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6 **Prey body size mediates the predation risk associated with being ‘odd’**

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26 **Running header:** Body size and oddity

27

28 **Abstract**

29 Despite selection pressures on prey animals to maintain phenotypically homogeneous
30 groups, variation in phenotype within animal groups is commonly observed. While many
31 prey animals preferentially associate with size-matched individuals, a lack of preference, or
32 a preference for non-matching group mates is also commonly observed. We suggest that
33 the assortative response to predation risk may be mediated by body size, because larger-
34 bodied prey may be at greater risk of predation than smaller bodied prey when in a mixed
35 group due to their greater potential profitability. We test this idea by observing attacks by
36 three-spine sticklebacks *Gasterosteus aculeatus* on mixed groups of large and small *Daphnia*
37 *magna* prey. We find that smaller *Daphnia* are at greatest risk when they form the majority
38 of the group, while larger *Daphnia* are at the greatest predation risk when they form the
39 minority. Thus, we predict that both large and small prey should benefit by association with
40 large prey, generating a potential conflict over group membership that may lead to the
41 mixed phenotype groups we observe in nature.

42 **Key words:** oddity effect, confusion effect, assortment, shoaling, group living.

43 **Introduction**

44 Prey animals across taxa commonly live in groups to reduce predation risk (although other
45 factors such competition, foraging and sociality also contribute to the decision to live in
46 groups; Krause and Ruxton 2002). Choosing to be in a group dilutes individual risk once the
47 group has been detected by a predator (Foster and Treherne 1981), even when the
48 increased attack rate on larger groups is accounted for (Turner and Pitcher 1986). The
49 oddity effect describes how a phenotypically different ('odd') individual in a prey group is at
50 greater risk of predation relative to its group-mates, as it is more easily isolated for attack by
51 a predator (Milinski 1977; Ohguchi 1978; Landeau and Terborgh 1986; Theodorakis 1989).
52 When a group is phenotypically homogeneous, a visual predator suffers from 'predator
53 confusion', reducing targeting accuracy and therefore risk to each prey individual (Neill and
54 Cullen 1974; Landeau and Terborgh 1986; Krakauer 1995), a phenomenon observed in 64%
55 of studies across taxonomic groups (reviewed in Jeschke and Tollrian 2007). Together, the
56 confusion and oddity effects predict that animals should chose to group into homogenous
57 aggregations in which they experience reduced individual risk.

58 We see this predicted phenotypic uniformity in groups across many species: birds (Smith et
59 al. 2002; Brightsmith and Villalobos 2011; Sridhar et al. 2012), mammals (Meldrum and
60 Ruckstuhl 2009), amphibians (Breden et al. 1982) and fish (Peuhkuri 1997; Croft et al. 2009)
61 assort by body size. Fish in particular have been the focus of many experimental studies
62 providing examples of a preference for associating with similarly sized shoal-mates (banded
63 killifish, Krause and Godin 1994; two-spotted goby, Svensson et al. 2000; swordtails, Wong
64 and Rosenthal 2005; and Trinidadian guppies, Croft et al. 2003). However, variation in body
65 size within groups is still observed (fish shoals: Krause et al. 1998; Hoare et al. 2000; Croft et

66 al. 2009; bird flocks: Farine et al. 2012) and preferences for non-uniformity or the absence
67 of a preference for similarly-sized group-mates have been shown experimentally. In
68 particular, while large-bodied prey fish show preferences for similarly sized conspecifics,
69 small-bodied individuals show either no preference (Svensson et al. 2000; Rodgers et al.
70 2011) or prefer larger bodied conspecifics (Jones et al. 2010).

71 One explanation for observations of non-assortment by size is because the assortative
72 response to risk (through oddity) is mediated by body size: differently sized prey exhibit
73 different grouping preferences because their relative risks of being odd differ. Optimal
74 foraging theory predicts that predators should select the most profitable prey (e.g. Stephens
75 and Krebs 1986; Ydenberg et al. 2007), and in the absence of handling constraints
76 associated with larger size, larger-bodied individuals should represent a better meal
77 (Wetterer and Bishop 1985; Manicom and Schwarzkopf 2010). Planktivorous fish
78 preferentially prey on larger forms of zooplankton, which are widely observed to be
79 overrepresented in their diet relative to availability (e.g. Wetterer and Bishop 1985; Li et al
80 1985). This can be the result of either active choice for particular prey types or reduced
81 encounter rates for small prey due to their smaller size and lower detectability. In many
82 species, however, selectivity for larger-bodied prey is thought to be due to active choice (Li
83 et al 1985; Wetterer and Bishop 1985; Holzman and Genin 2005). Thus, odd prey individuals
84 in a group are likely to be at greater risk of predation when they are large relative to small
85 individuals in a similar oddity situation. In support of this, Peuhkuri (1997; 1998)
86 demonstrated that large fish are more risk averse, reducing foraging when odd in a group,
87 while small fish do not adjust their foraging behavior in response to oddity.

88 While much work explores the effect of size oddity from the perspective of the prey (i.e.
89 prey behavior and assortment decisions), less is known about how predators balance
90 potentially conflicting predation preferences, and what implications this might have for prey
91 assortment decisions. Classically, Theodorakis (1989) found that both large and small prey
92 individuals were more likely to be attacked by predators (and therefore at greater risk of
93 predation) relative to their group mates when they were odd, but this does not explain the
94 size-mediated shoaling preferences observed in some species (Svensson et al. 2000; Jones et
95 al. 2010; Rodgers et al. 2011). Here, we further explore the interaction between body size
96 and oddity from the predator perspective, asking how important oddity is to predators
97 when active preference for particular body sizes (more profitable prey) may influence their
98 choice.

99

100 **Methods**

101 Three-spine sticklebacks (*Gasterosteus aculeatus*) preying on *Daphnia* are a classic model
102 for studying confusion and oddity effects (e.g. Milinski 1977; Heller and Milinski 1979;
103 Milinski 1979; Ioannou et al. 2009; Rodgers et al. 2012). Sticklebacks were collected from
104 Saltfleet, Lincolnshire and housed for approximately 1 year in the laboratory before trials
105 began. Fish were housed in groups of 50-150 in large opaque containers at 15°C, on a
106 12:12h light:dark cycle, and fed daily on defrosted frozen bloodworm (from a commercial
107 aquarium supplier). Fish with body lengths between 35 and 45mm were used in the trials.
108 The prey used in the experiments were *Daphnia magna* of second (small, approximately
109 1mm) and fifth (large, approximately 2mm) instar sizes (Anderson 1932), purchased from a
110 pet supplies shop in Leeds, UK, collected for sale from ponds in West Yorkshire.

111 Experiments were based on the protocol detailed in Rodgers et al. (2012), which we
112 summarize here. Externally, at one end of a test tank (20 x 20 x 45cm), we positioned a 3x4
113 array of *Daphnia* confined individually into transparent 1cm cubes. At the opposite end of
114 the tank, a removable opaque barrier defined an acclimatization zone for the predator
115 (15cm from the tank end), leaving a 30cm attack zone between the barrier and prey. The
116 tank was covered externally on three sides (not including the end where the grid was
117 positioned) with black plastic to minimize disturbance to the fish. Three treatments with
118 different ratios of *Daphnia* sizes were used: 1:11 large:small (large-bodied minority), 6:6
119 large:small (equal ratios), and 11:1 large:small (small-bodied minority). In the 6:6 treatment
120 prey were arranged with large and small alternating. In the two other treatments, the oddly
121 sized individual was randomly positioned in the grid. We did not observe any size-related
122 differences in the activity of the *Daphnia* when confined in the array.

123 A test fish was introduced to the acclimatization zone, where it had no visual access to the
124 *Daphnia*. After six minutes acclimatization, the barrier was removed and the stickleback's
125 behavior was filmed using a digital video camera positioned behind the *Daphnia* grid, to
126 enable accurate recording of the prey individual first attacked. Once the first attack had
127 been made, the trial finished and the test fish was removed. Fish that had not made an
128 attack within 10 minutes of the barrier being removed were excluded from the experiment.
129 We recorded 16/30 successful attacks in the 1:11 (large:small) treatment, with 18/28 and
130 19/44 on the 6:6 and 11:1 treatments respectively. Of those that did not attack, 17 fish did
131 not emerge from the acclimatization zone, and 29 emerged but did not attack. Three other
132 trials were discarded due to failures in the recording. The water in the test tank was
133 changed between each trial to control for olfactory cues from previous test fish. No

134 olfactory cues from the *Daphnia* were available to the predators. Each fish was used only
135 once then returned to the stock tanks. *Daphnia* were returned to a size-matched pool for
136 reuse in subsequent trials.

137 All statistical analyses were carried out using R v. 2.10.1 (R Development Core Team 2007).
138 Exact binomial tests were used to test for prey body size preferences of sticklebacks.
139 Expected proportions of attacks on large individuals (assuming random predation) were
140 dependent on the distribution of body sizes within the group. In the 1:11 large:small
141 treatment, we would expect the predator to target the large individual in 1 in every 12
142 trials, giving an expected proportion of 0.083. Expected proportions for the 6:6 and 11:1
143 large:small treatments were 0.5 and 0.917 respectively. Estimates of 95% confidence
144 intervals for the observed proportions were calculated using the 'modified Wald' method
145 (Agresti and Coull 1998). For illustrative purposes, we then converted the attack data into
146 per capita predation risk for both large and small individuals. If a group consisted entirely of
147 size-matched *Daphnia* (N=12), the per capita risk for each individual would be 0.0833
148 (=1/12). We calculated the per capita risk for each group composition as the proportion of
149 trials in which an individual of the size under consideration was targeted, divided by the
150 number of individuals of that size in that trial (Rodgers et al. 2012).

151

152 **Results**

153 The number of times the predator targeted the large individual was significantly higher than
154 random expectation in the equal ratios treatment (6:6 large:small, large individual targeted
155 in 17/18 trials, $p < 0.001$). The large individual was also preferentially targeted in the large-

156 bodied minority trials (targeted in 4/16 trials, $p=0.039$) but the small individual was not
157 preferentially targeted where it was in the minority (large individual targeted in 19/19 trials,
158 $p = 0.399$, figure 1a). Thus, predators target large individuals more often than expected by
159 chance when grouped with a higher or equal number of small individuals. When a group of
160 predominantly large prey includes a single small individual, predators attack both large and
161 small prey at a rate consistent with random expectation (although the small individual was
162 never attacked in this treatment this is not statistically distinguishable from random attack).

163 We next calculated the per capita predation risk for large and small individuals for each of
164 the group compositions tested (figure 1b). Per capita risk for large individuals is greatest
165 when they form the minority of the group, and decreases as the number of large individuals
166 in the group increases. For small individuals, absolute per capita risk is always lower than for
167 large ones, and they are also at greatest per capita risk when there is a single large prey in
168 the group, and their risk decreases as the number of large individuals in the group increases
169 (figure 1b).

170

171 **Discussion**

172 Here we have shown that large prey are at consistently greater risk of attack than small prey
173 when in mixed groups, and that the risk of attack by a predator changes according to the
174 composition of the group. For large prey, risk is greatest when it is in the minority in the
175 group. For small prey, however, being odd in a group does not translate into increased risk –
176 here, all observed attacks were on large individuals and attack rates were consistent with
177 random attack. Small prey have greater per-capita risk when they form the majority of the

178 group, and lowest risk when make up a smaller proportion. This contrasts with the work of
179 Theodorakis (1989), who found that both large and small individuals were preferentially
180 targeted, and suggests that the oddity effect alone does not explain predation risk in our
181 system. Instead, our results may be consistent with a preference for more profitable, larger
182 bodied prey (Wetterer and Bishop 1985; Li et al. 1985; Holzman and Genin 2005; Stephens
183 and Krebs 1986; Ydenberg et al. 2007) and this may override any confusion and oddity
184 effects (which are known to operate in the stickleback-*Daphnia* system; Milinski 1977;
185 Heller and Milinski 1979; Milinski 1979; Ioannou et al. 2009; Rodgers et al. 2012).

186 If predation risk is greater on larger individuals, and confusion effects operate in a particular
187 system, we would expect that predation pressure should lead to social preferences that
188 minimize risk, that is, assortment with large individuals for both large- and small-bodied
189 prey, a pattern observed in fish by Jones et al. (2010) and supported by Peuhkuri (1997) and
190 Rodgers et al. (2011), but in contrast to Lachlan et al. (1998) who observed the opposite
191 pattern. Our results also contrast with those of Theodorakis (1989) who found that both
192 large and small odd prey were preferentially targeted by fish predators. If both large and
193 small individuals can reduce risk by assorting with large conspecifics, this generates a
194 potential conflict between the two. Large individuals would benefit by excluding or avoiding
195 small individuals from their groups, while small individuals benefit from joining those
196 groups. It may be costly to exclude group members, particularly in free-entry groups such
197 as fish shoals (Krause and Ruxton 2002) resulting in the mixed phenotype groups that we
198 observe in nature (Tosh et al. 2007; Rodgers et al. 2012). Equally, there may be reasons
199 other than predation why individuals do not appear to assort by phenotype. In shoaling fish,
200 familiarity (Griffiths 2003; Ward and Hart 2003), recent shared experience of particular

201 habitats, mediated by olfactory cues (Ward et al. 2005), foraging competition (Metcalf and
202 Thomson 1995), nutritional state (Morrell et al. 2007) and crypsis relative to the
203 environment (Rodgers et al. 2012) all contribute to social decision-making and may lead to
204 non-assortative behavior.

205 Optimal association behavior may also be constrained by other factors. In mobile species
206 with fission-fusion dynamics, moving between groups may be common (Croft et al 2003;
207 Couzin 2006; Sueur et al 2011) allowing preferences to be expressed, but in other species,
208 aggregations may simply occur where environmental conditions are favourable, rather than
209 through social choice, leading to non-assorted groups. In contrast, in groups with defined
210 social structures, such as dominance hierarchies, these structures may constrain the
211 freedom to select optimal associates. For example, in mixed-species flocks of tits (*Paridae*),
212 subdominants are limited in their interactions in a group, and do not flock with similarly
213 sized heterospecifics, as might be predicted (Farine et al 2012).

214 From the predator's perspective, selection of odd individuals would overcome the confusion
215 generated by groups of moving prey (Neill and Cullen 1974, Ohguchi 1978; Landeau and
216 Terborgh 1986, Krakauer 1995), carrying with it both short and longer-term fitness benefits
217 (as well as increased attack success, the reproductive performance of goshawks *Accipiter*
218 *gentilis* increases with their selectivity for rare colour morphs of feral pigeons *Columbia livia*,
219 for example (Rutz 2012)). However our experiments show that predators do not always
220 select these odd individuals. Given a choice of equal numbers of both prey types, predators
221 selected the large prey in almost every case, suggesting that large prey are preferred,
222 potentially because they are nutritionally more valuable. Observations suggest that for
223 larger sticklebacks, as used in our experiment, handling time even for larger *Daphnia* is likely

224 to be negligible (Gill and Hart 1994), and so larger *Daphnia* (which likely contain 2-4x the
225 energy content of small *Daphnia*; Nuutinen and Ranta 1986) are very likely to be more
226 profitable, reflecting the widespread observation that larger zooplankton are preferred by
227 planktivorous fish (Wetterer and Bishop 1985, Li et al. 1985) resulting from active choice for
228 more profitable prey (Wetterer and Bishop 1985; Li et al. 1985; Holzman and Genin 2005).
229 Predators are therefore trading off the potential benefits of a better meal against the
230 reduced chance of success resulting from confusion effects (Krakauer 1995; Ioannou et al.
231 2007). We assume that large odd prey may be preferentially targeted because predators
232 benefit from both avoiding confusion and capturing a valuable target, but when small prey
233 are odd, the benefits of using oddity to overcome confusion are not balanced by the lower
234 nutritional value of the target prey. However, the increased conspicuousness of large odd
235 prey is also likely to play a role in predator targeting decisions (Rodgers et al. 2012),
236 potentially reducing the effectiveness of dilution effects for these prey.

237 But why was the large prey individual not always attacked? Both optimal foraging for more
238 profitable prey and oddity effects would predict that the large individual should always be
239 preferred when in the minority, and although we found a significant preference, in 75% of
240 trials where the large individual was odd, a small individual was attacked. One explanation
241 may be that predators were unable to accurately distinguish between large and small
242 *Daphnia* in our experimental set up, but the targeting rates of large prey in the equal ratios
243 treatment suggest that this was not the case, and predators could accurately distinguish the
244 large individual. Secondly, sticklebacks may not have been able to simultaneously view all
245 prey, and were selecting from among a subset, reflecting a pattern of sequential rather than
246 simultaneous encounter of prey types (see Stephens and Krebs 1986), which would predict

247 that small individuals would be attacked if large ones were not available at that time.

248 Planktivorous fish are able to detect and attack prey within around 60° of either side of their
249 heads (e.g. Flore et al. 2000; Asaeda et al. 2002; Cobcroft and Pankhurst 2006) which would
250 suggest that they are able to view the complete prey grid from the majority of locations
251 within the tank (only by approaching closer than 2cm would the angle subtended by the
252 group exceed 120°), and our prey group was within the range of *Daphnia* configurations of
253 previous confusion and oddity papers (Heller and Milinski 1979; Milinski 1979; Ioannou et al.
254 2009; Rodgers et al. 2012). We did not quantify reaction distances in our experiment, but
255 Ioannou et al. (2011) indicate that sticklebacks will attack groups of prey from distances of
256 up to 40cm, with a mean reaction distance of approximately 180mm. Thus, it seems likely
257 that all prey could be viewed simultaneously, and attacks began when this was the case.

258 Finally, attacking swarming prey requires additional cognitive attention, which must be
259 redirected from other activities, particularly anti-predator vigilance (Milinski and Heller
260 1978), potentially placing the predators themselves at increased risk of predation. A
261 predator must therefore balance these conflicting demands in selecting which individual(s)
262 from an aggregation to attack, and a small individual may be targeted even when a larger
263 one is available. Our results demonstrate that oddity effects interact with other individual
264 and group characteristics, and these complex interactions are likely to shape prey choice
265 decisions for predators, as well social decisions and patterns of assortment by prey in both
266 laboratory trials and free-living populations.

267

268

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277

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406 **Figure Legends**

407 **Figure 1 a)** Proportion of trials resulting in predator attacks on large *Daphnia*, for each of the
408 three prey group compositions (ratio of large:small individuals for each treatment are as
409 follows: 1:11 large-bodied minority, 6:6 equal ratios, 11:1 small-bodied minority). Error bars
410 represent 95% confidence intervals calculated using the 'modified Wald' method described
411 in Agresti and Coull (1998). Dashed horizontal lines show the proportion expected by
412 random prey selection, according to the prey group composition. Significant differences
413 between observed proportions and random expectation are shown with an asterisk. **b)**
414 Estimated per capita predation risk for large (open circles, dashed line) and small (filled
415 circles, solid line) individuals as a function of the number of large individuals in the group,
416 calculated from the attack data shown in a). The horizontal dotted line represents the per-
417 capita risk to each individual in a uniform group of 12. Lines connecting points are for
418 illustration only.

