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6   **Computerized stimuli for studying oddity effects**

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28 **Abstract**

29 Visually hunting predators must overcome the challenges that prey groups present.

30 One such challenge is the confusion effect where an overburdened visual system

31 means predators are unable to successfully target prey. A strategy to overcome

32 confusion is the targeting of distinct, or odd, individuals (the oddity effect). In live prey

33 experiments, manipulation of group member phenotypes can be challenging and prey

34 may differ on more than the single feature one intends to define as odd. The use of

35 highly controllable computerized stimuli to study predator-prey interactions is

36 increasingly popular in the field of behavioral ecology. However, to our knowledge,

37 the validity of computerized stimuli to study the oddity effect has not been

38 established.

39 Predator choice experiments were conducted using naive stickleback predators to

40 ascertain whether the oddity effect could be demonstrated in the absence of live prey.

41 We found evidence for both the oddity effect and preferential targeting of group

42 edges and low density regions, as would be predicted if predators targeted prey

43 individuals to minimize confusion. The oddity effect was evident at a low threshold,

44 above which dots were no longer perceived as odd, and no longer attacked more

45 often than expected by chance.

46 We conclude that computerized stimuli are an improved, practical method for

47 studying oddity effects while further validating the use of similar methods for studying

48 other aspects of visual predation. In addition to higher control of 'prey' appearance,

49 the replacement of live prey animals with digital stimuli is ethically beneficial and

50 reusing code improves experimental efficiency.

53   **Data accessibility**

54   Analyses reported in this article can be reproduced using the data located at
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Introduction

When predators approach a group of prey they are simultaneously presented with a choice of potential targets. Which prey within a group are selected by predators directly affects the composition of phenotypes within a group, in addition to driving the evolution of prey grouping behaviors (Croft et al., 2009; Rodgers et al., 2015). Visually hunting predators may select prey because of their position in the group (Hamilton, 1971), or because of their appearance (Ohguchi, 1978). Prey may be preferentially targeted because they appear slow or weak (Genovart et al., 2010), because they are the appropriate size to maximize energy gains (Turner, 1982), or because they are visually distinct from the rest of their group (the oddity effect, Almany et al., 2007; Penry-Williams et al., 2018).

Landeau and Terborgh (1986) used bass preying on groups of minnow to demonstrate that the presence of visually distinct 'odd' prey mitigates the confusion effect. The confusion effect describes the diminished ability of a predator to successfully target an individual within a group, resulting from cognitive limitations (Krakauer, 1995). Landeau and Terborgh (1986) is a well-cited oddity effect study, showing how individual appearance and overall group composition can affect predation decisions and outcome. However, a methodology that uses live, vertebrate prey, which are confined with the purpose of being attacked, is something we are less likely to deem ethically acceptable by today's standards (Buchanan et al., 2012; Brown, 2015; Sloman et al., 2019). A more common predator-prey system for studying confusion and oddity effects is that of stickleback (*Gasterosteus aculeatus*) preying on *Daphnia*. Putting aside any philosophical questions about ethics and (the lack of) vertebrae (although see Freelance, 2018), there are potential issues relating to efficiency and perception that may arise here.

79   In order to understand how phenotype contributes to the oddity effect, prey group

80   members should ideally only differ on a single feature. Many studies examining predator

81   selection of odd prey require prey individuals to be sorted by size and dyed, usually with

82   food coloring (Landeau and Terborgh, 1986; Wilson et al., 1990; Richards et al., 2011;

83   Rodgers et al., 2013; Penry-Williams et al., 2018). This process is time consuming and largely

84   reliant on a human judgment of prey similarity. Perception is highly subjective, even

85   between members of the same species (Brainard and Hurlbert, 2015) and consequently this

86   raises potential issues for repeatability. In addition, studies of confusion and oddity effects

87   use the human visual system to establish uniformity of prey appearance, yet stickleback, for

88   example, are able to see ultraviolet (UV) light (Modarressie and Bakker, 2007; Rick et al.,

89   2012). Hence, what might appear to be a largely homogenous stimulus group in visible light

90   might not be the case elsewhere in the electromagnetic spectrum. Although there are ways

91   to overcome between-species perceptual differences (e.g., Rowe et al, 2006), we submit

92   below that rendering digital stimuli monochromatically and through a UV-filter affords the

93   highest standard of stimulus control.

94   An alternative to altering prey appearance is to use color-morphs of the same species. In the

95   case of *Daphnia*, morphs can be obtained through manipulating water chemistry (Ohguchi,

96   1978). However, different behavioral phenotypes often present themselves alongside

97   differences in appearance. For example, higher levels of aggression are seen in melanic vs.

98   silver mosquito fish (*Gambusia holbrooki*, Horth, 2003) and blue vs. yellow cichlids

99   (*Astatotilapia burtoni*, Dijkstra et al., 2017). Black springbok (*Antidorcas marsupialis*) have

100   lower activity levels than their white or standard colored counterparts (Hetem et al., 2009),

101   and while both black and white mollies (*Poecilia latipinna*) shoal with color-matched

102   conspecifics, white morphs have a stronger overall shoaling tendency (Rodgers et al. 2013).

103   Uncontrolled differences in behavioral phenotype have the potential to confound studies

104   that are aiming to isolate a feature that may influence predator choice.

105   As we suggest above, a possible solution to improve experimental efficiency and to better

106   control prey phenotype is to use computerized stimuli in place of live prey. Individuals

107   within simulated 'prey' groups can be manipulated to differ from their group-mates only in

108   the specific, measurable ways intended by the experimenter. The use of computerized

109   stimuli to study visual search and attentional capture is well established in experimental

110   psychology (Bundesen and Habekost, 2008). There is also considerable research in the field

111   of behavioral ecology examining the confusion effect, with human predators preying on

112   computerized targets (Ruxton et al., 2007; Scott-Samuel et al., 2015; Hogan et al., 2017a;

113   Hogan et al., 2017b). Computerized stimuli are also gaining popularity for studying some

114   aspects of visual predation in non-humans (Ioannou et al., 2012; Woo et al., 2016; Duffield

115   and Ioannou, 2017; Ioannou et al., 2019). However, to our knowledge, the effectiveness of

116   similar methods for studying oddity is yet to be validated for non-human predators.

117   Here, we use stickleback targeting computerized prey-dots to establish the value of this

118   approach to the study of the oddity effect, defined here as the preferential targeting of a

119   minority phenotype (Ohguchi, 1978; Penry-Williams et al., 2018; Raveh et al., 2019). If the

120   use of digital stimuli is a valid methodology for exploring oddity effects, we would expect to

121   see that a minority phenotype becomes preferentially targeted below a certain threshold of

122   representation within the group. For applicability to the general study of visual predation,

123   predators should target computerized prey groups as they do live prey groups. Thus, we

124   would expect, in line with work on live prey, to also see preferential predation of those on

125   the edges of groups (Hirsch and Morrell, 2011).

126

Methods

Stickleback sourcing and maintenance

129 Three-spined stickleback (n=56) were sourced from Thwaite Hall Gardens, Cottingham, UK

130 (grid reference: TA 055 326) in October, 2015. A further 200, wild caught stickleback were

131 sourced from The Carp Co. (Bourne Valley Fish Farm, Kent, UK) in September, 2016. Fish

132 from the Thwaite Hall Gardens source were caught using telescopic landing nets and

133 transported back to the laboratory, by car, in a 20L bucket filled with pond water. No fish

134 died in transit or immediately after being transferred to the laboratory tanks.

135 All fish were quarantined for 3 weeks in two 150L tanks, aerated with two Tetra APS 50 air

136 pumps and two 30 mm air stones per tank. Manual water changes of 25-50% were made 2-3

137 times per week. After this period, fish were housed in groups of 12 on a closed, freshwater

138 system with ~20% new water introduced per week. Fish were fed daily on defrosted frozen

139 bloodworms and *Daphnia* spp. (Ings Lane Garden Centre, Hull, UK). Water temperature was

140 kept between 10-12°C and the day:night light cycle was set at 12:12 h to prevent the onset

141 of breeding condition. As a result, no attempt was made to determine the sex of individual

142 fish. Experimentation took place between 09:00 and 18:30 h, as stickleback are diurnal,

143 visual predators (Wootton, 1976; FitzGerald and Wootton, 1986).

144

Experimental tank setup

146 Experiments took place in a modified glass aquarium (figure 1). The aquarium was split into

147 a companion area spanning the full width of the tank at one end (10 cm x 20 cm, figure 1a)

148 and a larger focal area (20 cm x 20 cm, figure 1b). The companion area contained 3 non-

149 experimental fish. The companion fish acted to reduce stress to the test fish by providing a

150 social environment for this shoaling species (Jones and Godin, 2009; Voellmy et al., 2014). A

151 transparent, perforated partition allowed visual and olfactory contact between the

152 companion fish (in the companion area) and the focal fish (in the focal area). The walls of

153 the companion area were covered with black, opaque plastic to minimize brightness, and

154 therefore stress (Maximino et al., 2010), to the companion fish. An opaque lid covered the

155 companion area so companion fish were not disturbed when focal fish were netted in and

156 out of the experimental tank. The focal area of the tank was partially divided by a black,

157 opaque barrier. This provided a shaded refuge area for the test fish, from which the

158 projection (see below) was not visible. A plastic plant within the experimental area provided

159 further refuge for the test fish.

160 Simulated prey (see below for details of the simulation) were rear-projected onto a self-

161 adhesive, rear projection film (model: GR/Gray, brand: ARCHISTAR) adhered to the tank wall

162 (figure 1b). A Sony VPL-DX122 LCD projector connected to a Toshiba Portégé Z30-B-10G

163 Ultrabook was used to project the simulated prey. The progressive scanning of the 60Hz LCD

164 screen and the constant lamp output of the projector ensured that the critical flicker

165 frequency of stickleback, thought to be higher than humans (Healy et al., 2013), is unlikely

166 to be an issue here (for full explanation see Künzler and Bakker, 2001, pp 681-682).

167 To reduce brightness and glare, the projector was placed behind a screen (Solar Control

168 High Reflective Silver Window Film, The Window Film Company UK Ltd, Chesham, UK). The

169 screen also functioned to reduce heat and UV transmission by 77% and 99% respectively.

170 Two webcams (Microsoft LifeCam Cinema), connected to a second laptop (Samsung NP-

171   R780-JT3BUK) were placed outside of the tank, facing the projection wall, to allow for data

172   collection (see Experimental Procedure, below). Webcam 1 (figure 1) was positioned above

173   the waterline and allowed observation of the fish exploring the tank and approaching the

174   projection. Webcam 2 was placed directly below webcam 1 and allowed underwater

175   observation of the fish attacking the simulated prey group.

176

177   Simulation of prey

178   All simulations were carried out using OpenSesame v3.0.7 (Mathôt et al., 2012), using a

179   screen resolution (canvas) of 1360 x 768 pixels. The canvas was colored an intermediate

180   shade of grey, RGB(129,129,129). N_{group} dots (N_{group} = 16) were positioned on the canvas by

181   selecting pseudorandom integer values from a uniform distribution between x_{min} and x_{max},

182   and between y_{min} and y_{max} for each dot i (see supplementary table 1 for details of

183   parameters used in the simulation). The minimum and maximum values of x and y were

184   chosen to define an active area of the canvas suitable for projection onto the experimental

185   tank, and gave an approximate projected array area of 3 x 7 cm. Each dot had a radius r of

186   7.5 pixels, centered on (x_i, y_i), and a pseudorandom orientation (movement direction, d_i)

187   between 0 and 2π radians. Dots were colored (c_i) according to whether they were odd or a

188   distractor (the remainder of the group). Dots $1 \leq i \leq N_{odd}$ were colored as specified by shade

189   of the odd dot, and the remainder the shade of the distractors (see table 1 for number of

190   odd dots). 'Dark' dots were defined as RGB(1,1,1) and 'light' dots as RGB(255,255,255). Dots

191   therefore differed from one another in luminance, but not color. The combination of

192   achromatic stimuli presented through a UV-filter ensured that prey stimuli could not be

193   differentiated on the basis of hues that are invisible to humans (Oliveira et al., 2000; Baldauf

194   et al., 2008). A circular dot shape was chosen to represent the prey. This avoided the

195   assumption that other projected shapes, such as those of natural prey, would be viewed as

196   such by the stickleback.

197   In each timestep t, the position of each dot was updated such that:

198          $x_{i(t+1)} = x_{i(t)} + v * cos(d_i)$

199          $y_{i(t+1)} = y_{i(t)} + v * sin(d_i)$

200   The value of v (v = 1.5) was selected such that the dots appeared to move smoothly and

201   continuously to a human observer. To ensure that the dots did not move in straight lines,

202   after the position of dots had been altered, their orientation was adjusted such that:

203     $d_{i(t+1)} = d_{i(t)} + a_{max} * (b_i – 0.5)$, where b is a pseudorandom number between 0 and 1.

204   Random motion is common in many zooplankton species (Seuront et al., 2003; Komin et al.,

205   2004; Strickler et al., 2005) and the random elements of swimming behavior will elicit attack

206   from predatory fish (Matsunaga and Watanabe, 2012).

207   For any dots that left the canvas (where any of $x_i > x_{max}$, $x_i < x_{min}$, $y_i > y_{max}$ or $y_i < y_{min}$),

208   orientation was updated such that $d_{i(t+1)} = d_{i(t)} + \pi$, meaning that they reversed direction and

209   'bounced' back into the group. This ensured that the group did not become more dispersed

210   during the simulation, mimicking natural groups where compaction is maintained (Seghers,

211   1974; Magurran and Pitcher, 1987). The simulated dots will henceforth be referred to as

212   'prey-dots'.

213

214   **Experimental procedure**

215   The experimental tank (figure 1) was filled to a depth of 13 cm of system water, with an

216   olfactory cue added to stimulate predatory feeding behavior (Johannesen et al., 2012). The

217   olfactory cue was made by defrosting 2 blocks of Gamma brand frozen *Daphnia* in 20ml

218   system water. The *Daphnia* were then strained through a fine mesh net to ensure that the

219   cue contained no solids. Three non-experimental fish were carefully netted into the

220   companion area (figure 1a) 5-10 min before experimentation commenced. Companion fish

221   had visual and olfactory contact with the focal fish in both the refuge area (figure 1a) and

222   experimental area (figure 1b), but their view into the experimental area was partially

223   obstructed by a plastic plant. Companion fish were not used as test fish.

224   At the start of each trial, the focal fish was netted from the holding tank into the refuge

225   area, and the prey simulation was started. Within a single trial a fish was presented with up

226   to 7 arrays (prey-dot groups). Fish were allowed 20 min to attack the first group of prey-dots

227   within a trial. For each subsequent prey group, fish were allowed up to 10 min to attack. The

228   additional 10 min of time to attack the first group was to allow for acclimatization and tank

229   exploration. If an individual continued to show interest in the stimuli, by attacking prey-dots

230   within the allotted time, it was presented with up to 7 treatments out of a possible 11 (table

231   1). In a first set of trials (N=35 fish) prey-dot groups were homogenous (0-odd, 16 dark or 16

232   light prey-dots), equal (8-odd), 2-odd and 4-odd (table 1). In a second set of trials (N=34 fish)

233   prey-dot groups were homogenous, equal, 1-odd and 3-odd (table 1). Groups in both sets

234   were presented in a random order.

235   Each individual trial ended either when the fish made an attack towards a prey-dot, or when

236   the allotted attack time expired. As the fish attacked, the experimenter froze the moving

237   prey-dots by pressing the spacebar, then used the mouse to click at the position of the

238   attack. The coordinates and phenotype of each prey-dot, in addition to the coordinates of

239   the mouse click, were recorded for use in analysis. If the experimenter froze the array > 0.45

240   sec before or after the fish made contact with the screen this was noted as a failed trial and

241   the experimenter moved on to the next prey-dot group. 0.45 sec was equivalent to a

242   timescale where the dots had visually (to a human observer) shifted position. This occurred

243   on 93 out of 339 occasions in total. The proportion of these occurrences were similar across

244   each treatment type, with no significant difference between the greatest number of

245   occurrences (9/27 trials in the 4 light:12 dark array) and the fewest (4/27 trials in the 3

246   dark:13 light array; proportion test: x = 1.621, p = 0.203).

247

248   At the end of the trial, fish were measured to the nearest 0.1 mm (standard length) using

249   dial calipers before being put back in their system tank. A total of 87 fish were tested,

250   however 18 fish did not make a first attack within 20 min and 2 fish were removed from

251   analysis due to experimenter error, resulting in a final sample size of n=67, (standard length

252   28.4-51.7 mm), see table 1 for breakdown of sample sizes by treatment. A total of 197

253   attacks were made, with a mean of 2.95 attacks per fish.

254

255   **Data Analysis**

256   Data were analyzed in R v.3.3.1 (R Development Core Team, 2015). A binomial test was used

257   to assess whether the proportion of attacks made towards light and dark targets differed

258   from random expectation in the equal ratios treatment. As there was no significant

259   deviation from random (13 attacks to dark, 21 attacks to light; binomial test, p = 0.230), fish

260   could be said to express no particular preference for light or dark dots, so data were pooled

261   by the number of odd individuals for all further analysis.

262   We used generalized linear mixed effects models (package lme4 1.1–12; Bates et al. 2015)

263   to explore the effects of oddity status (odd or not), number of odd individuals (treatment),

264   position (center or edge of the group) and local density (distance to the nearest neighbor),

265   and their interactions on whether or not a dot was targeted (target = 1, not target = 0). Trial

266   number nested within fish ID was added as a random effect (random intercepts) to account

267   for the repeated measures nature of the data (multiple dots per trial and multiple trials per

268   fish). An observation-level random effect (random intercepts) was also added to account for

269   over dispersion in the data (Harrison, 2014). There was no collinearity between the main

270   effects (VIF≤2.5). Body length and the site from which fish were sourced were initially

271   checked and found to have no effect on target choice (supplementary table 2). Both were

272   left out of further analysis to focus on variables of interest.

273   We identified a set of candidate models, including all possible combinations of pairwise

274   interactions between the four variables, plus the model including all three-way (and lower

275   order) interactions and the model containing the 4-way interaction (and all lower order

276   interactions). Every model contained the 4 main effects. This gave a total of 66 candidate

277   models. We ranked these models by AIC_C scores and assigned them Akaike weights (ω_m)

278   based on these scores (package MuMIn 1.40.0, Barton, 2017). All models with AIC_C within 2

279   of the best model AIC_C ($\Delta AIC_C \leq 2$) were included in the top model set. We calculated full

280   averaged estimates for each variable and interaction appearing in the top model set (i.e.

281   model-weighted averages of predictor estimates over all top set models including those that

282   did not contain the predictor). We also calculated the relative importance of explanatory

283 variables (ω_p; the sum of Akaike weights of all top set models containing the variable). We

284 reanalyzed our data using the mean distances to the 2-4 closest neighbors in place of the

285 distance to the nearest neighbor and found the results to be broadly consistent

286 (supplementary table 3).

287 Further binomial tests were used to assess whether fish attacked odd individuals more often

288 than expected by chance given their frequency in the group, and a proportion test was used

289 to assess whether edge individuals were attacked more often than expected by chance,

290 given the likelihood of an individual being defined as 'edge'.

291

292 **Ethical statement**

293 Experiments were approved by the University of Hull's School of Biological, Biomedical and

294 Environmental Sciences and Faculty of Science and Engineering ethical review committees

295 before commencement (reference numbers U094 and U095), and followed the Association

296 for the Study of Animal Behaviour Society Guidelines for the treatment of animals in

297 behavioral research and teaching (ASAB/ABS, 2018). Care was taken to minimize stress to

298 the experimental fish by the provision of companion fish and refuge areas during the

299 experiment, and by careful handling.

300

301 **Results**

302 All models in the top model set (table 2) contained an interaction between oddity status and

303 the number of odd individuals in the array on the likelihood of a particular dot being

304 attacked (table 3). Odd individuals were more likely to be attacked, but only when there

305   were 1 or 2 (rather than 3 or 4) in the array (binomial tests: table 4; figure 2a). The models

306   also highlighted that edge individuals (table 3; proportion test: x^2=63.874, df=1, p<0.001;

307   figure 2b) were attacked more often than those in the center of the group. These results

308   were broadly robust to the choice of nearest neighbor distance as a measure of local density

309   (supplementary table 3), however, including 3 or 4 neighbors (but not 2) in the measure of

310   local density showed that those with higher average nearest neighbor distances (low local

311   density, or more isolated individuals) were more likely to be attacked (supplementary table

312   3b and c; figure 2c).

313

314   **Discussion**

315   Using luminance oddity, we have validated the use of computerized stimuli to study the

316   oddity effect. We were able to demonstrate preferential targeting of a minority phenotype,

317   in line with the oddity effect (Ohguchi, 1978; Penry-Williams et al., 2018). 2D arrays were

318   attacked as you would expect if they were 3D, confusing prey group, with preferential

319   targeting of the edges and low density regions (e.g. Hirsch and Morrell, 2011; Duffield and

320   Ioannou, 2017). Other studies have used virtual stimuli to successfully examine the

321   confusion effect (Scott-Samuel et al., 2015; Hogan et al., 2017b), marginal predation

322   (Duffield and Ioannou, 2017), the coordination of prey movement (Ioannou et al., 2012;

323   Lemasson et al., 2016) and the targeting success of humans predating odd prey (Ruxton et

324   al., 2007). However, to our knowledge, this is the first demonstration of the oddity effect

325   using a naïve, non-human predator preying on computerized prey.

326   The predatory response of fish to the 2D prey group adds to the work validating the use of

327   virtual prey for studying visually mediated predation (Ioannou et al., 2012; Woo et al., 2016;

16

328   Duffield and Ioannou, 2017; Ioannou et al., 2019). We found that individuals on the

329   periphery of the group were significantly more likely to be targeted than those in the center.

330   This aligns with what would be expected of a pursuit predator attacking a prey group (Hirsch

331   and Morrell, 2011), and with studies examining marginal predation in relation to confusion

332   effects (Duffield and Ioannou, 2017). Targets were significantly more likely to be further

333   away from their nearest neighbors, i.e. they had lower local density, or were more isolated

334   within the group. These findings are contrary to the idea that denser regions of a group

335   attract attention due to higher conspicuousness (Ioannou et al., 2009), but in line with

336   findings that show increased risk to prey at lower local densities (Ioannou et al., 2009;

337   Ioannou et al., 2019).

338   Detection and selection occur at different stages of the predation process. Fish may be

339   initially drawn to denser regions of the group at the detection stage but choose to target

340   less dense (and less confusing) regions at the attack stage (Milinski, 1977). While we did not

341   measure success, evidence suggests that attacks are more successful when local prey

342   density is lower (stickleback preying on *Daphnia*; Ioannou et al., 2009) or prey individuals

343   are isolated from the group (geckos *Eublepharis macularius* and marmosets *Callithrix*

344   *jacchus* preying on mealworms, Schradin, 2000). Consequently, a targeting preference for

345   less dense regions can be considered a strategy for overcoming the confusion effect.

346   Attacking dense regions is more perceptually challenging and therefore takes more focus, at

347   the expense of awareness of surroundings. Stickleback are less likely to notice a predator

348   when attacking a dense swarm, and when they are exposed to a predator before being

349   presented with a prey group, they will target areas of lower local density (Milinski, 1984).

350   Bees have increased difficulty finding a target flower within a group of higher density

351   distractor flowers (Spaethe et al., 2006). In humans, increased density, or visual clutter,

352   contributes to crowding effects, impairing the identification of targets (Whitney and Levi,

353   2011), although this phenomenon can be overcome if targets are salient because they are

354   visually distinct i.e. they are odd (Põder, 2002).

355   Odd prey-dots were significantly more likely to be targeted when groups contained 1 or 2

356   odd prey-dots, but not when there were 3 or 4. These results suggest that joining a majority

357   unmatched group may not necessarily increase predation risk for minority phenotype

358   individuals, above a low threshold. However, we cannot say whether this threshold is an

359   absolute number or proportion as we only tested a single group size of 16 individuals.

360   Landeau and Terborgh (1986) found that when 1 or 2 odd colored minnow, but not 4, were

361   present within a prey group of 8, bass were significantly more likely to make a successful

362   attack to any group member, odd or otherwise. This effect did not scale up to group sizes of

363   15, where no 5 minute trials ended in a successful attack, and thus the question of absolute

364   or proportional thresholds could not be answered. In longer experimental trials, lasting 24

365   hours, Theodorakis (1989) demonstrated bass preferentially targeting size-odd minnow

366   below a threshold of 5, but again this was only in a single group size of 30.

367   Fish are commonly used to study the oddity effect, however a diverse array of animal

368   species respond to digitally generated stimuli (e.g. blue jays *Cyanocitta cristata*, Bond and

369   Kamil, 2002; baboons *Papio papio*, Fagot et al., 2009; chameleons *Chamaeleo chamaeleo*n,

370   Katz et al., 2015; jacky dragon *Amphibolurus muricatus*, Woo et al., 2016) and therefore

371   computerized stimuli to study oddity, and other aspects of visual predation are applicable

372   across species. Computerized stimuli form the foundation of studies of attentional capture

373   in experimental psychology (Bundesen and Habekost, 2008) but little is known about

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374   attentional capture in other species, particularly fish. Adaptations of the present

375   methodology could be used to address the dearth of research in this area.

376   Computerized stimuli appear to be a viable and practical method for studying oddity effects,

377   but there is still much to learn about when and why oddity effects occur. While we have

378   demonstrated a preference for odd targets at a low threshold within a group, we cannot

379   make conclusions about what drives the preference we have observed here. The targeting

380   of odd prey may have resulted from attentional capture by odd targets, or because

381   targeting odd prey reduces confusion effects. Further work, using a similar methodology to

382   that presented here, could be used to establish the threshold of 'useful' oddity, i.e. oddity

383   that improves attack success, and how this interacts with prey group size. In addition, while

384   we found no evidence that oddity interacted with the preference for edge and low density

385   regions,

386   We propose that the use of computerized 'prey' is an improved method for studying oddity

387   effects, for the following reasons:

388   1. Digital stimuli are highly controllable and reduce the potential for confounding

389   factors.

390   2. Ethical practice is improved because the number of live prey required for

391   experiments are reduced.

392   3. Once written, code can be shared and reused, greatly improving experimental

393   efficiency and output.

394

395

396   **Table 1** The 11 possible prey-dot group compositions, including the number of experimental

397   trials (*N* experiments) per treatment.

Group type	*N* experiments	N_{odd}	dark : light	Set
1-odd	16	1	1:15	2
1-odd	15	1	15:1	2
2-odd	15	2	2:14	1
2-odd	19	2	14:2	1
3-odd	17	3	3:13	2
3-odd	15	3	13:3	2
4-odd	21	4	4:12	1
4-odd	12	4	12:4	1
equal	35	8	8:8	1 & 2
homogenous	16	0	16:0	1 & 2
homogenous	16	0	0:16	1 & 2

398   **Table 2:** The top model set according to AIC, drawn from models including and excluding

399   interaction terms. Terms in bold are significant at p<0.05 assessing the impact of individual

400   terms in the model (table 3 & supplementary table 4).

Rank	Single variable terms	Interaction terms	df	AIC$_C$	ΔAIC$_C$
1	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density	10	1274.018	0
2	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd**	9	1275.100	1.081
3	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Oddity status * local density Position * local density	11	1275.280	1.261
4	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Number odd * local density Position * local density	11	1275.756	1.737
5	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd** Oddity status * position Position * local density	11	1275.930	1.912
6	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density Position * number odd	11	1276.011	1.993

401   Variance and standard deviation of random effects was <0.001 in the best-fitting model

402

403　**Table 3:** Model-averaged parameters from the GLMM output with attack status (target or

404　not) as the response variable.

Fixed term	β	95% CI	ω_p	Z
(Intercept)	-3.883			
Position	**1.281**	**0.865, 1.697**	**1**	**6.033**
Local density	-0.104	-0.560, 0.352	1	0.446
Number odd	0.072	-0.031, 0.175	1	1.366
Oddity status	**1.049**	**0.453, 1.646**	**1**	**3.448**
Oddity * number odd	**-0.125**	**-0.234, -0.015**	**1**	**2.234**
Position * local density	0.309	-0.054, 0.805	0.82	1.262
Oddity * local density	0.019	-0.146, 0.378	0.16	0.273
Local density * number odd	0.001	-0.018, 0.031	0.13	0.169
Position * oddity	0.014	-0.589, 0.820	0.12	0.105
Position * number odd	< 0.001	-0.063, 1.697	0.11	0.049

405　Full model-averaged estimates (β), 95% confidence intervals (CIs), relative importance (ω_p) and Z are

406　shown for all models appearing in the top model set (ΔAIC$_C$ ≤ 2). Predictor CIs that do not overlap

407　with zero are shown in bold. Candidate models: 66, top set models: 6 (see table 2).

408 **Table 4** Binomial test output where the number of attacks to odd individuals were

409 compared to what would be expected if odd shaded dots were targeted at random, with

410 respect to overall group size and baseline probability (chance). Significance level is indicated

Treatment	# trials odd targeted in	total # trials	Expected probability	p
1 odd	9	31	0.063	**<0.001 ** **
2 odd	9	34	0.125	**0.026 ***
3 odd	9	32	0.188	0.139
4 odd	11	32	0.25	0.154

411 by terms in bold, with * for $p<0.05$, ** for $p< 0.01$ and *** for $p<0.0001$***.

412

413

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