, 2012) 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, Alston, & Sampaio, 2010; Daniels, Cavalli, & Smullen, 2010; Valenti, Daniels, New, & Correia, 2010; Valenti, New, Salin, & Ye, 2010), that might translate to a great range of light environments, which have the potential to impact prawns' behavior and productivity. In fact, one study has already shown that food color affects prawns' larvae feeding behavior (Yong, Kawamura, Lim, & Gwee, 2018). In different species, color preference has also been related to the selection of appropriate habitats (Gu et al., 2017; Havel & Fuiman, 2017; Strader, Davies, & Matz, 2015). 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 & Rhyne, 2015). Therefore, the study of

76   color preference by species of economic interest might exert an important role in animal

77   welfare and food productivity.

78   Morphologically, the eyes of *M. rosenbergii* change throughout ontogenetic

79   development, since larvae have functionally apposition eyes, whereas adults have functionally

80   reflecting superposition eyes (Nilsson, 1983). The superposition eyes are more efficient for

81   gathering light and can be advantageous in low light conditions, but the transformations

82   necessary for the appearance of a superposition eye may not be complete in post-larvae, as

83   seen in a caridean shrimp (Douglass & Forward, 1989). Regarding the visual sensitivity of the

84   species, it was found that dark-adapted individuals exhibit a light absorption peak at 563 nm,

85   which corresponds to the yellow-red region of the spectrum (Matsuda & Wilder, 2014),

86   although the authors don't specify how many photoreceptor types would be accounting for the

87   sensitivity curve. Still, in spite of the great deal of experiments that have already been

88   conducted with giant prawns (Chong-Carrillo et al., 2016), only recently their visual system

89   begun to be studied through behavioral experiments (Kawamura, Bagarinao, Yong, Faisal, &

90   Lim, 2018; Kawamura, Bagarinao, Yong, Fen, & Lim, 2017; Kawamura, Bagarinao, Yong,

91   Jeganathan, & Lim, 2016; Kawamura, Yong, Wong, Tuzan, & Lim, 2020).

92   Through visual modeling studies, a strategy that has currently gained popularity, it is

93   possible to assess which spectral information available in the environment could be exerting

94   an adaptive function. During visual modeling, we infer how a given animal's visual system is

95   stimulated by observing a particular object under a specific illuminant (Olsson, Lind, &

96   Kelber, 2018). In other words, just by knowing how many kinds of photoreceptors (and their

97   peak sensitivities) there are in an animal's eye, the spectrum of ambient light, and the color of

98   an object of interest, we can suppose how the object should be seen by that observer. Yet,

99   although variations in the type and number of photoreceptors are usually related to the

100   dimensionality of color vision, only behavioral tests can verify an animals' color perception

101   (Jacobs, 1996). So, it is important to couple visual modeling data with behavioral experiments

102   that can validate them (Lind & Kelber, 2009).

103   To our knowledge, availability of chromatic and achromatic cues to *M. rosenbergii*

104   have never been properly analyzed by means of visual modeling. The experiments already

105   carried out either did not try to control the brightness of the stimuli or tried to do so without

106   correctly taking into account the prawns' visual system. In color preference experiments, the

107   choice of stimuli colors should consider the eye of the beholder (Hill, 2002), not human

108   vision. By using visual modeling, we can control the colors of the stimuli to be presented to

109   prawns in a rigorous manner, as in studies with other animal species (Detto, 2007; Escobar-

110   Camacho et al., 2019; Olsson, Lind, & Kelber, 2015; Siebeck, Wallis, Litherland, Ganeshina,

111   & Vorobyev, 2014).

112   Therefore, here we developed the first color preference study on *M. rosenbergii*

113   employing visual modeling, as a more rigorous control for stimuli brightness and

114   chromaticity, according to the visual system of prawns. Our aim is to investigate whether their

115   preference for different colors and brightness changes over their development. Since *M.*

116   *rosenbergii* spontaneously occupies experimental shelters (Santos, Pontes, Campos, &

117   Arruda, 2015), we analyzed the preference that two benthic developmental stages (i.e.

118   juveniles and adults) show for shelters of different chromaticities and brightnesses. Our

119   hypothesis is that *M. rosenbergii* changes their color preference gradually throughout

120   ontogeny, regardless of the farming conditions. This ontogenetic shift would be adaptative in

121   natural populations because the spectral composition (i.e. color) of the surrounding natural

122   photic environment changes as they start migrating from estuaries to freshwater ecosystems.

123   Since this migration only begins when *M. rosenbergii* reaches its post-larvae developmental

124   stage, we predict that adults will be more prone than juveniles to exhibit strong preferences

125 for longer wavelengths, such as yellow and orange, which are colors associated to freshwater

126 bodies (Stoffels, 2013).

127

2. Material and methods

2.1 Ethical statement

130 Our research was approved by the Ethics Committee on The Use of Animals of our

131 institution (protocol 042/2018) and is in accordance with Brazilian law. It complies with

132 ARRIVE guidelines and was carried out in accordance with the U.K. Animals (Scientific

133 Procedures) Act, 1986, and associated guidelines, EU Directive 2010/63/EU for animal

134 experiments.

135

2.2 Animal maintenance

137 At the Laboratory of Sensory Ecology, of the Federal University of Rio Grande do

138 Norte, we kept 39 juveniles of *Macrobrachium rosenbergii*. Animals were housed in a

139 collective aquarium (100 x 50 cm, 40 cm water column), with transparent water, sandy

140 substrate and aeration. They were subjected to a 12-hour light/12-hour dark light cycle (light

141 from 6:00 a.m. to 6:00 p.m.). Two fluorescent lamps provided a light intensity of

142 approximately 320 lux (measured with an Extech Instruments HD 400 Light Meter), which

143 should be sufficient for color discrimination (Kawamura et al., 2018).

144 We kept the physical-chemical parameters of the water at optimum levels for the

145 prawns (pH: 7.0-7.5; ammonia: 0 ppt; temperature: 26-28 ℃), and fed the animals twice a day

146 (morning and afternoon) with commercial food containing 42% crude protein. Twenty percent

147 of the aquarium's water was changed twice a week.

148

2.3 Experimental apparatus

150   We also made available transparent water, sandy substrate and aeration in two

151   experimental aquaria, with aeration positioned, approximately, at the center of each aquarium.

152   In each experimental aquarium, we arranged ten shelters, in two rows of five. We build the

153   shelters with plastic coated paper, folded in an appropriate way. Each aquarium had six gray

154   shelters, each one with a different brightness, besides a blue, a green, a yellow and an orange

155   shelter (Figure 1).

156

157   [Insert figure 1 about here]

158

159   2.4 Shelters' colors and brightness

160   For choosing our stimuli colors, we printed 101 different color patches that were

161   coated with plastic and had their reflectance spectra measured by us with a spectrophotometer

162   (USB4000 UV-VIS Fiber Optic Spectrometer, Ocean Optics, Inc.). We coupled the

163   spectrometer to a bifurcated optical fiber (QR450-7-XSR, Ocean Optics, Inc.), also attached

164   to a light source (DH-2000-BAL, Ocean Optics, Inc.). A white standard surface (WS-1-SL,

165   Ocean Optics, Inc.), and the obstruction of the light source and optical fiber, were used as,

166   respectively, the white and the black standards, for system calibration. We also measured the

167   illuminant of the experimental room with the spectrometer coupled to an optical fiber

168   (QP450-2-XSR, Ocean Optics, Inc.), attached to a cosine corrector (CC-3-UV-S, Ocean

169   Optics, Inc.). We calibrated this spectrometric system with a calibration light source (LS-1-

170   CAL, Ocean Optics, Inc.).

171   We run visual models, through pavo 2 (Maia, Gruson, Endler, & White, 2019), a

172   package for R 3.4.1 (R Development Core Team, 2020), to infer how each color patch would

173   be seen according to the prawn's visual system. Our model computed the quantum catches

174   absorbed by each type of photoreceptor described for prawns, when the animals visualized

175 each shelter (reflectance spectra in Figure 2), that was illuminated by the fluorescent lamps of

176 our experimental room (Figure 3). The absorption peaks of the photoreceptors of another

177 prawn species, *Palaemonetes poludosus* (380 nm and 555 nm) (Goldsmith & Fernandez,

178 1968), were adopted in our model, since data were not available for *M. rosenbergii*. *P.*

179 *poludosus* is the taxon most closely related to *M. rosenbergii* for which photoreceptors'

180 absorption peaks have been established. Using photoreceptors' absorption peaks of related

181 species is a viable alternative, since small variations in estimated peaks do not carry a great

182 influence in visual modeling results (Lind & Kelber, 2009; Olsson et al., 2018).

183

184   [Insert figure 2 about here]

185   [Insert figure 3 about here]

186

187   In order to calculate the signal of each photoreceptor, we divided the amount of light

188 reflected by a stimulus (shelter) and captured by a specific photoreceptor class (stimulus

189 quantum catch), by the amount of light reflected by a perfect white surface (white standard)

190 and captured by the same photoreceptor class (maximum quantum catch). Following Detto

191 (2007), we computed achromatic signals for each stimulus, as the sum of signals of short

192 wavelength (S signals) and long wavelength (L signals) photoreceptors. For chromatic

193 signals, we divided S signals by L signals (Siebeck et al., 2014). Chromatic and achromatic

194 signals were plotted in a chromaticity-luminance diagram (Figure 4), that show how our

195 stimuli varied with respect to color and brightness. We chose not to use the RNL model

196 (Vorobyev & Osorio, 1998) because it demands visual parameters (Olsson et al., 2018) that

197 are still unknown for prawns.

198

199   [Insert Figure 4 about here]

200

2.5 Experimental design

201

202   In experiment 1, we individually tested 39 juveniles about two months after

203   metamorphosis (body weight: 0.46 ± 0.13 g; total length: 3.89 ± 0.36 cm), two juveniles per

204   day, each one in a smaller experimental aquarium (30 x 50 cm). The shelters, in experiment 1,

205   measured 7 cm depth x 6 cm width x 3 cm height. The position of the different shelters for

206   each animal was randomized.

207   In experiment 2, we individually tested 24 of the 39 previously tested individuals,

208   when they were already adults about seven months after metamorphosis (body weight: $6.4 \pm$

209   3.2 g; total length: 8.49 ± 1.84 cm), one adult prawn per day, in a larger experimental

210   aquarium (50 x 100 cm). The shelters, in experiment 2, measured 7 cm depth x 9 cm width x

211   5 cm height. Otherwise, the two experiments were identical. Differences in sample size

212   between experiments 1 and 2 were due to animal mortality.

213   In both experiments, we fed all prawns in the collective aquaria at 7:30 a.m., removed

214   each prawn, that was about to be tested, from the collective aquarium and transferred it to the

215   center of an experimental aquarium at 8:00 a.m. From 9:00 a.m. to 5:30 p.m, at every 30 min,

216   we recorded if the animal was inside/on top of a shelter (shelter occupancy), or if it was away

217   from any shelter (no choice), following Kawamura et al. (2017). After the experimental

218   session, we removed the prawn from the experimental aquarium, recorded its weight and total

219   length, and transferred it to another collective aquarium, in which individuals that had been

220   already tested were kept. All animals were fed again at the end of the day.

221

2.6 Statistical analysis

222

223   We performed ten chi-square tests, one for each shelter, for unequal expected

224   proportions, to verify if the occupancy of each shelter differed from the expected 10% of all

225   cases. We employed the Bonferroni correction to account for multiple comparisons and set

226   our α to 0.005. All tests were performed in BioEstat 5.3 (Ayres & Ayres Jr, 2007).

227

3. Results

3.1 Visual modeling

230   Regarding our stimuli, the blue shelter generated a chromatic signal that stood out

231   from green, yellow and orange shelters (Figure 4), a strong indication that the blue shelter

232   could be perceived, by the prawns' visual system, as being of a different color. In contrast,

233   these four colored stimuli (i.e. blue, green, yellow, and orange shelters) only showed discrete

234   variations of achromatic signals, with the yellow shelter being slightly lighter than the others

235   (Figure 4). Moreover, all these colored stimuli, according to the visual system of the prawns,

236   were of intermediate brightness when compared to gray shelters. That is, in the absence of

237   chromatic information, animals should not be able to tell colored and gray shelters apart, and

238   would have a great range of achromatic options, including darker (gray shelters), intermediate

239   (gray and colored shelters) and brighter (gray shelters) stimuli, from which they could choose.

240

3.2 Shelter preference

242   The records of juveniles and adults occupying the shelters are shown in Figure 5.

243   Juveniles occupied the bluest available shelter (i.e. the one with the highest chromatic signal)

244   significantly more than expected by chance ($p = 0.0034$), while occupied all the other

245   available shelters (i.e. those with intermediate and low chromatic signals) at expectancy levels

246   ($p \geq 0.009$). Adults, on the other hand, occupied two of the most darker available shelters (i.e.

247   those ones with the lowest achromatic signals), gray 1 ($p < 0.0001$) and gray 2 ($p = 0.0001$),

248   significantly more than expected by chance, while occupied the most brighter available shelter

249   (i.e. the one with the highest achromatic signal), gray 6 ($p = 0.0010$), significantly less than

250   expected. Adults occupied all other shelters (i.e. those with more intermediate achromatic

251   signals) at expectancy levels ($p \geq 0.0435$).

252

253   [Insert figure 5 about here]

254

255   4. Discussion

256   Our study is the first to employ visual modeling to study color preference in

257   *Macrobrachium rosenbergii*. The computation of quantum catches, for prawn's visual system,

258   enabled us to choose blue, green, yellow and orange stimuli, that satisfied two criteria: 1)

259   differed chromatically from the gray shelters, presenting a very high or a very low chromatic

260   signal; and 2) exhibited more intermediate brightness levels, when compared to gray stimuli.

261   Our visual model showed that, for the prawns, the blue shelter presented a chromaticity very

262   different from the chromaticity of the green, the yellow and the orange shelters. On the other

263   hand, the green, the yellow and the orange shelters were very similar in chromaticity for the

264   prawns, probably due to a dichromatic color vision maintained by the interaction of two

265   different types of photoreceptors (Jacobs, 1996). Nevertheless, we must emphasize that our

266   results should be interpreted with caution, since it is not already established if the visual

267   system of *M. rosenbergii* works through chromatic opposition.

268   Our prediction that adult subjects would prefer longer wavelength colors (i.e. yellow

269   or orange shelters) was not corroborated, since juveniles preferred blue shelters, while adults

270   preferred darker ones. In our study, the stimulus that caught juvenile's attention (i.e. the blue

271   shelter) was similar in brightness, and chromatically different, from other colored stimuli (i.e.

272   green, yellow, and orange shelters), which were disfavored. This is a strong indication that the

273   blue preference shown by juveniles was based on color alone, not brightness, which is the

274   first indication of color vision in these animals. Adult preference, on the other hand, was

275   probably based on brightness, since different neutral stimuli (gray shelters) were very similar

276   in chromaticity and very different in brightness. Still, our results are not enough to determine

277   whether adult *M. rosenbergii* enjoy color vision, since there is a possibility that they prefer

278   darker shelters despite of a color vision sense. In fact, it has already been reported that adults

279   favor the occupancy of shaded areas of the pond (Karplus & Harpaz, 1990) and that the use of

280   shelters by this species might be linked to a light avoidance behavior (Costa & Arruda, 2016).

281   So, the preference for darker shelters by adults, in our study, may be explained by a tendency

282   to avoid light expressed by the species, which should facilitate their escape from predators

283   (Dabbagh & Kamrani, 2011). This preference for darker shelters has also been observed in

284   other species of the genus *Macrobrachium* (Balasundaram, Jeyachitra, & Balamurugan, 2004;

285   Mariappan & Balasundaram, 2003).

286   The ontogenetic changes in color preference exhibited by our animals, from blue to

287   dark gray, are consistent with what has been found in less controlled experiments performed

288   by other laboratories (Juarez, Holtschmit, Salmeron, & Smith, 1987; Kawamura et al., 2017;

289   Kawamura et al., 2016; Kawamura et al., 2018; Yong et al., 2018), however, our data

290   demonstrate that these shifts in color preference seem to occur later in life. Regarding the

291   preference of juveniles, our findings are in line with what has been shown for the color

292   preference of the larvae of *M. rosenbergii* in studies employing different colors of beads

293   (Kawamura et al., 2016) and feed (Yong et al., 2018). Similarly, the preference for darker

294   stimuli by our adult subjects is in line with what has been verified in previous studies that

295   tested post-larvae of *M. rosenbergii* (Kawamura et al., 2017), which were shown to prefer

296   black shelters over blue or green ones, and juveniles (Juarez et al., 1987), that preferred black

297   over blue or white substrates. Kawamura et al. (2020), on the other hand, report that the

298   yellow background was the most preferred by larvae and was avoided by post-larvae. The

299   authors also claim that larvae preferred brighter backgrounds, while post-larvae preferred

300   darker ones. However, these authors were unable to satisfactorily consider the animal's own

301   visual system, since nothing was done to assess the chromaticity of the different stimuli.

302   The discrepancies found between our results and previous studies might result from

303   the lack of precise control over stimuli and also from methodological differences. For

304   instance, Kawamura et al. (2017), Kawamura et al. (2020) and Juarez et al. (1987) tested *M.*

305   *rosenbergii* in groups, while we adopted individual testing. We know these animals are

306   aggressive from a young age (Silva & Arruda, 2015), and since Kawamura et al. (2017)

307   reported agonistic interactions among their experimental individuals, we can´t rule out the

308   possibility that their results were biased by hierarchy. For example, in a group context, it is

309   plausible to imagine that a prawn might have avoided occupying a preferred spot that was

310   already occupied by a more dominant individual, forcing it to opt for a suboptimal choice.

311   Hierarchy can even influence the expression of vision-related genes. Aziz, Rahi,

312   Hurwood and Mather (2018) compared gene expression of the three morphotypes found in

313   populations of *M. rosenbergii* and found higher expression levels of long wavelength opsin

314   genes in the eyestalk and hepatopancreas of small males, which are the most subordinate

315   morphotype. Hence, they suggest that small males could present a better color discrimination,

316   which would help avoiding dominant and subdominant morphotypes, that carry blue and

317   orange claws, respectively. In addition, Santos et al. (2015) noticed a difference in color

318   preference between sex, verifying that females preferred red and orange shelters, while males

319   preferred black ones. Since we did not sex our prawns, and neither did Juarez et al. (1987),

320   Kawamura et al. (2017) or Kawamura et al. (2020), we should not rule out sex bias as a

321   possible explanation for the ontogenetic discrepancies found between studies. Additional

322   behavioral studies should be encouraged, with careful control of stimuli's chromaticity and

323   brightness, in order to study the development of a preference for chromatic and achromatic

324   cues in males and females of *M. rosenbergii* and to elucidate whether adults have color

325   vision.

326   In conclusion, our results strongly indicate that *M. rosenbergii* uses chromaticity alone

327   to distinguish between stimuli. Juveniles show a higher preference for blue shelters, which is

328   based on chromaticity, since, according to our visual model, other shelters with comparable

329   brightness were not preferred by the animals in the same way. Later in life, prawns direct their

330   preference to darker shelters, and avoid brighter ones, which seems to be based, mostly, on

331   brightness cues. We suggest that farmers should provide blue shelters for juveniles and dark

332   shelters for adults, to favor shelter occupancy, which can improve productivity and animal

333   welfare.

334

348

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491

492   **Figure legends**

493

494   Figure 1. Schematic view of the arrangement of shelters in an experimental aquarium. The

495   prawns were individually tested in aquaria with 10 colored shelters arranged in two rows of

496   five.

497

498   Figure 2. Reflectance spectra of experimental shelters. The reflectance of each curve is

499   represented as a percentage, compared to the maximum reflectance of the most reflective

500   curve. Each curve is represented approximately the same color as the respective shelter.

501

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

503   fluorescent lamps.

504

505   Figure 4. Chromaticity-luminance diagram for the visual system of prawns. Inferred

506   chromatic and achromatic signals, determined for a perfect white surface (asterisk) and for

507   shelters employed in our experiments (squares), are represented. Distance between squares

508   indicate color and brightness difference in chromatic and achromatic signal axes, respectively.

509   Shorter λ = shorter wavelengths (e.g. blues); Longer λ = longer wavelengths (e.g. yellows).

510

511   Figure 5. Preference for shelters of different colors by juveniles and adults of giant river

512   prawns (*M. rosenbergii*). The bars represent the number of records of occupancy for each

513   shelter. Black bars represent shelters that were chosen significantly above expectancy level.

514   Gray bars represent shelters chosen at expected frequencies. The white bar represents a shelter

515   chosen significantly below expectancy levels.

516

517

518

519

Chromatic signal (Short λ ← → Long λ) vs Achromatic signal (Dark ← → Bright)

Legend:
- Blue shelter
- Orange shelter
- Gray shelter 1
- Gray shelter 3
- Gray shelter 5
- Green shelter
- Yellow shelter
- Gray shelter 2
- Gray shelter 4
- Gray shelter 6

Juveniles

Adults

Shelter color

Shelter occupancy