Numerical ability and improvement through interindividual cooperation varied between two cyprinid fish species, qingbo and crucian carp

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Abstract

19 We used qingbo (*Spinibarbus sinensis*) and Chinese crucian carp (*Carassius auratus*) to test

20 whether numerical discrimination could be improved by the coexistence and possible

21 cooperation of conspecies or heterospecies. We conducted a spontaneous shoal choice test of

22 singletons, conspecific dyads and heterospecific dyads under different numerical comparisons (8

23 vs. 12, 9 vs. 12 and 10 vs. 12). Singletons of qingbo could discriminate only 8 vs. 12, whereas

24 the dyads of qingbo showed better numerical acuity, as they could discriminate 10 vs. 12.

25 Crucian carp may have poor numerical ability, as both singleton and dyads showed no significant

26 preference for larger stimulus shoals, even at the 'easier' numerical discrimination, i.e., 8 vs. 12.

27 Furthermore, heterospecific dyads of crucian carp and qingbo did not show significant

28 preference for larger shoals at any numerical comparison in the present study. It is suggested that

29 both the numerical ability and the possibility for improvement by interindividual interaction and

30 hence cooperation might vary among fish species, and the interaction between heterospecies in

31 the present study showed negative effect on numerical ability possibly due to the different

32 behavioral and cognitive traits which make the information transfer and consensus difficult to

33 reach.

34

Introduction

36   Many studies have demonstrated that the ability to discriminate between quantities is

37 widespread (Vallortigara, 2012, 2017) and has been exhibited in preverbal infants (Lipton &

38 Spelke, 2003) as well as in a range of nonhuman animals, such as dolphins (Kilian et al., 2003),

39 dogs (Ward and Smuts, 2007), chickens (Rugani, Regolin & Vallortigara, 2007, 2008), tortoises

40 (Gazzola, Vallortigara & Pellitteri-Rose, 2018), frogs (Stancher et al., 2015), fish (Agrillo &

41 Dadda, 2007; Agrillo, Dadda & Bisazza, 2007; Stancher et al., 2013; Miletto Petrazzini et al.,

42 2015) and invertebrates (Gross et al., 2009; Reznikova & Ryabko,2011). Numerical ability can

43 improve antipredation efforts of animals by allowing them to compare shoals and join larger

44 ones because larger shoals confer the ecological benefits of improved survivorship under the risk

45 of predation (Foster & Treherne, 1981; Landeau & Terborgh, 1986;). Thus, it has been assumed

46 that the ability to discriminate quantities and stay with a larger shoal is a vital advantage in fish

47 species that live in groups.

48   Improved cognitive ability through interindividual cooperation was suggested more than one

49   century ago (Galton, 1907), and the so-called 'collective intelligence' has frequently been proven

50   both in the field and in laboratory studies (Krause, Ruxton & Krause, 2010; Bisazza et al., 2014).

51   The improvement in numerical ability has also been found in grass carp (*Ctenopharyngodon*

52   *idellus*) (Bai, Tang & Fu, 2019) and guppy (*Poecilia reticulata*) (Bisazza et al., 2014). The

53   possible mechanisms might be due to the so-called 'meritocratic leadership', i.e., the

54   performance of a dyad is determined by the better member, which plays a leadership role in

55   decision making (Bisazza et al., 2014). In nature, mixed-species shoals are frequently found in a

56   wide range of animal taxa and provide advantages in terms of enhanced foraging efficiency and

57   predator avoidance (Goodale et al., 2010; Kleinhappel et al., 2016). Recently, using two cyprinid

58   fish species as experimental animals, we found that numerical ability might facilitate by

59   cooperation between mixed-species individuals of grass carp (*Ctenopharyngodon idellus*) (good

60   numerical ability) and Chinese bream (*Parabramis pekinensis*) (poor numerical ability) as the

61   latter exhibited shutter behavior between two stimulus shoals following those of grass carp and

62   hence improved numerical ability compared to either singleton Chinese bream and its

63   conspecific dyad (Bai, Tang & Fu, 2019). Furthermore, the preference for either larger or smaller

64   shoals might vary between singletons and dyads due to some emotional and (or) motivational

65   factor (Regolin, Vallortigara & Zanforlin, 1995). Thus, the aim of the present study was to test if

66   the abovementioned improvement also manifests in other cyprinid fish species.

67   In the present study, we selected qingbo (*Spinibarbus sinensis*) and crucian carp (*Carassius*

68   *auratus*) as the experimental animals. Both species prefer group living and are widely distributed

69   throughout China. The numerical ability of qingbo (in singletons is 2:3) was recently

70   documented (Xiong et al., 2018), while data on the numerical ability of crucian carp are

71   unavailable. To fulfill our goal, we conducted a spontaneous shoal choice test of singletons and

72   dyads (both conspecific and heterospecific) under a numerical comparison range of 8 vs. 12 to 10

73   vs. 12 (8 vs. 12 was used because almost all fish species showed a similar or higher numerical

74   ability at a 2:3 ratio). We tested our hypothesis by comparing the preference to choose the larger

75   stimulus shoal among singletons, conspecific and heterospecific dyads.

76   **Materials & Methods**

77   **Ethics statement**

78   This study was approved by the Animal Care and Use Committee of the Key Laboratory of

79   Animal Biology of Chongqing (Permit Number: Zhao-20161012-01) and was performed in strict

80   accordance with the recommendations in the Guide for the Care and Use of Animal at the Key

81   Laboratory of Animal Biology of Chongqing, China.

82   **Subjects and housing conditions**

83   Experimental juvenile qingbo (N = 400, standard body length 5.10 ± 0.05 cm; body mass 2.87

84   ± 0.09 g) and juvenile crucian carp (N = 400, standard body length 3.88 ± 0.04 cm; body mass

85   1.74 ± 0.07 g) were purchased from a local market. Prior to the experiment, both qingbo and

86   crucian carp were randomly divided into two groups and reared separately as either the stimulus

87   shoal or the test fish. All fish were reared in water tanks that included a biological filter with

88   recirculating water for four weeks. During this period, the temperature of the dechlorinated water

89   was maintained at 25 ± 1 °C, and the oxygen content was maintained above 90% saturation. The

90   photoperiod cycle was 12 h of light: 12 h of darkness. All fish were fed once daily at 8:00 am

91   with a commercial floating diet (Tongwei Company, China). The uneaten food and feces were

92   cleaned up using a siphon. Furthermore, the experimental measurements were performed

93   between 8:00 and 18:00 after four weeks of acclimation.

94   **Experimental design**

95   We conducted 360 spontaneous choice tests, i.e., 20 repetitions of choice tests for singletons

96   of qingbo, singletons of crucian carp, dyads of qingbo, dyads of crucian carp and dyads of

97   mixed-species pairs (one qingbo and one crucian carp). Either a single (singleton test) or a pair

98   of fish (dyad test) was used as the test fish for each choice test. The numerical comparison was 8

99   vs. 12, 9 vs. 12 and 10 vs. 12.

100   **Protocol and setup**

101   The experimental apparatus used to assess the spontaneous shoal choice test consisted of a test

102   tank (70 cm × 35 cm × 35 cm) with two stimulus tanks (20 cm × 35 cm × 35 cm) positioned at

103   both ends (Fig. 1). Two 16-watt fluorescent lamps were located at both ends of the stimulus tank.

104   The tanks were filled with 10 cm of water. To prevent other interference factors, all of the walls

105   of the test tank, except for the wall connected with the stimuli tank, were covered with white

106   paper, and an opaque curtain was stretched around the arena. During the test, the behavioral

107   responses of the test fish were recorded using a webcam (Logitech Pro 9000; Logitech Company,

108 Suzhou, China) located 100 cm over the test tank and above the arena and connected to a remote

109 computer..

110   To avoid foraging behavior, fish were fed to apparent satiation 2 h before the measurements.

111 Stimulus fish were first introduced to the stimulus tank 5 min prior to the test. The test fish were

112 then introduced to the center of the test tank with a holding device (plastic cylinder with 10 cm

113 of diameter and 15 cm of height) and remained in the device for 3 min. After that period, the

114 holding device was gently removed, and the position of the test fish was recorded for 15 min at

115 15 frames s^{-1}. Each individual test fish was used only once, whereas individuals of the stimulus

116 shoals may have been used more than once. Twenty repetitions of each treatment were recorded.

117 In the numerical preference assessmentfor singletons or conspecific dyads, all stimulus shoal

118 members were the same fish species. In the numerical preference assessmentfor heterospecific

119 dyads, half qingbo and half Chinese crucian carp formed a mix stimulus shoals of two species for

120 8 vs. 12 and 10 vs. 12 numerical comparison, whereas 10 groups of 5 qingbo mixed with 4

121 Chinese crucian carp and 10 groups of 4 qingbo mixed with 5 Chinese crucian carp for stimulus

122 shoal of 9 individuals. The positions of the test fish were analyzed by the automated tracking

123 software program id Tracker (v 2.1) (Pérez-Escudero et al., 2014; Tang et al., 2017). In

124 conspecific dyads, the video files of two of the measurements of 8 vs. 12 in qingbo, three of the

125 measurements of 9 vs. 12 in crucian carp and one measurement of 10 vs. 12 in crucian carp

126 failed to be decoded. Therefore, the final repetitions were 18, 17 and 19 in 8 vs. 12, 9 vs. 12 and

127 10 vs. 12, respectively. The preferences of the test fish were defined as the time spent by the test

128 fish within the 11 cm preference zones during the 15-min periods of recording (i.e., within 11 cm

129 of the wall adjacent to the stimulus tanks on either side) and were calculated as follows:

130 observations within the preference zone of either the larger or smaller shoal / (observations

131 within the preference zone of the larger shoal + observations within the preference zone of the

132 smaller shoal). In conspecific dyads, we measured each fish in the dyad independently and then

133 calculated the average for dyads.

134 **Statistical analysis**

135   Statistical tests were carried out using SPSS 11.5. The time spent in the preference zone was

136 recorded as a measure of the preference of each test fish for either the larger or smaller stimulus

137 shoal. All data were tested for normality by a one-sample Kolmogorov-Smirnov test. The

138 linearly mixed model (tested number as random factor) was used to test the significance of the

139   preference for larger or smaller shoals. All values are presented as the mean ± S.E., and $P < 0.05$

140   was used as the level of statistical significance.

Results

Experiment 1 Numerical ability of singletons

143   Qingbo showed a significant preference for larger shoals at only a numerical contrast of 8 vs.

144   12 ($F_{1,38} = 6.083$, $P = 0.018$), i.e., qingbo were able to discriminate at only a 2:3 ratio (Fig. 2).

145   No significant preference was observed for 9 vs. 12 ($F_{1,38} = 0.119$, $P = 0.732$), or 10 vs. 12 ($F_{1,38}$

146    $= 1.742$, $P = 0.195$). Crucian carp showed no significant preference for larger shoals at any

147   numerical comparison: 8 vs. 12 ($F_{1,38} = 0.223$, $P = 0.640$), 9 vs. 12 ($F_{1,38} = 3.741$, $P = 0.061$), or

148   10 vs. 12 ($F_{1,38} = 0.335$, $P = 0.567$).

Experiment 2 Numerical ability of conspecific dyads

150   Dyads of qingbo showed a significant preference for the larger shoal at numerical contrasts of

151   8 vs. 12 ($F_{1,34} = 7.874$, $P = 0.008$) and 10 vs. 12 ($F_{1,38} = 4.581$, $P = 0.039$) but not at 9 vs. 12

152   ($F_{1,38} = 2.662$, $P = 0.111$). However, no significant preference was observed at any numerical

153   comparison in crucian carp: 8 vs. 12 ($F_{1,38} = 0.235$, $P = 0.631$), 9 vs. 12 ($F_{1,32} = 0.064$, $P =$

154   0.801), or 10 vs. 12 ($F_{1,36} = 0.511$, $P = 0.479$).

Experiment 3 Numerical ability of heterospecific dyads

156   Neither qingbo nor crucian carp showed any significant preference for larger shoals at any

157   numerical comparison in the preset study; 8 vs. 12 (qingbo: $F_{1,38} = 0.818$, $P = 0.371$, crucian

158   carp: $F_{1,38} = 0.704$, $P = 0.407$), 9 vs. 12 ($F_{1,38} = 2.118$, $P = 0.154$, $F_{1,38} = 0.969$, $P = 0.331$), and

159   10 vs. 12 ($F_{1,38} = 0.297$, $P = 0.589$, $F_{1,38} = 0.155$, $P = 0.696$).

Discussion

161   The main aims of the present study were to test whether interaction (i.e., cooperation) between

162   individuals could facilitate the numerical abilities of two cyprinid fish species and whether the

163   interaction between different fish species could achieve similar performance compared to the

164   possible improvement between conspecific dyads. The numerical ability indicated by shoal

165   preference increased from a threshold of 8 vs. 12 in singleton qingbo to at least 10 vs. 12 (the

166   most subtle numerical difference in this study) in qingbo dyads. However, crucian carp may

167   show poor numerical ability as it showed no preference to larger shoal in any numerical

168   comparison in the present study. Thus, the possible improvement in numerical ability between

169   individual crucian carp and heterospecific dyads was difficult to assess; however, the

170   coexistence of heterospecies did show a negative effect on the numerical ability of qingbo, as

171   the qingbo in heterospecific dyads could not even discriminate in the numerical comparison of

172   8 vs. 12.

173   **Qingbo showed greater numerical ability indicated by shoal preference than crucian carp**

174   Given the ecological benefit of collective living, half of all fish species prefer group living

175   throughout life or for at least a part of their life history (Shaw, 1978). Thus, numerical

176   discrimination may play an important role in fish species (Miletto Petrazzini et al., 2015), and

177   such ability has been widely documented in fish species (Agrillo, Dadda & Bisazza, 2007;

178   Potrich et al., 2015; Xiong et al., 2018). In the present study, singletons of qingbo could

179   discriminate in the numerical comparison of 8 vs. 12, which fall within the data of other fish

180   species (Lucon-Xiccato & Bissazza, 2017), which usually varied from 0.5 to 0.75). However,

181   crucian carp showed no significant preference for larger shoals in any of the numerical

182   comparisons in the present study. It is suggested that differences in numerical ability might exist

183   in closely related fish species. This may be reasonable, as qingbo in the field prefer to live in

184   fast-flowing water and exhibit a group-living lifestyle (Killen et al., 2016; Tang et al., 2017).

185   However, crucian carp prefer to live in still water with a more complicated habitat, and selection

186   stress may be more severe on characteristics other than group living and numerical ability.

187   However, cognitive and behavioral traits may also be involved in such differences in the

188   artificial experimental conditions, as the crucian carp seemed much less bold and showed fewer

189   exploration activities than qingbo. According to our observation (not directly recorded), it

190   seemed that Chinese crucian carp performed considerably fewer shutters between two stimulus

191   shoals than qingbo in the present study. Further investigation on boldness and stress hormone

192   such as plasma cortisol level during choice test might provide useful information. Furthermore,

193   the data in Fig. 2 clearly show that the mean preference ratio of crucian carp singletons, under

194   the numerical comparison of 8 vs. 12 (possibly also under the 8 vs. 12 and 9 vs. 12 conspecific

195   dyads), was similar to that of the qingbo. It is suggested that the large interindividual variation

196   might mask the possible shoal preference of crucian carp under these situations. The reason

197   might be that some individuals were rather shy and would stay with the smaller stimulus shoal

198   once they made the wrong choice (Lucon-Xiccato et al., 2017). Therefore, we cannot tell if they

199   cannot discriminate in the numerical comparison, if the test fish dare not make a choice or if they

200   do not care about the difference under the conditions of the present study. Perhaps a further study

201   under a food choice test might provide more useful information, as a previous study found that

202   the numerical ability varied between different ecological contexts (Lucon-Xiccato and Dadda,

203   2017). Nevertheless, the present study suggested that the numerical discrimination threshold of

204   singleton qingbo is approximately 2:3, whereas the threshold of crucian carp is less than that if it

205   has any numerical ability or shoal preference.

206   **The dyads of qingbo showed better numerical acuity than sigletons**

207   Increased cognitive ability through interindividual interaction was again demonstrated in the

208   present study, as the numerical threshold of qingbo dyads improved profoundly when compared

209   to that of singletons. The previous studies in grass carp (Bai et al., 2019) and guppy (Bisazza et

210   al., 2014) found both species can discriminate at a ratio of 0.75 (i.e., 3:4) by interindividual

211   cooperation. In the present study, dyads of qingbo could even discriminate in the 10 vs. 12

212   comparison (i.e., 0.833). Given that it is the smallest numerical comparison treatment designed in

213   the present study, it is suggested that qingbo may achieve a considerably high numerical

214   discrimination performance through cooperation. However, it was worth noting that dyads of

215   qingbo fail to discriminate 9 vs. 12, even though the preference for larger stimulus shoals was 23%

216   higher than that for smaller shoals. It is possible that the aforementioned large interindividual

217   variation might mask the significant difference. The improvement in numerical ability by

218   interindividual cooperation has also been found in grass carp (*Ctenopharyngodon idellus*) (Bai,

219   Tang & Fu, 2019). Given the profound improvement in numerical ability, it is possible that the

220   'meritocratic leadership' might be involved in cooperation during the numerical discrimination

221   process. However, it has long been suggested that the emotional and (or) motivational factor

222   related to the numerical discrimination and spatial cognition might also be involved in the

223   improved performance between dyads and singletons (Regolin, Vallortigara & Zanforlin, 1995).

224   Both singletons and dyads of crucian carp showed no shoal preference at any shoal preference

225   in the present study; thus, we cannot draw any conclusions about the possibility for improvement

226   in numerical ability by the interindividual interaction of crucian carp. However, because qingbo

227   could improve from the numerical comparison of 8 vs. 12 in singleton to 10 vs. 12 in dyad, if

228   such improvement does exist in crucian carp, the threshold of singleton crucian carp must be

229   considerably lower than 7 vs. 12 (which is the best possible numerical contrast threshold of the

230   crucian carp dyad). Again, the spontaneous shoal choice test under another ecological context

231 (for example, mating or foraging) or a training protocol used before might provide more useful

232 information (Lucon-Xiccato and Bisazza, 2017).

233 **Qingbo in heterospecific dyads showed poor numerical ability even lower than singletons**

234   In the present study, the crucian carp in the heterospecific dyads showed no shoal preference

235 in any numerical comparisons. However, because we did not conduct an easier numerical

236 comparison than 2:-3, we cannot determine the thresholds of singleton or dyads of crucian carp,

237 if they have any. Thus, we also cannot draw any conclusions about the possibility of the

238 numerical ability (or shoal preference) of crucian carp increasing through heterospecific

239 cooperation. However, on the contrary, the company of crucian carp showed a negative effect on

240 the numerical ability of qingbo, as qingbo in heterospecific dyads could not even discriminate in

241 the 8 vs. 12 comparisons (the threshold of singletons). These mechanisms need further

242 investigation. Because these two fish prefer living in different habitats, the behavioral and

243 cognitive traits might be completely different, thus making the information transfer and

244 consensus difficult to reach, which may be the precondition of the collective intelligence. Further

245 investigation using fish species of naturally mixed shoals as experimental models might give

246 more useful information.

247

Conclusions

249   Qingbo showed a similar numerical acuity to previous studies with a threshold of 0.66, which

250 could be facilitated to at least 0.83 by interindividual cooperation. Crucian carp showed no shoal

251 preference in the present study, possibly due to low cognitive ability, large interindividual

252 variation in numerical ability, low boldness or no motivation for shoal preference, or improper

253 numerical comparison (i.e. only large numerical comparison), which might make this a poor

254 experimental model for numerical ability research. The interaction between heterospecific dyads

255 elicited a decreased numerical ability of qingbo, which became even lower than the threshold of

256 singletons. However, it is difficult to draw any safe conclusions about the difference in

257 cooperation efficiency on numerical comparisons between conspecific and heterospecific dyads

258 due to the poor performance of crucian carp and (or) lacking of small numerical comparison in

259 the present study.

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263

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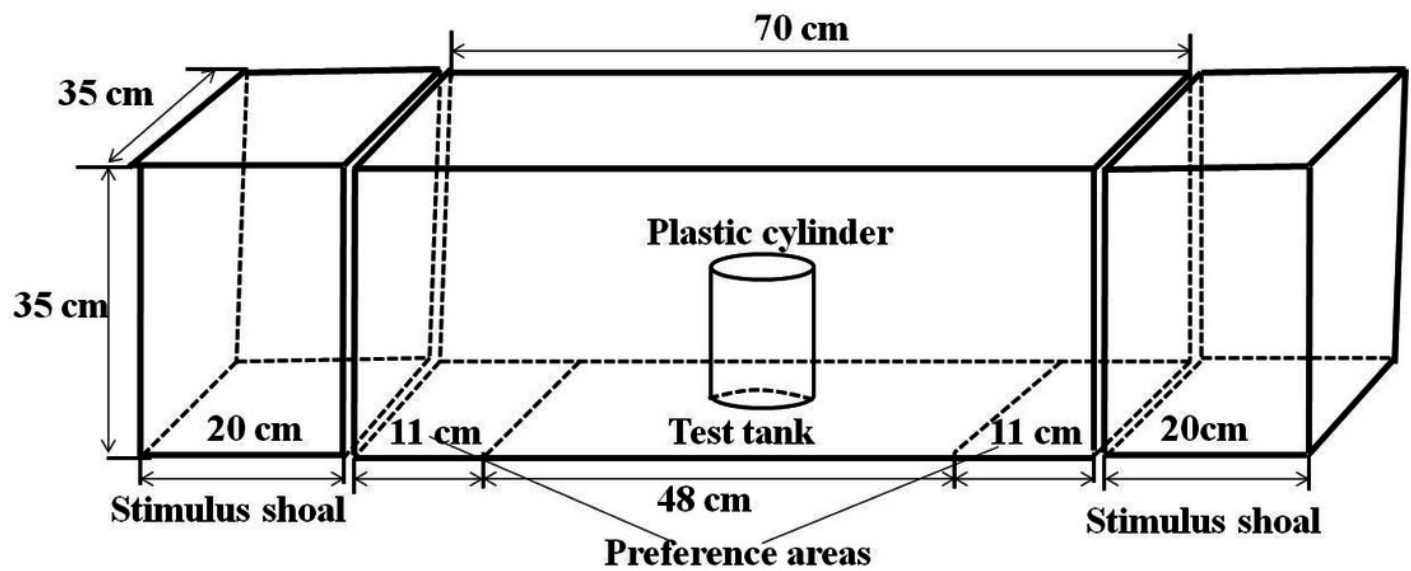
Figure 1

Experimental setup showing the structure of experimental arena.

The shoal choice test of qingbo and crucian carp in both singletons and dyads (both conspecific and heterospecific) under different numerical comparisons

Mean ± S.E., 20 repetitions, except N = 18 for 8 vs. 12 of conspecific dyad of qingbo, 17 for 9 vs. 12 and 19 for 10 vs. 12 of conspecific dyads of crucian carp. * indicates significant preference for larger shoals ($P <$ 0.05).

A) Singletons

■ Time near larger shoal
□ Time near smaller shoal

B) Conspecific dyads

■ Time near larger shoal
□ Time near smaller shoal

C) Heterospecific dyads

■ Time near larger shoal
□ Time near smaller shoal