1 **Context-dependent use of visual cues in the shell selection behaviour of the hermit**

2 **crab *Pagurus bernhardus***

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9

10 **Abstract**

11 Animals avoid predator attack in different ways; some carry defensive structures to

12 reduce predation, with the classic example being hermit crabs and their use of a mollusc

13 shell as a portable refugium. During shell selection, various shell characteristics are

14 investigated by the crab to determine their suitability. Here we consider the role of visual

15 cues. Previous research suggests that some hermit crabs are more likely to initially choose

16 a conspicuous shell but also to move to backgrounds against which they are less

17 conspicuous, suggesting a short-term/long-term trade-off. Across experiments in which we

18 manipulated shell and background colour, we show initially that *Pagurus bernhardus*

19 prefer black shells over white but this preference was lost in the absence of visual cues.

20 We then show that the strength of preference was dependent on background colour. We

21 repeated this last experiment with red and yellow shells against red or yellow

22 backgrounds to investigate whether this preference extended to chromatic hues. A

23 preference for darker (red) shells was expressed, but preference alteration with

24 background was not observed. *P. bernhardus* therefore discriminate between shells in

25 terms of shell and background colour, and discrimination may be rooted in a preference for

26 darker shaded shells.

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29 **Key words:** background, camouflage, crypsis, littoral, predation

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32 **1. Introduction**

33 There has been renewed interest over recent years in how animals avoid predator attack

34 through patterns of colouration and behaviour (e.g. Ruxton et al. 2004). Together with a

35 greater awareness of the perceptual abilities and receiver-psychology of predator species,

36 both theoretical and empirical advances have been made in terms of our understanding of

37 crypsis, camouflage, masquerade and aposematism (e.g. Stevens & Merilaita 2011;

38 Stevens 2013). Crypsis, broadly defined, is a trait that reduces the risk of detection by a

39 predator (Stevens & Cuthill 2006). More specifically, visual crypsis can be defined as the

40 colours and patterns of an organism that help to prevent detection by other organisms, in

41 this way distinguishing crypsis from hiding (Stevens & Merilaita 2009). Under this

42 definition, a variety of traits can be categorised as crypsis, including counter-shading

43 (Ruxton et al. 2004; Rowland et al. 2007), counter-illumination (Jones & Nishiguchi

44 2004) and camouflage (Wilson & Rouse 2010). Background matching is, however,

45 perhaps the best known - and most intuitively understandable - form of crypsis and helps

46 to explain the long-recognised observation that many animals tend to match their

47 background(s) in some way (Cott 1940; Stevens & Merilaita 2009).

48

49 For some animals, background matching may arise not through their own colouration,

50   but rather through the colour of the structures that they inhabit or the adornments with

51   which they provide themselves. In terms of structures, these may be assembled by the

52   animal, as in the case of caddis fly larvae (Williams, 1987), or they may be appropriated

53   intact from the environment, as for the classic case of hermit crabs. In hermit crabs, the

54   most visible surface seen by other organisms is the gastropod mollusc shell within which

55   the crab is housed, and the properties of which are shaped by selective pressures that had

56   acted upon the gastropod rather than the crab (Palmer 1979; Kemp & Bertness 1984).

57   Accordingly, any selective pressure to enhance shell crypsis in hermit crabs must act

58   upon the individual's shell selection behaviour. However, there will be constraints in

59   terms of the shells available (either free or already occupied by competitors), with those

60   constraints being exacerbated by the costs of a crab being unhoused and therefore

61   extremely vulnerable to predation. Moreover, crab growth is itself limited by the size of

62   available shells, adding another trade-off to shell-choice (Fotheringham, 1976).

63

64   Here we consider the role of visual cues and background-matching in the choice of shells

65   by the hermit crab *Pagurus bernhardus* (L.). Hermit crabs (Superfamily Paguroidea) are a

66   speciose and globally distributed group of decapods (Barnes et al. 2007; Grave et al.

67   2009). Characteristically, the majority of species occupy empty gastropod shells in order

68   to protect against both biotic and abiotic stresses (Bertness 1981; Pechenik & Lewis

69   2000). Hermit crabs select shells on the basis of a number of criteria, including shell

70   dimensions (Reese 1962; Mitchell 1976), shell species and morphology (Conover 1978;

71   Argüelles et al. 2009), and shell condition (Wilber 1990; Pechenik et al. 2001).

72   Nonetheless, the role of shell colour in hermit crab decision making remains under-

73   studied, even though colour may be important in terms of background matching, and given

74   that the shells they use are often polymorphic for colour (Smith 1976).

75

76   One constraint for visual shell discrimination is that the evidence for colour vision in

77   these crustaceans is limited (Kelber et al. 2003). There is, however, good evidence that

78   hermit crabs can distinguish between black and white, because they have been shown to

79   be better able to detect a shell that contrasts against its background (Reese 1963; Wilding

80   et al. 2008; Wilby et al. 2018). Conversely, hermit crabs also have been shown to alter

81   their location to minimise the contrast between their shell and background, thereby

82   minimising their conspicuousness (Partridge 1980), and there also is evidence that hermit

83   crabs are aware of their current level of conspicuousness (Briffa and Twyman 2011).

84

85   Here we tested whether or not *P. bernhardus* make context-dependent decisions over their

86   shells on the basis of firstly vision (Experiments 1 and 2), and secondly conspicuousness

87   (Experiments 3 and 4). To demonstrate the role of vision in shell selection, we predicted

88   that naked crabs would show a difference in the frequency of selection of painted shells

89   but no difference in preference when vision was eliminated as a selection factor. We tested

90   this in our first experiment by offering crabs black-painted shells and white-painted shells

91   against a light-coloured background. This was repeated in our second experiment, but we

92   removed visual cues by requiring crabs to choose a shell in the dark. If visual cues were

93   important in the first experiment, we expected random choice in the second experiment. In

94   our third experiment, we allowed crabs a 24 h period during which to choose and

95   potentially exchange shells. The crabs could, therefore, have made a rapid choice, but also

96   change that choice if, once occupying a shell, they then preferred less conspicuous

97   possible alternatives. For this latter experiment, we again offered crabs black and white

98   shells, against either a black or white background, allowing us to test whether shell

99   conspicuousness was a factor in selection. Finally, we repeated the third experiment using

100 red and yellow shells against red or yellow backgrounds in order to test whether any

101 preference extends to chromatic hues. Recently, individual *P. bernhardus* have been

102 shown to enhance their crypsis through contrast minimisation (Wilby et al. 2018).

103 Accordingly, although we were not explicitly testing for colour vision − because shell

104 discrimination could be based upon the achromatic shades of red or yellow shells − this

105 last experiment again offered crabs more or less conspicuous shells, in addition to the

106 opportunity both for short- and longer-term decision making.

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108

109 **2. Materials and methods**

110 **2.1. The study organism**

111 The common European hermit crab *P. bernhardus* exploits several different species of

112 gastropod mollusc shells for their protection. Commonly occupied shells on British coasts

113 include the grey-brown common periwinkle (*Littorina littorea* (L.)), the green-grey, and

114 often red-banded, top shell (*Gibbula umbilicalis* (da Costa)), and the polymorphic dog

115 whelk (*Nucella lapillus* (L.)) and flat periwinkle (*Littorina obtusata* (L.)). Both of the

116 latter species may present a range of shell colours including white, yellow, purple and

117 brown-black, with *N. lapillus* also showing some intensely striped colour patterns.

118 Potentially occupiable shells for *P. bernhardus* can thus vary markedly in terms of their

119 colour, pattern and gross morphology, and the heterogeneity of intertidal microhabitats

120 does, in itself, partly explain gastropod shell colour polymorphism (Wilbur & Steneck

121 1999). In the knowledge that *P. bernhardus* occupies intertidal communities of varied

122 background colouration − due to substratum type and macroalgal cover − we considered it

123 reasonable to expect hermit crabs to modify their shell colour preferences in order to

124 enhance their background matching.

125

126

2.2. Collection and maintenance of animals

127

128 Hermit crabs and shells of the periwinkle *L. littorea* were collected by hand from the rocky

129 intertidal zone on the Fife coast, UK (56°19'58.29"N, 24°6'26.03"W), between January and

130 March 2014. A single species of mollusc was used here to minimise variation in shell

131 morphology which could also influence hermit crab preference choices (Argüelles et al.

132 2009). Hermit crabs were maintained in an aquarium room under a continuous light regime

133 in 20L containers at an ambient temperature of 11-12°C, with running aerated seawater,

134 and fed crushed mussel (*Mytilus edulis* L.) once a week. Two separate stock aquaria were

135 used, and into which newly-collected animals were deposited alternately to ensure no

136 hermit crab was kept for > 4 wk.

137

138 *L. littorea* shells were cleaned of visible epibionts (e.g. barnacles) and boiled prior to

139 painting. Shells with noticeable aperture damage (erosion and/or cracks of 2 mm or

140 greater), or with holes through the shell wall, were discarded. Shells were dried for at least

141 48 h before being painted. Shells were painted with Humbrol enamel paints, specifically

142 matte black (paint No. 33), matte white (No. 34) (Experiments 1-3), red gloss (No. 19) or

143 yellow gloss (No. 69) (Experiment 4). Black and white shells then were painted also with

144 a glossy varnish (No. 35) to minimise the difference in their finish. After painting, all

145 shells were numbered with a permanent marker pen on the upright surface of the first

146 whorl (aperture face down). In order to randomise the shells assigned to each colour

147 group by size and shape, every fourth shell selected from the available pool was painted

148 the same colour.

149

150 For all the experiments, hermit crabs were selected haphazardly from the stock tanks and

151 carefully cracked from their shells using a bench vice. This is a standard means of hermit

152 crab extraction in studies involving *P. bernhardus* (Wilding et al. 2008; Elwood & Appel

153 2009). Naked crabs were maintained isolated in clear, colourless plastic containers for 30

154 min before any experiments were performed. Each crab was used once only, and at the

155 conclusion of the experiment all were cracked from their painted shells and provided

156 with empty unpainted *L. littorea* shells before being returned to the wild.

157

158

159 **2.3. Experiments 1 and 2: Initial shell selection**

160 Our first two experiments tested whether vision plays a role in the shell selection

161 behaviour of *P. bernhardus.* For Experiment 1, two randomly selected black shells and

162 two randomly selected white shells were placed aperture-up and equidistantly in a square

163 at the centre of a white coloured container (31x29x12.5 cm) filled with seawater (~13-

164 15°C). Shell selection was randomised by haphazardly drawing shells from the pool and

165 placing them into separate lines of each colour, from which experiments drew new shells

166 in turn. The position of each of the different shell colours was altered between trials. The

167 bottom of the container was layered with washed sand to ~0.5 cm depth in order to aid

168 hermit crab locomotion.

169

170 The naked hermit crabs were placed on their dorsal surface in the centre of the container

171 and allowed to select a shell. Crabs were placed on their dorsal surfaces to force them to

172 turn over, reducing the degree to which they were pointed in any specific direction. The

173 first shell entered by a hermit crab was recorded, then removed from the container along

174 with the occupying hermit crab. The water and sand within the container were replaced

175 between trials to remove any waterborne chemical cues and to maintain the temperature of

176 the seawater. The experiment was repeated for $N = 67$ crabs.

177

178 For Experiment 2, the same procedure was followed but modified by being performed in

179 darkness, to reduce the crab's use of visual cues. The containers were kept in darkness by

180 placing them within doubled, heavy-duty black polythene bags, which then were closed

181 once a hermit crab was introduced to the container. After 45 sec, the container was very

182 briefly inspected to determine whether the crab had entered a shell. If it had, the crab and

183 shell were removed and a new trial was initiated; otherwise the container was re-covered

184 and inspected again every 90 sec until a crab had either selected a shell or 10 min had

185 elapsed (recorded as 'no choice'). The sample size for this experiment was $N = 60$.

186

187

188 **2.4. Experiments 3 and 4: Shell colour selection**

189 To investigate the hypothesis that shell preference may vary with shell conspicuousness,

190 the two subsequent experiments were conducted, each with two treatments. For

191 Experiment 3, 20 black and 20 white painted shells were chosen at random from the

192 available pool as in Experiments 1 and 2 and scattered haphazardly into (1) a black

193 container, or (2) a white container (31x29x12.5 cm). Containers were filled with seawater

194 and held in an aquarium at 11-12°C, and seawater was continuously pumped through the

195 containers. The container was allowed to settle for at least 30 min before an experiment

196 began. Hermit crabs were randomly selected from the stock population and again cracked

197 from their shells and placed into individual clear, colourless plastic containers for 30 min

198 before beginning the experiment. Twelve hermit crabs then were placed haphazardly

199 around the container and left for 24 h under constant illumination. After 24 h, the shells

200   occupied by each crab were recorded. Four replicates were run for each treatment for a

201   total of N = 96 crabs.

202

203   Experiment 4 followed the same methodology as Experiment 3, except that here we used

204   20 red and 20 yellow painted shells placed either in a red or yellow container. Again, four

205   replicates were run for each treatment for a total of N = 96 crabs. No sand was placed in

206   the containers for Experiments 3 and 4 because that would disrupt the background

207   colouration. Pilot observations had previously shown that hermit crabs were able to adapt

208   to the substratum and effectively move around within 30 min of introduction.

209

210

211   **2.5. Statistical analysis**

212   All statistical analyses was performed using the open source R statistical package.

213   Experiments 1 and 2 were analysed with chi-square goodness-of-fit tests to determine

214   whether crabs selected one shell colour over the alternative under light and dark

215   conditions, respectively (with the null hypothesis that the selection of shells was equal for

216   each colour). Contingency tests were carried out to test for a difference in the frequency

217   of selection of black shells over white between Experiments 1 and 2, and to test for a

218   difference in the frequency of 'no choice' by crabs (with the null hypothesis that there

219   was no difference between the experiments in both cases). The few individuals that did

220   not make a choice were excluded from the main analysis. Experiments 3 and 4 were

221   analysed using a generalised linear mixed effects model (GLMM), including the *glmer*

222   function available in the *lme4* package. Shell colour and background colour were fitted as

223   main effects, along with an interaction between the two to determine whether shell

224 preference (if any) varied with respect to background. Replicate was fitted as a random

225 effect to take into account the multiple observations (=crabs) per replicate.

226

227

228 **3. Results**

229 The outcome for Experiment 1 was that hermit crabs preferred black shells over white

230 shells ($\chi^2_1 = 13.52$, P = 0.0002). However, when held under dark conditions (Experiment

231 2) this preference was lost, and shells were selected effectively at random (Experiment 2:

232 $\chi^2_1 < 0.01$, P > 0.99; Figure 1). The difference between the two experiments in terms of

233 preference for black shells was itself significant ($\chi^2_1 = 6.08$, P = 0.014). The number of

234 crabs that failed to make a choice within 10 min was small for both experiments, and did

235 not differ between them (9 out of 67 for Experiment 1, and 4 out of 60 for Experiment 2:

236 $\chi^2_1 = 0.93$, P = 0.34). In Experiment 3, the hermit crabs again expressed a preference for

237 black shells over white (GLMM: z = 3.53, P < 0.0001) but preference varied according to

238 background colour, being stronger on a black background (less conspicuous) than on a

239 white background (more conspicuous) (interaction: z = 2.21, P = 0.03; Figure 2).

240

241 In Experiment 4, the hermit crabs again expressed a preference for darker shells over

242 lighter shells (red over yellow: GLMM: z = 3.10, P = 0.002). This preference appeared to

243 vary somewhat with background colour, seeming greater for red as opposed to yellow

244 backgrounds (Figure 3); however, the interaction between shell colour and background

245 colour was statistically non-significant (z = 1.38, P = 0.17).

246

247

4. Discussion

248

249 Using experimental manipulations of shell colour we could show that vision plays a role

250 in the shell choices of *P. bernhardus* and that shell colour can affect preferences in a

251 context dependent manner: that is to say, preference varied with background colour. The

252 results of changing background colour from black to white were consistent with a drive to

253 reduce conspicuousness because fewer black shells were selected, although the preference

254 for darker shells did persist to some extent.

255

256 The outcome of Experiment 1 was that *P. bernhardus* discriminated between white and

257 black-painted shells, either as a result of active choice or arising from a passive attraction

258 to the black shells. This supports previous findings for *Pagurus samuelis,* which indicated

259 that hermit crab vision does indeed play a discriminating role in shell selection (Reese

260 1963). Our second experiment confirmed the role of visual cues, because the preference

261 for dark shells was lost under no-light conditions. These data agree also with previous

262 shell selection studies involving *P. bernhardus*, which indicated that the importance of

263 entering any occupiable shell rather than remaining naked is of a very high priority to

264 these crabs. Hence, a highly visible shell is the most likely to be initially occupied

265 (Wilding et al. 2008).

266

267 Having established that visual cues play a role in the selective behaviour of these crabs,

268 Experiments 3 and 4 were designed to investigate the preferences displayed by crabs when

269 they were allowed time to investigate a range of offered shells. Over a 24 h period, crabs

270 could potentially swap shells as they gathered more information from their environment,

271 reflecting a choice less influenced by an initial requirement to rapidly enter the first

272 available shell. Shell swapping is common in studies involving hermit crabs (Briffa &

273   Twyman 2011; Arce & Alcaraz 2012) and was frequently observed during the present

274   experiments, indicating that hermit crabs were continuing to inspect the available shells in

275   order to occupy the best individually-specific shell available. This behaviour is well

276   understood and has been modelled for other shell characteristics, including shell volume

277   and weight (Reese 1962; Lively 1988). Choice decisions therefore depend upon the

278   quality both of the shell occupied and of the alternative available shells (Elwood 1995). It

279   therefore seems reasonable to assume that if conspicuousness plays a role in the perceived

280   quality of a shell, hermit crabs will tend to select the preferred shells from a given

281   selection.

282

283   Within the context of the two sets of comparisons presented here, our data indicate that *P.*

284   *bernhardus* expressed a general preference for darker shells, and that this preference

285   appears to rank more highly in shell selection behaviour than an effort to enhance

286   background matching when the background colour is a light shade. In explaining possible

287   reasons for this preference, it is important to consider shells naturally occupied by *P.*

288   *bernhardus*. Although a range of gastropod species shells may be used (see Elwood et al.

289   1979), in this study the majority of crabs (85%) collected from the local shore occupied

290   shells of *L. littorea*. Given that those shells typically are a dark grey-brown in colour, our

291   experimentally determined preference may represent selection of the most commonly

292   available shell in the local habitat. It is notable also that the rocky intertidal habitat −

293   comprising solid substrata, and overlying rocks and crevices − occupied by this species

294   (Reimchen 1979; Wilbur & Steneck 1999; Williams 2009) is naturally achromatically

295   dark in shade, and thus may result in selection favouring a preference for darker shells,

296   because these are more likely to be cryptic. Although the present experiments cannot

297   explain the cause of this preference, they do demonstrate that at least two, sometimes

298 competing, visual factors (colour of shell and colour relative to the background) affect

299 selection behaviour.

300

301 In the present experiments we randomised shells with respect to their size. Shell size and

302 volume are well-known targets of shell preference amongst hermit crabs (Dominciano &

303 Mantelatto, 2004). Whilst we focused on only the one host species (*L. littorea*) future

304 experiments could explore the trade-offs associated with short- and longer-term decisions

305 regarding conspicuousness by varying the size and species of presented mollusc shells.

306 For example, a hermit crab may trade-off greater conspicuousness for a larger shell, with

307 its associated opportunities for future growth. But occupation of an excessively large

308 shell may hinder movement and escape behaviour when confronted by a potential

309 predator. If such additional trade-offs are important, under what conditions might they be

310 especially important? Relevant to such questions is the recent work that has revealed

311 individual variation in a measure of 'boldness' in *P. bernhardus*, because this is

312 correlated negatively with fecundity (Bridger et al. 2015). It may be predicted that

313 perhaps 'bolder' individuals are more prepared to accept the cost of conspicuousness than

314 are more risk-averse individuals.

315

316 Finally, it is likely that for many species background-matching will be more complex than

317 a simple correspondence to background colour of the immediate environment. For example,

318 effective background-matching might well require the individual to additionally assess

319 both shell and background patterns and textures in order to achieve effective crypsis

320 (Endler 1978; Rowland et al. 2007; Kang et al. 2013). Moreover, complex heterogeneous

321 habitats, such as the rocky intertidal, present a variety of background colourations and

322 textures on varying spatial scales and it may not be beneficial to adapt closely to a single

323   substratum (Stevens & Merilaita 2011). Accordingly, we acknowledge that the

324   combination of shell patterns, shades and colours − all of which can contribute to crypsis −

325   are likely to be more complex we have considered here. Further research in this area,

326   incorporating shell patterns and textures into preference experiments, may help to better

327   determine the role of these factors in hermit crab shell selection behaviour.

328

329

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337

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341

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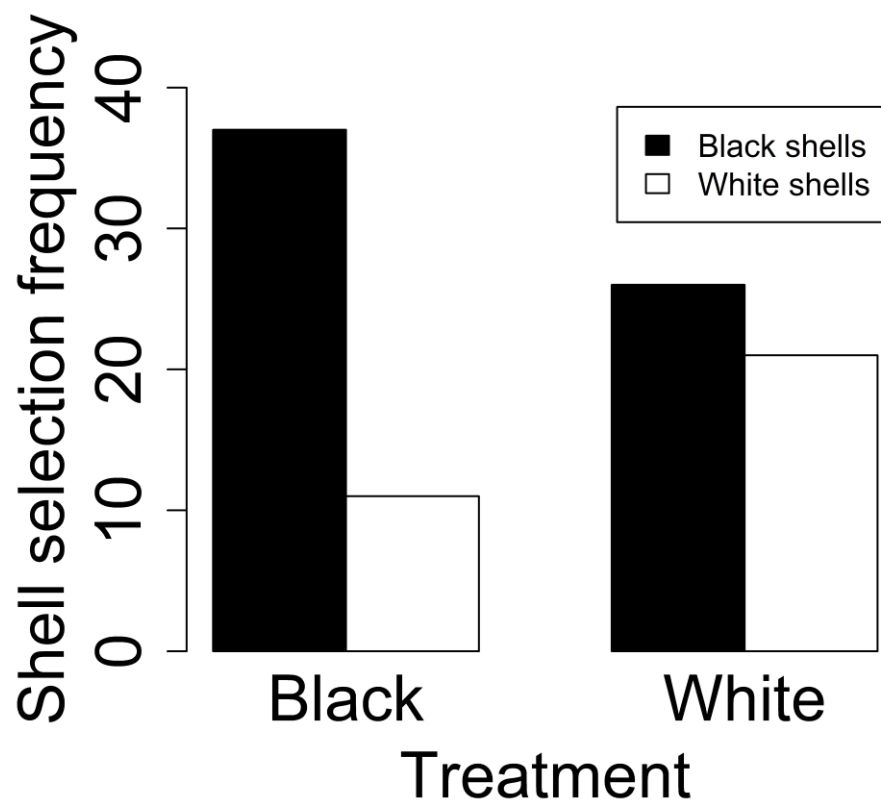
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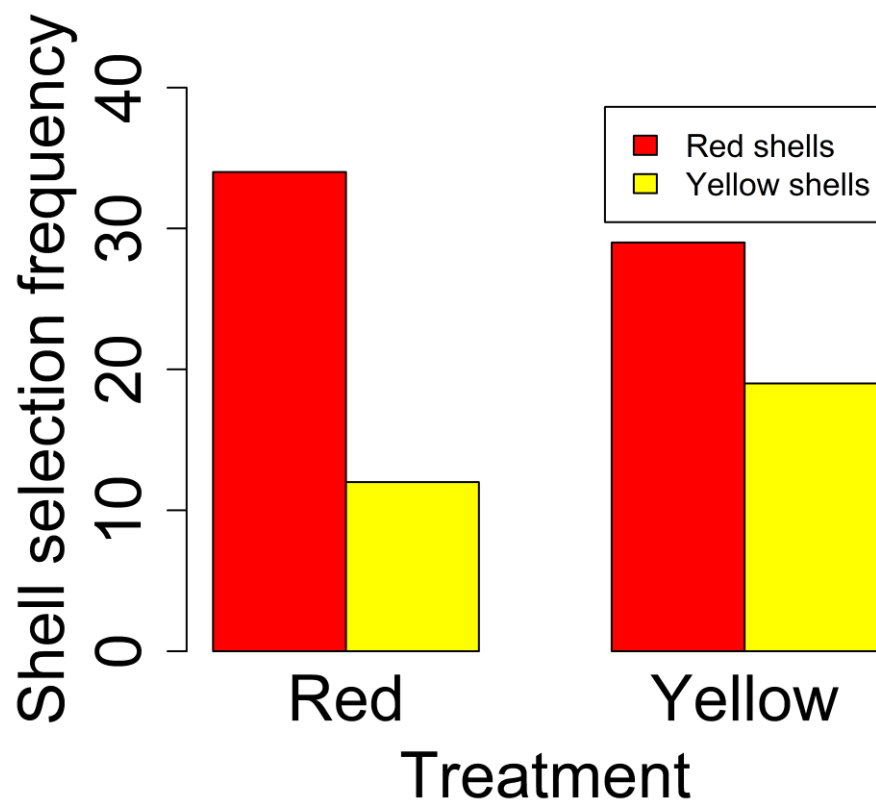
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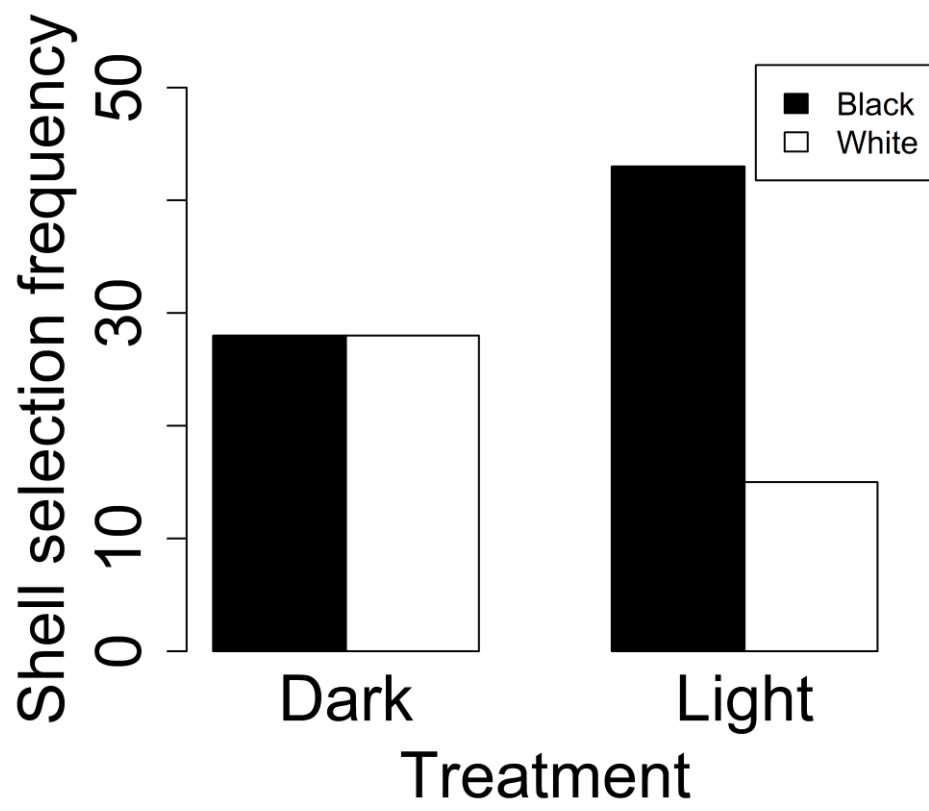
455   Figure 1

456   Figure 2

457   Figure 3