

1 **Predator recognition and anti-predatory behaviour in a recent aquatic**
2 **invader, the killer shrimp (*Dikerogammarus villosus*)**

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10

11 **Abstract**

12 The killer shrimp (*Dikerogammarus villosus*) is one of the most recent, but also most
13 damaging, aquatic invasive species in Europe, but information on how the species responds
14 to novel predation pressures in recently invaded areas is very limited. We employed an open
15 test arena to examine predator recognition and anti-predatory behaviour in killer shrimp
16 exposed to either blank water or water conditioned with fish kairomones to simulate a
17 predator threat. Within five years after their introduction, killer shrimp spent much more time
18 hiding in the presence of fish kairomones than when they were exposed to blank water.
19 However, no significant difference was found in aggregation behaviour, and killer shrimp
20 were strongly attracted to the scent of conspecifics regardless of predator threat. Given the
21 strong selective pressures that fish predators can exert on native and invasive gammarids, our
22 findings highlight the need to consider prey-predator interactions to better predict the
23 dispersal and likely impact of killer shrimp into invaded ecosystems.

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27 **Keywords**

28 Invasive species, Anti-predatory strategy, Chemical recognition, Aggregation behaviour,

29 Killer shrimp

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36 **Introduction**

37 From a prey-predator perspective two opposing selective forces may confront invasive
38 species when they colonise a new area: the absence of former predators may facilitate their
39 establishment (the enemy release hypotheses – Colautti et al. (2004), while their different
40 appearance (the oddity effect - Almany et al. (2007) and lack of co-evolutionary history (the
41 ‘naïve prey’ hypothesis - Sih et al. 2010) may curtail it. Thus, whether invasive species thrive
42 or flounder may depend on what predators they encounter, and how they respond to them.
43 This may result in ‘boom and bust’ cycles, reflecting prey-predator dynamics (Strayer et al.
44 2017). Surprisingly, very little is known about anti-predatory strategies of invasive species in
45 novel habitats.

46 The killer shrimp (*Dikerogammarus villosus*) is a freshwater gammarid indigenous to
47 the Ponto-Caspian region which has recently invaded Western Europe (Tricarico et al. 2010),
48 and which therefore constitutes a good system to examine anti-predatory strategies in novel
49 habitats. The species has a small size (1.8-30mm; Aldridge 2015) a flexible omnivorous diet
50 (Mayer et al. 2008), and lives in a wide variety of freshwater and brackish habitats (Devin &
51 Beisel 2008) where it faces many different potential predators. Despite its very recent
52 introduction, it is listed among the 100 most invasive species in Europe (DAISIE 2009) and
53 included in the RINSE (Reducing the Impact of Non-Native Species in Europe) black list
54 with a score of 9 out of 10 (Gallardo et al. 2016). It can displace and prey on local gammarids
55 and reduce native biodiversity (Eckmann et al. 2008; Macneil et al. 2013), and may already
56 be benefitting from a boom phase in some parts of Europe, having shed some of its former
57 parasites (Arundell et al. 2015; Grabner et al. 2015). The need for more information on this
58 aquatic invader has been flagged as a priority (Gallardo et al. 2016; Pöckl 2009), as it is
59 predicted that the species will cause major deleterious impacts on native fauna (MacNeil et
60 al. 2012).

61 Studies on the killer shrimp have focused mostly on its diet, there is very little information on
62 its predators. The species appears to be trophically very plastic (Bacela-Spychalska & van der
63 Velde 2013; Casellato et al. 2007; Platvoet et al. 2009), which would make it vulnerable to
64 many different predators. Gammarids are an important prey for many fishes (Mazzi & Bakker
65 2003; Perrot-Minnot et al. 2007) and there are reports that native brown trout and perch can
66 feed on killer shrimp in Britain (Aldridge 2015; Madgwick & Aldridge 2011). However,
67 knowledge on the predators of killer shrimp is mostly anecdotal and there is little information
68 on anti-predatory behaviour of this species in newly colonized areas, which is an important
69 aspect to consider for predicting its future spread and impact.

70 Hiding, aggregation and crypsis are three of the most common anti-predatory
71 strategies in aquatic species (Keenleyside 1979), which in the case of benthic gammarids are
72 intimately related to the nature of the substrate (Holomuzki & Hoyle 1990). Hiding behaviour
73 is particularly strong in gammarids (Goedmakers 1981; Jazdzewski et al. 2004), and
74 availability of suitable substrate to hide can be a key determinant of establishment success in
75 invasive gammarids (Devin et al. 2003), as different species may compete for shelter. For
76 example, De Gelder et al. (2016) reported that the killer shrimp's strong tendency to hide
77 during daytime can displace the European native gammarid *Gammarus roeselii* from their
78 shelters, which might put them at a higher risk of predation. Another common anti-predatory
79 strategy is aggregation behaviour, as being part of a group can confuse predators (Krakauer
80 1995; Krause & Ruxton 2002) and reduce the per-capita probability of being preyed (Codella
81 & Raffa 1995). Aggregation behaviour, however, also has costs as it is influenced by
82 competition for food and mating partners, and poses a greater risk of being parasitized, which
83 may put the group at a disadvantage (Krause & Ruxton 2002).

84 Thus, while killer shrimp invading Europe could be benefitting from a boom phase
85 caused by predator release, the oddity effect and prey naïvety of novel predators might make

86 them more vulnerable to native predators in the invaded waters. To shed light on this issue,
87 we tested two anti-predatory behaviours (hiding and aggregation) in killer shrimp exposed to
88 either dechlorinated water (control) or water conditioned with kairomones (i.e. semio-
89 chemicals emitted by predators that allow eavesdropping by prey without benefitting the
90 predator - Roberts & Garcia de Leaniz (2011) from a carnivorous fish predator, the three
91 spined stickleback (*Gasterosteus aculeatus*). We wanted to test if killer shrimp from a
92 recently colonized stream in Britain were able to recognise a common native fish as a
93 predator or, on the contrary, displayed prey naïvety that might make it more difficult to
94 mount an efficient anti-predatory response and, hence, make it more difficult to become
95 established in neighbouring waters.
96

97 **Materials and Methods**

98 *Collection and origin of samples*

99 Killer shrimp (average size = 16.8 ± 0.9 mm) were collected by live trapping in the Upper
100 Mother Ditch (Margam, Wales, 51°33'19.5"N 3°44'46.6"W) in May 2017, and three-spined
101 stickleback (weight range 0.9-2.0g) were hand-netted from an ornamental pond in Swansea
102 (Singleton Park, Wales 51°36'26.2 "N 3°58'52.4"W) in July 2017. We maintained the two
103 species in separate 100L recirculation aquaculture systems at CSAR facilities (Swansea
104 University) to avoid mixing their scents. Both species were fed frozen bloodworms, the
105 sticklebacks every day and the killer shrimp three times per week. Water temperature was
106 maintained at 15-16.5 °C with a weekly replacement of 20% volume.

107

108 *Experimental design*

109 We set up two experiments to examine the killer shrimp's anti-predatory behaviour in
110 relation to the presence of stickleback's kairomones (a fish predator that feeds on
111 gammarids). In the first experiment, we compared the hiding behaviour of individual killer
112 shrimp tested in water conditioned with stickleback kairomones compared to blank water. In
113 the second experiment, we examined the attraction of single killer shrimp to the scent of
114 conspecifics in an open-test arena scented with stickleback kairomones or with blank water.
115 We chose the three-spined stickleback as a test predator because it is a common predator of
116 gammarids (Macneil et al. 1999; Mazzi & Bakker 2003) and was present at the study site
117 (Upper Mother Ditch) where killer shrimp were first detected in 2011, having been detected
118 in a nearby reservoir one year earlier, in November 2010 (Madgwick & Aldridge 2011).

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122 *Water conditioning*

123 To obtain the kairomones used to simulate the presence of a predator, we housed 20
124 stickleback (biomass = 2.9 g/L) in a 10L tank of dechlorinated water for 24 hours. The
125 conditioned water was prepared freshly the day before the experiments.

126

127 *Experiment 1. Hiding behaviour under the threat of predation*

128 To quantify hiding behaviour under the threat of predation we used a 2L plastic tank
129 (L:20cm, W:10cm, H:10cm) fitted with artificial grass patches (3cm²) glued to the bottom in
130 a staggered fashion (Figure 1a), and a release cylinder (3.5cm diameter) located in the centre
131 of the tank. At the beginning of the experiment 250ml of either dechlorinated water (control
132 test) or fish-conditioned water (treatment) was added to the tank. One killer shrimp was
133 placed inside the release cylinder and left to acclimatise for 5 min. The cylinder was then
134 slowly lifted and the behaviour of the killer shrimp (time spent swimming or hiding in the
135 artificial grass patches) was recorded for 10 minutes with a GoPro Hero camera mounted
136 above the test tank (Figure 2A). In total, 20 individuals were tested with fish conditioned
137 water and 20 individuals with blank water, the order of which was determined at random.

138

139 *Experiment 2. Conspecific attraction*

140 To test if killer shrimp were more attracted to conspecifics under the threat of predation, we
141 used a tank of the same size and volume (2 L) as the one used in experiment 1, but in this
142 case the bottom was left bare and did not have artificial grass patches. At the two extremes of
143 the tank we attached two tea balls (diameter 5cm) and drew two lines in the tank to notionally
144 divide it into three equal sectors, two choice zones associated with the tea balls, and a middle
145 section that served as a neutral (no choice) zone (Figure 1b). Ten killer shrimp were
146 introduced in one of the two tea balls chosen at random, while the other one was left empty.

147 As for experiment 1, 250ml of fish conditioned water or dechlorinated water were added to
148 the tank and a single individual was introduced in the acclimatization cylinder, where it was
149 left to acclimatize for 5min The cylinder was then removed, and the activity of the killer
150 shrimp was recorded for 10 minutes with an overhead GoPro camera, as above. The time
151 spent in each of the three tank zones was used to describe its behaviour: the time spent in the
152 side containing the tea ball with conspecifics was interpreted as measure of attraction for
153 group protection, the time spent in the central part was interpreted as neutral behaviour, and
154 the time spent in the side with the empty tea ball was interpreted as avoidance of
155 conspecifics. After each trial, the position of the two tea balls was alternated to control for
156 possible external disturbances. In total, 40 killer shrimp were tested, 20 with dechlorinated
157 water and 20 with fish scented water. The killer shrimp inside the tea ball were replaced
158 between sessions to reduce aggressive behaviour due to confinement.

159

160 *Statistical analyses*

161 We used R 3.3 (Team 2017), for analysis. For both experiments, we used a paired t-test to
162 examine if (1) killer shrimp spent more time hiding than swimming when they were exposed
163 to fish kairomones than when they were exposed to blank water (Experiment 1), and if (2)
164 attraction to conspecifics was stronger when the killer shrimp were exposed to kairomones
165 from a fish predator than when they were exposed to dechlorinated water (Experiment 2) .

166

167 *Ethics Statement*

168 Experiments were carried out in accordance with Swansea University's Ethical guidelines
169 and were approved by the Ethics Committee (070917/24, Reference Number:
170 STU_BIOL_30638_060617140454_1). At the end of the experiments all sticklebacks were

171 released alive at the site of capture. The killer shrimp, due to the risk they may pose for
172 native communities, were disposed through incineration.

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175 **Results**

176 *Experiment 1. Hiding behaviour*

177 Killer shrimp spent significantly more time hiding when the water was conditioned with
178 kairomones from a predatory fish (mean time \pm 95CI = 543.45 \pm 13.7 s) than when they were
179 tested against blank water (mean time \pm 95CI = 386.75 \pm 18.5 s; behaviour x treatment
180 interaction $F_{1,76} = 544.02$, $P < 0.001$; Figure 2). Controls spent 50% of their time hiding and
181 50% swimming ($t_{19} = 1.416$, $P = 0.173$), whereas when they were exposed to fish kairomones
182 they spent 91% of their time hiding and only 9% swimming ($t_{19} = 34.789$, $P < 0.001$).

183

184 *Experiment 2. Attraction to conspecifics*

185 Killer shrimp spent much more time in the side of the tank scented with conspecifics (mean
186 time 477.5 \pm 20.5 s) than in the opposite side (mean time 39.1 \pm 12.2 s), but such preference
187 was not affected by the presence of fish kairomones ($t_{19} = 0.245$, $P = 0.808$; Figure 3).

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191 **Discussion**

192 Our study shows that within 6 years (approximately 20 generations) of their introduction into
193 a novel area in Britain killer shrimp display a strong tendency to hide when they are exposed
194 to the chemical scent of a native predatory fish (the three spined stickleback), but not when
195 they are exposed to dechlorinated water. Given that no evidence of predator avoidance was
196 detected on the same population in relation to the scent of non-predatory Nile tilapia (Rolla et
197 al. 2019), this strongly suggests that chemical recognition of stickleback kairomones
198 constitutes an evolved, adaptive trait.

199 Much of our knowledge on the invasive killer shrimp refers to its role as a predator,
200 there is little information regarding its role as a fish prey. This is unfortunate because
201 predatory fish can exert strong selective pressures on gammarids (Åbjörnsson et al. 2004;
202 Ahlgren et al. 2011; Kinzler & Maier 2006; Kotta et al. 2010; Wudkevich et al. 1997) and
203 could play a major role in determining the killer shrimp's invasion success. The killer shrimp
204 has been found in the diet of 17 fish species found in the introduced range (9 exotic and 8
205 native, Table 1), but predator recognition has only been reported for the European bullhead
206 *Cottus gobio* (Sornom et al. 2012), the racer goby *Babka gymnotrachelus* (Jermacz et al.
207 2017), and the spiny-cheek crayfish *Orconectes limosus* (Hesselschwerdt et al. 2009),
208 therefore little is known about its antipredator behaviour. Amphipods can change their
209 behaviour and habitat preferences when they detect chemical cues from potential predators
210 (Baumgärtner et al. 2003; Thiel 2010), but also from injured conspecifics (Wisenden et al.
211 2001; Wudkevich et al. 1997), similar to what has been observed among teleost fishes
212 (Roberts & Garcia de Leaniz 2011). Kairomone detection by gammarids has been reported
213 previously as an anti-predatory strategy (Wudkevich et al. 1997), but seldom in the context of
214 invasion biology (Hesselschwerdt et al. 2009).

215 Predation by native species could reduce, or at least slow down, invasions by non-
216 native species (Zuharah & Lester 2010; Zuharah & Lester 2011) because they may not be
217 able to recognise native predators (Sih et al. 2010), but also because their different
218 appearance could make them easier to detect, or make them more attractive, to native
219 predators (the ‘oddity prey effect’, (Penry & Williams et al. 2018). For example, killer shrimp
220 are typically larger than native freshwater gammarids (Devin et al. 2003), and this might
221 make it easier for visual predators to detect them. However, native predators may also be
222 reluctant to feed on novel prey due to neophobia (Champneys et al. 2018), and this could
223 result on lower predation pressure on invasive species (Crawley 1987; MacNeil et al. 2000;
224 Trowbridge 1995; Wells & Henderson 1993). Killer shrimp could also benefit from a
225 ‘shadow of safety’ effect if their relative low abundance during the earlier stages of invasion
226 deflects predation pressure to the more abundant native prey (Trillo et al. 2016). Killer
227 shrimp can rapidly become the dominant species in invaded benthonic communities (Dick &
228 Platvoet 2000) and can become the most abundant food resource for fish feeding on
229 macroinvertebrates. For example, field studies have indicated that killer shrimp can replace
230 native *Gammarus roeseli* in the diet of zoo-benthivorous fish (Eckmann et al. 2008), but
231 other studies have suggested the opposite, and reported that native fish prefer to feed on
232 native gammarids (Kinzler & Maier 2006).

233 Clearly, the role of predation on invasion dynamics is difficult to predict, but
234 knowledge of the time since introduction, and of prey-predator interactions appear important
235 in determining establishment success. This is particularly complicated in the case of the killer
236 shrimp in Great Britain because although its arrival is very recent, it may have already
237 learned to chemically recognise a range of novel predators during its long invasion of Europe.
238 Killer shrimp in the British Isles are genetically similar to those in continental Europe
239 (Rewicz et al. 2015), where the invasion started in 1992 after the opening of the Main-

240 Danube canal (Dick & Platvoet 2000), suggesting that they are stepping stones direct
241 descendants from the first invaders. Stepping stones strategies drive the long distance
242 dispersal of many species (Saura et al. 2014), and it is possible that repeated residencies in
243 different habitats may have enabled the killer shrimp to learn to recognise different predators.
244 Given that the three-spined stickleback is also widespread in continental Europe, our study
245 cannot rule out that the observed predator recognition was acquired in Britain, or represents
246 an older behavioural legacy from previous invasions.

247 Two common anti-predatory strategies in amphipods are to reduce mobility and
248 become more aggregated under the risk of predation (Åbjörnsson et al. 2000; Williams &
249 Moore 1985; Williams et al. 2016). Results from Experiment 1 in our study indicate that
250 killer shrimp spend more time hiding and less time swimming when they were exposed to
251 predator kairomones, as seen in other gammarids. These findings are also in agreement with
252 those of Sornom et al. (2012) who observed a decrease in mobility and an increase in hiding
253 time in killer shrimp exposed to the scent of another fish predator, the European bullhead
254 (*Cottus gobio*). However, our results on aggregation behaviour (Experiment 2) are more
255 equivocal. Unlike *Gammarus pulex*, which become increasingly aggregated when exposed to
256 stickleback kairomones (Kullmann et al. 2008), killer shrimp in our study showed the same
257 strong preference to remain in the vicinity of conspecifics even when there was no immediate
258 threat of predation. Exposure to bullhead kairomones also failed to elicit an increase in killer
259 shrimp aggregation (Sornom et al. 2012), but in this case aggregation was low. Jermacz et al.
260 (2017) have shown that killer shrimp prefer to hide in response to predator cues, rather than
261 aggregate, when refuges are present, and that they aggregate when there are no shelters and
262 staying in a group is the only antipredator strategy possible. It is possible that aggregation
263 behaviour in the killer shrimp depends on the availability of shelters, but also on the risk of
264 intra-guild predation. Compared to native gammarids, killer shrimp display higher sociability

265 and lower incidence of cannibalism (Kinzler et al. 2009; Truhlar & Aldridge 2015), which
266 may explain their strong tendency to aggregate. Aggregation behaviour can provide not only
267 protection from fish predators (Åbjörnsson et al. 2004), but could also facilitate dispersal, as
268 living in a group would increase the number of founders, and propagule pressure has been
269 found to be an important factor determining invasion success (Consuegra et al. 2011;
270 Ricciardi et al. 2010)

271

272 **Conclusions**

273 In conclusion, prey-predator dynamics are an important, but largely neglected, determinants
274 of invasion success and our study indicates that knowledge of anti-predatory strategies might
275 be important for predicting dispersal pathways and risk of establishment in the killer shrimp,
276 and likely also on other aquatic invaders. Killer shrimp are dispersing at an alarmingly fast
277 rate in Europe (DAISIE 2009; Gallardo et al. 2016), and prevention and control measures
278 might benefit from information on prey and predators present in communities at risk. In this
279 sense, behavioural profiling of anti-predatory strategies, using perhaps some of the simple
280 assays shown in our study, could be incorporated into risk assessments. Knowledge of how
281 invasive species might respond to resident predators can inform the development of more
282 efficient management actions, as these seldom consider biotic resistance (Robinson et al.
283 2019; Robinson et al. 2018). Given its strong aggregation behaviour, we also suggest that
284 even when complete eradication is not possible, control measures that aim to reduce the
285 density of killer shrimp might be beneficial, as a lower relative abundance and a smaller
286 group size can make them more vulnerable to fish predators, potentially reducing their impact
287 on native communities.

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294

295 **Author Contributions & Competing Interests**

296 MR and CGL designed the study. SC and CGL secured the funding. MR collected the data
297 and carried out the analyses with advice from CGL. MR and CGL wrote the MS with
298 contributions from SC. The authors declare no competing interests.

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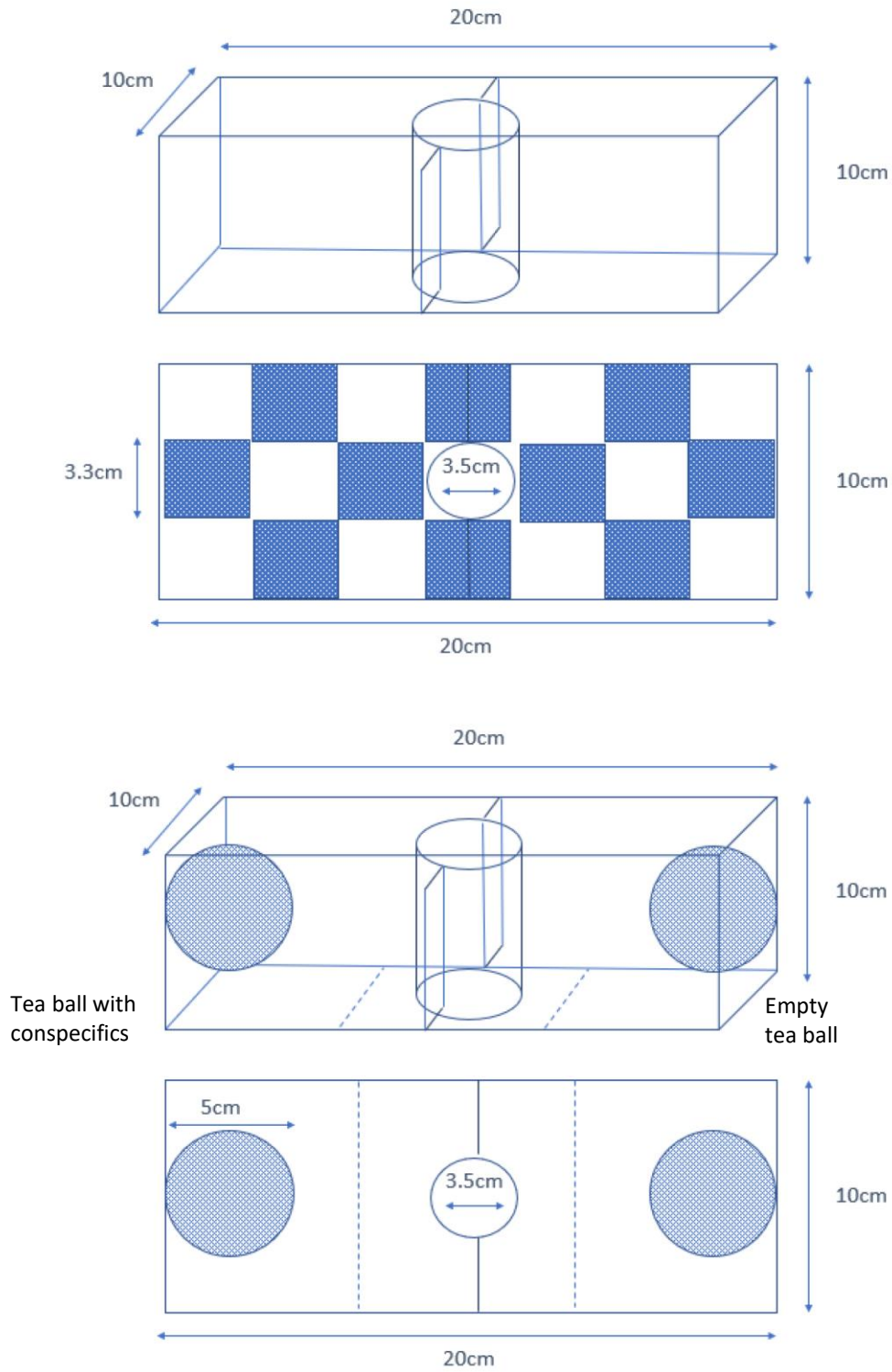
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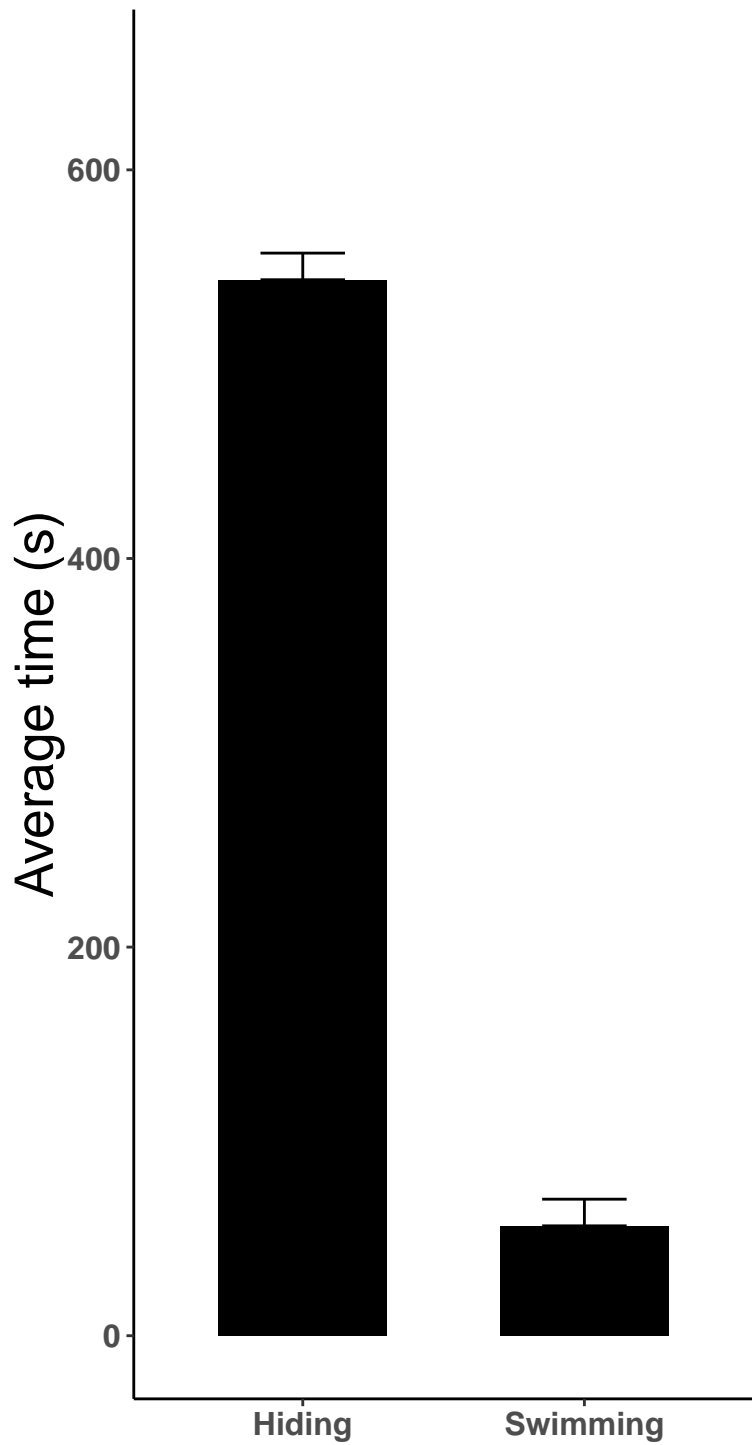
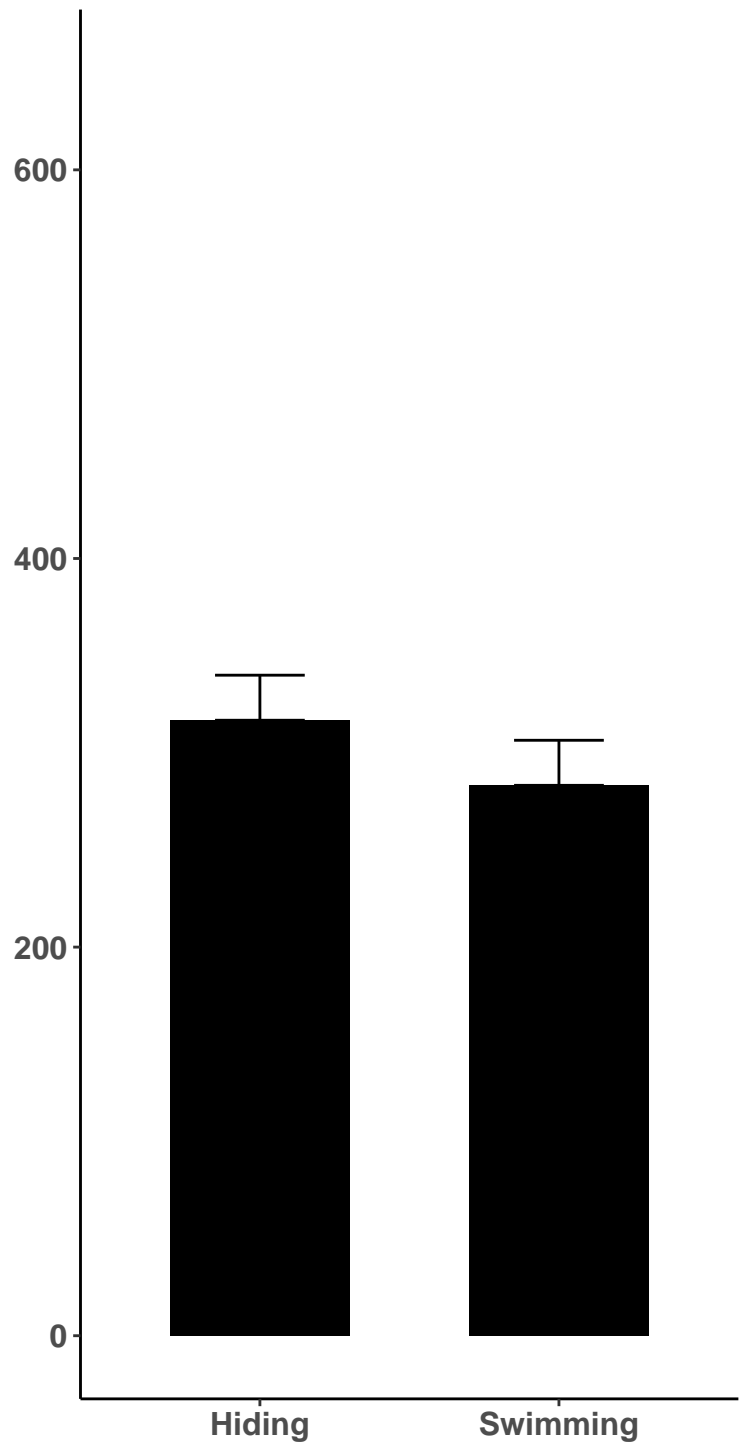
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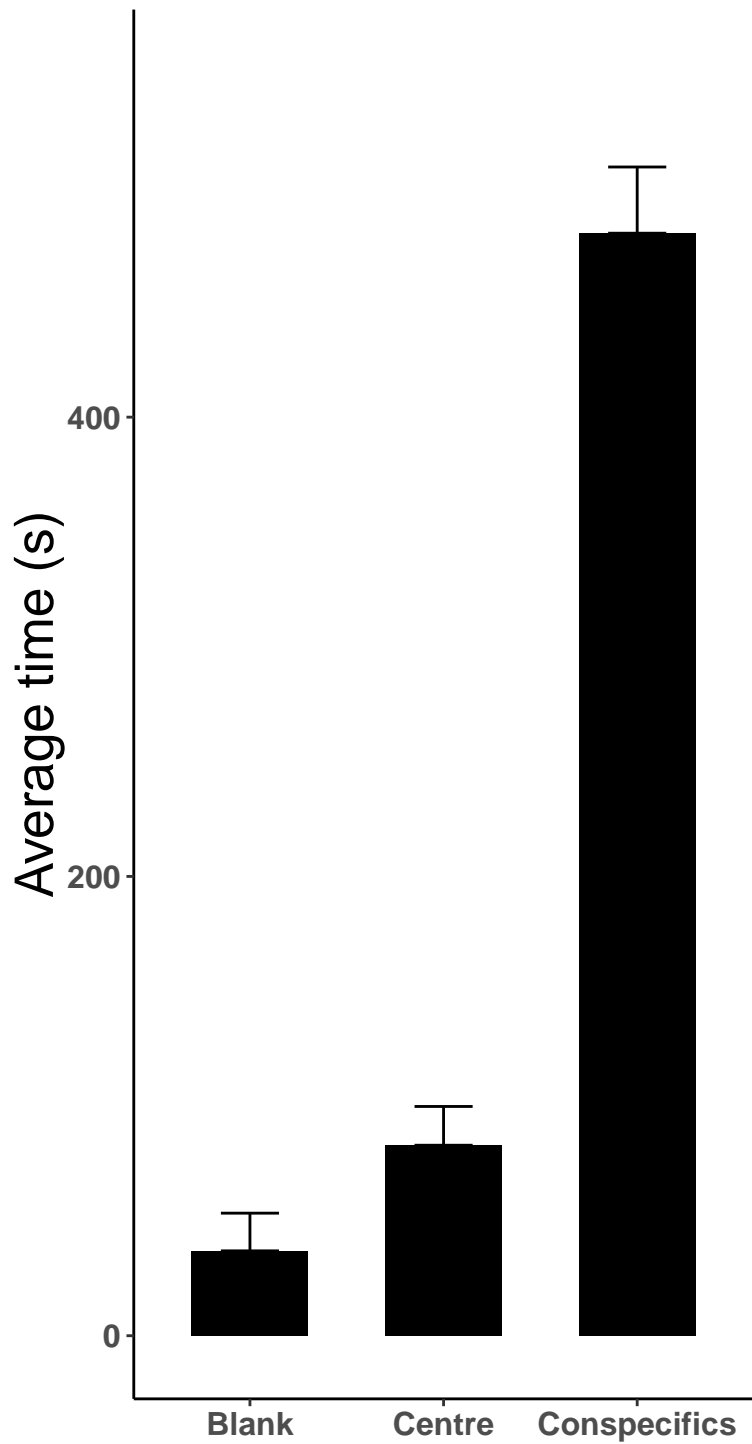
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