



Penry-Williams, I. L., Ioannou, C. C., & Taylor, M. I. (2018). The oddity effect drives prey choice but not necessarily attack time. *Ethology*, 124(7), 496-503. <https://doi.org/10.1111/eth.12754>

Peer reviewed version

Link to published version (if available):  
[10.1111/eth.12754](https://doi.org/10.1111/eth.12754)

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# 1 **The oddity effect drives prey choice but not necessarily attack time**

2 Running head: Choice and speed in the oddity effect

3

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## 11 **Acknowledgements**

12 We thank the University of East Anglia for the purchase of materials under the Ecology Research

13 Project Module (BIO-6022Y). CCI was supported by a NERC Independent Research Fellowship

14 NE/K009370/1.

15 **Abstract**

16 The tendency of predators to preferentially attack phenotypically odd prey in groups (the oddity  
17 effect) is a clear example of how predator cognition can impact behaviour and morphology in prey.  
18 Through targeting phenotypically odd prey, predators are thought to avoid the cognitive constraints  
19 that delay and limit the success of attacks on homogenous prey groups (the confusion effect). In  
20 addition to influencing which prey a predator will attack, the confusion and oddity effects would also  
21 predict that attacks on odd prey can occur more rapidly than attacking the majority prey type, as  
22 odd prey are more easily targeted, but this prediction has yet to be tested. Here, we used kerri tetra  
23 fish, *Inpaichthys kerri*, presented with mixed phenotypic groups of *Daphnia* dyed red or black to  
24 investigate whether odd prey in groups are preferentially attacked, and whether these attacks were  
25 faster than those on the majority prey type. In agreement with previous work, odd prey were  
26 targeted and attacked more often than expected from their frequency in the prey groups, regardless  
27 of whether the odd prey was red in a group of black prey, or vice versa. However, no difference was  
28 found in the time taken to attack odd versus majority prey items, contrary to our predictions. Our  
29 results suggest that the time taken to make an attack is determined by a wider range of factors or is  
30 subject to greater variance than the choice of which prey is selectively targeted in a group.

31

32 Keywords: Confusion effect, Oddity effect, Predation, Prey, Living in groups, Aggregation, Groups

33

34 **1. Introduction**

35 Predation is believed to be a major driver of group formation in prey species across a wide range of  
36 taxa (Ioannou, 2017). The tendency to aggregate into social groupings has been observed after both  
37 short (Hoare, Couzin, Godin, & Krause, 2004) and long term (Herbert-Read et al., 2017) exposure to  
38 an increased level of predation risk. Correspondingly, individuals in groups often experience higher  
39 survival rates compared to solitary individuals (Cresswell, 1994; Neill & Cullen, 1974; Santos et al.,  
40 2016; Treherne & Foster, 1982). A number of mechanisms act to reduce this per capita risk of  
41 predation, including risk dilution (Foster & Treherne, 1981; Turner & Pitcher, 1986), the group  
42 vigilance effect (Elgar, 1989; Treherne & Foster, 1981), the avoidance effect (Ioannou, Bartumeus,  
43 Krause, & Ruxton, 2011) and predator mobbing (Andersson & Wiklund, 1978).

44 Another widespread mechanism for reducing predation risk in prey groups is the confusion  
45 effect, whereby the greater number of targets present in a prey group causes difficulty in the  
46 predator's targeting and capture of a single individual (Ioannou, Tosh, Neville, & Krause, 2008;  
47 Krakauer, 1995). This is believed to be due to the sensory overload caused by many (often moving)  
48 targets within the visual field, an explanation that has been supported with neural network models  
49 (Krakauer, 1995; Tosh, Jackson, & Ruxton, 2006). The confusion effect has been documented in a  
50 wide range of taxa, including fish, bird, cephalopod and human predators (Cresswell, 1994; Landeau  
51 & Terborgh, 1986; Neill & Cullen, 1974; Schradin, 2000; Theodorakis, 1989; Tosh et al., 2006).

52 Although the formation of groups frequently reduces predation risk in prey, there are  
53 numerous mechanisms by which predators have adapted to minimise the effects of, or even to take  
54 advantage of, social behaviour in prey. Aggregation can, in some circumstances, increase risk for  
55 prey species hunted by predators with the ability to consume multiple prey in a single encounter  
56 (Turner & Pitcher, 1986), such as filter feeders (Rieucou, Fernö, Ioannou, & Handegard, 2015; Rode  
57 et al., 2013), or those that set traps for collectively foraging prey (Bauer, Federle, Seidel, Grafe, &  
58 Ioannou, 2015). In order to alleviate the confusion effect, predators can reduce vigilance for their  
59 own predators, allowing increased attention for prey capture but increasing their own risk of

60 predation (Milinski, 1984), target the edges of prey groups where prey may be less dense (Duffield &  
61 Ioannou, 2017), or selectively target phenotypically odd individuals within the prey group, which  
62 stand out from the 'background' of other, homogenous group members. This 'oddity effect' has  
63 been demonstrated among predatory fish targeting grouped prey of mixed colours (Landeau &  
64 Terborgh, 1986; Ohguchi, 1978), body size (Rodgers, Downing, & Morrell, 2015; Theodorakis, 1989)  
65 and species (Almany, Peacock, Syms, McCormick, & Jones, 2007). The strategy of initially focusing on  
66 conspicuously odd individuals in dense prey aggregations can be predicted from the optimal foraging  
67 theory (Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971), acting to maximise intake of  
68 energy per unit time while minimising the time required to obtain energy, which may be slowed by  
69 sensory confusion (Almany et al., 2007; Milinski & Heller, 1978). As a result, this frequency-  
70 dependent selection against rare phenotypes within groups is often used to explain non-random  
71 assortment in groups based on such phenotypic traits (Allan & Pitcher, 1986; Hoare, Krause,  
72 Peuhkuri, & Godin, 2000; McRobert & Bradner, 1998). Landeau & Terborgh (1986) demonstrated an  
73 increased attack rate and higher rate of capture when odd individuals were present in groups of  
74 silvery minnows (*Hybognathus nuchalis*) predated by largemouth bass (*Micropterus salmoides*)  
75 compared to homogeneous prey groups. Additionally, investigations on group predation have found  
76 shorter capture times for individual prey items than for grouped prey for both leopard geckos  
77 (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus*) (Schradin, 2000), as well as an  
78 increased capture/contact ratio for cephalopod and fish predators (Neill & Cullen, 1974).

79         Through focusing attacks on phenotypically odd individuals to minimise the confusion effect,  
80 the time required to target and successfully attack a prey item should be reduced, maximising  
81 predation efficiency (Landeau & Terborgh, 1986). Here, a system of artificially coloured *Daphnia*  
82 (Ohguchi, 1978) preyed upon by the predatory fish kerri tetra, *Inpaichthys kerri*, was used to test  
83 whether minority (odd) prey are selectively targeted by predators, as documented in previous  
84 experiments, and also the time taken to do so. Therefore, we tested whether the targeting of odd

85 prey can occur faster compared to attacks on majority prey phenotypes within the group, following  
86 the expected effects of confusion and oddity.

87

## 88 **2. Methods**

### 89 **2.1. Predatory fish**

90 In this study, an experimental predator-prey system was used, consisting of a kerri tetra predating  
91 upon mixed phenotypic groupings of *Daphnia magna*. Kerri tetra are native to South America  
92 (Aripuanã River and upper Madeira River basin, Mato Grosso State, Brazil) and are often kept in  
93 aquaria. Tetra maintain an omnivorous diet, consisting of detritus plant material as well as live foods  
94 including small crustaceans including *Artemia* and *Daphnia* spp. Thirty-five mixed-sex kerri tetra  
95 'Super Blue' were sourced from an aquarium wholesaler and were housed in 35L aquaria (31 x 31 x  
96 37cm) in groups of approximately nine individuals. A natural light cycle was present in the room with  
97 additional illumination of tanks from above by a 60-watt bulb. Water temperature was at 24°C and  
98 ad libitum feeding of Aqua One Brand tropical fish flakes and *Daphnia magna* was undertaken prior  
99 to the study period. During the predation trial period, fish were not fed for 17 hours prior to their  
100 trial.

101

### 102 **2.2. *Daphnia* prey**

103 Live *Daphnia magna* were obtained from Notcutts Garden Centres Ltd., Norwich, and housed in a  
104 large indoor container (47 x 61 x 61cm, ~175L) to establish a source population. *Daphnia* were fed  
105 on a mixture of live *Spirulina* sp., yeast (Fast Action Dried; The Pantry, Aldi) and crushed fish flakes  
106 (Aqua One Brand). *Daphnia* were kept under the optimum conditions as described by Jonczyk and  
107 Gilron (2005), of ~20°C and a cycle of 16 hours light to 8 hours dark.

108 To manipulate prey appearance, live *Daphnia* were dyed red or black using food colouring.  
109 Individuals were pipetted into 10ml beakers; each contained 2ml of tank water and 0.25ml of dye for  
110 a period of 30 minutes. The dyes (Sainsbury's Brand) ingredients consisted of: Red (Water, Colours:

111 Anthocyanins, Paprika Extract; Emulsifier: Polysorbate 80; Acidity Regulator: Citric Acid;  
112 Antioxidants: Alphanatocopherol, Ascorbyl Palmitate; Palm Oil, Preservative: Potassium Sorbate) and  
113 Black (Propylene Glycol, Water, Colour: Vegetable Carbon; Emulsifier: Acacia Gum; Preservative:  
114 Potassium Sorbate; Acidity Regulator: Citric Acid).

115

### 116 **2.3. Preference Tests**

117 All prey targeting experiments were carried out in tanks of the same dimensions as those housing  
118 the fish (i.e. 31 x 31 x 37cm, ~35L). The trial tank was positioned adjacent (without a gap) to another  
119 tank housing approximately nine kerri tetras from the population, to reduce acclimatisation time  
120 and stress caused to individuals due to the shoaling behaviour demonstrated in this family (Marcos  
121 Mirande, 2009). A single fish was introduced to the trial tank from the stock population, and after an  
122 acclimatisation period of 10 minutes the *Daphnia* group was poured in gently at the surface of the  
123 water. The time taken to make the first attack from the introduction of the prey was recorded from  
124 observations ~40cm from the tank, along with the colour of the prey attacked.

125 Preliminary testing was carried out to determine any preference in the predators for either  
126 colour of prey item. Ten kerri tetras were randomly selected from the population and individually  
127 presented with ten *Daphnia*, in an equal ratio of black and red (5:5). A second preliminary  
128 preference test was also carried out, with five *Daphnia* of a single colour presented in each trial for a  
129 random sample of 20 predators (n=10 per prey colour).

130

### 131 **2.4. Oddity Trials**

132 Trials testing for the oddity effect used the same protocol as detailed in 2.3, above, with ten *Daphnia*  
133 poured at the surface. Each predator (n=35) was subjected to the following treatments in a random  
134 order to reduce order effects over a series of weeks, with a minimum of 48 hours between an  
135 individual's trials: Red oddity (Red 1 : 9 Black), black oddity (Black 1 : 9 Red) and in equal ratio (Red 5  
136 : 5 Black).

137           The time taken from the prey being introduced to the first predation event (i.e. a prey was  
138 consumed) was again recorded, along with the colour of the attacked prey. If a second attack was  
139 made within three minutes of the first attack, the time taken (from the first attack) and the colour of  
140 the second attacked prey was also recorded. Trials were stopped after 3 minutes if there had been  
141 no attacks to ensure prey aggregation. Any fish from trials resulting in no predation were moved into  
142 a separate stock tank and the trial was repeated 24 hours later. Variation in extraneous variables  
143 was kept to a minimum by carrying out trials during the same hours each day (10am - 3pm) and  
144 keeping noise to a minimum. Filters were turned off in the trial tank during trials to avoid distraction  
145 and maintain the aggregation of *Daphnia* prey groups. Any remaining *Daphnia* were removed from  
146 the tank following the trial. All procedures were approved by the University of East Anglia Animal  
147 and Ethical Review Board, and were performed in accordance with national UK guidelines for the  
148 care and use of laboratory animals. The data supporting the findings of this study are available as  
149 Supplementary Information data.

150

## 151 **2.5. Statistical Analysis**

152 As the identities of individual fish could not be recorded between trials across treatments, each prey  
153 treatment was analysed separately to avoid pseudoreplication within the analysis, as each fish was  
154 used only once per prey treatment. Whether the fish showed a preference for a particular prey type  
155 (red prey in the equal ratio treatment or odd prey in the odd : majority prey treatments) was tested  
156 using binomial tests. The proportion of that prey type in the *Daphnia* group was used as the  
157 expected probability, assuming targeting by the predators was random. Due to the right skew in the  
158 distribution of the times taken to attack the prey, negative binomial General Linear Models (GLM)  
159 were used with a log link function to analyse the effect of prey type on the time taken to attack prey.  
160 The dispersion parameter was inspected to ensure it was approximately equal to 1 (0.5 to 2). All  
161 statistical tests were carried out in R version 3.3.3 (R Development Core Team, 2011).



162 In cases where there was no statistically significant effect of the targeted prey's colour on  
163 the time taken to make an attack, we carried out a randomisation-based power analysis to  
164 determine approximately how many trials would be required to achieve a statistically significant  
165 effect of target prey colour on the time taken. The observed data was resampled with replacement  
166  $N$  times, and the negative binomial GLMs as described above were repeated on this randomly  
167 sampled data.  $N$  is the simulated sample size, and we tested sample sizes from 40 to 1,000 trials in  
168 increments of 10 trials. At each value of  $N$ , 1,000 iterations were carried out and the P value  
169 associated with the effect of prey colour (from the negative binomial GLMs) at the 80% quantile was  
170 saved for each value of  $N$ . This 80% corresponds to a value of beta of 0.8, where beta is the test  
171 power to avoid incorrectly accepting the null hypothesis. Reported is the sample size ( $N$ ) where the P  
172 value at the 80% quantile is statistically significant at  $P < 0.05$ ; in other words, the sample size that is  
173 expected to be required to detect a statistically significant difference in 80% of repeats of the  
174 experiment.

175

### 176 **3. Results**

#### 177 **3.1. Prey colour preference**

178 In the first preliminary test with homogenous groups of 5 prey items, no evidence to support faster  
179 targeting based purely on colour alone was found. There was no significant difference in the time  
180 from introduction to first attack between the two colours (mean $\pm$ SD, Black: 13.17 $\pm$ 7.02s and Red:  
181 10.02 $\pm$ 6.55s, negative binomial GLM: deviance = 1.059,  $P = 0.30$ ). In the second preliminary test with  
182 a ratio of 5 red to 5 black *Daphnia* per trial, there was no evidence of selective predation based on  
183 colour. Each prey type was targeted and attacked in the first attack in exactly the same ratio that  
184 would be expected from random predation, with each colour being targeted in 50% of trials. There  
185 was also no significant difference in the time taken from prey introduction to attack between the  
186 prey colour conditions (mean $\pm$ SD, Black: 8.92 $\pm$ 5.29s and Red: 5.78 $\pm$ 1.91s, t-test:  $F=2.704$ ,  $df=8$ ,  
187  $p=0.247$ ).

188            In the main trials, the treatment with an equal ratio of red to black prey (5:5) showed that  
189 the proportion of red prey targeted in the first attack (15/35 trials) did not vary significantly from  
190 random targeting (Figure 1A, binomial test:  $P = 0.50$ ). In the 30 trials of this treatment where a  
191 second attack also took place, there was a tendency for the red prey to be attacked (20 trials),  
192 although this effect was not significantly different to that expected from chance alone (Figure 1B,  
193 binomial test:  $P = 0.099$ ; the expected probability of attacking red prey was calculated from the  
194 proportions of red to black prey remaining after the first attack in these trials), providing further  
195 evidence in support of no selective predation based on colour alone.

196

### 197 **3.2. Selection for prey oddity**

198 Of first attacks in the 35 trials, 11 trials resulted in the odd prey being targeted when the odd prey  
199 was red (1 red : 9 black), and the same number of trials resulted in the odd prey being targeted  
200 when the odd prey was black (1 black : 9 red). This proportion (31%) was significantly greater than  
201 that expected from random targeting (binomial test:  $P = 0.00042$ ), given the proportion of odd to  
202 majority prey (10%). There was thus evidence of an oddity effect in both treatments, seemingly  
203 unaffected by whether the odd prey item was red or black.

204            The oddity effect was also evident in the second attack made, excluding trials where the first  
205 attack resulted in the odd prey being consumed as there was no odd prey present in the second  
206 attack, thus changing the expected ratio from random predation (1 odd : 8 majority prey). In 8 out of  
207 24 trials the targeted prey was odd when it was red (binomial test:  $P = 0.0033$ ), and 8 out of 22 trials  
208 the targeted prey was odd when it was black (binomial test:  $P = 0.0018$ ). Overall, in each of the  
209 oddity treatments, 19 of the 35 trials resulted in an odd prey being consumed during either the first  
210 or second predation event, regardless of whether the odd prey was red or black (Figure 1).

211

### 212 **3.3. Time taken to attack prey**

213 No correlation was found between the time for the first and second attack within any treatment  
214 (Figure 2, Spearman's rank correlation: equal ratio treatment:  $r_s = 0.29$ ,  $P = 0.12$ ; red odd treatment:  
215  $r_s = -0.095$ ,  $P = 0.59$ ; black odd treatment:  $r_s = 0.12$ ,  $P = 0.51$ ). This indicates that the two latencies  
216 were likely driven by different factors; the first and second attacks of each treatment were therefore  
217 analysed separately. For the first attack by each fish, attacks on odd prey were not more or less rapid  
218 than attacks on majority prey (negative binomial GLM: red odd treatment: deviance = 0.20,  $P = 0.65$ ;  
219 black odd treatment: deviance = 1.11,  $P = 0.29$ ). The power analysis revealed sample sizes of >1,000  
220 and 230 trials for red odd and black odd treatments, respectively, would be required to reliably  
221 detect a statistically significant effect. Similarly, there was no difference in the time taken to make  
222 the second attack depending on whether the second attacked prey was odd or in the majority (red  
223 odd treatment: deviance = 0.00092,  $P = 0.98$ ; black odd treatment: deviance = 0.0034,  $P = 0.95$ ).  
224 Sample sizes of >1,000 were estimated to be required to detect statistically significant effects in both  
225 tests.

226 The time taken to make the second attack was also analysed as a function of whether the  
227 prey group still contained an odd prey (in trials where a majority prey was attacked first) or was  
228 homogeneous with only the majority prey type remaining (in trials where an odd prey was attacked  
229 first). In the red odd treatment, there was no indication that the presence of an odd prey in the  
230 second attack affected the time taken to make the attack (negative binomial GLM: deviance = 0.026,  
231  $P = 0.87$ ). However, the presence of a black odd prey made the time taken to attack the second prey  
232 significantly faster than if the prey group was homogeneously red (deviance = 4.81,  $P = 0.028$ ). This  
233 finding supports that of Landeau & Terborgh (1986) who also demonstrated that attacks on groups  
234 containing phenotypically odd prey were faster than those on homogeneous groups.

235 In the treatment with an equal ratio of red to black prey (5:5), there was no difference in the  
236 time taken to attack each prey type (Figure 3, negative binomial GLM: first attack: deviance = 0.13,  $P$   
237 = 0.72, second attack: deviance = 2.00,  $P = 0.16$ ), further supporting the finding that there was no  
238 preference for a certain prey colour. The power analysis determined >1,000 and 150 trials would be

239 required to detect a statistically significant effect of prey colour for first and second attacks,  
240 respectively.

241

#### 242 **4. Discussion**

243 In agreement with previous studies, mostly in fish (Almany et al., 2007; Landeau & Terborgh, 1986;  
244 Ohguchi, 1978; Rodgers et al., 2015; Theodorakis, 1989), we demonstrate a strong oddity effect in  
245 the kerri tetra predating artificially coloured *Daphnia* prey. There was no apparent preference for  
246 red or black coloured prey, but when the oddly coloured phenotype in a group was dominated by  
247 the other colour, both red and black coloured prey were attacked in a significantly greater  
248 proportion than expected from their frequency in the group. This frequency-dependent predation  
249 selects against rare phenotypes in prey groups, and provides a mechanism for prey groups to assort  
250 and be homogenous (Allan & Pitcher, 1986; Hoare et al., 2000; McRobert & Bradner, 1998).

251 The most widely accepted explanation for the oddity effect is that predators find it less  
252 cognitively demanding to attack prey that are visually different than others present in the group,  
253 where multiple prey in the visual field cause the confusion effect (Ioannou et al., 2008). Based on  
254 this cognitive explanation, we predicted that in addition to a preference for attacking phenotypically  
255 odd individuals, attacks on these prey should take less time because these prey are more quickly  
256 targeted, and should be easier to attack once a target prey is selected (compared to a non-odd,  
257 majority prey item). However, we found no evidence that attacks on odd prey were faster than  
258 those on majority prey items when attacks were made on groups with an odd individual. Attacks  
259 were faster, however, when the second attack was made on a group with the odd black prey  
260 remaining compared to a homogenous group of red prey, in which the odd prey had already been  
261 consumed (as previously demonstrated by Landeau & Terborgh, 1986). However, this was not  
262 consistently demonstrated, with no evidence presented when comparing groups containing odd red  
263 prey and homogeneously black groups in the second attack.

264           The time taken to complete cognitively demanding tasks is a widespread method used to  
265 measure the difficulty of a task in both cognitive psychology (Hockley, 1984; Wenger & Townsend,  
266 2000) and animal behaviour (Abbott & Sherratt, 2013; Passino & Seeley, 2006). It is thus surprising  
267 to find that a preference for odd prey exists but no evidence of any effect of the targeted prey type  
268 on the time taken in this study. Previous work, also using *Daphnia* as prey, has shown a reduced rate  
269 of attacks on larger groups (Ioannou et al., 2008; Milinski, 1977), suggesting that the confusion effect  
270 does indeed slow the speed at which attacks are made (although see Duffield & Ioannou, 2017, using  
271 virtual prey). Previous work using bluegill sunfish (*Lepomis macrochirus*) attacking a virtual prey  
272 population (Ioannou, Guttal, & Couzin, 2012) has shown a similar trend, where differences in the  
273 time taken to make an attack could not explain the predators' avoidance of polarised prey groups.  
274 Similarly, despite evolving the prey behaviours to create a population with fewer of the prey types  
275 preferentially selected in the initial population, there was no change in the time taken for the  
276 predators to attack prey.

277           There are a number of possible explanations for why the time taken to make an attack may  
278 not reflect prey phenotypes presented or selected for attack. One explanation is that the time taken  
279 to identify prey and make attacks tend to be highly variable (e.g. Figure 3), suggesting that inter-  
280 individual response varies greatly between trials, even when the prey group composition is the same  
281 within each treatment. Similar results were found in Neill & Cullen's (1974) study investigating  
282 cephalopod and fish hunting behaviour, noting that there was a great deal of variation in the time  
283 for predators to make initial contact with prey. This could be due to consistent behavioural  
284 differences between individual fish, i.e. animal 'personality'. Consistent variation in boldness (the  
285 response to perceived risk: Réale, Reader, Sol, McDougall, & Dingemanse, 2007) has been shown to  
286 correlate with the latency to approach and consume food (Ioannou & Dall, 2016). Mamuneas et al.  
287 (2014) showed bolder (typically male) three-spined sticklebacks (*Gasterosteus aculeatus*) to have  
288 faster information acquisition and decision making ability (determined from maze navigation to a  
289 food reward) than shyer conspecifics, but demonstrated no difference in decision-making accuracy.

290 Inter-individual variation can also be driven by shorter-term differences in hunger  
291 (McDonald, Rands, Hill, Elder, & Ioannou, 2016). Although such differences in motivation can often  
292 result in inter-trial variation that swamps any other measured effect such as the prey phenotype  
293 targeted (e.g. odd or majority). Our study showed no relationship between the time taken to attack  
294 the first prey from when the prey were introduced and the time taken to attack the second prey  
295 after the first prey was consumed (shown in Figure 2). This suggests that factors other than  
296 motivation drove the time taken to attack the first and second prey within the trials. The delay from  
297 the introduction of prey to the first attack may be primarily affected by the time needed to detect,  
298 recognise and decide to attack the prey, while the second attack should be predominantly  
299 influenced by the decision to attack another prey, given the level of perceived risk by the predator  
300 (Lima & Dill, 1990).

301 It is also possible that the prey group size was not large enough to create the required  
302 confusion to generate a difference between odd and majority prey in the time taken to make the  
303 attack (although the task did affect prey choice). The predation of *Daphnia* by aquatic predators has  
304 been prevalent in the literature on confusion and oddity (e.g. Landeau & Terborgh, 1986; Milinski,  
305 1977; Rodgers et al., 2015). Previous studies utilising a similar methodology have determined an  
306 increasing level of confusion with increasing group numbers. Landeau and Terborgh (1986)  
307 demonstrated an increased level of difficulty in prey capture in any group larger than one individual.  
308 The greatest level of difficulty was demonstrated in the larger groups of 8 and 15 individuals, with  
309 only 17% and 11% of the trials resulting in capture, respectively, and an increased number of attacks  
310 per kill. While tests into size oddity by Rodgers et al. (2015) utilised 12 individuals per group.  
311 Therefore, with reflective groups sizes present within our study (n=10 per trial), it can be assumed  
312 that the confusion effect was present.

313 Interestingly our results and those from other studies suggests that the time taken to make  
314 an attack may be more variable and hence less predictable than the choice of which prey to target.  
315 To the best of our knowledge, this issue has not been explicitly investigated in previous studies on

316 predator-prey interactions. It may suggest however that selection pressure from predator behaviour  
317 is asymmetric, with strong selection on prey phenotypes from predators' choice of which prey to  
318 attack, but relatively weak selection on predators being able to make faster attacks when attacking  
319 particular prey types. If this is the case, it brings into question why predators show such preferences,  
320 with a reduction in the time to initiate attacks perhaps being considered less important for predators  
321 than other factors such as vigilance for their own predators, which may apply a stronger selective  
322 pressure (e.g. Milinski, 1984).

323

324

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455

456 **Figure legends**

457

458 **Figure 1:** The frequency (total counts) of attacking each prey type (red or black) in the three different  
459 treatments (equal ratio, red odd prey and black odd prey) for the first (a) and second (b) attack in  
460 each trial. First attack: All treatments (n = 35 trials), Second attack: Equal ratio (n = 30 trials), red  
461 oddity (n = 24 trials) and black oddity (n = 22 trials). Trials are omitted from the second attack plot  
462 (and corresponding analysis) if the first attack was on the odd prey, as only majority prey type  
463 remained. Expected frequencies of attacking each prey colour, based on the frequency of each  
464 colour within the trials, is indicated by the horizontal dashed lines.

465

466 **Figure 2:** The correlation between the times (seconds) taken to attack the first and second prey in  
467 each trial. The data are arranged by treatment: equal ratio (a), red odd prey (b) and black odd prey  
468 (c). First attack: All treatments (n = 35 trials), Second attack: Equal ratio (n = 30 trials), red oddity (n =  
469 24 trials) and black oddity (n = 22 trials).

470

471 **Figure 3:** The time (seconds) taken to make the first (a) and second (b) attack in each treatment.  
472 Attacks are split within each treatment depending on prey type. First attack: All treatments (n = 35  
473 trials), Second attack: Equal ratio (n = 30 trials), red oddity (n = 34 trials) and black oddity (n = 33  
474 trials). Medians are illustrated by thick horizontal lines (black or white), the interquartile range (IQR)  
475 is enclosed within the boxes and the whiskers represent cases within  $1.5 \times$  IQR. The empty circles  
476 represent data points outside of the whiskers.