

2019-07-03

Distracted decision makers: ship noise and predation risk change shell choice in hermit crabs

Tidau, Svenja

<http://hdl.handle.net/10026.1/14368>

10.1093/beheco/arz064

Behavioral Ecology

Oxford University Press (OUP)

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1 **Distracted decision-makers: Ship noise and predation risk**
2 **change shell choice in hermit crabs**

3 This is a final accepted manuscript. The definitive published version is at Behavioral
4 Ecology, arz064, <https://doi.org/10.1093/beheco/arz064>

5

6 Svenja Tidau* and Mark Briffa

7

8 * Corresponding author: svenja.tidau@plymouth.ac.uk

9

10 *Address and contact*

11 Svenja Tidau

12 University of Plymouth | Marine Biology & Ecology Research Centre

13 Drake Circus | Plymouth, PL4 8AA | UK

14

15 Mark Briffa

16 University of Plymouth | Marine Biology & Ecology Research Centre

17 Drake Circus | Plymouth, PL4 8AA | UK

18 **Abstract**

19 Human induced rapid environmental change such as noise pollution alters the ability of
20 animals to integrate information cues. Many studies focus on how noise impacts single
21 sensory channels but in reality animals rely on multi-modal sources of information. In
22 this study, we investigated the effect of anthropogenic noise and the visual presence of
23 a predator on tactile information gathering during gastropod shell assessment in the
24 European hermit crab *Pagurus bernhardus*. For hermit crabs, empty gastropod shells
25 are a crucial resource affecting growth, reproduction and survival. We measured shell
26 assessment behavior and manipulated (i) the shell size (50% or 80% of the optimal),
27 (ii) sound condition (ship or ambient) and (iii) visual predator cue (absence/ presence).
28 Overall we found that crabs were less likely to accept an optimal shell in the presence
29 of ship noise, suggesting that exposure to ship noise disrupted the information
30 gathering ability of the crabs. We also found a significant interaction between noise,
31 predator presence and shell size on the mean duration for the final decision to accept
32 or reject the optimal shell. Hermit crabs in 50% shells took less time for their final
33 decision when exposed to both ship noise and predator cue while crabs in 80% shells
34 showed shorter decision time only when the predator cue was absent. Our results
35 indicate that anthropogenic noise can interact with predation threat and resource
36 quality to change resource acquisition, suggesting that noise pollution can disrupt
37 behavior in a non-additive way, by disrupting information use across multiple sensory
38 channels.

39

40 **Keywords**

41 Anthropogenic noise, hermit crabs, human induced rapid environmental change,
42 predation risk, resource assessment, sensory ecology

43 **Introduction**

44 Human induced rapid environmental change (HIREC) (Sih et al. 2011) encompasses
45 global processes such as climate change as well as examples of more localized and
46 transient pollution such as ship noise (Tuomainen and Candolin 2011). HIREC can either
47 affect behavior directly by impacting whole organism performance capacities (via
48 changes to development or physiological state) or indirectly by altering the sensory
49 environment and disrupting the information gathering and decision-making processes
50 that underpin behavior. Both routes have potential implications for survival and fitness.
51 Noise has been shown to affect the detectability (and recognizability) of cues both
52 through masking of sound (Brumm 2004; Foote et al. 2004; Sun and Narins 2005; Clark
53 et al. 2009; Barber et al. 2010; Halfwerk et al. 2012; Lampe et al. 2012; Ladich and Fay
54 2013; Heiler et al. 2016; Spiga 2016; Simpson et al. 2016) and by distracting an animal's
55 limited attention (Chan et al. 2010a; Chan et al. 2010b; Wale et al. 2013a; Kunc, et al.
56 2014; Simpson et al. 2015; Radford et al. 2016; Nedelec et al. 2017; Walsh et al. 2017;
57 Tidau and Briffa *In Press*). Since animals perceive and have to process information
58 across various modalities, their limited attention is a cognitive constraint (Dukas 2004).
59 As a consequence, the 'distracted prey hypothesis' (Chan et al. 2010b) suggests that
60 since animals have to divide their attention they may no longer respond appropriately to
61 predator cues in the presence of noise (Chan et al. 2010b). Thus, noise might not only
62 distract attention from acoustic cues but also from non-acoustic cues across visual,
63 chemical and tactile channels and in addition can also disrupt the integration of
64 information across sensory modalities (Halfwerk and Slabbekoorn 2015).

65 Recent decades have seen mounting evidence for effects of anthropogenic noise
66 pollution across a range of taxa, habitats and behavioral contexts (Barber et al. 2010;
67 Kight and Swaddle 2011; Williams et al. 2015). This includes shifts in the amplitude,
68 duration, timing and patterns of acoustic communication as possible means of

69 compensating for noise, with examples in birds (Brumm 2004; Halfwerk et al. 2012),
70 amphibians (Sun and Narins 2005), insects (Lampe et al. 2012), marine mammals (Foote
71 et al. 2004; Heiler et al. 2016), fish (Ladich and Fay 2013) and snapping shrimp (Spiga
72 2016). However, there is also evidence that behaviors in contexts other than
73 communication can be impacted by noise, and in these cases the scope for animals to
74 compensate may be more limited. Furthermore, due to distraction effects disruption is
75 not limited to behavior that relies on acoustic sources of information only. Examples of
76 the wide range of impacted behavioral contexts include reduced foraging performance
77 in the common shore crab *Carcinus maenas* (Wale et al. 2013a), the greater mouse-
78 eared bat *Myotis myotis* (Siemers and Schaub 2011) and the Black-tailed prairie dog
79 *Cynomys ludovicianus* (Shannon et al. 2014), decreased parental care in the spiny
80 chromis *Acanthochromis polyacanthus* (Nedelec et al. 2017), impaired shoaling in the
81 Bluefin tuna *Thunnus thynnus* (Sara et al. 2007) and reduced predator avoidance in the
82 European eel *Anguilla anguilla* (Simpson et al. 2015).

83 Anthropogenic noise not only disrupts the sensory environment of animals along
84 acoustic, unimodal sensory channels but also across non-acoustic channels for
85 information gathering and processing, such as the visual and tactile sensory systems
86 (Kunc et al. 2014; Tidau and Briffa *In Press*). It has been suggested that such cross-
87 sensory interference can distract organisms, thus explaining behavioral changes in
88 response to anthropogenic pollution in vertebrates and invertebrates alike (reviewed by
89 Halfwerk and Slabbekoorn 2015). However, different sources of information used by
90 animals tend to be studied in isolation. In contrast, few studies have taken a multi-
91 sensory approach to investigating the effects of anthropogenic noise on behaviors that
92 (in nature) are likely to be dependent on information from several channels (Sih et al.
93 2011; Halfwerk and Slabbekoorn 2015). For example, the European hermit crab *Pagurus*
94 *bernhardus* integrates tactile and visual information when assessing the value of an

95 empty gastropod shell. This is a critical resource that provides protection for their weakly
96 calcified abdomen and crabs are known to choose new shells based on information
97 about their mass, species, condition (Elwood and Neil 1992) and color (Briffa et al. 2008).
98 During the process of exchanging an old shell for a new one, hermit crabs are vulnerable
99 to attack and hence they adjust their shell assessment behavior in the presence of
100 predators (Briffa et al. 2008). Hermit crabs rely on a range of tactile, visual and chemical
101 cues in order to compare the quality of a potential new shell with that of the currently
102 occupied shell. Like other coastal species, however, hermit crabs are subject to noise
103 pollution caused by the motors of ships and boats. While *P. bernhardus* is found in
104 coastal intertidal rock pools, as they grow, these hermit crabs prefer to occupy *Buccinum*
105 *undatum* shells and are increasingly found in subtidal areas such as the English Channel.
106 Thus, for *P. bernhardus* noise from ships represents a relevant anthropogenic stimulus.
107 A recent laboratory study has shown that the time taken for *P. bernhardus* to choose a
108 new shell decreases significantly in the presence of white noise (Walsh et al. 2017).
109 While the effects of noise on shell assessment (Walsh et al. 2017) and antipredator
110 behavior (Chan et al. 2010a) have been analyzed in isolation in different species of
111 hermit crabs, the effects of noise on the ability to integrate information about the shell
112 resource and predation threat has yet to be investigated.

113 Here, we investigate the effects of ship noise on the ability of hermit crabs to use
114 tactile and visual information to choose a shell of optimal quality and to adjust their shell
115 assessment behavior in the visual presence of a predator. A common predator of *P.*
116 *bernhardus* is the common shore crab *Carcinus maenas* and previous studies have
117 shown that hermit crabs respond to their chemical cues (Rotjan et al. 2004; Briffa et al.
118 2008). Under normal circumstances the duration of shell investigation and chance of a
119 hermit crab exchanging shells increases with the potential gain in shell quality (Elwood
120 and Stewart 1985; Elwood 1995; Tricario and Gherardi 2007; Turra and Gorman 2014)

121 but decreases with predation risk (Rotjan et al. 2004; Bulinski 2007; Briffa and Austin
122 2009), reflecting a trade-off between the costs and benefits of changing shells. If this
123 trade-off between shell quality and predation risk is altered by the presence of noise, this
124 would indicate that anthropogenic noise reduces the ability of hermit crabs to integrate
125 pertinent information across different sensory channels. We predict that hermit crabs will
126 respond to the visual predator cue by altering their shell assessment and that this is
127 influenced by the quality of shell a hermit crabs occupies, i.e. crabs in small shells (50%
128 of its preferred shell based on the crabs own body mass) will have a large shell gain
129 (50%) but are also more exposed to predators while crabs in larger shells (80% of its
130 preferred shell) have a lower shell gain (20%) but are less exposed to a predator. We
131 predict that crabs in small shells will therefore show greater responses to the predator
132 cue. Moreover, if noise disrupts information gathering across sensory channels, we
133 expect crabs to alter their shell dependent predator response in the presence of noise.
134 Thus, the effect of original shell size on responses to a predator cue should be reduced
135 in the presence of noise. Thereby, we aim to address a current gap in knowledge about
136 how the effects of anthropogenic noise might impact the integration of behavior across
137 the different sensory channels that animals rely on in nature.

138 **Materials and methods**

139 ***Collection and husbandry of hermit crabs***

140 *P. bernhardus* inhabits subtidal as well as intertidal marine habitats. For practically of
141 sampling, we collected *P. bernhardus* from the rocky intertidal of Hannafore Point,
142 Cornwall, UK (50° 20' 42" N, 4° 28' 0" W) adjacent to the English Channel and next to a
143 local fishing harbor between November 2016 and January 2017. We transported the
144 animals directly to a temperature-controlled room at the University of Plymouth. The
145 room was maintained at 15 °C with a 12:12 hour light:dark cycle and hermit crabs kept

146 in a single holding tank containing 125 L of continuously filtered and aerated seawater
147 (Briffa et al. 2013) taken from the laboratory supply obtained from the seaward side of
148 Mount Batten pier (50° 21' 34" N, 4° 8' 8" W) in Plymouth Sound at spring tides. We fed
149 crabs in this stock tank once a week with white fish.

150 At least 16 hours before the observation, we removed crabs with a bench vice
151 from their shell, sexed and weighed each individual. Crab mass ranged from 0.18 g to
152 1.61 g (mean mass \pm SE = 0.798 g \pm 0.32 g, $N=59$). Each crab was assigned a *Littorina*
153 *littorea* shell of either 50% or 80% of its preferred shell mass based on a regression line
154 relating preferred shell mass to body mass (Dowds and Elwood 1983; Briffa and Elwood
155 2007). We housed the crabs in individual white plastic dishes of 15 cm diameter
156 containing continuously aerated seawater to a depth of 5 cm. Since the shell mass
157 preferences of females are subject to change during the breeding season, we used only
158 male crabs without damaged appendages, visible parasites or recent molting in the study
159 (Briffa and Elwood 2007). After the observations we returned the animals unharmed to
160 the sea at the collection point.

161 ***Tank set-up and sound analysis***

162 We carried out the observations in a 80 x 50 x 50 cm sized glass tank filled with ~ 130 L
163 (to a depth of 40 cm) of seawater from the laboratory supply. We placed the tank on a
164 free-standing trolley and cushioned it with at least 1cm Styrofoam plates between tank
165 and trolley as well as the trolley and floor. The speaker was suspended in the tank from
166 a cushioned bamboo stick at 20 cm distance to one end of the tank, such that it was fully
167 submerged in the seawater (Figure 1). In order to ensure that crabs were exposed to
168 similar sound conditions we designed two 20 x 20 cm arenas within the larger tank at
169 equal distances from the speaker. The center of each arena was 30 cm from the center
170 speaker and the other end of the tank. No substrate was provided on the arena floors,
171 as this is known to interfere with the locomotion and general activity of hermit crabs and

172 other non-swimming crustaceans (Wale et al. 2013; Walsh et al. 2017; Tidau and Briffa
173 *In Press*). The arenas were divided by an opaque 15 cm high plastic sheet. In order to
174 disrupt the particle motion resulting from the sound playbacks as little as possible while
175 preventing the crabs from directly escaping from the arena, we constructed the walls of
176 each arena from 1 x 1 cm mesh-size plastic mesh. For the predator cue, we placed a
177 plastic model crab of approximately 10 cm width in an upright position outside of the tank
178 and centered to the arena such that it was visible from inside the arena imitating the
179 natural predator *Carcinus maenas* (Rotjan et al. 2004; Briffa et al. 2008).

180 While some studies use white noise as a substitute sound source to test the effect
181 of anthropogenic noise pollution on animals (Chan et al. 2010a; Stahlman et al. 2011;
182 Walsh et al. 2017), most noise studies utilize playbacks of actual anthropogenic
183 pollutants, for example ships. Ship noise and white noise playbacks not only differ in their
184 spectral properties (frequency, amplitude) but also in their temporal pattern and
185 predictability. Compared to white noise, which is characterized by equal energy intensity
186 across frequencies (Barber et al. 2010), ships produce unique acoustic signals
187 depending on factors such as speed and load (Hildebrand 2009). Consequently, ships
188 produce a more unpredictable signal compared with artificial white noise. It is known that
189 the stress induced by a stimulus is linked to its predictability (Koolhass et al. 2011;
190 Francis and Barber 2013) and that for this reason less predictable stimuli are likely to be
191 more distracting to animals. Relatively few studies have formally compared the effect of
192 artificial white noise and playbacks of anthropogenic noise pollutants (Holles et al. 2013;
193 Bent et al. 2018; Bermúdez-Cuamatzin et al. 2018), but where this has been done noise
194 from anthropogenic pollutants tends to be similarly (Bermúdez-Cuamatzin et al. 2018) if
195 not more distracting than white noise in terms of behavior (Holles et al. 2013; Bent et al.
196 2018). For these reasons we used three ship noise playbacks along with corresponding
197 ambient control sounds from the same sites recorded at three major UK harbors. These

198 recordings were used in previous studies in which the sample location, ship size and
199 speed were detailed (for instance Wale et al. 2013a; Simpson et al. 2015). We used
200 Audacity 2.1.2 (Audacity Team, 2017) to create a total of six sound tracks for playback
201 to the crabs, of either ambient control sound or ship noise. In the case of ship noise
202 tracks, we alternated 2 minutes of ship noise with 2 minutes of ambient sound including
203 15 seconds fading in and out to simulate noise of passing ships. We assigned the crabs
204 randomly to one of the two sound treatments (ambient control or ship noise). Within each
205 of these treatments crabs received one of three alternative sound recordings of ship
206 noise or ambient sound, as appropriate for their treatment group. These recordings were
207 alternated between the successive observations (for details on the noise exposure and
208 behavioral observation see section below).

209 For the playbacks of the sound tracks, we used a Toshiba Portégé R830-13C
210 laptop (Tokyo, Japan) connected to a Lvpin LP-200 amplifier (Lvpin Technology Suzhou
211 Co., Taiping Town, China) and an underwater speaker (DNH Aqua-30 underwater
212 speaker, effective frequency range 80-20 000 Hz, DNH A/S, Kragerø, Norway). To
213 characterize the acoustic properties of our playbacks within the laboratory aquarium we
214 undertook a spectral analysis as follows. We re-recorded the six sound tracks at the
215 center of the arena at 30cm distance to the speaker and 10cm to the tank wall at 1-2 cm
216 distance to the bottom of the tank with an omnidirectional hydrophone HTI-96-MIN (with
217 inbuilt preamplifier, manufacturer-calibrated sensitivity -165 dB re 1 V μ Pa-1; frequency
218 range 0.002-30 kHz, High Tech Inc., Gulfport, MS, USA) and Linear Sony PCM-M10
219 recorder (48 kHz sampling rate, Sony Corporation, Tokyo, Japan; recording level
220 calibrated using pure sine wave signals from a function generator with a measured
221 voltage recorded in line on an oscilloscope). At this position, the three ambient sound
222 tracks were played back so that they had an average maximum sound pressure level of
223 119.4 dB RMS re 1 μ Pa (ambient A: 119.7, ambient B: 118.8, ambient C: 119.8) and

224 the ship noise had an average maximum of 143.6 dB RMS re 1 μ Pa (ship A: 143.0, ship
225 B: 143.8, ship C: 143.9). These sound levels were similar to those in previous studies on
226 crustaceans (Wale et al. 2013a, Wale et al. 2013b). We note that hermit crabs are likely
227 to perceive the particle motion component of sound rather than the measured sound
228 pressure levels (Popper et al. 2001; Breithaupt 2002). However, as in in previous studies
229 (see for instance Wale et al. 2013), and due to unresolved challenges of tank acoustics
230 (Rogers et al. 2016) we analyzed the power spectrum of the sound pressure for each
231 playback to make sure that we exposed crabs to two distinctive sound conditions namely
232 ship noise and ambient control, rather than attempting to establish absolute noise
233 sensitivity levels for hermit crabs. We used PAMGuide (Merchant et al. 2015) for
234 MATLAB R2015b (MathWorks, Inc. 2015) to perform a power spectrum analysis of 60
235 seconds recording with Hann evaluation window, overlap 50%, 0.25 second window
236 length, 1 - 48 000 Hz bandwidth normalized to 1 Hz (Figure 2).

237 ***Experimental design and behavioral analysis***

238 We designed a fully orthogonal experiment with the three factors; sound condition
239 (ambient control or ship noise), predator cue (present or absent) and initial shell size (50%
240 adequate or 80% adequate). The combination of these treatments resulted in 8 treatment
241 groups. During each observation session, our set up containing two arenas allowed us
242 to concurrently expose two individuals (that were unable to interact with one another) to
243 the same sound track. At the start of the session we placed a shell of 100% preferred
244 size for the crab allocated to each arena with the aperture facing downwards in the
245 middle of each arena. After starting the sound playback, we placed the crabs in their
246 allocated arenas with the aperture of their gastropod shells facing upwards. To avoid the
247 effect of shell size being confounded by time of day, we always observed concurrently a
248 crab starting in the observation in a 50% adequate shell and a crab starting the
249 observation in an 80% adequate shell, one in each of the two observation arenas. To

250 avoid confounding the data through any directional bias the position (left or right arena)
251 we alternated the two shell size treatments between arenas across consecutive
252 observations. On each day of observation we collected data from a similar number of
253 crabs from each of the four ship noise and predator cue combinations, and the order of
254 treatment combinations was varied from day to day.

255 The shell assessment behavior was recorded with a Canon Legria HF R47
256 (Tokyo, Japan) for a maximum of 25 minutes (up to 5 minutes were allowed for crabs to
257 emerge from their gastropod shell at the start of the observation and 20 minutes of
258 behavior were then quantified). The videos were scored using The Observer version 12
259 (Noldus IT, Wageningen, The Netherlands) event logger software blind to the sound
260 and predator cue treatments. We scored the frequency, duration and latency for each of
261 the behaviors. The observation started when the crab had emerged from its shell and
262 placed at least one of its appendages on the bottom of the tank. During the 20 minutes
263 of observation the crabs were continuously exposed to either ambient control sound or
264 ship noise playback as described above. We recorded the total decision time defined by
265 the time from the start of the observation when crabs contacted the bottom of the tank
266 with at least one walking leg to the point where the crabs had made a clear decision to
267 reject either the new, optimal shell or the initially occupied shell. We designated the final
268 decision point as that time at which crabs had moved one body length away from either
269 the rejected optimal shell or the previously occupied shell. We also recorded whether
270 crabs contacted the optimal shell with their antennae, whether they entered the optimal
271 shell. For those crabs that did enter the optimal shell we recorded whether or not they
272 finally accepted the optimal shell. Observations were terminated when one of the
273 following conditions was met: The crab swapped into the optimal shell and moved at
274 least as far away from the old shell as the length of its body (“optimal shell accepted”),
275 the crab had contact with the 100% shell but did not swap into it and moved away at

276 least as far as the length of its body (“optimal shell rejected”) or after 20 minutes, if the
277 crab had no shell contact (“no decision”). Of the initial 77 observations conducted, 18
278 crabs made no contact with the optimal shell. Since their decision was not affected by
279 any of the predictors (sound: $\chi^2_1 = 0.34$, $P = 0.56$; predator cue: $\chi^2_1 = 1.17$, $P = 0.28$,
280 occupied shell: $\chi^2_1 = 0.02$, $P = 0.89$) or their interaction (see supplemental files for a
281 complete results table), we excluded those 18 crabs from the analysis. This left a sample
282 size of $N = 59$ crabs (see Table 1 for details).

283 ***Statistical analysis***

284 To determine the effects of noise condition, predator cue and shell size on shell
285 assessment behavior we used General and Generalised Linear Mixed Effect Models, as
286 appropriate, implemented in the R-package lme4 (Bates et al. 2015) in R version 3.3.2
287 (R-Core-Team 2017). The fixed effects were sound treatment (ship noise or ambient
288 control), predator cue (present or absent) and initial occupied shell size (50% or 80%),
289 and their interactions. Crab body mass was included as a covariate. In order to account
290 for the potential pseudo-replication that might arise from re-using each of the three ship
291 noise and three ambient control recordings across multiple observations, we included
292 playback identity as a random (intercept) effect. Furthermore, we included a second
293 random intercept to account for the paired observations within each observation session.
294 Where necessary the data (i.e. latency to contact the optimal shell, total decision time to
295 accept or reject the optimal shell) were log transformed to improve normality, so that the
296 assumption of the linear models would be met. For the binary response variables
297 (displaying antennal contact, entering the optimal shell, accepting the optimal shell) we
298 used a binomial distribution and for continuous data (duration and latency) we used a
299 Gaussian distribution. For models with non-Gaussian data we used likelihood ratio tests.
300 To assess model fit we visually inspected the distribution of residuals.

301

302 *Ethical note:* No animals were harmed during the experiments. After the experiment each
303 crab was supplied with an optimal shell, was fed and returned to the sea at the location
304 of collection. No licenses or permits were required for this study.

305

306 **Results**

307 There was no effect of the interaction between sound, predator cue and occupied shell
308 size ($\chi^2_1 = 3.08$, $P = 0.08$) or any of the main effects, i.e. sound ($\chi^2_1 = 2.11$, $P = 0.15$),
309 predator cue ($\chi^2_1 = 0.34$, $P = 0.56$) or initially occupied shell size ($\chi^2_1 = 0.99$, $P = 0.32$)
310 on the latency to contact the optimal shell (see supplement for all results tables).

311 Larger hermit crabs approached the optimal shell faster than smaller crabs ($\chi^2_1 = 7.44$,
312 $P = 0.006$). Furthermore, there was a significant three-way interaction between sound,
313 predator cue and shell size on the total decision time to accept or reject the optimal
314 shell ($\chi^2_1 = 5.0$, $P = 0.03$; Figure 3). Crabs in a 50% adequate shell and exposed to a
315 predator took a longer total decision time under ambient control compared to ship
316 noise. In the contrary crabs in 80% shells showed the opposite pattern, taking more
317 time to decide under ambient sound than ship noise when the predator was absent, but
318 being unaffected by the sound treatment when the predator was present. The total
319 decision time decreased with crab mass ($\chi^2_1 = 7.23$, $P = 0.007$).

320 For crabs that contacted the optimal shell, we analyzed the effect of the predictors
321 on the occurrence of antennal contact. Since not every crab decided to contact the
322 optimal shell, we did not have sufficient data on the occurrence of antennal contact to
323 calculate the three-way interaction. For those crabs that did contact the optimal shell,
324 there were no significant two-way interactions: sound and predator cue ($\chi^2_1 = 1.51$, $P =$
325 0.22) or predator cue and occupied shell ($\chi^2_1 = 3.08$, $P = 0.08$). However, under ambient

326 sound conditions, hermit crabs in 50% shells were less likely to contact the optimal shell
327 with their antennae compared to crabs in 80% shells whereas this pattern was absent in
328 the presence of ship noise. ($\chi^2_1 = 10.0$, $P = 0.002$; Figure 4). In the presence of a predator
329 cue, more crabs displayed antennal contact with the optimal shell ($\chi^2_1 = 4.07$, $P = 0.04$;
330 Figure 5).

331 Crabs which occupied a 50% shell were more likely to enter the optimal shell than
332 crabs in 80% shells ($\chi^2_1 = 5.46$, $P = 0.02$; Figure 6). We could not reliably calculate the
333 three-way interaction for this decision since relatively few crabs with an 80% shell that
334 were exposed to ship noise decided to enter the optimal shell (see supplement Table 4).
335 None of the two-way interactions sound and predator ($\chi^2_1 = 1.57$, $P = 0.21$), sound and
336 occupied shell ($\chi^2_1 = 3.15$, $P = 0.08$), predator cue and occupied shell ($\chi^2_1 = 0.67$, $P =$
337 0.41) or the main effects other than occupied shell (sound: $\chi^2_1 = 2.58$, $P = 0.11$; predator
338 cue: $\chi^2_1 = 0.17$, $P = 0.68$) had a significant effect on whether crabs entered the optimal
339 shell. None of the factors or their interaction affected the latency to swap into the optimal
340 shell (see supplement Table 5).

341 For the final decision to accept the optimal shell we could not calculate the three-
342 way interaction as relatively few individuals with an 80% adequate shell that were
343 exposed to noise chose to enter the optimal shell (see supplement Table 6). The decision
344 was not affected by the interactions between sound and predator cue ($\chi^2_1 = 0.34$, $P =$
345 0.56), sound and occupied shell ($\chi^2_1 = 2.19$, $P = 0.14$), predator and occupied shell (χ^2_1
346 $= 0.005$, $P = 0.94$) or predator cue ($\chi^2_1 = 0.38$, $P = 0.54$). However, under ambient sound
347 conditions, crabs accepted the optimal shell more frequently than under noise conditions
348 ($\chi^2_1 = 8.0$, $P = 0.005$; Figure 7). Crabs in a 50% shell accepted the optimal shell more
349 often than crabs in an 80% shell ($\chi^2_1 = 11.67$, $P = 0.0006$; Figure 8).

350 **Discussion**

351 Noise exposure significantly influenced the shell assessment behavior of hermit crabs,
352 disrupting both activities during shell assessment and the final decision to accept or
353 reject the optimal. *P. bernhardus* responded to noise in interaction with other (naturally
354 occurring) cues in the case of shell assessment activities but also in isolation in the case
355 of the final decision to accept the optimal shell. For hermit crabs, gastropod shells
356 represent a critical resource, which determines not only survival but also growth and
357 fecundity. Therefore, the assessment process and decision to exchange the current shell
358 for an optimal one will directly influence an individual's fitness. These decisions can be
359 complex because the benefits of swapping into a better shell must be balanced against
360 the temporary predation risk during the assessment process, which might attract the
361 attention of predators. On swapping shells, the weakly calcified abdomen is briefly
362 exposed. Thus, crabs are usually less likely to swap shells when the risk of predation is
363 high (Briffa et al. 2008). The current data show that the way hermit crabs use information
364 on these benefits and risks can be disrupted by changes to the sensory environment
365 caused by anthropogenic noise.

366 The total decision time taken to find, assess and then finally accept or reject the
367 optimal shell was influenced by a complex three-way interaction between sound
368 treatment, size of the initially occupied shell and the visual predator cue. That crabs in a
369 50% shell show shorter decision time than crabs in an 80% shell under the control
370 conditions (without predator cue and noise) is in line with previous studies demonstrating
371 that the potential gain in shell quality influences the motivation for changing shells
372 (Elwood 1995). Further, predator cues affected crabs differently depending on the shell
373 quality they hold and generally crabs exposed to predation risk tend to behave more
374 cautiously (Briffa et al. 2008). Here, crabs showed more cautious shell assessment steps
375 such as the antennal contact in the presence of a predator cue. For crabs in a low quality

376 50% adequate shells the visual predator cue led to an increase in decision time under
377 ambient sound but this effect was absent when ship noise was present. Thus, for crabs
378 with the potential for a large increase in shell quality, ship noise appears to negate the
379 normal effect of predator presence. Compared to crabs in a 50% shell, crabs in 80%
380 shells took longer to assess shells in the absence of a predator cue than in its presence
381 and the normal pattern observed under ambient sound was absent in the presence of
382 ship noise (as in the case of crabs in 50% shells). A recent study on the hermit crab
383 *Clibanarius vittatus* showed that the shell quality affects the response time to a predator
384 cue and that crabs in better quality shells show longer startle response without predation
385 risk than crabs exposed to a predator cue (Gorman et al. 2018) as we observed. Here,
386 the decision-making duration of hermit crabs was influenced by two naturally occurring
387 cues, shell quality and predation risk, as well as anthropogenic noise. Therefore, the
388 present data show that anthropogenic noise can lead to changes in behavior through
389 interactions with other sources of information. Previous studies on the response to noise
390 in crustaceans suggest that they adjust the timing or duration of their behavior when
391 noise is the only factor animals were exposed to. The common shore crab *Carcinus*
392 *maenas* retreated more slowly into shelters exposed to ship noise playbacks (Wale et al.
393 2013a) and the hermit crab *P. bernhardus* investigated shells more quickly under white
394 noise (Walsh et al. 2017). Likewise exposed to white noise, the marine rock lobster
395 *Panulirus longipes* took longer to emerge from shelter (Meyer-Rochow et al. 1982) and
396 the Caribbean hermit crab *Coenobita clypeatus* let a predator approach closer before
397 hiding (Chan et al. 2010a). Expanding on those studies, our results indicate that rather
398 than acting in isolation, noise effects are also influenced by at least two other, naturally
399 occurring factors, shell size and predation risk, both of which hermit crabs are likely to
400 experience frequently in nature (as pointed out in the introduction on the natural habitat
401 of *P. bernhardus*). The shell quality has been shown to determine behavior and
402 physiological state in hermit crabs (Briffa and Elwood 2000; Briffa and Elwood 2005).

403 One of the few examples on the effects of ship noise and predation risk in interaction
404 with physiological condition was on the European eel *Anguilla anguilla*. Here, juveniles
405 in poor condition decreased their startle response to ship noise (Purser et al. 2016). Even
406 though the exact mechanisms remain unknown, the differences observed between
407 hermit crabs in 50% (poorer condition) and 80% (better condition) adequate shells seem
408 similar. Future research on examining the mechanisms underpinning interactions
409 between noise and physiology could help to better explain these observed behavioral
410 responses.

411 Further we found evidence that noise effects animals differently depending on
412 the resource quality they hold and the complexity of the task. Under ambient conditions,
413 crabs initially in 80% shells (which had relatively little to gain) employed more antennal
414 contact during shell investigation compared to crabs initially in 50% shells (which could
415 make a relatively large gain). This difference is likely to reflect the fact that those crabs
416 in 80% shell had been presented with a more difficult choice than those in 50% shells
417 and hence made greater efforts to assess the empty shell. In the presence of ship noise,
418 however, this difference between crabs presented with easy and difficult choices (in
419 terms of potential gain in shell quality) was absent, with no difference in the amount of
420 antennal contact shown by crabs supplied with 50% and 80% adequate shells. Although
421 it is difficult to disentangle the effects of motivation from those of task complexity it is
422 likely that animals with more difficult decisions to make are susceptible to distraction by
423 anthropogenic noise. As animals possess a finite amount of attention and hence any
424 attention directed towards a novel cue (e.g. ship noise) is unavailable for other tasks
425 (Dukas 2004). Thus, routine tasks that require attention, such as assessing empty shells,
426 can be disrupted by novel stimuli. Blue jays *Cyanocitta cristata* have been shown to divert
427 their attention from a predator stimulus under more difficult and complex foraging tasks
428 (Dukas and Kamil 2000). That the difficulty of a task has an impact on the ability to detect

429 and respond to a stimulus (such as a predator) is known from other studies on several
430 bird species and the three-spined sticklebacks *Gasterosteus aculeatus* (for an overview
431 see Lawrence 1985). In humans it has been shown that with increasing difficulty of a
432 task less attention was spent on a second stimulus; the perception of the distracting
433 stimulus depends on the cognitive load of the focus task (Rees et al. 1997). Therefore,
434 the fact that crabs with less motivation and a more difficult decision were more
435 susceptible to the effects of noise provides additional support for the distracting effect of
436 noise (such as in the distracted prey hypothesis) which has been shown across humans
437 and non-human vertebrates and invertebrates. Future research on the cognitive
438 processes underlying these observations will allow to better understand the causes and
439 consequences of noise.

440 Anthropogenic noise exposure can also alter the final outcome of critical decision-
441 making. Under anthropogenic noise fewer crabs accepted the optimal shell; a similar
442 result to that recently obtained in crabs exposed to white noise (Walsh et al. 2017).
443 Rather than being affected by noise in interaction with the additional factors of predator
444 cue and shell size, the final decision to accept or reject the optimal shell was influenced
445 by noise itself. Suboptimal shells can inhibit growth and reproductive success as females
446 carry their eggs within the shell (Bertness 1981). Furthermore, shell fit is important for
447 protection against predators. When shells are too small hermit crabs cannot withdraw
448 fully into the shell and hence are most exposed (Angel 2000). As a consequence,
449 anthropogenic noise could have implications beyond individual crabs at the population
450 level. This effect could also be multiplied as vacated shells serve as a resource for
451 smaller crabs and cascade through the population, a process known as vacancy chain
452 previously described in hermit crabs (Briffa and Austin 2009; Lewis and Rotjan 2009).
453 Thus, noise appears to make it more difficult for hermit crabs to utilize information about
454 predation risk and shell quality. The decisions that are underpinned by such information

455 are also dependent on motivational state and here we also investigated whether noise
456 might interact with the motivation of crabs to change shells.

457 Our findings are broadly in line with the “distracted prey hypothesis” which
458 suggests that animals seem to get distracted by noise when assessing the potential
459 threat of a predator, allocating part of their limited attention away from the threat towards
460 the distracting stimulus (Chan et al. 2010b). For instance, prey showed decreased anti-
461 predator response (Bruitjes and Radford 2013; Bruitjes et al. 2016; Purser et al. 2016),
462 were slower to be startled by a stimulated predator attack (Simpson et al. 2015) and
463 were caught more efficiently and quickly (Nedelec et al. 2015). What we now show is
464 that these patterns of altered responses to information concerning predation threat
465 interact with altered responses to other cues, in this case tactile and visual information
466 gathering concerning resource quality. Moreover, distraction appears to alter the ability
467 of crabs to integrate this information on resource value with information on the risk of
468 predation. Thus, anthropogenic noise pollution alters the multisensory integration of cues
469 during the information gathering, assessment and decision-making process surrounding
470 utilization of a critical resource in the European hermit crab. To the best of our knowledge
471 there are no other studies that have compared the effect of noise (an anthropogenic
472 pollutant) with the effects of variation in the complexity of a cognitive task (driven in this
473 case by the size of the initial occupied shell) and the visual presence of an external threat
474 (visual presence of a predator). As animals live in complex environments with competing
475 information and attention demands (Talsma et al. 2010), it is important to understand the
476 interactive effect of anthropogenic noise with biologically relevant factors such as
477 predator cue and resource value. Under noise, stimulus-selective attention, where less
478 relevant information is ignored (Dukas 2002), seems to be compromised. The result that
479 hermit crabs choose an optimal shell less often under anthropogenic noise is likely a
480 consequence of distraction of their limited attention away from the pertinent natural cues

481 towards the anthropogenic stimuli. The decision to accept or reject an optimal shell has
482 not only implications for the fitness and survival of an individual but potentially cascades
483 up to the population level by reproduction, exposure to predators and freeing resources
484 for conspecifics. Our results provide evidence that pollutants such as noise can act
485 across sensory modalities (Halfwerk and Slabbekoorn 2015) and distract information
486 gathering and decision making of animals, here in using tactile and visual cues for
487 resource assessment. Cross-modal distraction from noise is not limited to the predation
488 context (common cuttlefish *Sepia officinalis* changed its color more frequently during a
489 playback of anthropogenic noise, Kunc et al. 2014) or animals but has been shown in
490 humans as well (Parmentier et al. 2011; Ljungberg and Parmentier 2012). Here, we
491 demonstrate multi-modal effects of human-induced rapid environmental change (HIREC)
492 on the sensory environment of animals and compromises the use of biologically relevant
493 cues, specifically that ship noise disrupts both tactile and visual information gathering
494 under predation risk in the European hermit crab by interacting with these information
495 channels.

496 *Funding*

497 This work was supported by the Erasmus Mundus Joint Doctoral Programme on
498 Marine Ecosystem Health & Conservation and the University of Plymouth who awarded
499 a PhD scholarship to S.T..

500

501 *Acknowledgements*

502 We thank Stephen Simpson and Andrew Radford for providing the sound files and
503 advising us at the initial stage of the experiment, Matthew Wale for his support in the
504 sound analysis and Ann Torr for technical assistance during fieldwork and the animal
505 husbandry.

506

507 *Data Accessibility*

508 Analyses reported in this article can be reproduced using the data provided by Tidau
509 and Briffa 2019.

510 **References**

- 511 Angel JE. 2000. Effects of shell fit on the biology of the hermit crab *Pagurus*
512 *longicarpus* (say). J Exp Mar Biol Ecol. 243:169-184.
- 513 Audacity Team. 2017. Audacity(R): Free Audio Editor and Recorder [Computer
514 application]. Version 2.2.1. Available from: <https://audacityteam.org/> (Accessed
515 September 2016)
- 516 Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for
517 terrestrial organisms. Trends Ecol Evol. 25:180-189.
- 518 Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models
519 using lme4. J Stat Softw 67:1-48.
- 520 Bent AM, Ings TC, Mowles SL. 2018. Anthropogenic noise disrupts mate searching in
521 *Gryllus bimaculatus*. Behav Ecol. 29:1271-1277.
- 522 Bermúdez-Cuamatzin E, López-Hernández M, Campbell J, Zuria I, Slabbekoorn H.
523 2018. The role of singing style in song adjustments to fluctuating sound
524 conditions: A comparative study on Mexican birds. Behav Process. 157:645-
525 655.
- 526 Bertness MD. 1981. The influence of shell-type on hermit crab growth rate and clutch
527 size (Decapoda, Anomura). Crustaceana 40:197-205.
- 528 Breithaupt T. 2002. Sound perception in aquatic crustaceans. In: Wiese K, editor. The
529 crustacean nervous system. Berlin, Heidelberg: Springer. p. 548-558.
- 530 Briffa M, Austin M. 2009. Effects of predation threat on the structure and benefits from
531 vacancy chains in the hermit crab *Pagurus bernhardus*. Ethology 115:1029-
532 1035.
- 533 Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel
534 analysis of plasticity, personality and predictability in hermit crabs. Anim Behav.
535 86:47-54.

536 Briffa M, Elwood RW. 2000. Cumulative or sequential assessment during hermit crab
537 shell fights: Effects of oxygen on decision rules. P Roy Soc Lond B Bio.
538 267:2445-2452.

539 Briffa M, Elwood RW. 2005. Rapid change in energy status in fighting animals: Causes
540 and effects of strategic decisions. Anim Behav. 70:119-124.

541 Briffa M, Elwood RW. 2007. Monoamines and decision making during contests in the
542 hermit crab *Pagurus bernhardus*. Anim Behav. 73:605-612.

543 Briffa M, Haskell P, Wilding C. 2008. Behavioural colour change in the hermit crab
544 *Pagurus bernhardus*: Reduced crypticity when the threat of predation is high.
545 Behaviour 145:915-929.

546 Bruintjes R, Purser J, Everley KA, Mangan S, Simpson SD, Radford AN. 2016. Rapid
547 recovery following short-term acoustic disturbance in two fish species. Roy Soc
548 Open Sci 3: 150686.

549 Bruintjes R, Radford AN. 2013. Context-dependent impacts of anthropogenic noise on
550 individual and social behaviour in a cooperatively breeding fish. Anim Behav.
551 85:1343-1349.

552 Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial
553 bird. J Anim Ecol. 73:434-440.

554 Bulinski KV. 2007. Shell-selection behavior of the hermit crab *Pagurus granosimanus*
555 in relation to isolation, competition, and predation. J Shellfish Res. 26:233-239.

556 Chan AAY-H, David Stahlman W, Garlick D, Fast CD, Blumstein DT, Blaisdell AP.
557 2010a. Increased amplitude and duration of acoustic stimuli enhance
558 distraction. Anim Behav. 80:1075-1079.

559 Chan AAY-H, Giraldo-Perez P, Smith S, Blumstein DT. 2010b. Anthropogenic noise
560 affects risk assessment and attention: The distracted prey hypothesis. Biol Lett.
561 6:458-461.

562 Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D.
563 2009. Acoustic masking in marine ecosystems: Intuitions, analysis, and
564 implication. *Mar Ecol Prog Ser.* 395:201-222.

565 Dowds BM, Elwood RW. 1983. Shell wars: Assessment strategies and the timing of
566 decisions in hermit crab shell fights. *Behaviour* 85:1-24.

567 Dukas R. 2002. Behavioural and ecological consequences of limited attention. *Philos T*
568 *Roy Soc B.* 357:1539-1547.

569 Dukas R. 2004. Causes and consequences of limited attention. *Brain Behav Evol*
570 63:197-210.

571 Dukas R, Kamil AC. 2000. The cost of limited attention in blue jays. *Behav Ecol.*
572 11:502-506.

573 Elwood RW. 1995. Motivational change during resource assessment by hermit crabs. *J*
574 *Exp Mar Biol Ecol.* 193:41-55.

575 Elwood RW, Neil SJ. 1992. Assessments and decisions: A study of information
576 gathering by hermit crabs. London; New York: Chapman & Hall.

577 Elwood RW, Stewart A. 1985. The timing of decisions during shell investigation by the
578 hermit crab, *Pagurus bernhardus*. *Anim Behav.* 33:620-627.

579 Foote AD, Osborne RW, Hoelzel AR. 2004. Environment: Whale-call response to
580 masking boat noise. *Nature* 428:910-910.

581 Gorman D, Ragagnin MN, McCarthy ID, Turra A. 2018. Risk-taking and risk-avoiding
582 behaviors by hermit crabs across multiple environmental contexts. *J Exp Mar*
583 *Biol Ecol.* 506:25-29.

584 Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in
585 response to noise-dependent female feedback. *Funct Ecol.* 26:1339-1347.

586 Halfwerk W, Slabbekoorn H. 2015. Pollution going multimodal: The complex impact of
587 the human-altered sensory environment on animal perception and performance.
588 *Biol Lett.* 11:20141051.

589 Heiler J, Elwen SH, Kriesell HJ, Gridley T. 2016. Changes in bottlenose dolphin whistle
590 parameters related to vessel presence, surface behaviour and group
591 composition. *Anim Behav.* 117:167-177.

592 Hildebrand JA. 2009. Anthropogenic and natural sources of ambient noise in the
593 ocean. *Mar Ecol Prog Ser.* 395:5-20.

594 Holles S, Simpson SD, Radford AN, Berten L, Lecchini D. 2013. Boat noise disrupts
595 orientation behaviour in a coral reef fish. *Mar Ecol Prog Ser.* 485: 295-300.

596 Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: An
597 integrative, mechanistic review. *Ecol Lett.* 14:1052-1061.

598 Koolhaas JM, Bartolomucci A, Buwalda B, de Boer SF, Flügge G, Korte SM, Meerlo P,
599 Murison R, Olivier B, Palanza P, et al. 2011. Stress revisited: A critical
600 evaluation of the stress concept. *Neurosci Biobehav R.* 35:1291-1301.

601 Kunc HP, Lyons GN, Sigwart JD, McLaughlin KE, Houghton JDR. 2014. Anthropogenic
602 noise affects behavior across sensory modalities. *Am Nat.* 184:E93-E100.

603 Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest package: Tests in
604 linear mixed effects models. *J Stat Softw.* 1: 1-26.

605 Ladich F, Fay RR. 2013. Auditory evoked potential audiometry in fish. *Rev. Fish Biol.*
606 *Fish.* 23:317-364.

607 Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: Grasshoppers from
608 noisy roadside habitats produce courtship signals with elevated frequency
609 components. *Funct Ecol.* 26:1348-1354.

610 Lawrence ES. 1985. Vigilance during easy and difficult foraging tasks. *Anim. Behav.*
611 33:1373-1375.

612 Lewis SM, Rotjan RD. 2009. Vacancy chains provide aggregate benefits to *Coenobita*
613 *clypeatus* hermit crabs. *Ethology* 115:356-365.

614 Ljungberg JK, Parmentier FBR. 2012. Cross-modal distraction by deviance functional
615 similarities between the auditory and tactile modalities. *Exp Psychol* 59:355-
616 363.

617 The MathWorks, Inc. 2015. MATLAB and Statistics Toolbox Release 2015b. Natick:
618 USA.

619 Merchant ND, Fristrup KM, Johnson MP, Tyack PL, Witt MJ, Blondel P, Parks SE.
620 2015. Measuring acoustic habitats. *Methods Ecol Evol* 6:257-265.

621 Meyer-Rochow VB, Penrose JD, Oldfield BP, Bailey WJ. 1982. Phonoresponses in the
622 rock lobster *Panulirus longipes* (Milne Edwards). *Behav Neural Biol* 34:331-336.

623 Nedelec SL, Radford AN, Pearl L, Nedelec B, McCormick MI, Meekan MG, Simpson
624 SD. 2017. Motorboat noise impacts parental behaviour and offspring survival in
625 a reef fish. *P Roy Soc Lond B Bio.* 284: 20170143.

626 Nedelec SL, Simpson SD, Morley EL, Nedelec B, Radford AN. 2015. Impacts of regular
627 and random noise on the behaviour, growth and development of larval atlantic
628 cod (*Gadus morhua*). *P Roy Soc Lond B Bio.* 282: 20151943.

629 Parmentier FBR, Ljungberg JK, Elsley JV, Lindkvist M. 2011. A behavioral study of
630 distraction by vibrotactile novelty. *J Exp Psychol Human.* 37:1134-1139.

631 Popper AN, Salmon M, Horch WK. 2001. Acoustic detection and communication by
632 decapod crustaceans. *J Comp Physiol A* 187:83-89.

633 Purser J, Bruintjes R, Simpson SD, Radford AN. 2016. Condition-dependent
634 physiological and behavioural responses to anthropogenic noise. *Physiol*
635 *Behav.* 155:157-161.

636 R-Core-Team. 2017. A language and environment for statistical computing. Vienna:
637 Austria: R Foundation for Statistical Computing. Available from: [https://www.r-](https://www.r-project.org/)
638 [project.org/](https://www.r-project.org/) (Accessed January 2017)

639 Rees G, Frith CD, Lavie N. 1997. Modulating irrelevant motion perception by varying
640 attentional load in an unrelated task. *Science* 278:1616-1619.

641 Rogers PH, Hawkins AD, Popper AN, Fay RR, Gray MD. 2016. Parvulescu revisited:
642 Small tank acoustics for bioacousticians. In: Popper AN, Hawkins A, editors.
643 Effects of noise on aquatic life II. p. 933-941.

644 Rotjan RD, Blum J, Lewis SM. 2004. Shell choice in *Pagurus longicarpus* hermit crabs:
645 Does predation threat influence shell selection behavior? Behav Ecol Sociobiol.
646 56:171-176.

647 Sara G, Dean JM, D'Amato D, Buscaino G, Oliveri A, Genovese S, Ferro S, Buffa G,
648 Lo Martire M, Mazzola S. 2007. Effect of boat noise on the behaviour of bluefin
649 tuna *Thunnus thynnus* in the Mediterranean Sea. Mar Ecol Prog Ser. 331:243-
650 253.

651 Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic
652 noise modifies behaviour of a keystone species. Anim Behav. 94:135-141.

653 Siemers BM, Schaub A. 2011. Hunting at the highway: Traffic noise reduces foraging
654 efficiency in acoustic predators. P Roy Soc Lond B Bio. 278:1646-1652.

655 Sih A, Ferrari MCO, Harris DJ. 2011. Evolution and behavioural responses to human-
656 induced rapid environmental change. Evol Appl 4:367-387.

657 Simpson SD, Purser J, Radford AN. 2015. Anthropogenic noise compromises
658 antipredator behaviour in European eels. Glob Change Biol. 21:586-593.

659 Spiga I. 2016. Acoustic response to playback of pile-driving sounds by snapping
660 shrimp. In: Popper AN, Hawkins A, editors. Effects of noise on aquatic life II.
661 New York: Springer. p. 1081-1088.

662 Stahlman WD, Chan AAY-H, Blumstein DT, Fast CD, Blaisdell AP. 2011. Auditory
663 stimulation dishabituates anti-predator escape behavior in hermit crabs
664 (*Coenobita clypeatus*). Behav Process. 88:7-11.

665 Sun JWC, Narins PM. 2005. Anthropogenic sounds differentially affect amphibian call
666 rate. Biol Conserv. 121:419-427.

667 Talsma D, Senkowski D, Soto-Faraco S, Woldorff MG. 2010. The multifaceted interplay
668 between attention and multisensory integration. *Trends Cogn Sci* 14:400-410.

669 Tidau S, Briffa M. 2019. Data from: Distracted decision-makers: Ship noise and
670 predation risk change shell choice in hermit crabs. *Behav Ecol*. DOI:
671 doi:10.5061/dryad.4sm0dq1

672 Tidau S, Briffa M. In Press. Anthropogenic noise pollution reverses grouping behaviour
673 in hermit crabs. *Anim. Behav.*

674 Tricarico E, Gherardi F. 2007. Resource assessment in hermit crabs: The worth of their
675 own shell. *Behav Ecol*. 18:615-620.

676 Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced
677 environmental change. *Biol Rev*. 86:640-657.

678 Turra A, Gorman D. 2014. Subjective resource value and shell abandoning behavior in
679 hermit crabs. *J Exp Mar Biol Ecol*. 452:137-142.

680 Wale MA, Simpson SD, Radford AN. 2013a. Noise negatively affects foraging and
681 antipredator behaviour in shore crabs. *Anim Behav*. 86:111-118.

682 Wale MA, Simpson SD, Radford AN. 2013b. Size-dependent physiological responses
683 of shore crabs to single and repeated playback of ship noise. *Biol Lett*. 9:
684 20121194.

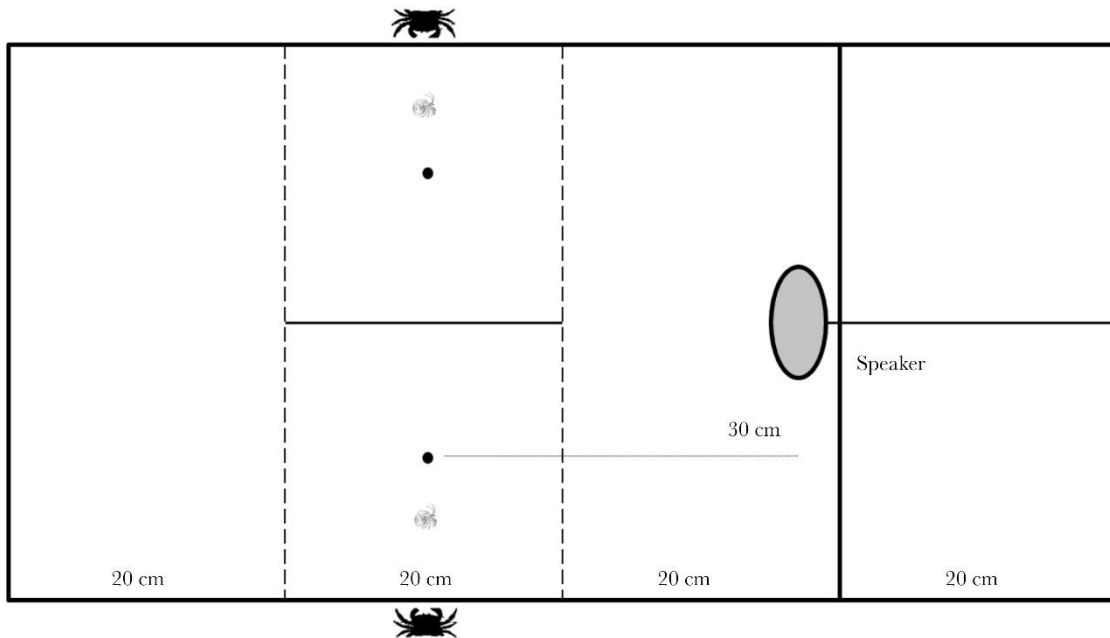
685 Walsh EP, Arnott G, Kunc HP. 2017. Noise affects resource assessment in an
686 invertebrate. *Biol Lett*. 13: 20170098.

687 Williams R, Wright AJ, Ashe E, Blight LK, Bruintjes R, Canessa R, Clark CW, Cullis-
688 Suzuki S, Dakin DT, Erbe C, et al. . 2015. Impacts of anthropogenic noise on
689 marine life: Publication patterns, new discoveries, and future directions in
690 research and management. *Ocean Coast. Manage*. 115:17-24.

691 **Figure legends**

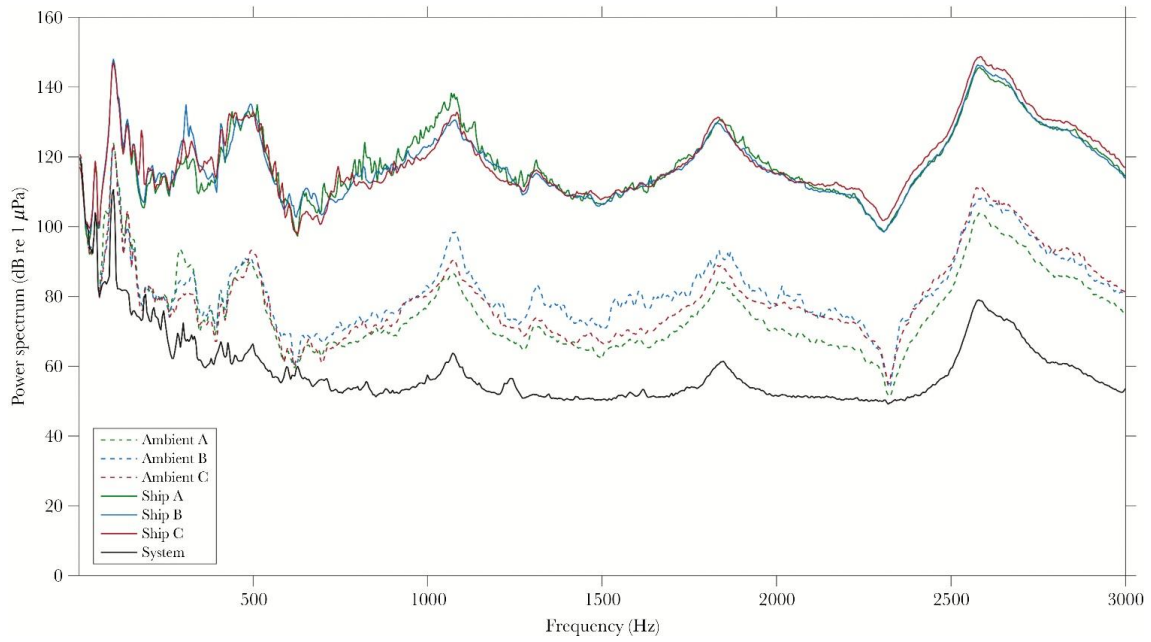
692

693



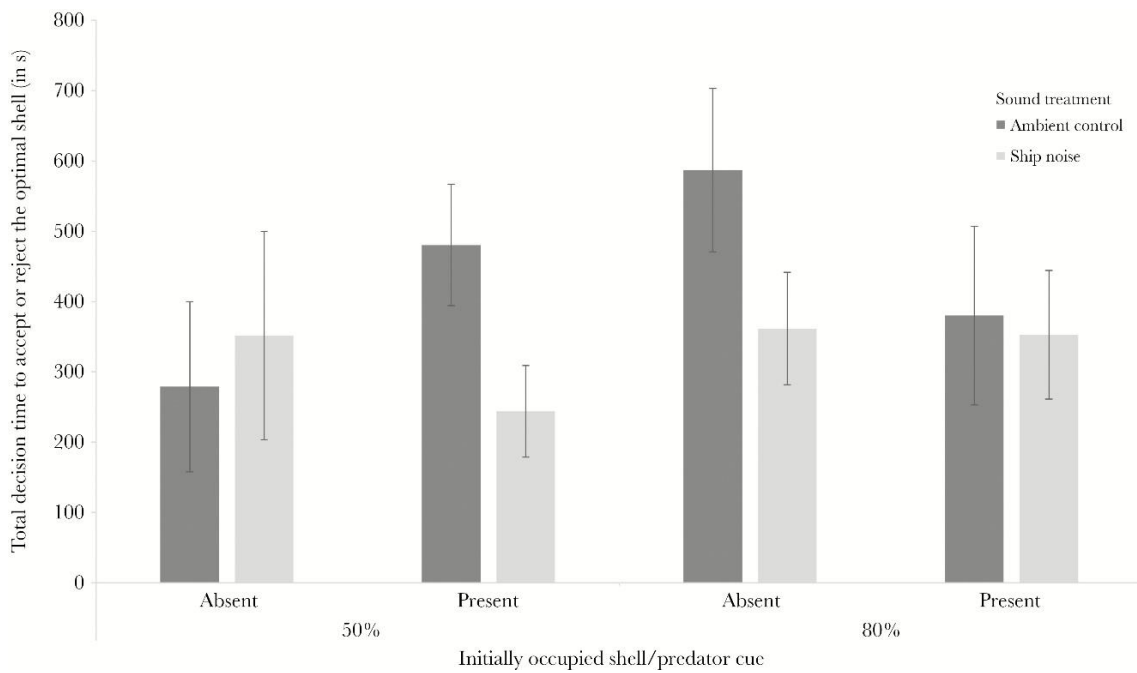
694

695 **Figure 1** Tank set-up and arena (plan view). The dotted lines represent the mesh to
696 separate the arena from the rest of the tank. The blank line represent the opaque
697 plastic sheet to separate the hermit crabs. The empty shells were placed in the center
698 of the arena at 30 cm distance to the speaker. The visual predator cue was placed
699 outside the tank and hermit crabs were placed between the shell and the predator cue.



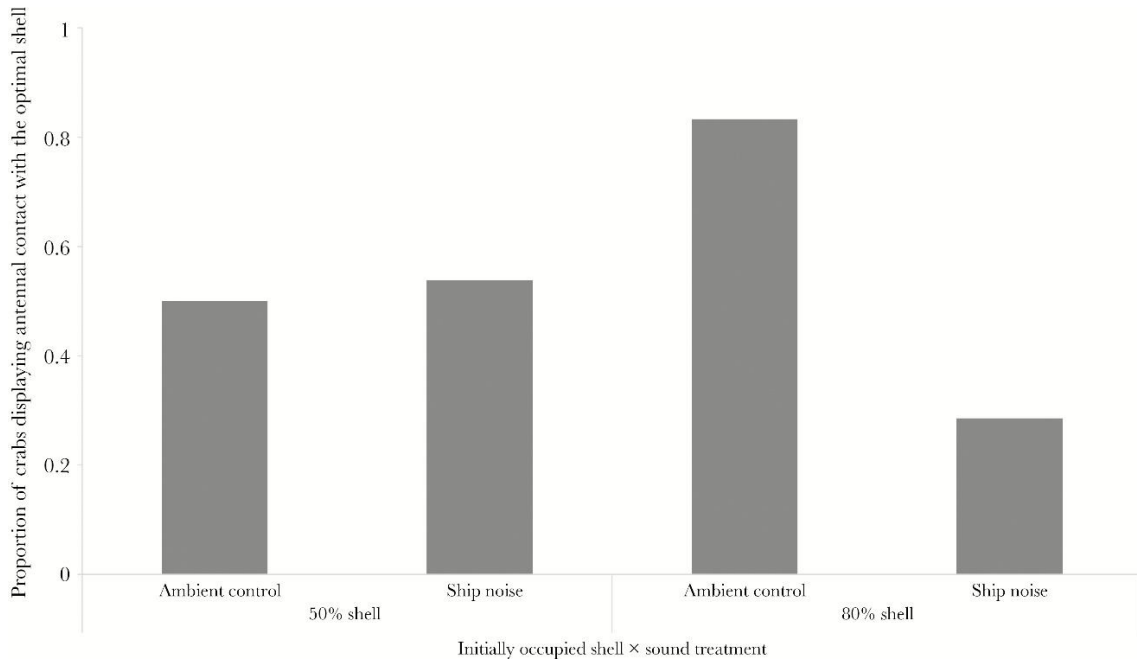
700

701 **Figure 2** Power spectrum analysis of the playbacks of all six recordings (3 ship noise
 702 playbacks, 3 ambient playbacks) in the tank and the system's self-noise (equipment
 703 switch on but no playback).



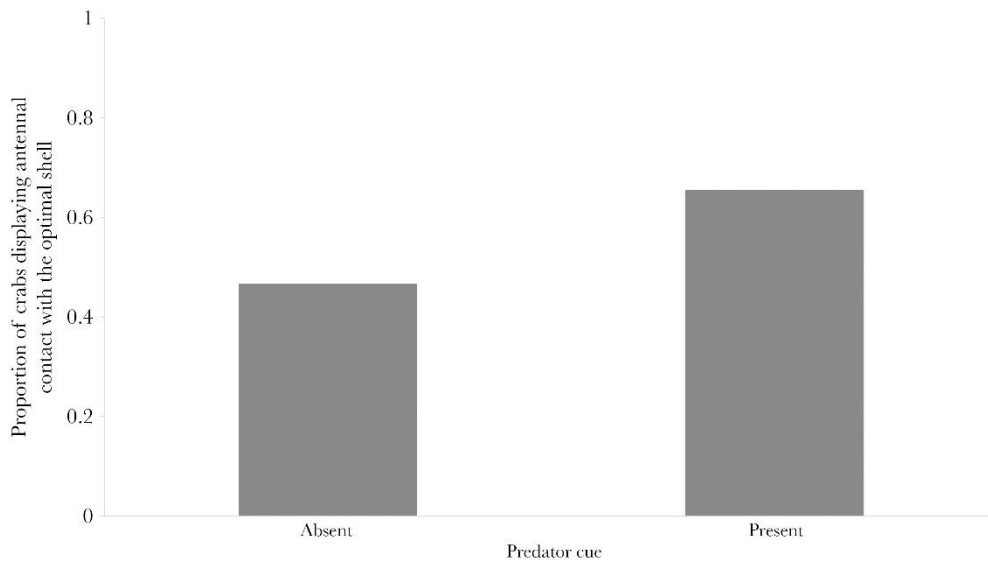
704

705 **Figure 3** The three-way interaction between sound treatment, predator cue and initially
 706 occupied shell size on the total decision time to accept or reject the optimal shell. Error
 707 bars show standard errors.



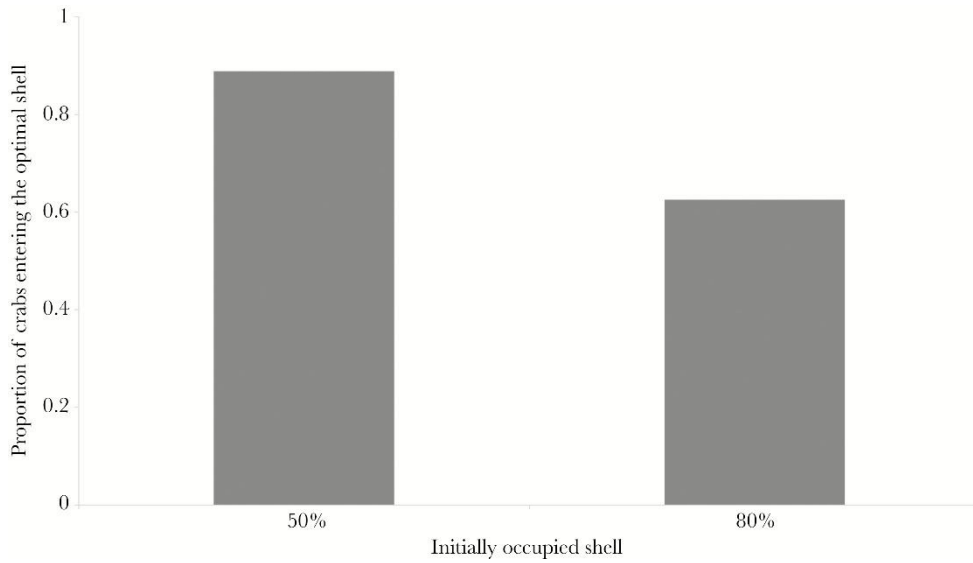
708

709 **Figure 4** The interaction effect between sound treatment and initially occupied shell
 710 size on the proportion of crabs that contacted the optimal shell with their antennae.



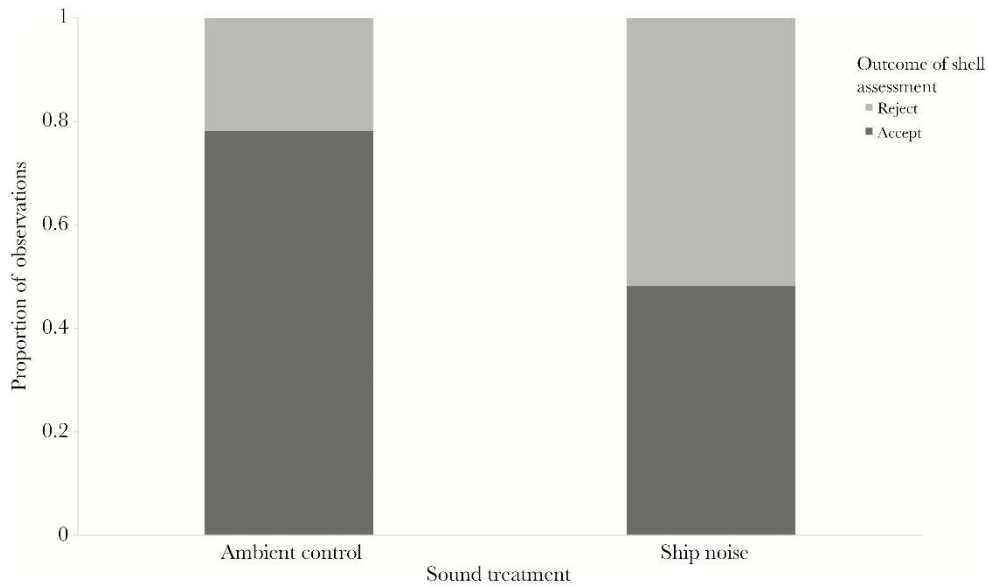
711

712 **Figure 5** The effect of a visual predator cue on the proportion of crabs that contacted
 713 the optimal shell with their antennae



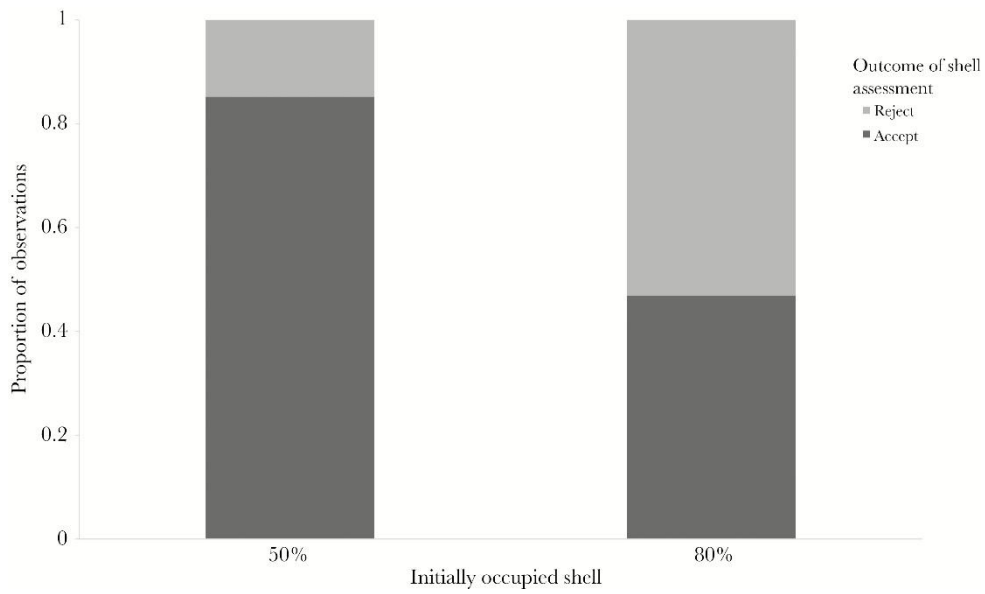
714

715 **Figure 6** The effect of initially occupied shell size on the proportion of crabs that swap
 716 and did not swap into the optimal shell.



717

718 **Figure 7** Effect of sound treatment on the decision of hermit crabs to accept or reject
 719 the optimal shell.



720

721 **Figure 8** Effect of initially occupied shell on the decision of hermit crabs to accept or
 722 reject the optimal shell.

723 **Tables and table legends**

724

725 **Table 1.** Summary of number of observations in each treatment combination, with the number
 726 of crabs that changed shell in each case given in parentheses.

	<i>Predator absent</i>			<i>Predator present</i>								
	<i>50% shell</i>			<i>80% shell</i>			<i>50% shell</i>			<i>80% shell</i>		
	<i>n</i>	<i>entered</i>	<i>accepted</i>	<i>n</i>	<i>entered</i>	<i>accepted</i>	<i>n</i>	<i>entered</i>	<i>accepted</i>	<i>n</i>	<i>entered</i>	<i>accepted</i>
Ambient <i>(n=32)</i>	6	(6)	(6)	10	(8)	(7)	8	(8)	(8)	8	(4)	(4)
Noise <i>(n=27)</i>	7	(5)	(5)	7	(4)	(2)	6	(5)	(4)	7	(4)	(2)

727

728 **SUPPLEMENT**

729

730 **Table 1** Latency to contact the new shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	3.08	1	0.08
sound * predator cue	0.02	1	0.88
sound * shell size	0.01	1	0.91
predator cue * shell size	2.11	1	0.15
sound	1.95	1	0.16
predator cue	0.34	1	0.56
shell size	0.99	1	0.32
mass	7.44	1	0.006

731

732 **Table 2** Total decision time (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	5.0	1	0.03
mass	7.23	1	0.007

733 Note that results were obtained using a model simplification approach, and as such reporting is restricted to the highest
734 order effects, where significant interactions are present.

735

736 **Table 3** Occurrence of antennae contact (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	1.51	1	0.22
sound * shell size	10.0	1	0.002
predator cue * shell size	3.08	1	0.08
predator cue	4.07	1	0.04
mass	1.91	1	0.17

737 Note that since not every crab decided to contact the optimal shell, we did not have sufficient data on the occurrence of
738 antennal contact to calculate the three-way interaction.

739

740 **Table 4** Enter the optimal shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	1.57	1	0.21
sound * shell size	3.15	1	0.08
predator cue * shell size	0.67	1	0.41
sound	2.58	1	0.11
predator cue	0.17	1	0.68
shell size	5.46	1	0.02
mass	0.88	1	0.35

741 Note that since relatively few crabs with an 80% shell that were exposed to ship noise decided to enter the optimal shell,
742 there was not sufficient data to calculate the three-way interaction.

743 **Table 5** Latency to enter the optimal shell

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	1.62	1	0.20
sound * predator cue	0.20	1	0.66
sound * shell size	0.41	1	0.52
predator cue * shell size	0.91	1	0.34
sound	0.30	1	0.59
predator cue	1.88	1	0.17
shell size	0.56	1	0.45
mass	0.95	1	0.33

744

745 **Table 6** Final decision to accept new shell (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	NA	NA	NA
sound * predator cue	0.34	1	0.56
sound * shell size	2.19	1	0.14
predator cue * shell size	0.005	1	0.94
sound	8.0	1	0.005
predator cue	0.38	1	0.54
shell size	11.67	1	0.0006
mass	0.48	1	0.49

746 Note that since relatively few individuals with an 80% adequate shell that were exposed to noise chose to enter the
747 optimal shell, there was not sufficient data to calculate the three-way interaction.

748

749 **Table 7** Total decision time (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	5.0	1	0.03
mass	7.23	1	0.007

750

751 **Table 8** Locomotion (bold indicates significant effects)

Factors and their interactions	χ^2	df	P-value
sound * predator cue * shell	0.005	1	0.94
sound * predator cue	0.23	1	0.63
sound * shell size	0.58	1	0.45
predator cue * shell size	0.02	1	0.90
sound	0.11	1	0.75
predator cue	1.42	1	0.23
shell size	1.32	1	0.25
mass	7.35	1	0.007

752

753

754