

1 This is a pre-copyedited, author-produced PDF of an article accepted for publication in
2 Oecologia following peer review. The final publication is available at Springer via
3 <http://dx.doi.org/10.1007/s00442-012-2473-y>

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5 **Mixed phenotype grouping: the interaction between oddity and crypsis**

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18 Author contributions: GMR, HK and LJM conceived and designed the experiments. GMR and
19 HK performed the experiments. GMR, HK and LJM analysed the data. GMR and LJM wrote
20 the manuscript.

21

22 **Abstract**

23 Aggregations of different-looking animals are frequently seen in nature, despite well-
24 documented selection pressures on individuals to maintain phenotypically homogenous
25 groups. Two well-known theories, the 'confusion effect' (reduced ability of a predator to
26 accurately target an individual in a group) and the 'oddity effect' (preferential targeting of
27 phenotypically distinct, 'odd', individuals) act together to predict the evolution of
28 behaviours in prey that lead to groups of animals that are homogeneous in appearance. In
29 contrast, a recently-proposed mechanism suggests that mixed groups could be maintained if
30 one species in a mixed group is more conspicuous against the habitat than the other, as
31 confusion effects generated by the conspicuous species impede predator targeting of the
32 cryptic species; thus, cryptic species benefit from association with conspicuous ones. We
33 test these contrasting predictions from the perspective of both predators and prey, and
34 show that cryptic individual *Daphnia* are at reduced risk of predation from three-spine
35 sticklebacks *Gasterosteus aculeatus* when in mixed phenotype groups, a risk that is reduced
36 further as the number of conspicuous individuals increases, supporting the hypothesis for
37 the evolution of mixed groups. In contrast, while the preference for associating with colour-
38 matched conspecifics by mollies (*Poecilia sphenops*) was reduced when they were cryptic,
39 we found no evidence for active association with conspicuous conspecifics. We conclude
40 that prey animals must balance the relative risks of oddity and conspicuousness in their
41 social decisions, and that this could potentially lead to the evolution of mixed phenotype
42 grouping as a response to predation risk alone.

43

44 **Keywords**

45 Mixed-species group, inter-specific grouping, oddity effect, confusion effect, predation

46 **Introduction**

47 Predators play a key role in ecological communities with well-established direct and indirect
48 effects on prey abundance and behaviour (Sih et al. 1985; Lima and Dill 1990; Schmitz et al.
49 2004). Theoretical understanding of predator-prey interactions is generally based on the
50 assumption of homogeneous, randomly distributed prey. For example, although functional
51 response models (predicting predation success in response to prey density) have been
52 developed that account for handling and digesting time of predators, such models assume
53 spatial and phenotypic homogeneity in prey (Jeschke et al. 2002). Other theoretical
54 approaches in ecology that include these assumptions include population dynamics
55 (Tenhumberg et al. 2009), group formation (Morrell et al. 2011) and biological self-
56 organisation (Couzin et al. 2005). The assumptions of prey homogeneity can be violated in
57 two important ways: 1) a violation of the assumption of spatial homogeneity via prey
58 aggregation and 2) a violation of the assumption of phenotypic homogeneity where prey
59 differ in appearance or behaviour. Including these factors into models of predator-prey
60 interactions can have significant effects on their predictions (Fryxell et al. 2007; Pettorelli et
61 al 2011).

62

63 Aggregation is a widespread phenomenon across the animal kingdom carrying with it
64 numerous benefits for individuals living in groups (Krause & Ruxton 2002). Perhaps the most
65 well recognised benefits relate to a reduction in predation risk through several mechanisms
66 including the dilution (Foster and Treherne 1981), encounter-dilution (Turner and Pitcher
67 1986), selfish herd (Hamilton 1971) and confusion (Miller 1922; Krakauer 1995) effects. The
68 confusion effect describes the inability of a predator to accurately target individual prey
69 items within a group of moving individuals, resulting in a reduced attack-to-kill ratio and

70 benefiting all individuals in the group (Krakauer 1995; Krause & Ruxton 2002). This effect is
71 predicted to be enhanced by increased synchrony of movement, larger group size, increased
72 density and phenotypic uniformity within a group. Where there is variation in phenotypes
73 in a group, predators can increase their success rate if they select prey that are
74 phenotypically distinct from the rest of the group. This is known as the oddity effect, and
75 results in preferential predation on 'odd'-looking individuals (Milinski 1977; Ohguchi 1978;
76 Krause & Ruxton 2002). Predator confusion and the oddity effect are complementary
77 mechanisms that select for behaviours in prey that should result in the formation of
78 phenotypically-assorted (homogeneous) groups. In systems where the predator hunts
79 visually prey groups should consist of individuals that are all very similar in appearance, and
80 evidence suggests that this is often the case. Shoaling fish have been well-studied in this
81 regard where assortment by species (Ward et al. 2002), body size (Krause et al. 1996),
82 kinship (Fitzgerald and Morrisette 1992), parasite load (Barber et al. 1998) and colour
83 (Rodgers et al. 2011) are observed.

84

85 However, there are many cases where there is considerable variation in phenotype within a
86 group. This is particularly clear in communities where mixed-species grouping occurs.
87 Mixed-species associations are frequently observed in birds (Moynihan 1968), mammals
88 (Smith et al. 2004), and fish (Barlow 1974). Although mixed-species grouping has been the
89 subject of scientific investigation for over 100 years (Morse 1977) we do not fully
90 understand the evolutionary causes and the mechanisms by which it is maintained in the
91 face of selection for phenotypic assortment in groups (via the confusion and oddity effects;
92 Tosh et al. 2007). A number of possible benefits of associating with individuals that are not
93 reliant on phenotype-matching (i.e. not linked to avoiding oddity) have been described

94 which may explain the occurrence of mixed-species and mixed-phenotype groups, including
95 increased foraging efficiency and predator detection for all group members (Stensland et al.
96 2003). Alternatively, the benefits of mixed species grouping may be asymmetric.
97 Experimental evidence suggests that a solitary individual may benefit from joining a group
98 of dissimilar con- or heterospecifics rather than remaining alone (Landeau and Terborgh
99 1986), may preferentially associate with more vulnerable individuals (Mathis and Chivers
100 2003) or with ones better able to detect predators (Diamond 1981; Krause and Ruxton
101 2002). This active choice by some group members means that the costs of oddity may be
102 greater for some individuals in a group than for others (Mathis and Chivers 2003; Rodgers et
103 al. 2011).

104

105 Using neural network models Tosh et al. (2007) proposed a predation-based mechanism to
106 explain mixed-species grouping. They introduce the idea that the interaction between
107 crypsis, confusion and oddity can lead to the evolution of mixed species grouping. Here
108 crypsis (or conspicuousness) refers to the animal's colouration relative to the habitat,
109 contrasting with oddity, which refers to colouration relative to the rest of the group. Tosh et
110 al. (2007) demonstrate theoretically that when groups consist of both cryptic and
111 conspicuous individuals, confusion effects generated by the conspicuous group members
112 are of particular benefit to cryptic individuals. They suggest that the anti-predator benefits
113 of crypsis (Ruxton et al. 2004; Caro 2005) may be enhanced by association with conspicuous
114 species as this worsens predator targeting of the cryptic individuals beyond that predicted
115 by either their crypsis alone or by the confusion effect, but there is no experimental
116 evidence to confirm this.

117

118 Both the mechanism presented in Tosh et al. (2007) and the standard confusion/oddity
119 framework described above predict asymmetric (phenotype dependent) predation risk on
120 prey, but these predictions differ dependent upon whether the prey animals are
121 conspicuous or cryptic relative to the habitat. Table 1 outlines the contrasting predictions
122 for the two possible mechanisms, which can be summarised as follows: Tosh et al. (2007)
123 predict that phenotypically distinct (odd) individuals should only be targeted if they are
124 conspicuous, and that individuals that are both cryptic against the habitat and odd relative
125 to the group are targeted less often than expected by chance. In contrast the
126 confusion/oddity framework predicts that odd individuals should always be targeted,
127 regardless of their crypsis against the habitat (table 1a). From the perspective of the prey
128 (table 1b), the confusion/oddity framework predicts that individuals should preferentially
129 associate with colour-matched group-mates (leading to the evolution of homogeneous
130 groups), while Tosh et al (2007) predict that this should only be true for individuals that are
131 conspicuous against the habitat; cryptic individuals should choose to associate with
132 conspicuous (and therefore phenotypically different from themselves) rather than colour-
133 matched group-mates (table 1b), potentially leading to the evolution of mixed grouping.

134

135 We examine these hypotheses from the perspective of both predators (three-spined
136 sticklebacks *Gasterosteus aculeatus* attacking individuals in groups of colour dyed *Daphnia*)
137 and prey (black and white morphs of the molly *Poecilia sphenops* choosing to shoal with
138 matched or dissimilarly coloured shoal mates). By exploring both the predator and prey
139 perspectives our work will more fully explore the various pressures that shape predator-
140 prey interactions and lead to the evolution of the mixed-phenotype groups of prey animals
141 we see in nature. Our aim is to explore patterns that apply broadly to groups of prey

142 animals by using two different model systems to address the prey and predator angles of
143 this phenomenon. Each system was selected to be the most suitable available to us for
144 those particular experiments. This integrated approach allows a greater understanding of
145 the mechanisms involved in the evolution and maintenance of mixed-phenotype
146 aggregations.

147

148 **Materials and methods**

149 Experiment 1: Prey targeting by sticklebacks

150 Approximately 150 three-spine sticklebacks (*Gasterosteus aculeatus*) were collected from
151 Saltfleet, Lincolnshire in October 2009 and housed in large opaque containers at a
152 temperature of 15°C under a 12:12hr light:dark cycle. Fish were fed daily on frozen
153 bloodworm. Live *Daphnia magna* were obtained from a local pet shop. To obtain cryptic and
154 conspicuous prey, live *Daphnia* were dyed red or blue by placing large numbers of individuals
155 in 1000ml of water containing 5ml of either red or blue food dye (Dr. Oetker brand) for a
156 period of 7-10 days. Red and blue were chosen as both colours are present in stickleback
157 breeding colouration and there is evidence that these fish rank shades of these colours in a
158 similar way to humans (Rowe et al. 2006). Blue food colouring contained: water, colour
159 (brilliant blue), acidity regulator (citric acid) and preservative (potassium sorbate). Red food
160 colouring contained: colours (beetroot red, paprika extract), mylose syrup, emulsifier
161 (polysorbate 80), glycerine, water, antioxidants (disodium EDTA, sodium ascorbate) and
162 preservative (potassium sorbate).

163

164 Prey targeting experiments were carried out in a small aquarium (20x20x50cm). The tank
165 was divided into two sections: a horizontal wire positioned on the base of the tank marked

166 out the third of the tank furthest from the prey (the predator zone). At the opposite end of
167 the tank, a removable grid of 1cm transparent cubes positioned on the external wall of the
168 tank held the *Daphnia*. Twelve cubes were arranged in a 3x4 grid and placed centrally on the
169 outside of the tank end. Each cube contained coloured water (red or blue at 3ml/litre) and a
170 single *Daphnia*. The concentration of food dye in the cubes was slightly lower than that used
171 to dye the *Daphnia* to ensure that individual *Daphnia* were visible to the observer, while
172 enhancing crypsis where water and *Daphnia* were the same colour. The grid design ensured
173 that the 12 *Daphnia* prey were unable to aggregate, as predators are known to target
174 denser areas of groups (Ioannou et al. 2009). Inside the tank, flush with the wall containing
175 the prey, we positioned a removable opaque barrier to conceal the prey from the predator
176 during an acclimatisation period. The tank was surrounded by opaque screens to minimise
177 disturbance to the fish. Trials were recorded using a digital video camera (Panasonic NV-
178 GS280) placed behind the grid containing the prey, such that the predator was viewed
179 through the prey grid and the prey item targeted could be easily identified.

180

181 Each section of the grid contained dyed water and a single *Daphnia*. We considered 4
182 primary treatments:

- 183 1) Control: 12 undyed *Daphnia* in either red or blue water, to test for any innate
184 preference for red or blue (20 trials)
- 185 2) 6:6 treatment (even treatment): equal numbers of red and blue dyed *Daphnia* (40
186 trials)
- 187 3) 1:11 treatment (cryptic minority): a single cryptic individual and 11 conspicuous
188 individuals (40 trials)

189 4) 11:1 treatment (cryptic majority): 11 cryptic individuals and a single conspicuous
190 individual (40 trials)

191 The specific predictions for each experiment in relation to our hypotheses (table 1a) can be
192 found in table 2a. For treatment 1 (control), 6 cells contained red-dyed water and 6 cells
193 contained blue-dyed water arranged such that the immediate neighbours of any cell were of
194 the opposite colour. Treatments 2-4 had a single colour background (i.e. all cells contained
195 red or blue water) and were repeated with both red and blue backgrounds (N=20 for each
196 colour background). Cryptic individuals were those that were the same colour as the
197 background, conspicuous ones were those that were the opposite colour. In treatment 2,
198 individual *Daphnia* were positioned so that the direct neighbours of each individual was of
199 the opposite colour to avoid any clustering of particular phenotypes. In treatments 3 and 4
200 the position of the odd individual was changed systematically between trials to control for
201 any centre or edge preferences in the attacking predator. Once filled, the prey grid was
202 positioned externally on the tank. *Daphnia* were taken from pools of similarly coloured
203 individuals to which they were returned between trials. Pools contained approximately 50
204 *Daphnia* of 3mm +/- 0.25mm.

205

206 An individual stickleback was placed into the predator zone in the test tank and given 2
207 minutes to acclimatise. After the acclimatisation period we raised the opaque barrier
208 concealing the prey, using a pulley to reduce disturbance to the fish. If the stickleback was
209 not in the predator zone, the barrier was raised once the fish returned there. We recorded
210 the colour and crypsis of the first prey individual attacked by the fish, using the video
211 recordings. Fish that did not enter the predator zone within 10 minutes were removed. Fish
212 that did not attack the prey within 15 minutes of the barrier being removed were excluded

213 from the analysis. Final sample sizes were N = 16 (control; 4 fish did not attack), N = 40
214 (even treatment; all fish attacked), N = 38 (cryptic minority; 2 fish did not attack) and N = 38
215 (cryptic majority; 2 fish did not attack)). Fish were not reused and the water in the test tank
216 was changed between trials.

217

218 Experiment 2: Shoal choice in mollies

219 Mollies (*Poecilia sphenops*) occur in two distinct colour morphs (black and white) but are
220 phenotypically similar in other aspects of morphology. 70 black and 70 white individuals
221 were obtained from Neil Hardy Aquatica in December 2009 and maintained in small aquaria
222 (200x200x500mm) with a gravel substrate, small filter and artificial plant, at a salinity of
223 1.004ppt at 26°C and on a 12:12hr light:dark cycle. Each tank contained 10-12 individuals,
224 with equal numbers of each morph. On arrival in the laboratory, fish were randomly
225 assigned to be either test fish (approximately 60 individuals of each colour) or in the initial
226 pool of stimulus fish (10 individuals of each colour; see also below). Test and stimulus fish
227 were held separately, and within a category (test/stimulus) individuals were moved
228 between tanks twice a week for the duration of the experiment to reduce any confounding
229 effects of familiarity (Griffiths 1997; Griffiths and Magurran 1997a). Fish were housed in
230 these conditions for approximately 6 weeks until commencement of the trials, and were fed
231 commercial fish food twice daily.

232

233 Shoal choice experiments were carried out in 2 test aquaria. Each tank (200x500x170mm)
234 was divided into 3 sections using transparent glass to ensure visual but not olfactory
235 communication to reduce confounding effects of habitat similarity (Webster et al. 2007).
236 The two end compartments (stimulus compartments) measured 150x200mm and contained

237 the stimulus fish. Three of the external surfaces of each tank were covered with opaque
238 adhesive film, leaving only the side facing the observer transparent. One tank was covered
239 with white film, the other with black film. A 20mm layer of white or black gravel respectively
240 was also added. By performing the trial in either a black tank or a white one, each of the fish
241 morphs could be made cryptic or conspicuous against the background. Preference zones
242 were marked on the observer side of the central compartment at a distance of 82mm (twice
243 the mean body length of 20 fish) from the stimulus compartments. A test fish was
244 considered to be shoaling with a stimulus shoal when more than 50% of its body was in the
245 preference zone, giving a conservative estimate of shoaling tendency.

246

247 Only fish with a standard body length of between 38 and 46mm were used in the
248 experiment, and there was no significant difference in body size between black and white
249 fish ($F_{1,106} = 1.845$, $p = 0.177$). 4 black individuals were taken from the pool of stimulus fish
250 and placed in one stimulus compartment and 4 white individuals were placed in the other
251 stimulus compartment. A test fish was placed in the central compartment and allowed 10
252 minutes to acclimatise before preferences were recorded. We recorded the cumulative time
253 (in seconds) that the fish spent in each of the preference zones over the course of a 10-
254 minute trial. All 4 combinations of test fish colour and crypsis (background colour) were
255 investigated. The specific predictions for each combination in relation to our hypotheses are
256 outlined in table 2b. The stimulus compartment containing the black fish was alternated
257 between experiments to control for side bias. Once fish had been used as test fish they were
258 added to the pool of stimulus fish, but stimulus fish were never used as test fish. 30 trials
259 were conducted where the test fish was white and cryptic (i.e. a white fish on a white

260 background), 30 on white conspicuous fish, 28 on black cryptic fish and 26 on black
261 conspicuous.

262

263 Statistical analysis

264 Binomial tests were used to investigate the prey selection preference of sticklebacks.

265 Expected proportions are given in the relevant section below. For the shoaling experiment

266 we used a generalised linear model with quasi-binomial error distribution (to account for

267 overdispersion in the data) and a logistic link function to investigate the proportion of time

268 spent shoaling with the colour-matched shoal as a function of test fish colour and test fish

269 crypsis. The interaction between test fish colour and test fish crypsis was not significant and

270 so was removed to give the minimum adequate model. To investigate whether the shoaling

271 preference exhibited by each colour/crypsis combination differed significantly from a

272 random preference, we tested (preference for matched shoal)-(preference for unmatched

273 shoal) against a null expectation of zero using one-sample t-tests. Data were arcsin square

274 root transformed to meet the assumptions of normality. Correction for multiple tests was

275 carried out using False Discovery Rate control (Benjamini & Hochberg 1995). Both original

276 and adjusted (in italics) p-values are shown.

277

278 **Results**

279 Experiment 1: Prey targeting in sticklebacks

280 There was no colour preference for undyed *Daphnia* on red or blue backgrounds (binomial

281 test, $P = 1.00$ ($P = 1.00$)) and no difference between colour treatments (i.e. whether the trials

282 were performed on a red or blue background) for any of the ratios tested (binomial tests

283 1:11 $P=1.00$ ($P=1.00$); 6:6, $P = 0.44$ ($P=0.572$); 11:1, $P = 0.45$ ($P=0.532$). Therefore all data
284 have been pooled and analysed on the basis of cryptic/conspicuous alone.

285

286 The number of times the cryptic individual was targeted by the predator was significantly
287 lower than random expectation in the 6:6 (cryptic individual targeted in 7/40 trials, against a
288 random expectation of 0.5, $P<0.001$ ($P<0.001$)) and 11:1 experiments (cryptic individual
289 targeted in 26/38 trials, against an expectation of 0.9167 (11/12), $P<0.001$ ($P<0.001$)), but
290 not in the 1:11 experiment (cryptic individual targeted in 1/38 trials, against a random
291 expectation of 0.0833 (1/12), $P = 0.370$ ($p=0.535$), figure 1a). Thus, cryptic individuals are
292 targeted less often than expected by chance when grouped with a lower or equal number of
293 conspicuous individuals. When a single cryptic individual is in a group with predominantly
294 conspicuous individuals, it is attacked at a rate consistent with random attack. Table 2a
295 summarises these results in relation to the specific predictions of both the Tosh and oddity
296 mechanisms.

297

298 We next investigated the per capita predation risk for cryptic and conspicuous individuals
299 for each of the group compositions tested (figure 1b). In a group consisting entirely of one
300 type or the other ($N = 12$ in figure 1b), the per capita risk for each individual is 0.0833
301 ($=1/12$). We calculated the per capita risk for each composition as the proportion of trials in
302 which an individual of the type under consideration was targeted divided by the number of
303 individuals of that type in that trial. Thus, for the 1:11 treatment, per capita risk for cryptic
304 individuals was calculated as $(1/38)/1$ (one cryptic target in 38 trials, with 1 cryptic individual
305 in the trial) and risk for conspicuous individuals as $(37/38)/11$ (37 conspicuous targets in 38
306 trials divided by the 11 cryptic individuals in each trial). Per capita risk for cryptic individuals

307 in greatest when in a uniform group and decreases as the number of conspicuous
308 individuals in the group increases. In contrast, per capital risk for conspicuous individuals is
309 lowest in a uniform group and increases with the number of cryptic group-mates (figure 1b)

310

311 Experiment 2: Shoal choice in mollies

312 Fish colour and fish crypsis had significant independent effects on the proportion of time
313 spent shoaling with the colour-matched shoal (quasi-binomial GLM, colour: $t = 2.861$, $df =$
314 106 , $P = 0.0038$ ($P = 0.0083$), crypsis: $t = -2.320$, $df = 105$, $P = 0.0197$ ($P = 0.0366$), non-
315 significant interaction between crypsis and colour removed from the model). Conspicuous
316 fish showed a stronger preference for the colour-matched shoal than cryptic fish and white
317 fish showed a stronger preference than black fish (figure 2). Preference for the colour
318 matched shoal differed significantly from random choice for white conspicuous fish ($t =$
319 7.4733 , $df = 28$, $P < 0.001$ ($P < 0.001$)), black conspicuous fish ($t = 4.3172$, $df = 25$, $P < 0.001$
320 ($P < 0.001$)), and white cryptic fish ($t = 6.3823$, $df. = 26$, $P < 0.001$ ($P < 0.001$)) but not for
321 black cryptic fish ($t = 1.2425$, $df = 25$, $P = 0.2256$ ($P=0.3666$)). Table 2b summarises these
322 results. There was no difference in overall shoaling tendency between cryptic and
323 conspicuous test fish (t-test, $t = 0.201$, $P = 0.841$).

324

325 **Discussion**

326 The two theoretical frameworks for the evolution of mixed phenotype groups that we have
327 investigated predict different suites of predator targeting of prey, prey risk and prey group
328 choice behaviour. The confusion/oddity framework (preferential predation on
329 phenotypically distinct, odd individuals in a group) selects against the evolution of mixed
330 grouping, but mixed aggregations are selected for by the mechanism proposed in Tosh et al

331 (2007). Here, grouping is driven primarily by one partner in a species/phenotype pair, as the
332 confusion effect generated by a species that is conspicuous against the habitat impedes
333 predator targeting of a more cryptic one. Our results (summarised in table 2) lend support
334 to both mechanisms and suggest that animals may face conflicting selection pressures
335 within the context of phenotypic similarity in group assortment. We show that individuals
336 that are cryptic against the habitat are at reduced risk of predation when in mixed
337 phenotype groups and this risk is reduced further as the number of individuals that are
338 conspicuous against the habitat increases, providing support for Tosh's model. In contrast,
339 and in support of the confusion/oddity framework, we did not find any evidence that cryptic
340 fish preferentially chose to associate with conspicuous ones. Instead, in the majority of our
341 tests, fish associated with phenotypically similar individuals, avoiding being odd in the
342 group, but this preference was reduced when individuals were cryptic against the habitat.
343
344 We provide evidence for asymmetric costs to individuals in mixed groups: in our prey
345 targeting experiment, cryptic individuals benefitted by association with conspicuous ones
346 while conspicuous ones were put at increased risk by the presence of cryptic individuals
347 (figure 1b). As Tosh et al (2007) suggest, mixed grouping could therefore be maintained by
348 the association preferences of cryptic individuals (or those that are simply at lower risk of
349 predation). There are many examples of associations in mixed species groups being
350 maintained by one party: associations between fathead minnows (*Pimephales promelas*)
351 and brook sticklebacks (*Culaea inconstans*) are maintained by the less vulnerable
352 sticklebacks (Mathis and Chivers 2003), and cowtail stingrays (*Pastinachus sephen*) maintain
353 the association with whiprays (*Himantura uarnak*) because of the whiprays faster
354 antipredator response (Semeniuk and Dill 2006). Similar patterns are seen within species: in

355 European minnows (*Phoxinus phoxinus*), good foraging competitors choose to actively
356 associate with poor competitors but not vice versa (Metcalf and Thomson 1995). The
357 results of our shoal choice experiment, however, do not support the idea that cryptic
358 individuals preferentially associate with conspicuous ones; instead suggesting that crypsis
359 allows more flexibility in shoaling decisions.

360

361 The context and visual background in which prey animals are being observed is important
362 when considering crypsis (Endler 1990). When a predator is at some distance from prey,
363 crypsis against the background (e.g. vegetation or substrate) is likely to be of primary
364 importance in concealing a prey group. As predators must identify and then select a group
365 to attack, this would select for all group members to match their background (Ruxton et al.
366 2004) producing phenotypically uniform groups. At closer range, once the group has been
367 detected, predator focus switches to identifying and targeting an individual within a group.
368 Relative risks within the group become important and behaviours that reduce an individual's
369 risk relative to his group mates are selected for (Morrell et al. 2011). Our findings from the
370 shoal choice experiments may represent a trade-off between reducing risk pre- and post-
371 detection.

372

373 Conflicting selection pressures in social decision-making are not uncommon. The decision to
374 join one group over another depends on many more factors than phenotypic appearance
375 alone. Group size (Krakauer 1995), nutritional state (Krause 1993a; Morrell et al. 2007),
376 parasitism (Barber and Huntingford 1995), predation risk (Hoare et al. 2004), familiarity
377 (Griffiths and Magurran 1997b) and recent experience (Webster et al. 2007) all interact to
378 shape shoaling decisions. Membership of a larger group, for example, may benefit

379 individuals through the dilution effect (Foster and Treherne 1981; Turner and Pitcher 1986),
380 but this must be traded off against the relative ease of detection of larger groups by
381 predators (Ioannou and Krause 2008; Morrell and James 2008) and the importance of
382 familiarity in shoal choice decisions decreases as group size increases (Griffiths and
383 Magurran 1997b).

384

385 There may be other pressures selecting for phenotypic uniformity in groups, including
386 activity synchrony (Conradt and Roper 2000) and foraging efficiency (Ranta et al. 1994).
387 Conradt and Roper (2001) propose that uniformity is maintained by the higher cost of
388 performing synchronous activities for mixed groups, while Ranta et al. (1994) suggest that
389 foraging success should be higher in uniform groups, particularly for small individuals. In
390 addition, there may be social pressure to maintain uniform groups. One can imagine that
391 high-risk (here, conspicuous) individuals would benefit by 'evicting' low-risk (cryptic) ones
392 from their group. There is little evidence that individuals can control group membership in
393 'free entry' groups such as fish shoals (Krause and Ruxton 2002), but where groups are
394 stable and social hierarchies exist, entry to a group may be restricted (Stephens et al. 2005;
395 Jordan et al 2010). Even in free entry groups, less favoured group members may be
396 restricted to the periphery (Krause and Godin 1994; Barber et al. 2000) where predation risk
397 is higher (Hamilton 1971; Krause 1993b). Alternatively, high-risk individuals made vulnerable
398 by new low-risk members could choose to leave the shoal when the risks associated with
399 leaving are outweighed by the risks imposed by non-uniformity of the group.

400

401 It is possible that the animals used in our experiments did not perceive colour differences in
402 the same way as the human observers. However, sticklebacks are known to rank red and

403 blue in a similar way to humans (Rowe et al. 2006) and so individuals that appeared cryptic
404 and conspicuous to us are likely to appear similarly to the fish. Little is known about colour
405 perception in mollies, but previous work suggests a perception of black and white that is
406 consistent with ours (Bradner and McRobert 2001). We found that black fish generally
407 showed a weaker preference for the colour-matched shoal, but this reflects previous
408 findings (McRobert and Bradner 1998) and may result from a reduced perception of risk by
409 black fish (perhaps due to an increased perception of crypsis or safety) or selected
410 differences in shoaling preferences resulting from domestication.

411

412 We acknowledge the limitations of using captive-bred, domestic animals in some of our
413 experiments. Captive-bred animals have not been subject to the selection pressures which
414 their wild counterparts experience, and in the case of the mollies, the captive breeding and
415 selection regimes necessary to produce distinct black and white morphs likely means that
416 black fish are more closely related to other black fish than to white fish and vice-versa. This
417 potentially confounds any effect of colour with that of kinship, by which fish are also known
418 to assort (Krause and Ruxton 2002; Ward & Hart 2003). However, while our finding that fish
419 preferentially associate with similarly coloured individuals could be explained as a
420 preference for associating with more closely related individuals, the key finding is that
421 preferences change according to the conspicuousness of the potential shoal-mates. This
422 suggests that there are other colour-associated factors at play in determining shoal choice in
423 mollies. We suggest that our results demonstrate association patterns based on colour,
424 oddity and crypsis that go beyond the confounding effects of relatedness resulting from
425 domestication.

426

427 We chose to use black and white mollies because of their very similar morphologies,
428 distinctly different colours, their history of use in similar experiments and their documented
429 ability to discriminate between different colour morphs and associate on the basis of colour,
430 with variation in preference strength depending on the characteristics of the shoal and
431 environment (McRobert and Bradner 1998, Bradner and McRobert 2001a, b). These studies
432 are often cited as the classic examples showing that fish assort by colour and their authors
433 have suggested that shoal-choice abilities and preferences for particular phenotypes in
434 shoal-mates is so important to group living fishes it is likely to be highly conserved and still
435 present even in domestic morphs (Bradner and McRobert 2001a). Domestic morphs of
436 group-living fishes have been successfully used to demonstrate and explain patterns of
437 association and social learning seen in wild animals (Laland and Williams 1998; Reader and
438 Laland 2000; Engeszer et al. 2004; Morrell et al. 2007; Gomez-Laplaza 2009). Examples of
439 the colour assortment seen here in domestic fish reflect those seen in wild fishes (Crook
440 1999; Rodgers et al. 2010).

441

442 The oddity effect is predicted to operate most strongly in small, highly asymmetric groups
443 (Krause and Ruxton 2002), the conditions tested here. We also investigate oddity in two
444 very different taxonomic groups on which different selection pressures may operate,
445 resulting in different patterns. Further work is needed to elucidate the conditions under
446 which oddity effects shape animal aggregations in nature, and the effects of interactions
447 between oddity and other selection pressures (including crypsis) across species. The
448 majority of work investigating the oddity effect in relation to colour has used either
449 domesticated morphs (McRobert and Bradner 1998; Bradner and McRobert 2001; Gomez-
450 Laplaza 2009) or artificially dyed prey (Ohguchi 1978; Landeau and Terborgh 1986; Thomas

451 et al. 2010) and future work should also consider natural variation in prey colouration, on
452 which predators must base their choice of target and prey base their social decisions.

453

454 When confusion effects associated with aggregation are incorporated into functional
455 response models, they significantly alter predicted rates of consumption relative to prey
456 density (Jeschke and Tollrian 2005). Similarly, considering groups as a functional unit in
457 models of predator-prey dynamics fundamentally alters predicted food intake rates and
458 stabilises interactions (Fryxell et al. 2007). Thus, the processes and patterns involved in the
459 formation and maintenance of animal groups are a key component in predator-prey
460 interactions and the structure of animal communities. Variation between individuals is also
461 thought to influence predator-prey dynamics (Pettorelli et al. 2001): understanding how
462 predators select from among available prey types may have implications for concepts
463 ranging from the evolution of aggregation (Couzin et al. 2005; Morrell et al. 2011) and
464 aposematic colouration (Ruxton et al. 2004) to understanding species diversity (for example,
465 if predators preferentially consume rare prey species resulting in local extinctions; Almany
466 et al. 2007). Here we show that prey animals must balance the relative risks of oddity and
467 conspicuousness in their group choices and suggest that the complex selection pressures
468 enforced by predation can lead to the evolution of mixed-phenotype grouping through
469 response to these risks alone.

470

471 **Acknowledgements**

472 We thank Colin Tosh for invaluable discussions in the early stages of this project, Scott
473 Fawcett and the CBS staff practical advice and fish husbandry services, Ása Johannesen for
474 help with collection of fish, and Jennifer Kelley, Katherine Jones, Scott Peacor and two

475 anonymous referees for insightful comments on the manuscript. This work was funded
476 through a Biotechnology and Biological Sciences Research Council Doctoral Training Grant to
477 GMR, Natural Environment Research Council Postdoctoral Fellowship (NE/D008921/1) to
478 LJM, and the University of Leeds (HK).

479

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676

677 **Tables**

678 **Table 1:** Contrasting predictions of the confusion/oddity framework and the mechanism
 679 proposed by Tosh et al. (2007), for situations where **a)** predators are selecting from among
 680 available prey types, which may be phenotypically distinct from the majority of the group
 681 ('odd/rare' in the table) and may also be cryptic or conspicuous against the habitat; and **b)**
 682 when prey are selecting group-mates with whom to associate.

Prey phenotype	Tosh et al. (2007) predict:	Confusion/oddity
		framework predicts:

a) Predators selecting from among available prey types

A prey animal which is:	Should be targeted:	
Odd/rare relative to the rest of the group	When conspicuous against the habitat	Always targeted
Cryptic against the habitat	Less often than expected by chance when grouped with conspicuous individuals	When odd/rare
Conspicuous against the habitat	Always targeted	When odd/rare

b) Association preferences of prey

An individual which is:	Should associate with a group which is:	
Cryptic against the habitat	Conspicuous (and therefore of a different	Cryptic (phenotypically matched to the choosing

	phenotype)	individual)
Conspicuous against	Conspicuous (matched)	Conspicuous (matched)
the habitat		

683

684

685

686 **Table 2:** A summary of our hypotheses relating to the predictions of the Tosh et al. (2007)

687 model and the confusion/oddity framework, together with the qualitative results of the

688 prey targeting (a) and shoal choice (b) experiments, indicating the model supported.

a) Prey targeting experiment

Cryptic: conspicuous ratio	Prediction for cryptic individuals Tosh et al. (2007)	Confusion/ oddity	Conflict between predictions?	Result	Support for:
1:11	Attacked less than random	Attacked more than random	Yes	Attacked at random	-
6:6	Attacked less than random	Attacked at random	Yes	Attacked less than random	Tosh

11:1	Attacked	Attacked	No	Attacked	Both
	less than	less than		less than	
	random	random		random	

b) Shoal choice experiment

Focal fish	Shoaling preference prediction	Conflict between predictions?	Result	Support for:
	Tosh et al. (2007)	Confusion/ oddity		
White, cryptic	Black	White	Yes	No preference
White, conspicuous	White	White	No	Prefer white
Black, cryptic	White	Black	Yes	Prefer black
Black, conspicuous	Black	Black	No	Prefer black

689

690

691 **Figure legends**

692

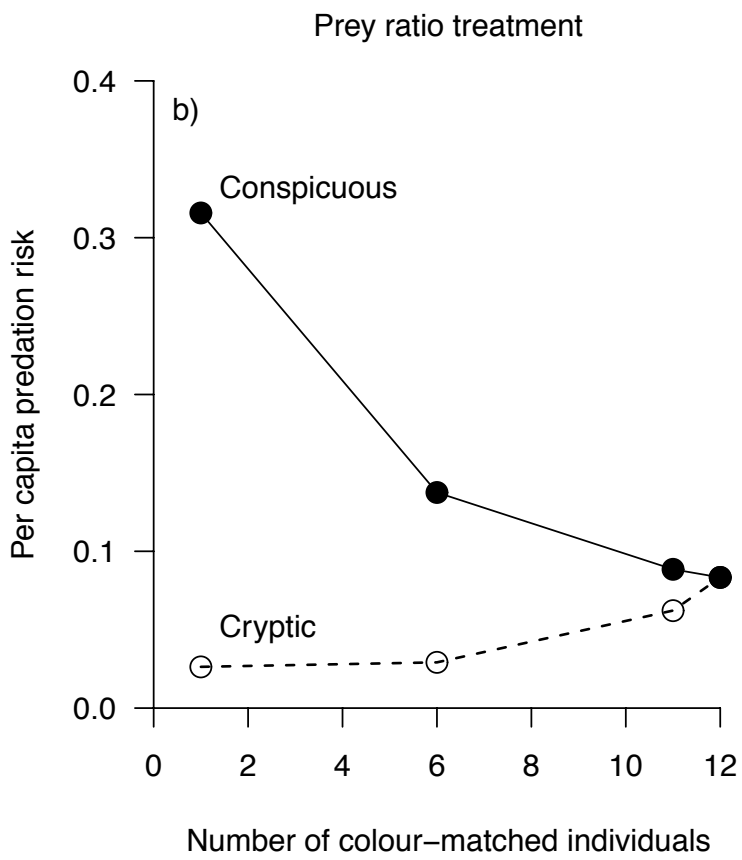
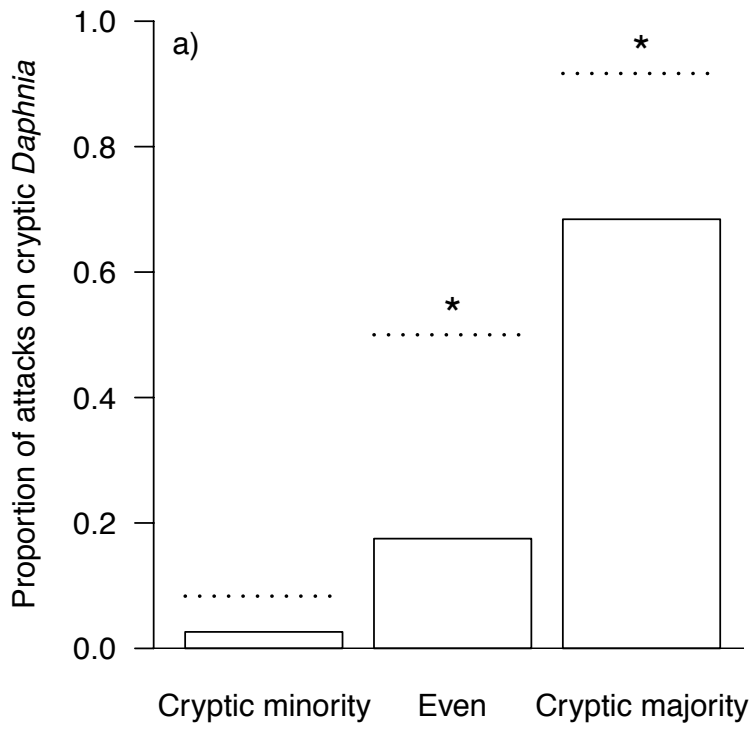
693 **Fig. 1 a)** The proportion of attacks on cryptic *Daphnia* by three-spine sticklebacks in the
694 three different prey ratio treatments (ratio of cryptic:conspicuous individuals for each
695 treatment are as follows: 1:11 Cryptic minority, 6:6 Even, 11:1 Cryptic majority). Dotted
696 lines indicate the expected proportion of attacks targeting a cryptic *Daphnia*, based on
697 random expectation. Stars indicate significant differences between observed and expected
698 proportions in binomial tests for 1:11 ($P = 0.535$, $N = 38$), 6:6 ($P < 0.001$, $N = 40$) and 11:1 (P
699 < 0.001 , $N = 38$). **b)** Per capita predation risk for cryptic (open circles, dashed line) and
700 conspicuous (filled circles, solid line) individuals as the number of individuals of each type in
701 the group increases

702

703 **Fig. 2** The proportion of time spent by black and white colour morph mollies (test fish) with
704 colour-matched shoals for conspicuous (grey bars) and cryptic individuals (open bars), mean
705 ± 2 SE. Significant effect of fish colour (GLM, $t = 2.861$, $df = 106$, $P = 0.0083$) and fish crypsis
706 ($t = -2.320$, $df = 105$, $P = 0.0366$) on the proportion of time spent with the colour-matched
707 shoal was found. The horizontal dashed line indicates a random expectation of equal time
708 spent with each shoal. Asterisks indicate significant ($P < 0.05$) deviation from this
709 expectation based on one-sample t-tests (black-conspicuous: $df = 25$, $P < 0.001$; black-
710 cryptic: $df = 25$, $P = 0.367$; white-conspicuous: $df = 28$, $P < 0.001$; white-cryptic: $df = 26$, $P <$
711 0.001)

712

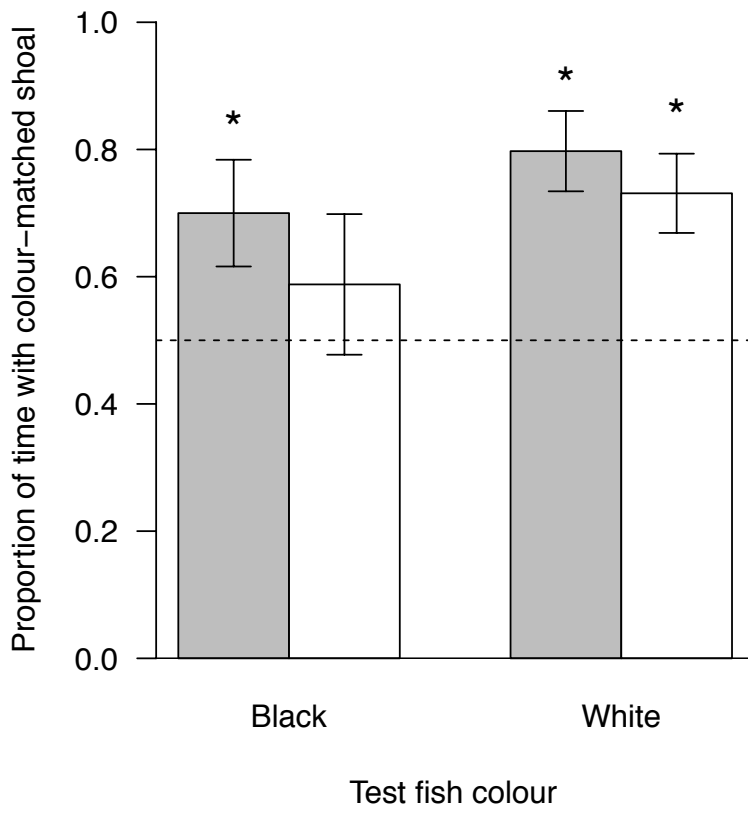
713 Figure 1



714

715

716 Figure 2



717

718

719 **Electronic supplementary material**

720

721 **Mixed phenotype grouping: the interaction between oddity and crypsis**

722

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732

733 **Table of key terms**

734

735 The table below summarises the key terms that we use in the manuscript.

Term	Description
Confusion effect	A benefit of group living, whereby the attack-to-kill ratio of a predator (success rate) is reduced when individual prey animals aggregate (Miller 1922; Krakauer 1995; Krause & Ruxton 2002).
Oddity effect	A mechanism where predators attack individuals within a group that are phenotypically distinct from the majority of the group ("odd"; Milinski 1977; Ohguchi 1978; Krause & Ruxton 2002). The confusion effect and oddity effect operate together select for behaviours in prey leading to the evolution of phenotype-assorted groups (e.g. preference for associating with phenotypically matched group-mates).
Phenotype-assorted group	A group of individuals that are visually very similar. The terms "uniform group" and "homogeneous group" are equivalent (Krause & Ruxton 2002)

Mixed-phenotype group	A group of individuals that differ in appearance from one another (Tosh et al. 2007). This might include variation in appearance within the same species, or groups of two or more species (mixed-species group).
Visual background	The background against which a prey animal would be viewed by a predator (Endler 1990; Ruxton et al. 2004). We distinguish here between two components of the visual background: the habitat (substrate/tank wall), and the other individuals in the group (for schooling fish, this may be an equally or more important component of the visual background than the habitat; Endler 1990). We use different terminology when discussing an animal's appearance relative to these different components of the visual background.
Conspicuous	An animal that stands out (visually) against the visual background (Ruxton et al. 2004). Here, we use 'conspicuous' or 'cryptic' to refer to the contrast/similarity between the animal's body colouration and the colour of the habitat or substrate, and 'odd' or 'phenotypically-matched' to refer to the contrast/similarity between the animal's colouration and the other members of the group.
Cryptic	An animal that closely matches (visually) the characteristics of the habitat (Ruxton et al 2004).
Odd	An individual which is phenotypically distinct (visually) from the other members of the group (Milinski 1977; Ohguchi 1978; Krause & Ruxton 2002)
Phenotypically matched	An individual which is of the same visual phenotype as the other members of the group

736

737 **References**

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