# Hermit crab response to a visual threat is sensitive to looming cues

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Prior work in our lab has shown that an expanding image on a computer screen elicits a hiding response in the Caribbean terrestrial hermit crabs (Coenobita clypeatus). We conducted two experiments to identify what properties of the expanding stimulus contribute to its effectiveness as a visual threat. First we found that an expanding geometric star evoked a strong hiding response while a contracting or full-sized stationary star did not. A second experiment revealed that the more quickly the stimulus expanded the shorter the latency to hide. These findings suggest that the anti-predator response to looming stimulus relies heavily on visual cues relating to the manner of approach. The simulated visual threat on a computer screen captures key features of a real looming object that elicits hiding behavior in crabs in the wild.

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21   **Abstract**

22   Prior work in our lab has shown that an expanding image on a computer screen elicits a hiding

23   response in the Caribbean terrestrial hermit crabs *(Coenobita clypeatus)*. We conducted two

24   experiments to identify what properties of the expanding stimulus contribute to its effectiveness

25   as a visual threat. First we found that an expanding geometric star evoked a strong hiding

26   response while a contracting or full-sized stationary star did not. A second experiment revealed

27   that the more quickly the stimulus expanded the shorter the latency to hide. These findings

28   suggest that the anti-predator response to looming stimulus relies heavily on visual cues relating

29   to the manner of approach. The simulated visual threat on a computer screen captures key

30   features of a real looming object that elicits hiding behavior in crabs in the wild.

31

32 **Introduction**

33 Many species rely on vision for threat detection. The ability to appropriately respond to an

34 approaching predator requires the ability to detect the visual threat and estimate its imminence

35 (Fanselow & Lester, 1988). In a natural context, rapidly approaching visual stimuli elicit the

36 looming response (Chan et al., 2010a). It can be challenging to experimentally manipulate

37 individual features of the looming stimulus to determine their effectiveness. By using a looming

38 image on a computer screen, it is possible to simulate an approaching predator in controlled

39 laboratory conditions and measure the nature and timing of responses. Using such methods,

40 many species have been shown to flee or hide from looming images (e.g., Chan et al., 2010b;

41 Fotowat & Gabbiani, 2011; Preuss et al., 2006; Rind & Simmons, 1999; Sun & Frost, 1998, &

42 Yilmaz & Meister, 2013).

43     But not all looming images are associated with an increased predation risk. Thus, other

44 studies have manipulated the image content to determine whether a variety of images are

45 similarly evocative. For instance, Curio (1974) manipulated the structure of a looming predator

46 image to show that pied flycatchers *(Ficedula hypoleuca)* used a complex combination of visual

47 cues to discriminate both between predators and non-predators, and between similar types of

48 predators. Similar discriminative abilities have been reported from observational field

49 experiments. For instance, Walters (1990) showed that three species of lapwings (Charadriidae:

50 *Vanellus* spp.) also use visual cues to identify predators while Seyfarth and Cheney (1990)

51 demonstrated that vervet monkeys (*Chlorocebus pygerythrus*) emitted different alarm calls in

52 response to the sight of different predators (see Yilmaz & Meister, 2013, for similar results in

53 mice).

54     Species are also sensitive to the rate at which an object expands because rate contains

55 potential information about the time to impact. Studies of crayfish (*Procambarus clarkii*, Glantz,

56 1974), fish (*Carassius auratus*, Pruess et al., 2006), and fiddler crabs (*Neohelice granulate*,

57 Hemmi & Pfeil, 2010; Oliva & Tomsic, 2012) have measured response differentiation when the

58 speed or size of the looming image was changed, showing that species are sensitive to alter the

59 timing of their response based on calculations of the timing of collision.

60  Caribbean terrestrial hermit crabs *(Coenobita clypeatus*) are an ideal invertebrate system to

61 test looming image discrimination and processing. Prior work in our lab demonstrated that

62 hermit crabs have a binary escape response; they hide (or fail to hide) in their shells when

63 presented with a looming image of a predator or geometric shape presented on a computer screen

64 (Chan et al. 2010b; Ping et al., 2015; Ryan et al. 2012; Stahlman et al. 2011; Watanabe et al.

65 2012).

66  Using procedures developed in our lab, we designed two experiments to manipulate specific

67 aspects of the image and then measured responses by recording the number of trials to

68 habituation, the latency to hide, and the latency to emerge from their shells. The goal of the

69 experiments was to determine which factors contributed to the effectiveness of the looming

70 visual stimuli used in our prior research to elicit antipredator hiding responses. The first

71 experiment compared the typical looming stimulus produced by the gradual expansion of the

72 image with two other conditions. In one condition, the stimulus was presented suddenly at full

73 size, and in the other the stimulus began at full size and contracted to a single pixel. The second

74 experiment tested how changing the rate of image expansion affected response times.

75 **General Methods**

76  The subjects were 57 hermit crabs acquired from a pet supply company (California

77 Zoological Supply). Experimentally-naïve crabs were used for each experiment. The hermit

78    crabs' shells aperture length ranged from 3 to 4 cm across. Crabs were housed in UCLA's

79    Comparative Cognition Laboratory (http://pigeonrat.psych.ucla.edu) in groups of one to six.

80    Each had its claw numbered with non-toxic OPI nail polish for identification. Subjects were

81    housed in 50 x 25 x 25 cm clear plastic bins. Bins were lined with coconut fiber substrate (Zoo

82    Med Eco Earth, San Luis Obispo, CA, USA) and each contained two ceramic water dishes, a

83    paper plate under which the crabs could comfortably rest, a wet sponge to maintain humidity,

84    and a plastic food cup. Crabs always had access to distilled drinking water in one dish and a 1%

85    salt solution in the other, and were given Tetrafauna Hermit Crab meal pellets daily (Blacksburg,

86    VA, USA). The coconut substrate was checked daily for fungus and changed three times a week

87    or more often as necessary to prevent infection. The dishes containing water were cleaned and

88    replenished daily, and the coconut substrate was replaced on Mondays, Wednesdays, and

89    Fridays. Each bin was mostly covered with a clear acrylic sheets (0.5 cm thick) to maintain

90    humidity, with a small opening to allow air circulation. The room contained a Vicks humidifier

91    (Proctor & Gamble, Cincinnati, OH, USA) to maintain the atmosphere at 50-75% humidity in

92    the bins. Two 9.5 Watt heat lamps were used to provide warmth for the bins, maintaining a room

93    temperature of 25°C. A timer provided a 14:10 hour light: dark cycle, with lights turning on at

94    8:00 AM.

95        All experimental trials were performed in a test arena located on a desktop (Fig. 1). We

96    constructed a wooden, matt black arena 18.2 cm W x 30.5 cm L, x 14.5 cm H). A 15-inch LCD

97    monitor (Dell 1704FPVt, Round Rock, TX, USA) with a screen resolution of 1024X 768 pixels

98    was used to display visual stimuli. Subjects were secured in a crab-holder using Fun Tak™ blue

99    and white putty (Henkel Removable Poster Putty™, model 1084014, Duseldorf, Germany)

100    attached to the crab's shell. The holder was positioned in front of and 13.3 cm away from the

101 LCD screen. Subjects were oriented so that the aperture of their shell was angled up and

102 perpendicular in relation to the ground when secured.

103     We used a custom program developed in-house to automatically recorded latency to hide and

104 re-emerge (Ryan et al., 2012). A web camera (Logitech, model C250, Lausanne, Switzerland)

105 was placed 5 cm in front of the clamp, below the LCD monitor. The program detected activity in

106 a 300 x 150 pixel region in the camera's visual field. At the beginning of a session, the subject

107 was placed on its back into the putty and clipped into the apparatus. The square-shaped visual

108 detection field was positioned so that the bottom 1/3$^{rd}$ contained the crab's shell and the top 2/3$^{rds}$

109 was empty to allow detection space for when the crab emerged. We then set the number of

110 "hiding pixels" (i.e., the number of pixels the detector registered when the crab was hiding), and

111 the program computed a value to set a variable called "ExtraPixelsOut" to determine when the

112 crab had emerged from its shell. The value of "ExtraPixelsOut" was calibrated for each

113 individual crab at the beginning of each session to account for each individual crab's size.

114 Furthermore, to account for variation in individual size, we calculated a variable labeled

115 "ClawSize" for each crab. To calculate "ClawSize" we set the baseline for a hiding crab at zero

116 pixels, recorded the minimal number of pixels once the crab emerged, subtracted 1000 from this

117 number, and divided it by 0.5. After this calibration was complete, a crab was scored as hiding

118 until this additional number of pixels was detected in the recording square on the monitor. We

119 found this method to reliably discriminate the state of the crab being emerged from its shell from

120 the state of it hiding within its shell (Ryan et al., 2012).

121     A variable labeled "ExtraPixelsIn" was computed to ensure the program accurately registered

122 when the crab returned to hiding. After emerging from its shell, a hiding response did not always

123 result in the crab returning as far into its shell as when the initial "hiding pixels" baseline was set

124   at the beginning of the session. Thus, to increase sensitivity to detecting hiding responses,

125   "ExtraPixelsIn" was set to 1/6th the hiding pixels. Once the crab emerged, the program did not

126   consider the crab as being "hiding" until the number of pixels detected fell below this number of

127   additional pixels (Ryan et al., 2012).

128       The criterion for number of trials to habituation was defined as two consecutive trials with no

129   registered hide response. Both experiments were video recorded and the results of the automatic

130   detector were verified on the video and hand scored when necessary to include cases where the

131   automatic detector failed to detect response.

132       If a subject failed to emerge for 20 min at the beginning of a session it was returned to its

133   home cage and was tried again after all the other crabs had completed their session for the day. If

134   a hermit crab still failed to emerge from its shell, it was not included in the experiment.

135   **Experiment 1**

136   In this experiment we compared the effectiveness of an expanding stimulus, a contracting

137   stimulus, and a full-sized stationary stimulus on eliciting the hide response.

138   *Methods*

139   *Subjects*. We tested 30 experimentally-naïve crabs. 10 crabs were tested on day 1, another 10

140   were tested on day 2, and the remaining 10 crabs were tested on day 3 of the experiment. Each

141   day, about 1/3rd of the crabs were tested in each of the three conditions: Expanding, Contracting,

142   and Static. Test order was counterbalanced using a Latin square design to account for

143   confounding effects of time of day and day of the week.

144   *Stimuli*. The stimulus consisted of a white star shape, 1024 x1024 pixels, on a black background

145   (Fig. 2a).

146   *Procedure*. A session started with the crab being placed in the apparatus as described in the

147  General Methods. Each trial began as soon as the crab was automatically detected as being out of

148  its shell for 30 consecutive seconds. If the program detected that the crab hid again during this

149  interval, the pre-trial timer would reset and not restart until the crab was detected as being "out"

150  again. Once the crab had been detected as "out" for 30 consecutive seconds, the trial began with

151  a 30-s delay followed by the presentation of the visual stimulus. Figure 3 provides a schematic

152  for the time course of each of the three types of presentation of the stimulus. The Expanding

153  image started as a single pixel at the top of the screen and enlarged at an exponentially increasing

154  rate such that it simulated the approach of the stimulus at a constant rate. From the start

155  presentation, the stimulus reached its full width of approximately 900 pixels in 17 s. Once the

156  stimulus reached its largest size, it filled the lower part of the screen and remained on the screen

157  for an additional 5 s. For Static presentations, the stimulus was presented at full size at the center

158  of the screen for 22 s. For Contracting presentations, the stimulus was initially presented at its

159  full size and contracted at an exponentially decreasing rate to simulate the image receding at a

160  constant rate. The contracting presentation took 17 s to go from full size to a single pixel at the

161  top of the screen, after which the single pixel remained on the screen for an additional 5 s.

162       For all conditions, trials were repeated until either the visual stimulus had been presented

163  15 times, the session reached a time ceiling of 30 min, or until the crab had two consecutive trials

164  on which it did not hide at all during the stimulus presentation (i.e., reached the habituation

165  criterion).

166  **Results**

167       Very few subjects in the Contracting or Static conditions hid to the stimulus presentation

168  on any trial, precluding a group comparison of rates of habituation. Therefore, we instead

169  analyzed proportion of crabs that hid on the first trial in each of the three conditions using a two-

170   tailed Freeman-Halton extension of Fisher's exact test. For all tests, we interpret two-tailed *p*-

171   values < 0.05 as significant.

172         Stimulus presentation had a large effect on hiding responses ($p = 0.023$; Fig. 4), with the

173   Expanding stimulus eliciting the most reliable response. A larger proportion of crabs in the

174   Expanding condition hid as compared to the Static or Contracting conditions (Fisher's exact test:

175   $p = 0.023$). There was no difference in the proportion of crabs that had in the Static or

176   Contracting conditions *($p = 1.000$)*. These results suggest that the expanding stimulus was

177   perceived as much more threatening than either the static or contracting stimuli.

178   **Experiment 2**

179         In this experiment we evaluated the effect of varying rate of stimulus expansion on

180   probability and latency to hide. Rate of expansion correlates with the changes in the amount of

181   stimulus that fills the visual field of the perceiver of a real looming object. Thus, to the degree

182   that rate of approach of a looming object elicit differences in latency and probability of a hiding

183   response, similar effects should be observed when rate of expansion of a two-dimensional

184   stimulus on a computer screen is varied.

185   *Methods*

186   *Subjects*. We tested 26 experimentally-naïve crabs randomly allocated to one of three groups

187   (*n*=8 for Group 8s and 32s, and *n*=10 for Group 16s). Subjects were maintained as in Experiment

188   1.

189   *Stimuli*. To assess the generality of the effect of expansion, two stimuli were used; an image of a

190   red-tailed hawk (*Buteo jamaicensis*, 1024x796 pixels at full size) and the image of a coconut

191   crab (*Birgus latro*, 1024x430 pixels at full size, Fig. 2b, c). All other aspects of the apparatus

192   were as described for Experiment 1.

193    *Procedure.* Each subject received one session per day for two days. Each crab received one

194    session with the hawk stimulus and one session with the coconut crab stimulus, with test order

195    counterbalanced across subjects such that half of each group was shown the hawk on the first day

196    and the coconut crab on the second day while the order was reversed for the remaining crabs.

197    Groups differed in the rate of stimulus expansion from onset to reaching full size. The three

198    expansion rates tested were 8 s (fast velocity), 16 s (medium velocity), and 32 s (slow velocity).

199    Expansions occurred exponentially such that, in each condition, the stimulus appeared to

200    approach at a constant rate throughout the presentation.

201       Each session began and trials were conducted as described for Experiment 1. Each trial

202    consisted of the expansion from a single pixel to a full size image of either a coconut crab picture

203    or a hawk picture. Trials with the same visual stimulus were repeated until either the visual

204    stimulus had been presented 15 times, the session reached a time ceiling of 30 min, or until the

205    crab had two consecutive trials on which it did not hide at all during the stimulus presentation

206    (i.e., reached the habituation criterion).

207    **Results**

208       A two-way mixed ANOVA conducted on latencies to hide on the first trial with

209    Expansion Rate (8s, 16s, and 32s) as a between-subject factor and Stimulus Type (Hawk and

210    Coconut Crab) as a repeated measure revealed a main effect of Expansion Rate $F(1, 23) = 7.05$,

211    $p < 0.01$, $\eta p^2 = 0.38$, but no effect of Stimulus Type, $F(1, 23) = 1.06$, $p = 0.31$, nor interaction

212    between Expansion Rate and Stimulus Type, $F < 1.0$. Planned comparisons revealed hide

213    latencies differed between the 8s and 32s presentation times $F(1, 23) = 13.24$, $p = 0.01$, and

214    between the 16s and 32s presentation times $F(1, 23) = 7.29$, $p < 0.05$ (Fig. 5), but not between the

215    8s and 16s presentation times, $F(1, 23) = 1.29$, $p = .27$. A similar ANOVA conducted on

216  latencies to emerge failed to reveal any main effects or interactions, $F_S(1, 22) < 1.58$, $p_S > 0.23$

217  (latency to emerge data were missing from one subject in Group 16s, and thus $n = 23$ for this

218  analysis). Because a large number of subjects failed to habituate, trials to habituation was not

219  analyzed as a measure of reaction (Figure 6). These results suggest that rate of expansion serves

220  as a proxy for rate of approach of a looming stimulus, with faster rates eliciting shorter latencies

221  to hide.

222  **Discussion**

223     An expanding image was much more effective than a static or contracting image at eliciting

224  the anti-predatory hide response in hermit crabs. This supported the hypothesis that hermit crabs

225  perceived the expanding image as threatening and probably as a looming object. Moreover, the

226  faster the rate of expansion, the shorter the latency to hide, which is also consistent with how

227  animals react to looming stimuli under natural conditions.

228     Collectively, these experiments demonstrate that for Caribbean terrestrial hermit crabs, the

229  visual system plays an essential role in identifying and responding to potential threats. While

230  dynamic features of an expanding stimulus likely simulate the key aspects of a looming stimulus,

231  it is difficult to determine whether crabs perceived the pictorial or representational aspects of the

232  images. Many species show mixed evidence of perceiving photographs or pictures presented on a

233  computer screen as representations of real 3D objects versus as only 2D colored patterns. For

234  example, evidence is mixed as to whether pigeons (*Columba livia*) can perceive the pictorial or

235  representational aspects of pictorial displays (Fagot, 2000). We've found evidence that the

236  Caribbean hermit crab lacks color vision (Ping et al., 2015). Unpublished studies from our lab

237  also fail to find evidence that hermit crabs can distinguish between pictorial content that is

238  naturalistic (e.g., photographs of a hawk, coconut crab, sea gull), man-made real objects (e.g., a

239  picture of a couch), and simple geometric shapes (e.g., a square, star, or oval). More research

240  would be needed to definitively answer this question for the Caribbean hermit crab.

241  Nevertheless, the fact that hermit crabs were particularly sensitive to an expanding stimulus

242  suggests that some aspects of real, looming objects are perceived in the dynamic 2D stimuli in

243  our study. Out results are consistent with much prior work exploring the neural basis of

244  antipredator responses to looming stimuli in arthropods (Hemi, 2005; Oliva et al., 2007; Oliva &

245  Tomsic 2012).

246      While we documented the visual detection abilities that these crabs possessed, previous

247  experiments have shown the importance of the acoustic environment to the crab's ability to

248  respond to visual stimuli (Chan et al. 2010b; Ryan et al. 2012), indicating that hermit crabs use

249  multisensory channels to evaluate their environment. This is consistent with research on other

250  invertebrates such as fiddler crabs (*Uca vomeris*) that employ multiple detector systems to

251  evaluate different aspects of a possible threat (Hemmi, 2005; Hemmi & Pfeil, 2010). Future

252  studies would profitably examine how assessment works in a multi-modal paradigm. Finally, it is

253  worth noting that this and prior published work from our lab demonstrates the value of going

254  from field research into the lab and back again. Field research is valuable for its ability to gather

255  questions about an organism's behaviors in its natural habitat. Laboratory research can then

256  provide a more controlled setting within which to untangle distinct behavioral processes.

257  **Conclusion**

258      Computer technology can provide a valuable tool for investigating the perceptual and

259  cognitive processes that contribute to natural behavior observed in the field. Knowledge gathered

260  from laboratory work can in turn inform new directions for field work, including tailoring

261  improvements that protect animals from potentially deleterious anthropogenic effects.

262

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264 encouragement.

265

266 **Ethical approval**

267 All applicable international, national, and/or institutional guidelines for the care and use of

268 animals were followed. All procedures performed in studies involving animals were in

269 accordance with the ethical standards of the institution or practice at which the studies were

270 conducted.

271

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324 **Figure Legends**

325 **Figure 1** A schematic of our experimental set-up. The monitor displays the fully enlarges image

326 of the coconut crab stimulus. Figure not drawn to scale.

327

328 **Figure 2** Visual stimuli. Star image for Experiment 1 (a), Hawk and Coconut Crab images for

329 Experiment 2 (b, c). At maximum size, the Hawk image is 1024 x 796 pixels and the Coconut

330 Crab image is 1024 x 430 pixels.

331

332 **Figure 3** Schematic of the conditions: A) expanding, B) full-sized, and C) contracting stimulus

333 for Experiment 1.

334

335 **Figure 4** Percent of crabs that hid to the Expanding, Contracting, and Static conditions in

336 Experiment 1. Asterisk indicates significant difference from remaining groups, $p < .05$.

337

338 **Figure 5** Mean latency (s) to hide to the 8s, 16s, and 32s presentation time stimuli using both a

339 Hawk and Coconut Crab image in Experiment 2. Error bars depict standard errors of the means.

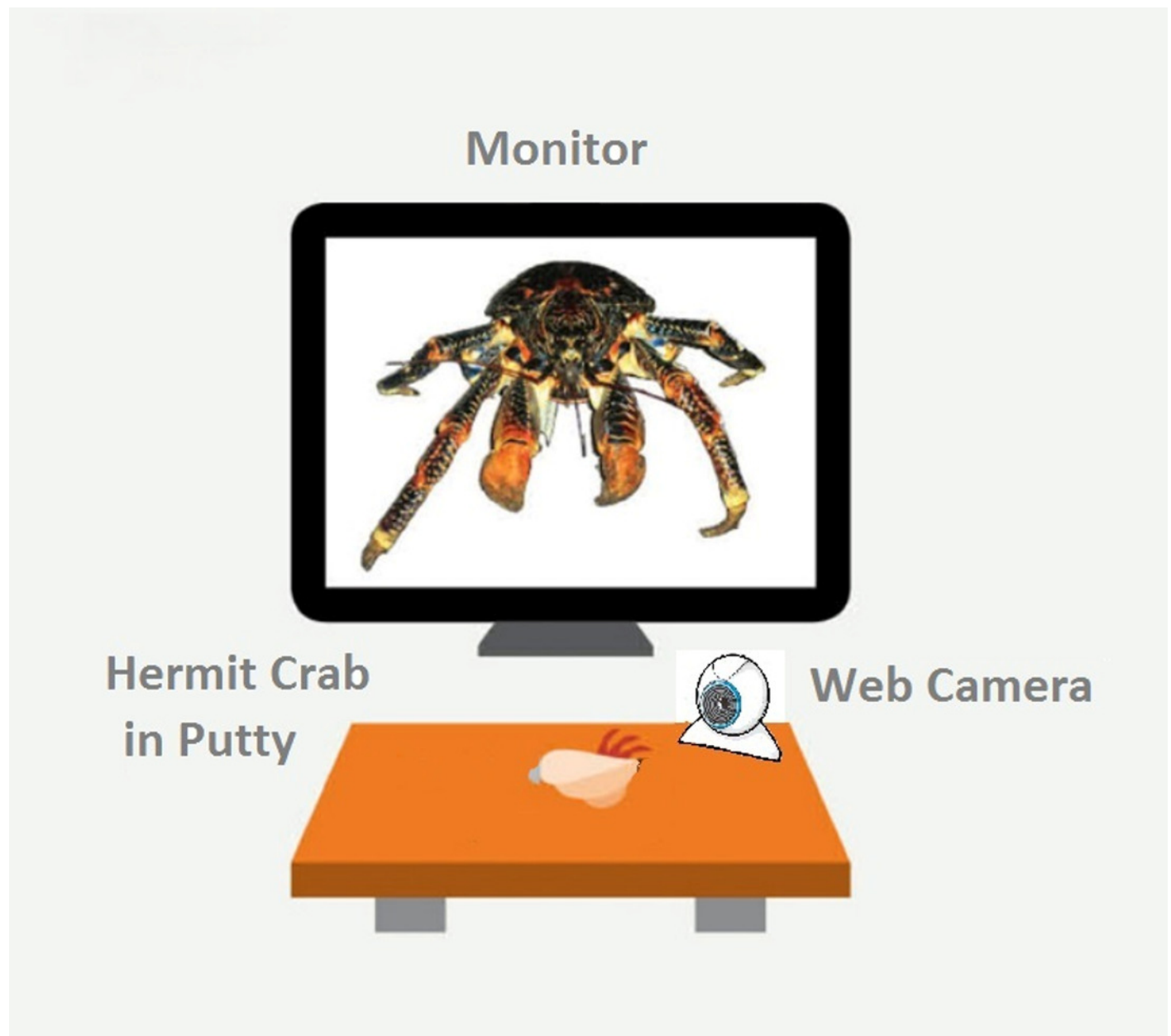
340

341 **Figure 6** Percentage of subjects that reached the habituation criterion in each condition of

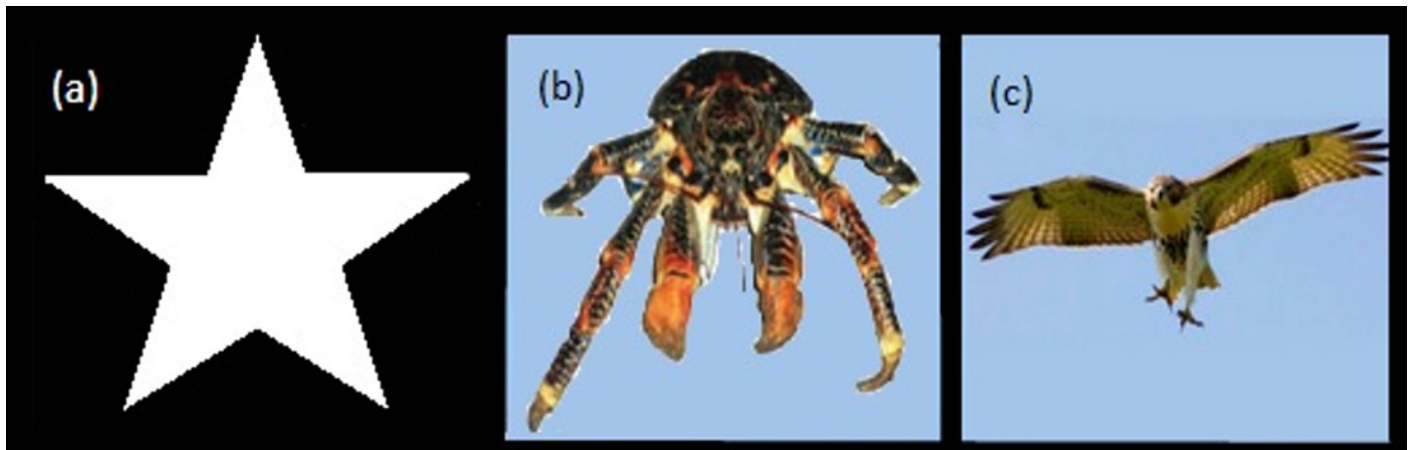
342 Experiment 2.

# Figure 1

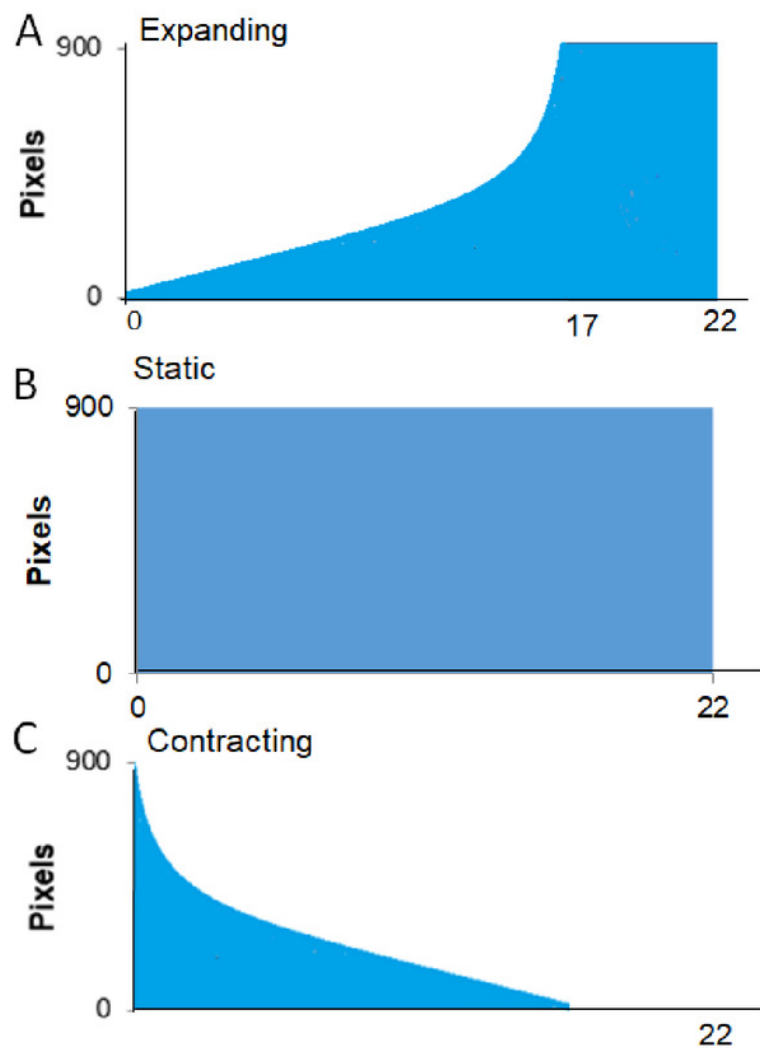
A schematic of our experimental set-up.

The monitor displays the fully enlarges image of the coconut crab stimulus. Figure not drawn to scale

# Figure 2

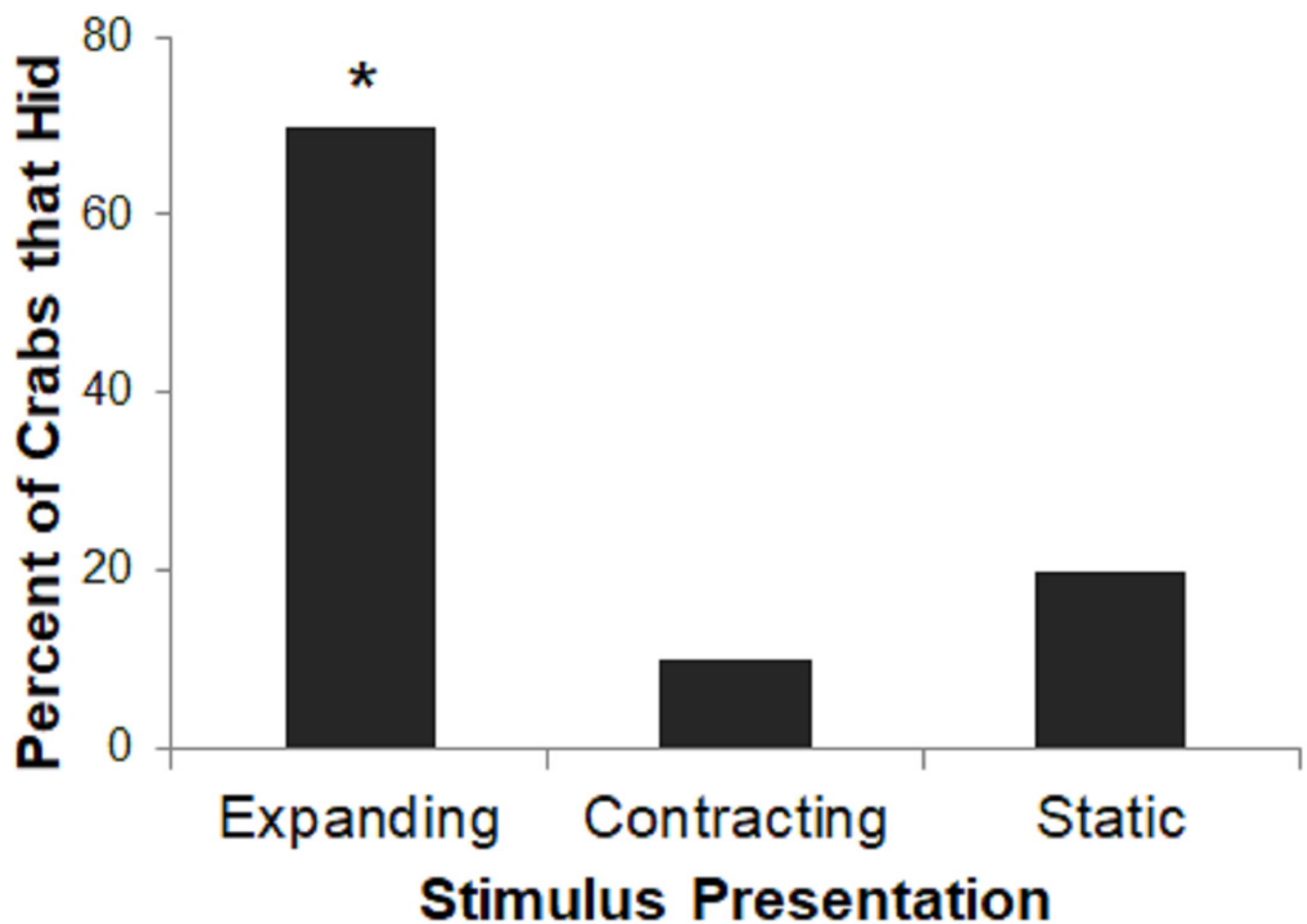
Visual stimuli.

Star image for Experiment 1 (a), Hawk and Coconut Crab images for Experiment 2 (b, c).

# Figure 3

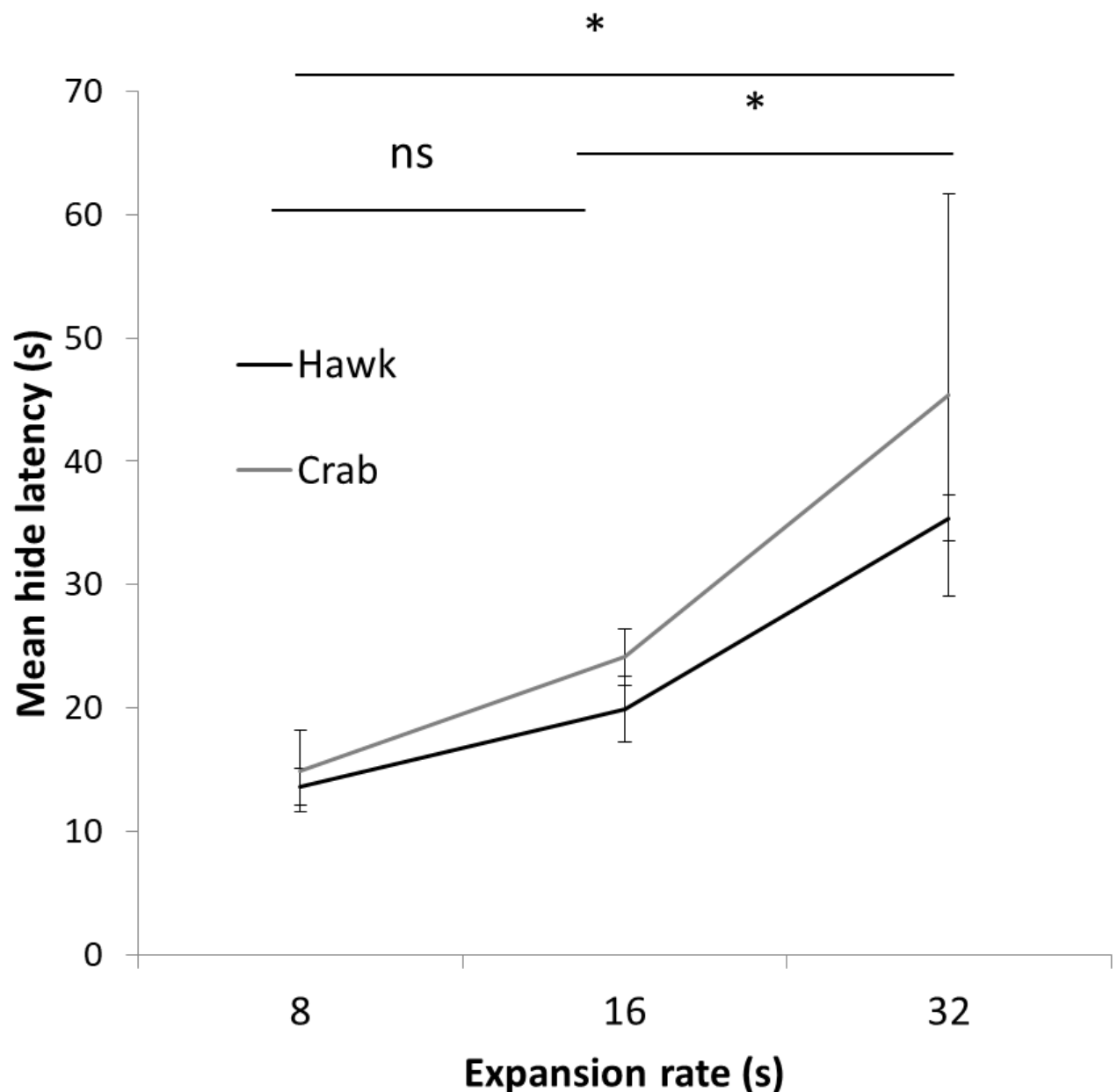
Presentation formats for Experiment 1

Schematic of the conditions, expanding, full-sized, and contracting stimulus for Experiment 1.

# Figure 4

Percent of crabs that hid to the Expanding, Contracting, and Static conditions in Experiment 1.

Asterisk indicates significant difference from remaining groups, $p < .05$.

# Figure 5

Results Experiment 2

Mean latency (s) to hide to the 8s, 16s, and 32s presentation time stimuli using both a Hawk and Coconut Crab image in Experiment 2. Error bars depict standard errors of the means.

# Figure 6

Percentage of subjects that reached the habituation criterion in each condition of Experiment 2.

|  | Hawk Expansion rate (s) | | |
|---|---|---|---|
|  | 8 | 16 | 32 |
| Habituated | 37.5% | 60% | 50% |
| Not habituated | 62.5% | 40% | 50% |