Are blue tits more likely to use social information from live demonstrators compared to video playback?

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Video playback provides a promising method to study social interactions, and the number of video playback experiments has been growing in recent years. Using videos has advantages over live individuals as it increases the repeatability of demonstrations, and enables researchers to manipulate the features of the presented stimulus. How observers respond to video playback might, however, differ among species, and the efficacy of video playback should be validated by investigating if individuals' responses to videos are comparable to their responses to live demonstrators. Here we use a novel foraging task to compare blue tits' (*Cyanistes caeruleus*) responses to social information from a live conspecific versus video playback. Birds first received social information about the location of food, and were then presented a three-choice foraging task where they could search for food from locations marked with different symbols (cross, square, plain white). Two control groups saw only a foraging tray with similar symbols but no information about the location of food. We predicted that socially educated birds would prefer the same location where a demonstrator had foraged, but we found no evidence that birds copied a demonstrator's choice, regardless of how social information was presented. Social information, however, had an influence on blue tits' foraging choices, as socially educated birds seemed to form a stronger preference for a square symbol (against two other options, cross and plain white) than the control birds. Our results suggest that blue tits respond to video playback of a conspecific similar to a live bird, but how they use this social information in their foraging decisions, remains unclear.

1 **Are blue tits more likely to use social information from live demonstrators**

2 **compared to video playback?**

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21 **ABSTRACT**

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24 playback experiments has been growing in recent years. Using videos has advantages over live

25 individuals as it increases the repeatability of demonstrations, and enables researchers to

26 manipulate the features of the presented stimulus. How observers respond to video playback might,

27 however, differ among species, and the efficacy of video playback should be validated by

28 investigating if individuals' responses to videos are comparable to their responses to live

29 demonstrators. Here we use a novel foraging task to compare blue tits' (*Cyanistes caeruleus*)

30 responses to social information from a live conspecific versus video playback. Birds first received

31 social information about the location of food, and were then presented a three-choice foraging task

32 where they could search for food from locations marked with different symbols (cross, square,

33 plain white). Two control groups saw only a foraging tray with similar symbols but no information

34 about the location of food. We predicted that socially educated birds would prefer the same

35 location where a demonstrator had foraged, but we found no evidence that birds copied a

36 demonstrator's choice, regardless of how social information was presented. Social information,

37 however, had an influence on blue tits' foraging choices, as socially educated birds seemed to form

38 a stronger preference for a square symbol (against two other options, cross and plain white) than

39 the control birds. Our results suggest that blue tits respond to video playback of a conspecific

40 similar to a live bird, but how they use this social information in their foraging decisions, remains

41 unclear.

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46 **INTRODUCTION**

47 The number of studies investigating social information use in animals has been expanding during

48 the last few decades, and it is now well documented that many species use social information in

49 their decision-making (Galef & Laland, 2005). Acquiring social information can be beneficial in

50 many different contexts. Animals can, for example, use social information in their foraging

51 decisions, mate choice, breeding habitat selection, or when avoiding predators (Danchin et al.,

52 2004). Social transmission is also taxonomically widespread, with evidence of social information

53 use found in birds (Aplin, 2019), mammals (Whiten, 2000), fish (Brown & Laland, 2003), reptiles

54 (Noble, Byrne & Whiting, 2014; Kis, Huber & Wilkinson, 2015) and even insects (Dawson &

55 Chittka, 2012; Baracchi et al., 2018). Social information is predicted to benefit individuals by

56 reducing the costs of personal learning (Laland, 2004; Kendal et al., 2005; Kendal et al., 2018).

57 When foraging, for example, individuals can gather social information about the location of food

58 sources or food palatability, and learn novel foraging skills (reviewed in Galef & Giraldeau, 2001),

59 which could increase their foraging efficiency.

60

61   As the number of social learning studies has grown, also the number of techniques to study

62 social interactions has increased. A common method is to use artificial stimuli that enables

63 researchers to control and standardize what information is presented (D'Eath, 1998; Woo &

64 Rieucau, 2011). Artificial stimuli have been used for a long time in animal behaviour research,

65 starting from simple dummies and leading up to robotic animals. Cardboard models were first used

66 by Tinbergen & Perdeck (1950) to investigate the importance of various stimulus characteristics

67 on the begging response of herring gull chicks. Subsequently, simple models have been used in

68 many experiments, including studies investigating mate choice (Halnes & Gould, 1994; Höglund

69 et al., 1995), or individuals' responses to predators (Powell, 1974; Petersson & Järvi, 2006) and

70 brood parasites (Thorogood & Davies, 2016). Over the recent years, new technology has enabled

71 researchers to use also more sophisticated techniques, such as robotic animals (Taylor et al., 2008;

72 Krause, Winfield & Deneubourg, 2011). For example, male satin bowerbirds were found to adjust

73 their displays in response to signals from robotic females (Patricelli et al., 2002), and wild grey

74 squirrels were shown to respond to a robotic model of a conspecific displaying alarm behaviour

75 (Partan, Larco & Owens, 2009).

76

77   Another promising technique to study social interactions is video playback. Videos can be

78 easily edited and manipulated, allowing researchers to alter the stimulus features that are presented

79 to observers and reduce the variation among presentations (D'Eath, 1998). Furthermore, with

80 technological advances it is now possible to create realistic computer-generated animations to

81 study social interactions (Woo & Rieucau, 2011). Video playback has been used successfully in

82 many bird species (Ophir & Galef, 2003; Bird & Emery, 2008; Rieucau & Giraldeau, 2009;

83 Guillette & Healy, 2017; Thorogood, Kokko & Mappes, 2018; Smit & Oers, 2019), as well as

84 across a range of other taxa, including mammals (Hopper, Lambeth & Schapiro, 2012; Gunhold,

85 Whiten & Bugnyar, 2014), fish (Rowland et al., 1995; Trainor & Basolo, 2000), reptiles (Clark,

86 Macedonia & Rosenthal, 1997; Ord et al., 2002) and spiders (Clark & Uetz, 1992). Video playback

87 does, however, have limitations such as the lack of depth cues, the lack of interaction between an

88 observer and an individual on the video, and differences between animal and human visual systems

89 (D'Eath, 1998; Zeil, 2000). Birds, for example, have higher critical flicker-fusion frequences (>

90   100 Hz) than humans (60 Hz) and they might therefore perceive the video image as flickering,

91   instead of continuous motion (D'Eath, 1998; Bird & Emery, 2008). However, this degree of visual

92   resolution often occurs when light stimuli are very bright (e.g. 1500 cd/m^2 in blue tits, (Boström

93   et al., 2016)) and beyond the normal brightness of most video screens. Nevertheless, video

94   playback does not always generate the same responses in observers when compared to studies

95   using live demonstrators (see Schlupp, 2000). For example, a recent study with California scrub-

96   jays (*Aphelocoma californica*) found that observing a video of a conspecific eavesdropping on a

97   caching event did not influence focal individuals' caching and re-caching behaviour, in contrast to

98   previous studies with a live conspecific (Brecht et al., 2018). The strength of the responses to

99   video and live demonstrations may also differ even when observers are found to respond to videos.

100 Zebra finch (*Taenopygia guttata*) males, for example, copy the nest material choice from a video

101 demonstrator but this preference is stronger when birds observe a live demonstrator (Guillette &

102 Healy, 2019). Most of these studies, however, have compared individuals' responses to video

103 playback to previous experiments with live demonstrators, and therefore have not accounted for

104 possible differences in test conditions, such as individual differences among the demonstrators.

105 Here our aim was to compare these two methods in one study by investigating whether blue tits'

106 response to the same demonstrator differs between video and live presentation.

107

108   The applicability of video playback in studies with blue tits is so far unclear. We found

109 recently that blue tits' behaviour changed when they were presented video playback of a

110 conspecific, but social information from videos did not influence their foraging decisions in a later

111 foraging task (Hämäläinen et al., 2017). In contrast, great tits (*Parus major*) have been

112 demonstrated to respond to videos of a conspecific (Snijders, Naguib & van Oers, 2017), and use

113   social information from videos in their foraging decisions (Thorogood, Kokko & Mappes, 2018;

114   Smit & Oers, 2019; Hämäläinen et al., in press), suggesting that video playback can be used

115   successfully in other parid tit species. It is, however, possible that even closely related species

116   differ in their response to video stimuli. For example, Roberts, Gumm & Mendelson (2017) tested

117   the efficacy of video playback in two species of darters, *Etheostoma barrenense* and *Etheostoma*

118   *zonale,* and found that despite the same experimental set-up and close relatedness of the species,

119   only *E. zonale* females' responses to video playback of conspecific males were comparable to live

120   males, whereas *E. barrenense* females showed a preference only for live males. Similarly, blue tits

121   might respond to videos differently than great tits. Alternatively, our previous result of blue tits

122   not copying a demonstrator (Hämäläinen et al., 2017) might be because blue tits were simply not

123   using acquired social information, regardless of how it was presented. Indeed, studies using live

124   demonstrators have also found that only about half of the tested blue tits learn a novel foraging

125   task socially (Sasvári, 1979; Sasvári, 1985; Aplin, Sheldon & Morand-Ferron, 2013), compared to

126   great tits that are more likely to solve the task after observing others (Sasvári, 1979; Sasvári, 1985).

127   To disentangle the effect of video playback and blue tits' tendency to use social information, we

128   designed an experiment where we investigated whether birds were more likely to use social

129   information from a live demonstrator, compared to a video presentation.

130

131   In this experiment, we presented blue tits a three-choice foraging task: an ice cube tray with

132   three wells covered and marked with different symbols (cross, square and plain white). One group

133   of the birds received social information about the location of food from a live conspecific, whereas

134   another group saw a video playback of a conspecific demonstrator. In addition, we had two control

135   groups that only saw a foraging tray (live/video presentation) but no information about the location

136 of food. We predicted that the birds in the control group would not have a preference for any of

137 the symbols and would choose each of them equally often. Socially educated birds were predicted

138 to choose the same symbol and location where they had observed a demonstrator foraging. We

139 predicted that blue tits would copy a demonstrator's choice equally often regardless of how social

140 information was presented (live/video demonstrator). However, finding that blue tits were less

141 likely to copy a demonstrator's choice from videos would indicate that video playback might not

142 be a suitable method for social learning studies in the species. Finally, we predicted that birds that

143 received social information would start the foraging task faster than control birds (Hämäläinen et

144 al., 2017; Thorogood, Kokko & Mappes, 2018).

145

146 **METHODS**

147 **Birds**

148 The experiment was conducted at Konnevesi Research Station in Central Finland during January

149 and February 2017. We tested social information use in 40 juvenile blue tits. In addition, five adult

150 birds were used as demonstrators. Birds were caught from the feeding site and housed in individual

151 plywood cages (80 cm × 65 cm × 50 cm) with a daily light period of 12.5 hours, and free access

152 to food (sunflower seeds, tallow and peanuts) and fresh water. Before and during the experiment

153 food was restricted to make sure that birds were motivated to forage. Birds were kept in captivity

154 for approximately one week and then released back at the capture site. Before this, each bird was

155 weighted and ringed for identification purposes. The work was carried out with permission from

156 the Central Finland Centre for Economic Development, Transport and Environment and license

157 from the National Animal Experiment Board (ESAVI/9114/ 04.10.07/2014) and the Central

158   Finland Regional Environmental Centre (VARELY/294/2015). Birds were treated following the

159   ASAB guidelines for the treatment of animals in behavioural research and teaching (2012).

160

Foraging task and pre-training

162   We investigated whether blue tits used social information about the location of food by presenting

163   them a three-choice foraging task where they had to find mealworms from a white plastic ice cube

164   tray (modifying a protocol used in Hodgson & Healy, 2005). The tray had 21 wells in three rows

165   and we covered three of these (in the middle row) with a piece of white paper that had either (i) a

166   black cross symbol, (ii) a black square symbol, or (iii) no symbol (plain white) printed on top (Fig.

167   1a). The same symbols were also attached in front of the foraging tray to increase their visibility

168   to the observers during demonstration. In the experiment birds had to lift up the paper covers to

169   find a food reward and we investigated whether social information influenced their first choice.

170

171   Before the experiment, we trained birds in their home cages to forage from an ice cube tray.

172   The training was done step-wise by first offering birds a tray with four of the wells (randomly

173   chosen) containing a mealworm. After birds had eaten these, we next presented them a tray with

174   four wells partly covered (again, randomly chosen), so that the mealworms were still visible.

175   During the training, we covered the wells with brown paper to prevent birds associating the reward

176   with white colour that was used in the experiment. In the next step birds received a tray where four

177   wells were covered with brown paper, so that the mealworms were completely hidden. After birds

178   had completed these steps (i.e. found and consumed all mealworms), we finally presented them a

179   tray with seven wells covered but only four of them containing a mealworm. This was done to

180   increase individuals' uncertainty about food reward in the wells, so that they would be more likely

181   to use social information in the experiment. Training was completed once individuals had found

182   and consumed all mealworms. All birds finished the training in one day.

183

184   **Demonstrators**

185   We used five individuals (all adults, i.e. > 1 year old) as demonstrators in the experiment. Each

186   individual was used twice in the live demonstration and also filmed for the video playback that

187   was presented to two observers (i.e. each individual was demonstrator for four observers).

188   Demonstrators were first trained to forage from an ice cube tray in their home cages, following a

189   similar step-wise protocol that we used with observers (see above). However, instead of covering

190   the wells with brown paper, we presented demonstrators a similar tray that we used in the

191   experiment, with three wells covered with different symbols (cross, square, plain white; Fig. 1a).

192   Food reward was placed only under one of the symbols (cross or square) whereas the wells covered

193   with other symbols were always empty. Demonstrators therefore learned to associate food reward

194   with one of the symbols and searched food from that location during the demonstrations. We

195   trained two of the demonstrators to associate food reward with a cross symbol, and two with a

196   square symbol. The last demonstrator was trained first with a square and later with a cross, so that

197   the number of demonstrations for each symbol was balanced among observers.

198

199   For the video playback, we filmed each demonstrator (with an HD camcorder Canon Legria

200   HF R66) performing the foraging task (i.e. finding a mealworm by lifting up the paper cover)

201   through the plexiglass wall of the test cage (a 50 × 66 × 50 cm sized plywood cage with the

202   plexiglass front wall). Three mealworms were hidden in the well (with either a cross or a square

203   symbol), and birds were filmed finding and eating all of them, so the demonstration was repeated

204   three times. We then edited these videos (using Windows Movie Maker), so that they were all 150

205   seconds long. We also filmed a five-minute long video of a demonstrator in the cage without a

206   tray, which was presented to observers before the foraging task demonstration. Finally, we filmed

207   control videos that contained of a tray only (with different symbols) but no bird (150 secs). The

208   order of symbols on the tray was randomized among videos (in both control and social information

209   videos).

210

211   **Experimental protocol**

212   In the experiment observers were randomly allocated to four treatments (n = 10 in each): (i) social

213   information from a live demonstrator, (ii) social information from video playback, (iii) live control

214   (the feeding tray only), (iv) video playback control (video of the feeding tray only). In all

215   treatments, birds were first allowed to habituate to the test cage for two hours. During this time,

216   we repeated the foraging task training one more time by presenting birds an ice cube tray with

217   seven wells covered with brown paper and four of these containing a mealworm. After this food

218   was restricted for 1 hour to make sure that birds were motivated to search for food during the

219   experiment.

220

221   The live demonstration was conducted in a plywood cage that was divided into two

222   individual compartments (each 50 × 66 × 50 cm) that were separated by a plexiglass wall (Fig.

223   1b). An individual that was tested was placed on one side of the wall, and a demonstrator bird (or

224   a tray only for the control group) on the other side. Outside the experiment, the plexiglass was

225   covered (with a cardboard sheet), so that the birds could not see each other, and the cover was

226   removed only for the duration of the demonstration. The front wall of each compartment was also

227   made of plexiglass, so that we could observe the birds during the experiment. The demonstrator

228   was placed to the test cage 2 hours before the test (with plexiglass between the two cage

229   compartments covered). Demonstrators were then given one more training session with the

230   symbols to ensure that they were foraging in the test cage, and that they were choosing the right

231   symbol (the symbol they had been trained to associate with reward). After this, demonstrators were

232   food-deprived for one hour, so that they were motivated to forage during the demonstration. We

233   then removed the cover of the plexiglass between the observer and the demonstrator, and let the

234   birds to habituate to this new situation for five minutes before presenting the foraging tray to the

235   demonstrator. The tray had three wells covered and one of them (the well with either a cross or a

236   square symbol) contained three mealworms. The order of the symbols was randomized across

237   presentations. We waited until the demonstrator found and ate all three mealworms which took on

238   average 230 seconds (range = 154–492 secs).

239

240   Once the demonstration was finished (i.e. the demonstrator had consumed all three

241   mealworms), we covered again the plexiglass between the cages, so that the birds could not see

242   each other. We then presented observers a foraging tray with the same three symbols. The order

243   of the symbols in the presented tray was the same as in the demonstration, so that observers could

244   use both symbol and spatial cues about the location of food reward. This time all the wells were

245   empty to make sure that birds could not get any additional cues about food. We recorded observers'

246   first choice to search for food (i.e. the well where they first lifted up the cover) and the latency to

247   make this choice. The live control treatment was conducted in a similar way but instead of seeing

248   a demonstrator, birds saw only the tray in an empty cage for 150 seconds.

249

250   When birds received information from videos, the experiment was conducted in a 50 (w) ×

251   66 (h) × 50 (d) cm sized plywood cage with the front wall made of plexiglass. We presented birds

252   videos by placing an LCD monitor (Dell E198FPF, 19", resolution 1280 × 1024, 75 Hz, 300 cd/m²)

253   against the plexiglass (Fig. 1c), following previously validated methods (Hämäläinen et al., 2017;

254   Thorogood, Kokko & Mappes, 2018; Hämäläinen et al., in press). The size of the demonstrator on

255   the screen was slightly smaller than the size of the live bird (approximately 70 % of the real size).

256   How birds perceive the demonstrator's size is, however, difficult to estimate because of depth cues

257   (Zeil, 2000) and differences in viewing distance, depending on an observer's position in the cage.

258   Nevertheless, previous studies have demonstrated that great tits use social information from the

259   videos with a similar sized demonstrator (Thorogood, Kokko & Mappes, 2018, Hämäläinen et al.,

260   in press). Birds were first let to habituate to the monitor for 15 min before starting the video. Birds

261   that received social information were then presented a five-minute video of a demonstrator in the

262   cage without the foraging tray, so that the protocol was similar to the live demonstration treatment

263   where birds could observe each other for five minutes before the demonstration. Birds were then

264   presented a 150 seconds long video of a demonstrator finding and consuming three mealworms

265   under one of the symbols. Birds in the control group saw a video of the feeding tray only (150

266   secs). After this, the computer monitor was removed and we presented birds the foraging task,

267   following the same protocol as in live demonstration. Again, the order of the symbols was the

268   same as in the videos, and we recorded birds' first choice and the time before they started the task.

269

270   **Statistical analyses**

271   We first investigated whether birds had an overall preference towards any of the symbols using a

272   binomial test (compared to equal probability of choosing any of the three symbols). We then

273   investigated whether these preferences differed between socially educated and control birds.

274   Because we did not find differences in information use between video and live demonstration

275   treatments (see results), we combined these treatments and used a G-test to compare distributions

276   of the preferences between all socially educated birds (live and video treatment; n = 20) and control

277   birds (live and video treatment; n = 20). We also used a G-test to investigate (i) if birds had a

278   preference for the spatial location on the tray (left/middle/right), i.e. if they chose any of the

279   locations more often than expected by chance (1/3 probability) and to (ii) compare the choices of

280   socially educated birds that saw a demonstrator choosing a square to those seeing a demonstrator

281   choosing a cross (video and live treatments combined). Because birds seemed to prefer a square

282   symbol (see results), we did this by comparing the likelihoods to choose a square (over alternative

283   options cross/white), i.e. testing if birds chose a square more often after seeing a demonstrator

284   choosing it, compared to seeing a demonstrator choosing a cross. We next used a Fisher's exact

285   test to investigate if birds were more likely to copy a demonstrator's choice when they were

286   presented a live demonstrator, compared to video playback. This was done by simply comparing

287   the number of birds whose choice matched that of a demonstrator (whether a demonstrator chose

288   a cross or a square) to those who chose a different symbol than a demonstrator. Finally, we tested

289   if social information influenced the latency to start the foraging task using a generalized linear

290   model with a negative binomial error distribution. The time to choose the well was used as a

291   response variable and explanatory variables included an interaction between social information

292   treatment (social information/control) and the way information was presented (live/video

293   demonstration). All the analysis were conducted using software R.3.3.1 (R Core Team 2016).

294

295   **RESULTS**

296   Overall, birds chose the well with a square symbol more often than predicted by chance (binomial

297   test, 25/40, p < 0.001). This preference, however, differed between socially educated and control

298   birds (G-test, G = 7.16, p = 0.028; Fig. 2a): individuals that received social information (live and

299   video treatments combined) showed a strong preference towards a square symbol (binomial test,

300   15/20, p < 0.001), whereas this preference was not significant in the control groups (binomial test,

301   10/20, p = 0.15). Against our prediction that socially educated birds would choose the same symbol

302   as a demonstrator, we did not find evidence that a demonstrator's choice (cross/square) influenced

303   an observers' likelihood to choose a square symbol (G-test, G = 0.51, p = 0.47). Instead, socially

304   educated birds seemed to prefer a square, regardless of a demonstrator's choice (Fig. 2a). This did

305   not differ between live and video presentations, i.e. birds were not more likely to copy the choice

306   of a live demonstrator compared to video playback (Fisher's exact test, p = 1; Fig. 2b). They also

307   did not prefer any location (left/middle/right) on the tray (location that birds chose did not differ

308   from that expected by random chance; G-test, G = 3.62, p = 0.16). Finally, social information did

309   not influence how fast birds started to forage (effect of social information: estimate = -0.178 ±

310   0.469, Z = -0.379, p = 0.70) and the effect of social information on foraging time did not depend

311   on the way the information was presented (social information*type of presentation: estimate =

312   0.657 ± 0.934, Z = 0.704, p = 0.48). Instead, both control and socially educated birds started the

313   foraging task faster after seeing a video demonstration, compared to live demonstration groups

314   (effect of video presentation: estimate = -1.013 ± 0.469, Z = -2.162, p = 0.03).

315

316   **DISCUSSION**

317   In this experiment, we tested whether blue tits were more likely to copy the food choice of a live

318   conspecific, compared to video playback. However, we found that blue tits did not copy a

319   demonstrator's choice of symbol, regardless of how social information was presented. Instead,

320   individuals chose the well with a square symbol more often than other options (Fig. 2a). Because

321   of this preference and the lack of evidence that observers copied a demonstrator's choice, it is

322   difficult to compare the effectiveness of video playback and live demonstration. However, birds'

323   preference for a square symbol was stronger after they received social information, compared to

324   the control groups. This response was consistent across both social information treatments,

325   indicating that even though birds did not choose the same symbol as a demonstrator, they

326   responded to video playback similarly than to a live demonstrator.

327

328   Blue tits might not value social information when the foraging task is relatively simple.

329   Similar to our previous video playback study (Hämäläinen et al., 2017), we did not find evidence

330   that blue tits copied the foraging choice of a conspecific from the video, and neither did they copy

331   the choice of a live demonstrator. Other studies with live demonstrators have similarly failed to

332   find a strong effect of social information in blue tits, showing that only approximately 50% of

333   tested birds learn a novel foraging task socially (Sasvári, 1979; Sasvári, 1985; Aplin, Sheldon &

334   Morand-Ferron, 2013). Social learning seems to be also age- and sex-biased with juveniles

335   (Sasvári 1985) and especially juvenile females being most likely to learn socially (Aplin, Sheldon

336   & Morand-Ferron, 2013). To increase the chances to detect social information use, we therefore

337   decided to test only juveniles, but we were not able to determine the sex of the tested individuals.

338   Birds were also provided with both visual and spatial cues about food reward (the location of the

339   symbols in the foraging task mirrored that in the demonstration), so individuals could have used

340   either type of information. Despite this, we failed to find evidence of blue tits copying a

341   demonstrator's foraging choice. In contrast to our previous study (Hämäläinen et al., 2017), we

342   also did not find evidence that social information influenced birds' latency to start the foraging

343   task. Instead, birds started the task faster after seeing video playback (either control or social

344   information) compared to seeing live stimuli. This probably results from slight differences between

345   the test conditions (i.e. different test cages). After the live demonstration, we covered the

346   observer's view of the demonstrator's cage by sliding a cardboard sheet between the two cage

347   compartments, and this disturbance might have affected the observers more than simply removing

348   the computer monitor following the video demonstration. Therefore, the test with live stimuli

349   might have been slightly more stressful for the birds which could explain the longer hesitation to

350   start the foraging task.

351

352   Despite failing to find evidence that blue tits copied the foraging choice of a demonstrator,

353   social information had an influence on their foraging choices. In all treatments, birds chose the

354   square symbol more often than other two options (cross or white). However, this preference for

355   squares was even stronger when birds received social information from a live or video

356   demonstrator, regardless of the demonstrator's choice. This indicates that simply seeing a

357   demonstrator foraging from the tray enhanced blue tits' preference towards the square symbol.

358   This result is difficult to explain, but it is possible that birds saw a demonstrator as a competitor,

359   which made them to choose the most visible and preferred prey item. Blue tits were found to prefer

360   squares also in our other experiment, where birds were allowed to choose between two prey items

361   with cross and square symbols (Hämäläinen et al., unpublished). Conspicuous square therefore

362   seems to be a more salient cue for blue tits, and contrasting social information about food location

363   did not override this preference. Great tits were recently found to have a high level of self-control

364   ability (Isaksson, Utku Urhan & Brodin, 2018), but to our knowledge this has not been tested in

365   blue tits, and it is possible that blue tits were simply too impulsive to inhibit their response to the

366   preferred signal. This initial preference makes our results difficult to interpret, and different

367   symbol choice might have provided us better evidence of social information use. Interestingly, the

368   preference for square symbols has not been found in great tits (Lindström et al., 2001; Hämäläinen

369   et al., in press), and artificial prey with cross and square symbols have been used in many

370   avoidance learning experiments (e.g. Alatalo & Mappes, 1996; Lindström et al., 1999; Lindström

371   et al., 2001; Thorogood, Kokko & Mappes, 2018). In these experiments squares often represent

372   unpalatable aposematic prey and great tits acquire avoidance to squares faster after receiving social

373   information about their unpalability (Thorogood, Kokko & Mappes, 2018; Hämäläinen et al., in

374   press). Despite the initial preference for squares, blue tits also learn to avoid them faster after

375   observing a negative foraging experience of a conspecific (Hämäläinen et al., unpublished) which

376   shows that blue tits can switch their foraging preferences according to acquired social information.

377   However, our experiment suggests that this is context-dependent, and blue tits do not change their

378   preferences when they receive positive social information and the foraging task is relatively

379   simple.

380

381   Our study highlights the importance of comparing animals' response to real and video

382   stimuli when testing the applicability of video playback (D'Eath, 1998). Without the live

383   demonstrator treatment, it would have been difficult to separate the effect of video presentation

384   from blue tits' tendency to use social information. However, because birds were not more likely

385   to copy the choices of live demonstrators, we can now be more confident that our result is not

386   explained only by the lack of response to video playback. Comparing individuals' response

387   between video and live demonstrations might be important even when videos are found to have an

388   effect on observers' behaviour, as these responses could be different compared to live stimuli. The

389   responses to videos might also be context-dependent: zebra finch males showed a stronger

390   preference for the nest material choice of a live conspecific (Guillette & Healy, 2019), whereas

391   female zebra finches courted video images of males more actively than live males, possibly

392   because of the lack of reciprocal response from males on the video (Swaddle, McBride &

393   Malhotra, 2006). The efficacy of video playback seems to also depend on the features of the video

394   presentation, such as the sound on the video. Zebra finches were shown to copy foraging choices

395   from video playback only when videos did not have sound (Guillette & Healy, 2017), whereas the

396   opposite was true in Burmese red junglefowl (*Gallus gallus spadecius*) that used social information

397   only from videos with sound (McQuoid & Galef, 1993). Together, these studies indicate that video

398   playback can be a useful tool in behavioural studies but its applicability might vary among species

399   and different contexts.

400

401   **Conclusion**

402   The aim of our study was to test the effectiveness of video playback in social learning studies in

403   blue tits by comparing social information use between live and video demonstrations. This

404   comparison proved to be difficult, as we found no evidence of social learning from either live or

405   video demonstrators, indicating that blue tits do not rely on social information in simple foraging

406   tasks. In our experiment the cost to search for food (i.e. lift up the paper cover) was probably low

407   and birds might have ignored social information because personal information was easy to acquire

408   (Laland, 2004; Kendal et al., 2005). It is also possible that birds would have needed to observe

409   several demonstrations from different individuals before relying on social information. In our

410   experiment individuals received information from one demonstrator only, whereas in nature blue

411 tits form foraging flocks and have opportunities to gather information from both conspecifics and

412 heterospecifics (Farine et al., 2015). Individuals are also likely to vary in their tendency to use

413 social information (Sasvári, 1979; Aplin, Sheldon & Morand-Ferron, 2013) and we might have

414 needed a bigger sample size to detect social learning. Furthermore, instead of using positive social

415 information about the location of food, some observers might have seen the demonstrator as a

416 competitor and therefore avoided the same symbol. Nevertheless, we found that blue tits responded

417 to video playback similar to a live demonstrator, as both demonstrations enhanced observers'

418 preference towards squares, indicating that videos had the same effect on birds' behaviour as live

419 demonstrators. However, because of the difficulties to detect social learning in blue tits, the

420 efficacy of videos should be tested also in other contexts before making conclusions of its

421 applicability for this species.

422

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426

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588

589

Figure 1

The experimental set-up.

(A) An example of the ice cube tray that was presented to birds. The tray had 21 wells and three of them (left, middle and right well in the middle row) were covered with a piece of white paper that had either a black cross or a square printed on top, or no symbols (plain white). The same symbols were attached in front of the tray to increase their visibility to observers. The order of the symbols was randomized among birds. (B) The set-up of the live demonstration. The demonstrator (left) and the observer (right) were in individual cages that were separated by plexiglass, so that birds could see each other. In the control treatment the birds saw only the tray. (C) The set-up of the video playback. A computer monitor was placed against a plexiglass front wall of the test cage. Birds were then presented a video of a demonstrator or a control video of the tray.
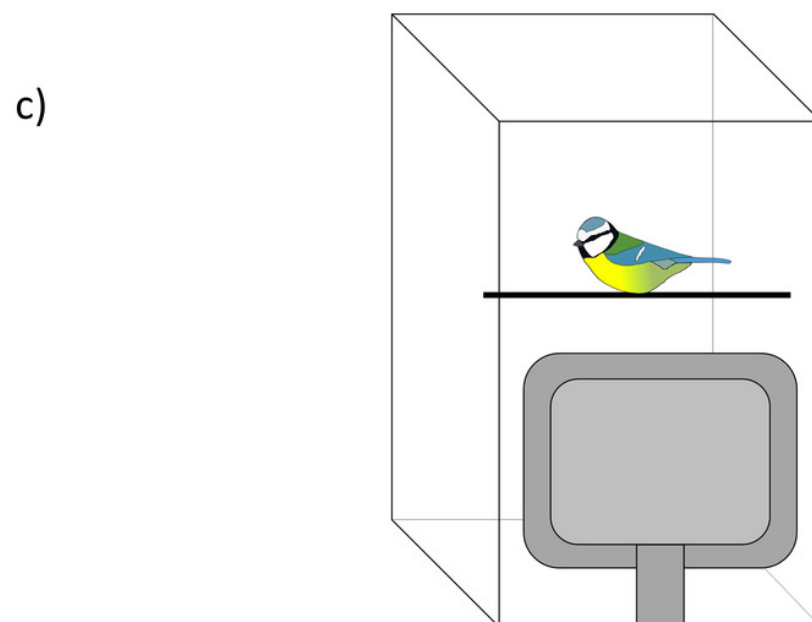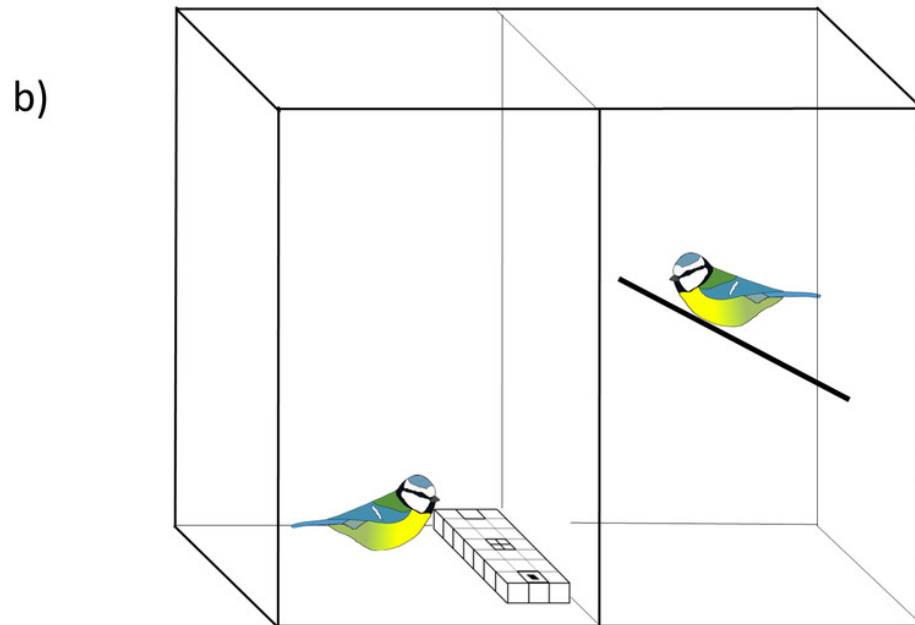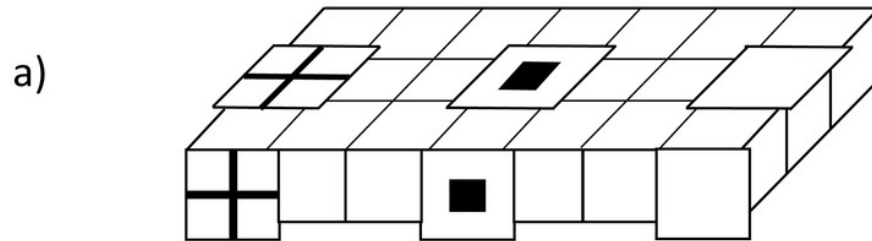
Figure 2

Birds' (n = 40) foraging choices in the experiment.

(A) The percentage of birds choosing each symbol when they were presented (live and video demonstrations combined) (i) a tray only (light grey bars, n = 20), (ii) social information of a demonstrator choosing a cross (dark grey bars, n = 10), or (iii) social information of a demonstrator choosing a square (black bars, n = 10). If birds did not have any preferences towards the symbol, each symbol was predicted to be chosen with 1/3 probability. This is represented by the dotted line (33 %) and the bars above the line indicate birds' preference towards that symbol. (B) Percentage of socially educated birds that copied the demonstrator (i.e. chose the same symbol as a demonstrator vs. one of the other two symbols) after seeing a live demonstrator (light grey bars, n = 10) or video playback of a demonstrator (dark grey bars, n = 10).