Can video playback provide social information for foraging blue tits?

Liisa Hämäläinen [Corresp., 1] , Hannah M Rowland [1, 2] , Johanna Mappes [3] , Rose Thorogood [1, 4]

[1] Department of Zoology, University of Cambridge, Cambridge, United Kingdom

[2] Institute of Zoology, Zoological Society of London, London, United Kindgom

[3] Centre of Excellence in Biological Interactions, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

[4] Department of Biosciences, University of Helsinki, Helsinki, Finland

Corresponding Author: Liisa Hämäläinen
Email address: llh35@cam.ac.uk

Video playback is becoming a common method for manipulating social stimuli in experiments. Parid tits are one of the most commonly studied groups of wild birds. However, it is not yet clear if tits respond to video playback or how their behavioural responses should be measured. Behaviours may also differ depending on what they observe demonstrators encountering. Here we present blue tits (*Cyanistes caeruleus*) videos of demonstrators discovering palatable or aversive prey (injected with bitter-tasting Bitrex) from coloured feeding cups. First we quantify variation in demonstrators' responses to the prey items: aversive prey provoked high rates of beak wiping and head shaking. We then show that focal blue tits respond differently to the presence of a demonstrator on a video screen, depending on whether demonstrators discover palatable or aversive prey. Focal birds faced the video screen more during aversive prey presentations, and made more head turns. Regardless of prey type, focal birds also hopped more frequently during the presence of a demonstrator (compared to a control video of a different coloured feeding cup in an empty cage). Finally, we tested if demonstrators' behaviour affected focal birds' food preferences by giving individuals a choice to forage from the same cup as a demonstrator, or from the cup in the control video. We found that only half of the individuals made their choice in accordance to social information in the videos, i.e. their foraging choices were not different from random. Individuals that chose in accordance with a demonstrator, however, made their choice faster than individuals that chose an alternative cup. Together, our results suggest that video playback can provide social cues to blue tits, but individuals vary greatly in how they use this information in their foraging decisions.

1 **Can video playback provide social information for foraging blue tits?**

2 Liisa Hämäläinen[1], Hannah M. Rowland[1,2], Johanna Mappes[3] and Rose Thorogood[1,4]

4 1. Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

5 2. Institute of Zoology, Zoological Society of London, Regents Park, London, NW1 4RY, UK

6 3. Centre of Excellence in Biological Interactions, Department of Biological and Environmental

7 Science, University of Jyväskylä, P.O. Box 35, 40014 Jyväskylä, Finland

8 4. Department of Biosciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland

10 **Corresponding author**

11 Liisa Hämäläinen, llh35@cam.ac.uk

19   **ABSTRACT**

20   Video playback is becoming a common method for manipulating social stimuli in experiments.

21   Parid tits are one of the most commonly studied groups of wild birds. However, it is not yet clear

22   if tits respond to video playback or how their behavioural responses should be measured.

23   Behaviours may also differ depending on what they observe demonstrators encountering. Here we

24   present blue tits (*Cyanistes caeruleus*) videos of demonstrators discovering palatable or aversive

25   prey (injected with bitter-tasting Bitrex) from coloured feeding cups. First we quantify variation

26   in demonstrators' responses to the prey items: aversive prey provoked high rates of beak wiping

27   and head shaking. We then show that focal blue tits respond differently to the presence of a

28   demonstrator on a video screen, depending on whether demonstrators discover palatable or

29   aversive prey. Focal birds faced the video screen more during aversive prey presentations, and

30   made more head turns. Regardless of prey type, focal birds also hopped more frequently during

31   the presence of a demonstrator (compared to a control video of a different coloured feeding cup in

32   an empty cage). Finally, we tested if demonstrators' behaviour affected focal birds' food

33   preferences by giving individuals a choice to forage from the same cup as a demonstrator, or from

34   the cup in the control video. We found that only half of the individuals made their choice in

35   accordance to social information in the videos, i.e. their foraging choices were not different from

36   random. Individuals that chose in accordance with a demonstrator, however, made their choice

37   faster than individuals that chose an alternative cup. Together, our results suggest that video

38   playback can provide social cues to blue tits, but individuals vary greatly in how they use this

39   information in their foraging decisions.

40

41

42

43

INTRODUCTION

Potential prey items differ in their nutritional benefits and palatability (Skelhorn, Halpin & Rowe, 2016). Therefore, when foraging, animals face decisions that require an estimation of the profitability of prey (Pyke, Pulliam & Charnov, 1977), in order to maximize their fitness. As well as learning from their own experience with prey (Skelhorn, Halpin & Rowe, 2016), predators can gather social information from observing the foraging experiences of others (Galef & Giraldeau, 2001). For example, observing conspecifics consuming palatable food positively influences food preferences in many avian species (Mason & Reidinger, 1981; McQuoid & Galef, 1993; Fryday & Greig-Smith, 1994). However, the potential for information to be available from observing an encounter with less palatable prey has received far less attention.

Many bird species show a clear disgust response by vigorously wiping their beaks on a perch (Clark, 1970; Ganchrow, Steiner & Bartana, 1990). This cue might provide social information about the profitability of food resources to others: for example, young chicks that observe beak wiping and head shaking are less likely to peck at, or consume, the same foods (Johnston, Burne & Rose, 1998; Skelhorn, 2011) and red-winged blackbirds will avoid feeding cups if demonstrators are induced to vomit after eating (Mason & Reidinger, 1982). Parid tits are one of the most studied wild birds in Europe, with an increasing focus on their social behavior and learning (e.g. Sasvári,

62   1979, Marchetti & Drent, 2000; Aplin, Sheldon & Morand-Ferron, 2013). While previous studies

63   have shown that Parid tits can learn a novel foraging task by observing other individuals (Sasvári,

64   1979, Aplin, Sheldon & Morand-Ferron, 2013), it is not yet known how they use social information

65   about food palatability in their foraging decisions.

66

67   Our first aim was to investigate how wild-caught blue tits use information from foraging

68   conspecifics, and if their response differs depending on the palatability of food that demonstrators

69   encounter. However, when studies involve experimentally manipulating social behaviour, it can

70   be difficult to control what stimuli focal birds observe (McQuoid & Galef, 1993). Issues can also

71   arise because of social characteristics of the birds themselves (e.g. dominance, Nicol & Pope,

72   1999). Video playback might circumvent these issues and provide many advantages over live

73   demonstrators. With videos, it is possible to manipulate the characteristics presented and control

74   the timing of the video presentation, thus enabling controlled and standardized stimuli to be

75   presented to focal individuals (D'Eath, 1998, Woo & Rieucau, 2011). Furthermore, use of video

76   playback also has ethical implications. For instance, using video playback to study how individuals

77   use social information about food palatability requires fewer demonstrators to be encouraged to

78   eat unpalatable food (e.g. Mason & Reidinger, 1982).

79

80   Video playback also has potential shortcomings, however, that should be considered when

81   using these stimuli in behavioural studies (D'Eath, 1998, Woo & Rieucau, 2011). For instance, in

82   many species, physical interactions between an observer and a demonstrator play an important role

83   in certain behaviours, such as in aggressive contests and courtship, so the applicability of video

84   playback in these contexts may be limited (D'Eath, 1998). To be able to study focal individuals'

85   responses to specific stimuli, we also need to be sure that individuals pay attention to subtleties in

86   demonstrators' behaviour instead of simply responding to their presence in a video (McQuoid &

87   Galef, 1993). To date, video presentations have been used successfully in both captive (Rowland

88   et al., 1995; Ord et al., 2002; Bird & Emery, 2008) and field studies (Clark, Macedonia &

89   Rosenthal, 1997; Burford, McGregor & Oliveira, 2000; Gunhold, Whiten & Bugnyar, 2014) across

90   different contexts, including studies of mate preference (e.g. Ophir & Galef, 2003), social learning

91   (e.g. McQuoid & Galef, 1993), and predator recognition (e.g. Evans, Macedonia & Marler, 1993),

92   and for a range of taxa, including mammals (Gunhold, Whiten & Bugnyar, 2014), fish (Rowland

93   et al., 1995), lizards (Ord et al., 2002), spiders (Clark & Uetz, 1992), and birds (Rieucau &

94   Giraldeau, 2009; Zoratto et al., 2014). Surprisingly, however, the validity of video playback has

95   not been tested for Parid tits. Therefore, the second aim of our study was to investigate its

96   applicability.

97

98   In this study, we presented focal birds with videos of a demonstrator encountering palatable

99   and aversive prey items in novel, coloured feeding cups. We first quantified variation in

100   demonstrator blue tits' behaviour when encountering these two prey types before presenting

101   standardized videos of these encounters to focal birds. These videos also included a control section

102   that consisted of a different coloured feeding cup in an empty cage; we predicted that individuals

103   would pay more attention to the videos when a conspecific was present. The control section was

104   presented to focal birds both before and after a demonstrator appeared on the screen to investigate

105   if birds' response to control cups would change after they had seen a demonstrator foraging from

106   a different cup. Because demonstrators were more active during the encounter with aversive prey,

107   we also predicted that this might provide more cues and therefore elicit more vigorous response in

108   focal birds, compared to a video of palatable prey.

109

110   Recent studies have shown that acquiring information by observing others does not always

111   result in use of that social information (Carter et al., 2014, Mesoudi et al., 2016). To investigate

112   whether video playback can be used to manipulate social information for blue tits, we used a simple

113   choice test to record if observers preferred to feed from a similarly coloured cup as the

114   demonstrator, or from the different coloured cup (present in the control video). We predicted that

115   focal birds observing a demonstrator encountering a palatable prey, would choose to feed from the

116   same cup as the demonstrator, whereas observation of an encounter with aversive prey would lead

117   them to avoid the cup in which the demonstrator found the distasteful prey item.

118

119   Finally, familiarity with the demonstrator may influence responses to playback. Previous

120   studies have shown that Japanese quail (*Coturnix japonica*) females identify specific males that

121   they see in videos (Ophir & Galef, 2003), and that rooks (*Corvus frugilegus*) spend more time

122   looking at a video of their partner, compared to a video of a nonaffiliated conspecific (Bird &

123   Emery, 2008). The value of social information may also vary depending on familiarity (Firth,

124   Sheldon & Farine, 2016, Mesoudi et al., 2016), or previous experiences (Farine, Spencer &

125   Boogert, 2015), with the demonstrator. We attempted to account for this by including a measure

126   of association strength from our study population's social network, and predicted that the identity

127   of the demonstrator would influence the behavioural responses of observers.

128

129   **METHODS**

130   *Birds and housing*

131   The study was conducted from January to March 2016 at Madingley Wood (0°3.2'E, 52°12.9'N),

132   an established study site in Cambridge. There is an ongoing long-term study of great tit and blue

133   tit populations in the area and birds have been given British Trust of Ornithology (BTO) ID rings

134   and fitted with small passive integrated transponder (PIT) tag fitted to a colour ring since 2012. In

135   January, five sunflower seed feeders were fitted with PIT tag reading antennae and data loggers

136   that scanned birds' unique PIT tag codes when they landed on a feeder. During the winter great

137   tits and blue tits form loose fission-fusion flocks that move between food sources (Ekman, 1989).

138   This flocking behaviour allows us to use the records from the feeders to identify individuals that

139   forage in the same flock. We used a Gaussian mixture model to detect these gathering events

140   (Psorakis et al., 2012), and then calculated social associations (i.e. edge weights in the social

141   network) between individuals based on how often they were present in the same group (gambit of

142   the group approach, Franks, Ruxton & James, 2010).

143

144   Wild blue tits (n = 25) were captured with mist nets (by HMR) in February 2016. Individuals

145   were chosen from the population randomly but PIT tag records enabled us to calculate association

146   strengths for each observer- demonstrator pair used in the experiment. All captured birds were

147   adults (based on plumage) but their sex was unknown. Birds were housed indoors in individual

148   plywood cages (80 cm x 65 cm x 50 cm) with a daily light period of 12 hours. Food (sunflower

149   seeds, peanuts and tallow) and water were provided ad libitum except prior and during the

150   experiment when food restriction was necessary. This restriction lasted no longer than one hour,

151   following guidelines to the operation of the Animal (Scientific Procedures) Act 1986 (2009), and

152   the Association for the Study of Animal Behaviour's Guidelines for the treatment of animals in

153 behavioural research and teaching (2012). Birds were kept in captivity for a maximum of four

154 days until released at the capture site, and they were in auditory (but not visual) contact during

155 housing and experiments. The study was conducted under existing Home Office (PPL 60/4322)

156 and Natural England (2015-6665-SCI-SCI-3**)** licenses held by HMR.

157

158 *Experimental protocol*

159 Prey types

160 We created two types of prey: a palatable mealworm and an aversive mealworm that was injected

161 and coated with 2.5% solution of denatonium benzoate (Bitrex). Bitrex tastes bitter to humans

162 (Chandrashekar et al., 2000) and elicits beak wiping in birds (Skelhorn & Rowe, 2009).

163

164 Video recording

165 We used six individual blue tits as demonstrators for the videos. Three of these birds were first

166 used as observers in the social information use test before recording them as demonstrators. Birds

167 were moved from their home cage to wooden test cages (66 cm x 50 cm x 50 cm) that differ from

168 the home cage in that they have a front wall made of plexiglass. We coated the plexiglass with

169 tinted film that made it possible to observe and film the birds while minimising effects on their

170 behaviour

171

172   We first filmed the demonstrators eating a palatable mealworm in a coloured feeding cup

173 (yellow or green). We then filmed the same individual eating a Bitrex mealworm in a different

174 coloured cup (blue or purple). Because an experience of prey with chemical defences was likely

175   to affect birds' response towards palatable prey and their willingness to consume it, we always

176   filmed responses towards palatable prey first.

177

178   From the videos, we quantified differences in demonstrators' response to palatable and

179   aversive prey from first contact with the prey item until 10 seconds after eating. We measured (i)

180   how long demonstrators spent wiping their beaks on a perch (in seconds), (ii) the number of beak

181   wipes they performed, and (iii) the number of times the head was shaken. We then used these

182   videos to create standardized videos to present to observers (see Videos S1 and S2).

183

184   Video presentation

185   All videos included 45 seconds of a demonstrator finding a prey item in a coloured cup and

186   a demonstrator's response to that prey. In addition, each video included 60 seconds of a different

187   coloured cup in an empty cage to make sure that observers were familiar with both cup colours

188   and their foraging choice would depend on the information in the video instead of novelty of cups.

189   30 seconds of this control video was shown to observers before a demonstrator appeared on the

190   screen and 30 seconds was shown after a demonstrator, as we predicted that observers might pay

191   attention to the cups differently after seeing a foraging conspecific. We used green and yellow

192   cups when demonstrators encountered palatable prey (randomizing which cup colour was shown

193   with a demonstrator and which in an empty cage), and blue and purple cups when demonstrators

194   encountered aversive prey. We showed each observer (n = 22) two videos, once for each prey type.

195   These two videos were shown on sequential days and the order was randomized among birds. We

196   did not change the demonstrator between different prey types, so observers saw the same

197   demonstrator encounter both palatable and aversive prey. Therefore, we think that any differences

198   in responses of the observers are likely due to the prey type, not the demonstrator's identity.

199

200   Observers were moved to a test cage 2 hr before the video presentations to allow habituation

201   to the cage. We then placed a computer monitor (Dell 1908FPc, 19") against the plexiglass front

202   wall of the cage for 15 minutes before showing the video (Fig. 1). This did not seem to stress the

203   birds and they got used to the monitor quickly. We recorded observers during the video-playback

204   (using a DBPOWER 1080P action camera; see Video S3), so that we could classify their behaviour

205   during the different sections of the video playback: when they were shown i) cups before the

206   demonstrator appeared (30 s), ii) the demonstrator's response to the prey (45 s), and iii) the same

207   cups once the demonstrator was no longer present (30 s). From these recordings, we analyzed (i)

208   the time that a bird spent facing the screen or flying, (ii) the number of head turns indicating

209   increased vigilance, and (iii) the number of hops a bird performed on a perch, suggested to indicate

210   increased nervousness such as neophobia (e.g. Heinrich, 1988).

211

212   The entire cage was not in the field of view of the camera, so sometimes birds flying close

213   to the roof of the cage, or holding on near the roof, could not be seen in the video. Therefore, we

214   excluded individuals from our dataset that were visible for less than 30 seconds during the whole

215   105 seconds video (60 seconds of cups only and 45 seconds of a demonstrator). After removing

216   these individuals, our dataset included 13 individuals that were shown videos of a demonstrator

217   encountering both palatable and aversive prey, and 3 individuals that were visible only when they

218   were shown a video of a demonstrator encountering palatable prey. The final sample size for video

219   analysis was therefore 16 observers when prey was palatable (mean time that observers were

220   visible = 81 seconds, range = 38–105 seconds) and 13 observers when it was aversive (mean time

221   that observers were visible = 90 seconds, range = 43–105 seconds).

222

223   Observer social information use test

224   Immediately following each session of video playback, we tested if focal birds (n = 22) used

225   social information from the videos by giving them a choice between two different coloured cups:

226   the cup that a demonstrator fed from, and the cup that was shown in an empty cage without a

227   demonstrator (Fig. 1c). Both cups were filled with sand, so that birds could not see their contents

228   and the time cost to search for prey was higher. Before the test, focal birds had been trained in

229   their home cages to search for food hidden in the sand by offering them mealworms in a white

230   feeding cup. Training was done stepwise, by first offering mealworms that were clearly visible,

231   and then covering them partly with sand, until birds learned to search for worms that were

232   completely hidden. Focal birds were therefore familiar with the foraging task in the experiment.

233   We filmed the focal birds during the test and from these, recorded the time that it took birds to

234   land on a first cup, and their choice. The test was finished after birds had landed on both cups, or

235   after 20 minutes. Two birds in the palatable prey test and one individual in the aversive prey test

236   did not land on either cup in 20 minutes, and were excluded from analyses.

237

238   *Statistical analyses*

239   All analyses were conducted using software R 3.2.2 (R Core Team, 2015). We used *asnipe* package

240   (Farine, 2013) to construct a social network of wild great tit and blue tit populations. We first

241   tested if the associations in the network were non-random by conducting permutation tests on the

242   group matrix. The mean weighted degree of our network was significantly greater than values from

243   the permutations (p = 0.001), demonstrating that our network differed significantly from random.

244   We then calculated association between observers and demonstrators within our network of 331

245   individuals (217 blue tits and 114 great tits). Association strengths were scaled between 0 (never

246   observed in the same flock) and 1 (always observed in the same flock), and in our experiment,

247   these values ranged from 0 to 0.070 (mean = 0.018, sd = 0.021). In addition, we calculated the

248   total number of interactions (i.e. times observed in the same flock) between demonstrators and

249   observers: these ranged from 0 to 107 (mean = 24, sd = 30.803). As both association measures

250   gave similar results when analysing observer's behaviour, we decided to use only association

251   strength in our final analyses.

252

253   We used a Wilcoxon signed ranked test to analyse differences in demonstrators' behaviour

254   when encountering aversive or palatable prey, to allow for the small sample size (n = 6). As the

255   time that birds spent on foraging differed among demonstrators (palatable prey: range = 38–170

256   seconds, median = 77 seconds; aversive prey: range = 16–115 seconds, median = 62 seconds) we

257   first divided the time spent on beak wiping and a number of beak wipes and head shakes with the

258   total time foraging, and then compared these rates between aversive and palatable prey.

259

260   For analyses of observers' behaviour, we next used generalized linear mixed effects models

261   with appropriate error distributions, implemented using the *lme4* package (Bates et al., 2014).

262   Explanatory variables in all models included an interaction between the effects of a demonstrator

263   being present (cups before/demonstrator/cups after) with the prey type (palatable/aversive), the

264   observer's association with its demonstrator as determined from the social network, and the test

265   order (first/second test). In addition, we included an observer's identity and a demonstrator video

266   as random effects. The baseline level of each model included an initial cup presentation, aversive

267   prey type, and a first video presentation. As the length of time that birds were visible in videos

268   differed, we modeled the time observers faced the screen or spent flying versus the length of time

269   observers performed other behaviours (i.e. total time visible – time facing a video or flying) as a

270   bound response variable with a binomial error distribution. Similarly, we converted the number of

271   head turns and hops into a rate by dividing the number of times they occurred by the total time a

272   bird was visible. We then converted these rates to integers by multiplying them by 30 seconds,

273   which was the most common length of time a bird was visible during each section of the videos.

274   We modeled head turns using a Poisson error distribution, but hopping with a negative binomial

275   error distribution as it was right-skewed.

276

277   Finally, we analysed if social information in the videos affected which cup observers landed

278   on first and how fast they made their choice, using again generalized linear mixed effects models.

279   To test the effects of video on birds' first choice, we included the choice (same/different cup that

280   a demonstrator fed from) as a response variable, and prey type (palatable/aversive), the observer's

281   association with its demonstrator, and the test order as explanatory variables, using binomial error

282   distribution. The baseline level of the model included the video playback of aversive prey and a

283   first video presentation. As the distribution of time before birds chose the cup was right-skewed,

284   we modeled it with a negative binomial error distribution, using the time before a choice as a

285   response variable, and an interaction between prey type (palatable/aversive), social information

286   use (0/1, i.e. not matching/matching a demonstrator's behaviour), and the test order as explanatory

287   variables. The baseline level of the model included the video playback of aversive prey, a first

288   video presentation and individuals that did not match a demonstrator's behaviour. Bird identity

289 and a demonstrator video were included as random effects in both models. Most of the birds landed

290 on a cup during the first five minutes after cups were presented. Two individuals, however, were

291 considerably slower at choosing in the aversive prey test, and landed on a cup only after 15

292 minutes. We therefore considered them as outliers, and removed them from the final analysis.

293

294 **RESULTS**

295 *Demonstrators' response*

296 Demonstrators responded differently to palatable and aversive prey. The time demonstrators spent

297 wiping their beaks on a perch (Wilcoxon signed-ranked test, $P = 0.03$) as well as the total number

298 of beak wipes (Wilcoxon signed-ranked test, $P = 0.03$, Fig. 2a) were both significantly greater

299 when demonstrators encountered aversive prey (time spent on beak wiping: median = 14 seconds,

300 range = 4–23 seconds; number of beak wipes: median = 49, range = 20–107), compared to

301 palatable prey (time spent on beak wiping: median = 1.5 seconds, range = 0–5 seconds; number of

302 beak wipes: median = 5.5, range = 0–17). Demonstrators also performed more headshakes when

303 eating aversive prey (median = 17.5, range = 5–27) than when eating palatable prey (Wilcoxon

304 signed-ranked test, $P = 0.03$; Fig. 2b; median = 0, range = 0–5).

305

306 *Focal birds' response to video-playback*

307 Facing the screen

308 The time observers faced the video screen depended on the prey type a demonstrator encountered

309 (Fig. 3a): observers faced the screen less during (demonstrator presence * prey type; estimate = -

310   0.836 ± 0.252, Z = -3.320, p < 0.001) and after (cups after demonstrator playback * prey type:

311   estimate = -0.570 ± 0.269, Z = -2.118, p = 0.03) the presentation of palatable prey compared to

312   aversive prey. There were no significant differences between video types in the way observers

313   responded to cups only before the presentation of a demonstrator (estimate = 0.318 ± 0.720, Z =

314   0.441, p = 0.66), suggesting that it was the behaviour of the demonstrator that influenced how long

315   observers faced the video screen. Following presentation of any demonstrators, observers paid

316   overall less attention to the screen showing cups only (estimate = -0.392 ± 0.181, Z = -2.167, p =

317   0.03; Fig. 3a). Focal birds also faced the screen more during the second test (estimate = 0.386 ±

318   0.144, Z = 2.679, p = 0.007). In addition, association strength with a demonstrator had a significant

319   effect on focal birds' behaviour, showing that individuals faced the screen less when they were

320   more closely associated with a demonstrator (estimate = -28.099 ± 12.296, Z = -2.285, p = 0.022).

321   The distribution of association scores, however, was skewed, as most of the individuals had low

322   association scores with a demonstrator, and it is therefore difficult to interpret this result. Finally,

323   bird identity (variance = 0.674) and demonstrator video (variance = 1.417), included to the model

324   as random effects, explained some of the observed variation. The final model is presented in

325   Supplemental information (File S1, Table 1).

326

327   Flying

328   Although observers varied in how much time they spent flying during video playback (range = 0–

329   29 seconds, mean = 4.8 seconds), there was no effect of demonstrator presence and prey type on

330   this behaviour (compared to initial cup presentation, demonstrator present * prey type: estimate =

331   0.185 ± 0.289, Z = 0.640, p = 0.52; cups after demonstrator playback * prey type: estimate = 0.169

332   ± 0.310, Z = 0.544, p = 0.59) and their interactions were therefore removed from the final model.

333   The final model shows that a demonstrator's presence, regardless of prey type (estimate = -0.248

334   ± 0.144, Z = -1.729, p = 0.16), the test order (estimate = 0.114 ± 0.158, Z = 0.718, p = 0.47) or the

335   association between observer and demonstrator (estimate = 14.913 ± 13.957, Z = 1.069, p = 0.29)

336   did not affect the time that observers were flying during video playback, but random effects

337   explained some of the observed variation (variance for bird identity = 0.908; variance for

338   demonstrator video = 0.987; Table 2 in File S1).

339

340   Head turns

341   The number of head turns observers performed depended on a demonstrator's presence in the video

342   and prey type a demonstrator encountered (Fig. 3b). Observers performed less head turns during

343   (demonstrator presence * prey type; estimate = -0.393 ± 0.196, Z = -2.002, p = 0.045) and after

344   (cups after demonstrator playback * prey type: estimate = -0.543 ± 0.199, Z = -2.726, p = 0.006)

345   the presentation of palatable prey compared to aversive prey. During the initial cup presentation

346   observers' responses did not differ significantly between these video types (estimate = 0.015 ±

347   0.278, Z = 0.055, p = 0.96). The test order (estimate = 0.188 ± 0.141, Z = 1.337, p = 0.181), or

348   association between demonstrator and observer (estimate = -8.142 ± 5.062, Z = -1.608, p = 0.11)

349   had no effect on the number of head turns performed, and also the variance estimates for the

350   random effects were small (variance for bird identity = 0.081; variance for demonstrator video =

351   0.158; Table 3 in File S1).

352

353   Hops

354   The number of hops that observers performed did not depend on the prey type a demonstrator

355   encountered (compared to initial cup presentation, demonstrator present * prey type: estimate = -

356   1.375 ± 0.951, Z = -1.446, p = 0.15; cups after demonstrator playback * prey type: estimate = -

357   0.636 ± 1.015, Z = -0.626, p = 0.53), so we removed these interactions from the final model. The

358   final model shows that birds were hopping significantly more in the presence of a demonstrator

359   compared to initial cup presentation (estimate = 1.967 ± 0.565, Z = 3.482, p < 0.001; Fig. 3c), or

360   to the cup presentation after a demonstrator (estimate = 0.953 ± 0.460, Z = 2.071, p = 0.04). Again,

361   the test order (estimate = 0.135 ± 0.452, Z = 0.297, p = 0.77), or the association with a demonstrator

362   (estimate = 6.237 ± 10.131, Z = 0.616, p = 0.54) had no effect on an observer's behaviour and the

363   variance estimates for random effects were small (variance for bird identity < 0.001; variance for

364   demonstrator video < 0.001; Table 4 in File S1). One individual hopped considerably more than

365   the others, but re-running analyses without it did not change the results. In particular, the increase

366   in hopping in the presence of a demonstrator remained significant (hops during presence of a

367   demonstrator versus initial cup presentation: estimate = 1.653 ± 0.415, Z = 3.981, p < 0.001).

368

369   *Social information use*

370   Prey type in the video (estimate = 0.372 ± 0.814, Z = 0.457, p = 0.65), the test order (estimate =

371   0.829 ± 0.745 Z = 1.113, p = 0.27), or the association score with a demonstrator (estimate = -

372   17.137 ± 14.739, Z = -1.163, p = 0.25) did not have a significant effect on an observer's cup choice

373   but demonstrator video, included as a random effect, explained some of the observed variation

374   (variance for bird identity = 0.031; variance for demonstrator video = 0.442; Table 5 in File S1).

375   After observing a demonstrator discovering palatable prey in a coloured cup, only 10 birds landed

376   first on that cup, whereas 10 birds chose the alternative coloured cup (binomial test, 10/20

377   compared to equal probability, p = 1). Similarly, after video-playback of a demonstrator's response

378   towards aversive prey, only 12 birds avoided the cup that the demonstrator fed from, whereas 9

379   birds landed on it first (binomial test, 9/21 compared to equal probability, p = 0.66). Only 5 birds

380   matched our predictions in both tests, choosing the same cup colour as a demonstrator after

381   receiving information about palatable prey, and avoiding that colour after seeing a demonstrator's

382   disgust response. Again, this was not different from what would be expected if birds foraged

383   randomly (binomial test, 5/20 compared to probability of 0.25, p = 1).

384

385   Information in the video, however, did appear to affect the latency of observers' cup choice.

386   Observers made their choice faster when they chose a cup matching the social information

387   provided in the video (compared to birds that did not match our predictions, estimate = -0.837 ±

388   0.265, Z = -3.154, p = 0.002; Fig. 4). This did not vary between the prey types observed (estimate

389   = -0.024 ± 0.262, Z = -0.092, p = 0.93), or between the first and the second test (estimate = 0.009

390   ± 0.226, Z = 0.043, p = 0.97). Therefore, in both tests birds chose the cup faster when their decision

391   matched a demonstrator's behaviour. The variance estimates for random effects were small

392   (variance for bird identity = 0.167; variance for demonstrator video = 0.062; Table 6 in File S1).

393

394   **DISCUSSION**

395   Our experiment shows that blue tits, like many other species tested (e.g. McQuoid & Galef, 1993;

396   Rieucau & Giraldeau, 2009; Zoratto et al., 2014) pay attention to video playback of a conspecific.

397   Focal birds were more active in the presence of a demonstrator than when videos showed a cage

398   without a conspecific present, and observers' behaviour differed depending on which prey type

399   was being sampled in the demonstration video. Furthermore, the identity of the demonstrator also

400   explained some variation in observers' behaviour. Despite our predictions, however, we found that

401   only half of the focal birds then chose to forage from the cup according to the information that

402   demonstrators had provided, the same as if birds foraged randomly. Information from video

403   playback, however, did influence how quickly birds made a choice: those that chose in accordance

404   with the demonstrator did so more quickly. Together, these results suggest that social cues in video

405   playback could provide blue tits with information about prey profitability, but the birds either did

406   not acquire or chose not to use this social information in their decision-making.

407

408   Similar to previous studies, (Clark, 1970; Skelhorn, 2011), we found that demonstrators

409   responded to aversive prey by performing beak wipes and headshakes. Head shaking and beak

410   wiping has been proposed to provide observers with information about potentially toxic prey

411   (Johnston, Burne & Rose, 1998; Skelhorn, 2011). This kind of 'disgust' behavior could increase

412   the benefits for paying attention to a demonstrator, as encounters with aversive prey can elevate

413   internal toxin levels (Skelhorn, Halpin & Rowe, 2016) or even increase the risk of mortality when

414   prey are lethal (Longson & Joss, 2006). Perhaps this explains why we observed differences in focal

415   birds' behavior between different video types, and why observers continued to pay more attention

416   to a cup in an empty cage after observing a demonstrator encounter aversive prey. Alternatively,

417   it is possible that focal birds faced the video screen and made more head turns when demonstrators

418   discovered aversive prey simply because demonstrators were more active during this presentation.

419   This could be investigated further by presenting focal birds videos that contain different cues but

420   show similar amounts of activity.

421

422   Other research on social information use by blue tits also finds that use of social information

423   is low: only approximately 50 % of individuals learn to solve a novel feeding task after observing

424   a conspecific solve it (Sasvári, 1979; Aplin, Sheldon & Morand-Ferron, 2013). These studies differ

425   from our experiment because in task solving tests, none of the individuals are expected to solve

426   the task without demonstration or training; in our experiment, individuals had a 50 % probability

427   to choose the predicted cup just by chance. Our result, that focal birds' foraging decisions do not

428   differ from what would be expected if birds were choosing the cup randomly, is difficult to

429   interpret. Individuals that chose the predicted cup in our experiment may have used social

430   information, or may have just chosen by chance a cup that matched a demonstrator's behaviour.

431   However, we found that individuals made their choice faster when choosing a cup that matched

432   the information in the video. It has been suggested that one of the costs of personal information

433   use is time and energy that individuals need for information gathering (Dall et al., 2005), and the

434   observed time difference in our experiment indicates that the time cost to make a decision might

435   be higher if individuals do not use social information. However, if we assume that all birds that

436   chose the cup according to our predictions used social information because they made their choices

437   more quickly, it is difficult to explain why all the other birds would have chosen an alternative

438   cup, as we would expect their choices to be random. Alternatively, if we assume that none of the

439   birds used social information from the videos, it is difficult to explain the observed difference in

440   their decision times.

441

442   One possibility is that some of the focal birds used the cues from videos differently than

443   others. For example, neophobia or competition could have affected observers' foraging choices

444   (Gibelli & Dubois, 2016). After seeing a demonstrator eating palatable prey from a coloured cup,

445   some observers might interpret that cup to be empty and therefore choose an alternative cup to

446   avoid competition. On the other hand, observers might interpret the video of a cup in an empty

447   cage so that demonstrators did not want to forage from that cup. Individuals might therefore choose

448   the same cup as a demonstrator just to avoid novelty, even after seeing a demonstrator eating

449   aversive prey. Furthermore, birds were pre-trained to locate favourable prey items from food cups,

450   albeit of different colour, so instead of using social information about food unpalatability, they

451   might have relied on their previous experience with prey (e.g. Kendal, Coolen & Laland, 2004).

452   In addition, individuals might have had preferences for different cup colours, but we did not find

453   that they chose any of the coloured cups more often than others, and the cup colours for

454   demonstrator and control videos were randomized.

455

456   It has been suggested that individuals are more likely to rely on social information when the

457   costs to acquire personal information increase (Kendal, Coolen & Laland, 2004; Kendal et al.,

458   2005), and it is possible that in our experiment the cost of foraging from the "wrong" cup was too

459   low to detect information use. In addition, some characteristics of observers such as sex and age

460   (Loukola, Seppänen & Forsman, 2012; Aplin, Sheldon & Morand-Ferron, 2013, Guillette &

461   Healy, 2014), personality (Marchetti & Drent, 2000), or dominance status (Nicol & Pope, 1999),

462   could have made it more difficult for us to detect an effect of social information on cup choice. In

463   a previous study of social learning in blue tits, for example, juvenile females were almost twice as

464   likely to learn the novel foraging task than other age/sex classes, and only 37.5% of adults overall

465   learned by observing others (Aplin, Sheldon & Morand-Ferron, 2013). In our study, all observers

466   were adult birds and we do not know their sex. Future work should therefore present blue tits with

467   more complicated tests with higher foraging costs (e.g. Aplin, Sheldon & Morand-Ferron, 2013),

468   and ensure sex and age are known. Still, in our experiment only five birds made their choice in

469   accordance with the demonstrator in both tests, so individuals were not consistent in their

470   information use and it is therefore unlikely that their sex would explain the observed variation.

471   The variation in information use between the two tests, however, is not surprising, as individuals

472   might value different type of social information differently. For instance, individuals' current toxin

473   levels and energetic state might influence their decision to attack aversive prey (Skelhorn, Halpin

474   & Rowe, 2016), and also increase the value of social information about prey unpalatability.

475

476   To further investigate the effectiveness of video playback in Parid tits, it could be useful to

477   compare focal birds' responses to videos to their response to live demonstrators. This, however,

478   would be difficult to conduct as live demonstrators vary in when and how they perform behaviours.

479   For example, individuals' propensity to eat aversive prey could depend on intrinsic differences,

480   such as their current energetic state (Skelhorn, Halpin & Rowe, 2016) that might vary over time.

481   In our experiment, the time that demonstrators spent eating aversive prey differed considerably

482   among individuals, and some of the demonstrators showed a stronger disgust response (more beak

483   wipes and head shakes) than others. With video playback, we could present focal birds

484   standardized videos of demonstrators' responses but the use of live demonstrators would include

485   much more variation, and therefore require a high number of individuals to be tested. A second

486   potential problem with our experiment was that vocal communication between observer and

487   demonstrator was impossible. However, we did not hear any of the focal birds vocalize during

488   playback, nor did any of the demonstrators vocalize during filming. We therefore suggest that our

489   results of focal birds' behavioural changes during video playback, the different responses

490   depending on demonstrator identity, and the effect we detected on the latency to forage, provide

491   adequate evidence that blue tits pay attention to video playback. We assert that this could be a

492   valid method for studying social information use.

493

494   **Conclusion**

495   In conclusion, our study showed that blue tits respond to video playback of a conspecific,

496   and that individuals paid more attention to demonstrators encountering aversive prey. This

497   indicates that they did not only respond to the presence of a demonstrator but also observed

498   differences in a demonstrator's behaviour. The cues from videos then influenced focal birds'

499   behaviour in a foraging task, as individuals that chose to forage in accordance with a demonstrator

500   made their foraging choice faster. The proportion of birds that made their choice according to

501   information from videos, however, did not differ from random, and we are therefore unable to

502   explain the differences in these two measures of foraging. Together, our results suggest that video

503   playback of a conspecific can provide social cues to blue tits, and video playback therefore

504   provides a promising method for studying social behaviour and learning in Parid tits, with potential

505   application for studies in both captivity and the wild. However, we do not know how these social

506   cues are later used in decision-making, and this seems to vary greatly among individuals.

507

508   **Acknowledgements**

509   We are grateful to Maggie Dinsdale, Sam Melvin and Sarah Manley for taking care of the birds,

510   Ian Millar for helping to build experimental facilities and Karen Spencer for Home Office support.

511   We also thank Neeltje Boogert and Rebecca Kilner for helpful comments on the study and

512   manuscript.

513

514 **REFERENCES**

515 Aplin, L.M., Sheldon, B.C. & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning
516   and individual variation in the blue tit, Cyanistes caeruleus. *Animal Behaviour*, 85, 1225–
517   1232. http://dx.doi.org/10.1016/j.anbehav.2013.03.009

518 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models
519   using lme4. Journal of Statistical Software, 67, 1–48.
520   http://dx.doi.org/10.18637/jss.v067.i01

521 Bird, C.D. & Emery, N.J. (2008). Using video playback to investigate the social preferences of
522   rooks, Corvus frugilegus. *Animal Behaviour*, 76, 679–687.
523   http://dx.doi.org/10.1016/j.anbehav.2008.04.014

524 Burford, F.R.L., McGregor, P.K. & Oliveira, R.F. (2000). Response of fiddler crabs (Uca
525   tangeri) to video playback in the field. *Acta ethologica*, 3, 55–59.
526   http://dx.doi.org/10.1007/s102110000020

527 Carter, A. J., Marshall, H. H., Heinsohn, R. & Cowlishaw, G. (2014). Personality predicts the
528   propensity for social learning in a wild primate. *PeerJ*, 2, e283.
529   https://doi.org/10.7717/peerj.283

530 Chandrashekar, J., Mueller, K. L., Hoon, M. A., Adler, E., Feng, L., Guo, W., Zuker, C.S. &
531   Ryba, N. J. (2000). T2Rs function as bitter taste receptors. *Cell*, 100, 703–711.
532   http://dx.doi.org/10.1016/S0092-8674(00)80706-0

533 Clark, D.L. & Uetz, G.W. (1992). Morph-independent mate selection in a dimorphic jumping
534   spider: demonstration of movement bias in female choice using video-controlled courtship
535   behaviour. *Animal Behaviour*, 43, 247–254. http://dx.doi.org/10.1016/S0003-
536   3472(05)80220-9

537 Clark, D. L., Macedonia, J. M. & Rosenthal, G. G. (1997). Testing video playback to lizards in
538   the field. *Copeia*, 2, 421–423. http://dx.doi.org/10.2307/1447764

539 Clark, G.J. (1970). Avian Bill-Wiping. *The Wilson Bulletin*, 82, 279–288.

540 D'Eath, R.B. (1998). Can video images imitate real stimuli in animal behaviour experiments?
541   *Biological Reviews*, 73, 267–292. http://dx.doi.org/10.1111/j.1469-185X.1998.tb00031.x

542 Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M. & Stephens, D. W. (2005).
543   Information and its use by animals in evolutionary ecology. *Trends in ecology & evolution*,
544   20, 187–193. http://dx.doi.org/10.1016/j.tree.2005.01.010

545 Ekman, J. (1989). Ecology of non-breeding social systems of Parus. *The Wilson Bulletin*, 101,
546 263–288.

547   Evans, C.S., Macedonia, J.M. & Marler, P. (1993). Effects of Apparent Size and Speed on the
548 Response of Chickens, Gallus gallus, to Computer-Generated Simulations of Aerial
549 Predators. *Animal Behaviour*, 46, 1–11. http://dx.doi.org/10.1006/anbe.1993.1156

550 Farine, D.R. (2013). Animal social network inference and permutations for ecologists in R using
551 asnipe. *Methods in Ecology and Evolution*, 4, 1187–1194. http://dx.doi.org/10.1111/2041-
552 210X.12121

553 Farine, D. R., Spencer, K. A. & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra
554 finches to switch social learning strategies. *Current Biology*, 25, 2184–2188.
555 http://dx.doi.org/10.1016/j.cub.2015.06.071

556 Firth, J. A., Sheldon, B. C. & Farine, D. R. (2016). Pathways of information transmission among
557 wild songbirds follow experimentally imposed changes in social foraging structure.
558 *Biology letters*, 12. http://dx.doi.org/10.1098/rsbl.2016.0144

559 Franks, D.W., Ruxton, G.D. & James, R. (2010). Sampling animal association networks with the
560 gambit of the group. *Behavioral Ecology and Sociobiology*, 64, 493–503.
561 http://dx.doi.org/10.1007/s00265-009-0865-8

562 Fryday, S. L. & Greig-Smith, P. W. (1994). The effects of social learning on the food choice of
563 the house sparrow (Passer domesticus). *Behaviour*, 3, 281–300.
564 http://dx.doi.org/10.1163/156853994X00299
565
566 Galef, B. G. & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: causal
567 mechanisms and adaptive functions. *Animal behaviour*, 61, 3–15.
568 http://dx.doi.org/10.1006/anbe.2000.1557

569 Ganchrow, J. R., Steiner, J. E., & Bartana, A. (1990). Behavioral reactions to gustatory stimuli in
570 young chicks (Gallus gallus domesticus). *Developmental psychobiology*, 23, 103–117.
571 http://dx.doi.org/10.1002/dev.420230202

572 Gibelli, J., & Dubois, F. (2016). Does personality affect the ability of individuals to track and
573 respond to changing conditions? *Behavioral Ecology*.
574 http://dx.doi.org/10.1093/beheco/arw137

575 Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in Zebra Finches.
576 *Behavioural Processes,* 108, 177–182. http://dx.doi.org/10.1016/j.beproc.2014.10.011
577

578 Gunhold, T., Whiten, A. & Bugnyar, T. (2014). Video demonstrations seed alternative problem-
579 solving techniques in wild common marmosets. *Biology letters*, 10, 1–5.
580 http://dx.doi.org/10.1098/rsbl.2014.0439

581   Heinrich, B. (1988). Why do ravens fear their food? *The Condor*, 90, 950–952.
582   http://dx.doi.org/10.2307/1368859

583   Johnston, A., Burne, T. & Rose, S. (1998). Observation learning in day-old chicks using a one-
584   trial passive avoidance learning paradigm. *Animal behaviour*, 56, 1347–1353.
585   http://dx.doi.org/10.1006/anbe.1998.0901

586   Kendal, R. L., Coolen, I., & Laland, K. N. (2004). The role of conformity in foraging when
587   personal and social information conflict. *Behavioral Ecology*, 15, 269-277.
588   http://dx.doi.org/10.1093/beheco/arh008

589   Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use
590   of social and asocial learning. *Advances in the Study of Behavior*, 35, 333-379.
591   http://dx.doi.org/10.1016/S0065-3454(05)35008-X

592   Longson, C. G., & Joss, J. M. P. (2006). Optimal toxicity in animals: predicting the optimal level
593   of chemical defences. *Functional Ecology*, 20, 731–735.
594   http://dx.doi.org/10.1111/j.1365-2435.2006.01148.x

595   Loukola, O. J., Seppänen, J. T., & Forsman, J. T. (2012). Intraspecific social information use in
596   the
597   selection of nest site characteristics. *Animal Behaviour*, 83, 629–633.
598   http://dx.doi.org/10.1016/j.anbehav.2011.12.004

599   Marchetti, C. & Drent, P. J. (2000). Individual differences in the use of social information in
600   foraging by captive great tits. *Animal Behaviour*, 60, 131–140.
601   http://dx.doi.org/10.1006/anbe.2000.1443

602   Mason, J. R. & Reidinger R. F. (1981). Effects of social facilitation and observational learning
603   on feeding behavior of the red-winged blackbird (Agelaius phoeniceus). *The Auk*, 778–784.

604   Mason, J.R. & Reidinger, R. F. (1982). Observational learning of food aversions in red-winged
605   blackbirds (Agelaius phoeniceus). *The Auk*, 99, 548–554.

606   Mesoudi, A., Chang, L., Dall, S. R. & Thornton, A. (2016). The Evolution of Individual and
607   Cultural Variation in Social Learning. *Trends in ecology & evolution*, 31, 215–225.
608   http://dx.doi.org/10.1016/j.tree.2015.12.012

609   McQuoid, L. M. & Galef, B. G. (1993). Social stimuli influencing feeding behaviour of Burmese
610   fowl: video analysis. *Animal Behaviour*, 46, 13–22.
611   http://dx.doi.org/10.1006/anbe.1993.1157

612   Nicol, C. J. & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging
613   success on social learning in laying hens. *Animal Behaviour*, 57, 163–171.
614   http://dx.doi.org/10.1006/anbe.1998.0920

615 Ophir, A.G. & Galef, B.G. (2003). Female Japanese quail affiliate with live males that they have
616   seen mate on video. *Animal Behaviour*, 66, 369–375.
617   http://dx.doi.org/10.1006/anbe.2003.2229

618 Ord, T. J., Peters, R. A., Evans, C. S. & Taylor, A. J. (2002). Digital video playback and visual
619   communication in lizards. *Animal Behaviour*, 63, 879–890.
620   http://dx.doi.org/10.1006/anbe.2001.1983

621 Psorakis, I., Roberts, S. J., Rezek, I. & Sheldon, B. C. (2012). Inferring social network structure
622   in ecological systems from spatio-temporal data streams. *Journal of the Royal Society*
623   *Interface*, 9, 3055–3066. http://dx.doi.org/10.1098/rsif.2012.0223

624 Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: a selective review of
625   theory and tests. *Quarterly review of Biology*, 52, 137-154.

626 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
627   Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
628
629 Rieucau, G. & Giraldeau, L. A. (2009). Video playback and social foraging: simulated
630   companions produce the group size effect in nutmeg mannikins. *Animal Behaviour*, 78,
631   961–966.
632   http://dx.doi.org/10.1016/j.anbehav.2009.06.023
633
634 Rowland, W. J., Bolyard, K. J., Jenkins, J. J. & Fowler, J. (1995). Video playback experiments
635   on stickleback mate choice: female motivation and attentiveness to male colour cues.
636   *Animal Behaviour*, 49, 1559–1567. http://dx.doi.org/10.1016/0003-3472(95)90077-2

637 Sasvári, L. (1979). Observational learning in great, blue and marsh tits. *Animal Behaviour*, 27,
638   767–771. http://dx.doi.org/10.1016/0003-3472(79)90012-5

639 Skelhorn, J. (2011). Colour biases are a question of conspecifics' taste. *Animal Behaviour*, 81,
640   825–829. http://dx.doi.org/10.1016/j.anbehav.2011.01.017

641 Skelhorn, J. & Rowe, C. (2009). Distastefulness as an antipredator defence strategy. *Animal*
642   *Behaviour*, 78,761–766. http://dx.doi.org/10.1016/j.anbehav.2009.07.006

643 Skelhorn, J., Halpin, C. G., & Rowe, C. (2016). Learning about aposematic prey. *Behavioral*
644   *Ecology*, 27, 955–964. http://dx.doi.org/10.1093/beheco/arw009

645 Woo, K.L. & Rieucau, G. (2011). From dummies to animations: A review of computer-animated
646   stimuli used in animal behavior studies. *Behavioral Ecology and Sociobiology*, 65, 1671–
647   1685. http://dx.doi.org/10.1007/s00265-011-1226-y

648 Zoratto, F., Manzari, L., Oddi, L., Pinxten, R., Eens, M., Santucci, D., Alleva E. & Carere, C.
649   (2014). Behavioural response of European starlings exposed to video playback of

650   conspecific flocks: effect of social context and predator threat. *Behavioural processes*, 103,
651   269–277. http://dx.doi.org/10.1016/j.beproc.2014.01.012

652 Government UK, 2009. Guidance to the operation of the Animals (Scientific Procedures).
653   (1986). ScotPIL manual - avian species.

654 Guidelines for the treatment of animals in behavioural research and teaching. (2012). *Animal*
655   *Behaviour,* 83, 301-309. http://dx.doi.org/10.1016/j.anbehav.2011.10.031

656

Figure 1

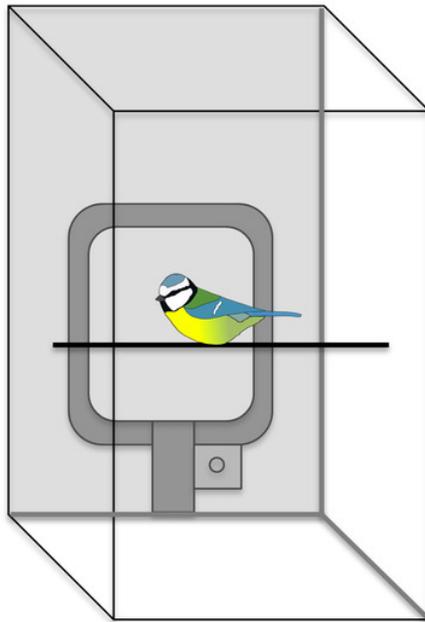
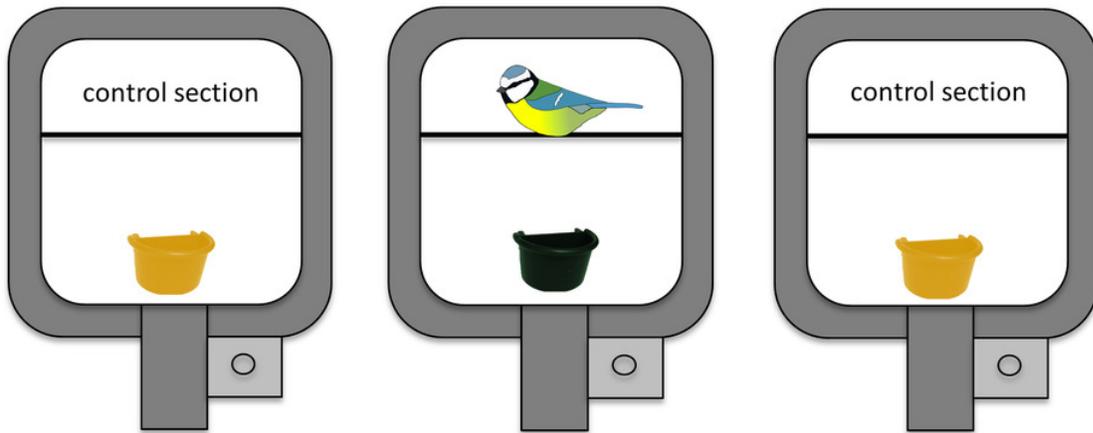
The experimental set-up.

a) The view of the test cage (a computer monitor and a camera recording focal birds' behaviours were placed against a plexiglass wall of the cage), b) presentation of video playback including a demonstrator discovering prey from a coloured feeding cup (45 seconds) and two control sections of a different coloured cup (30 seconds before and 30 seconds after a demonstrator), c) social information use test, where focal birds had a choice to forage from the same cup as the demonstrator, or from the cup in the control video.

a)

b)

control section

control section

c)

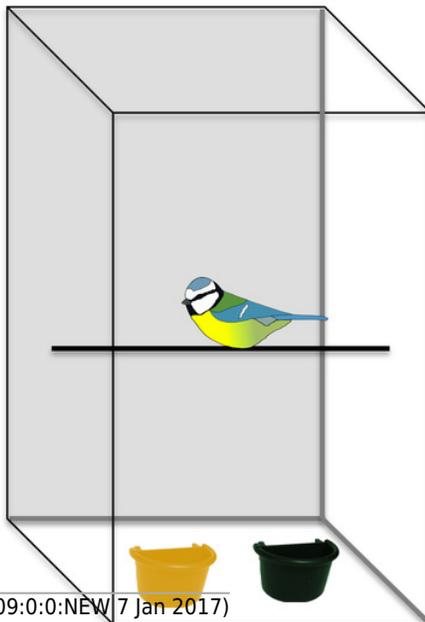



Figure 2

Demonstrators' response.

The number of beak wipes (a) and headshakes (b) demonstrators (n = 6) performed when encountering aversive or palatable prey.

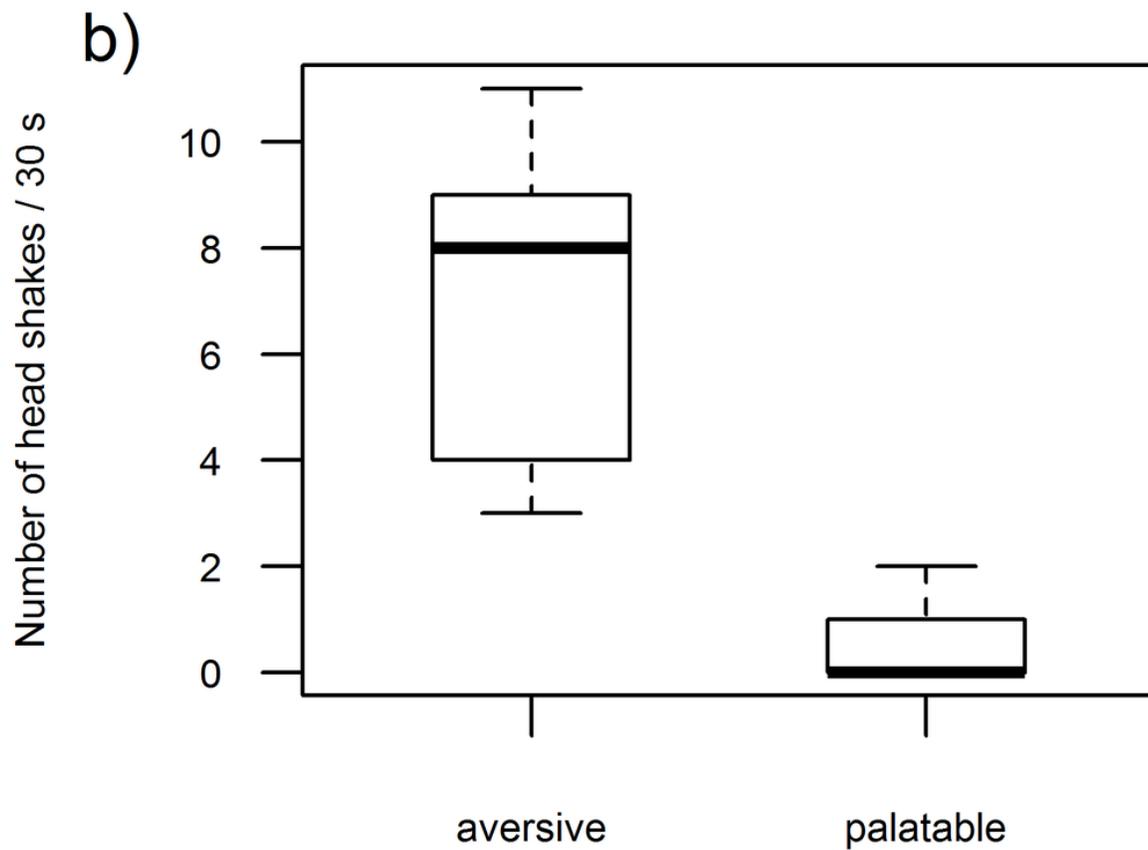
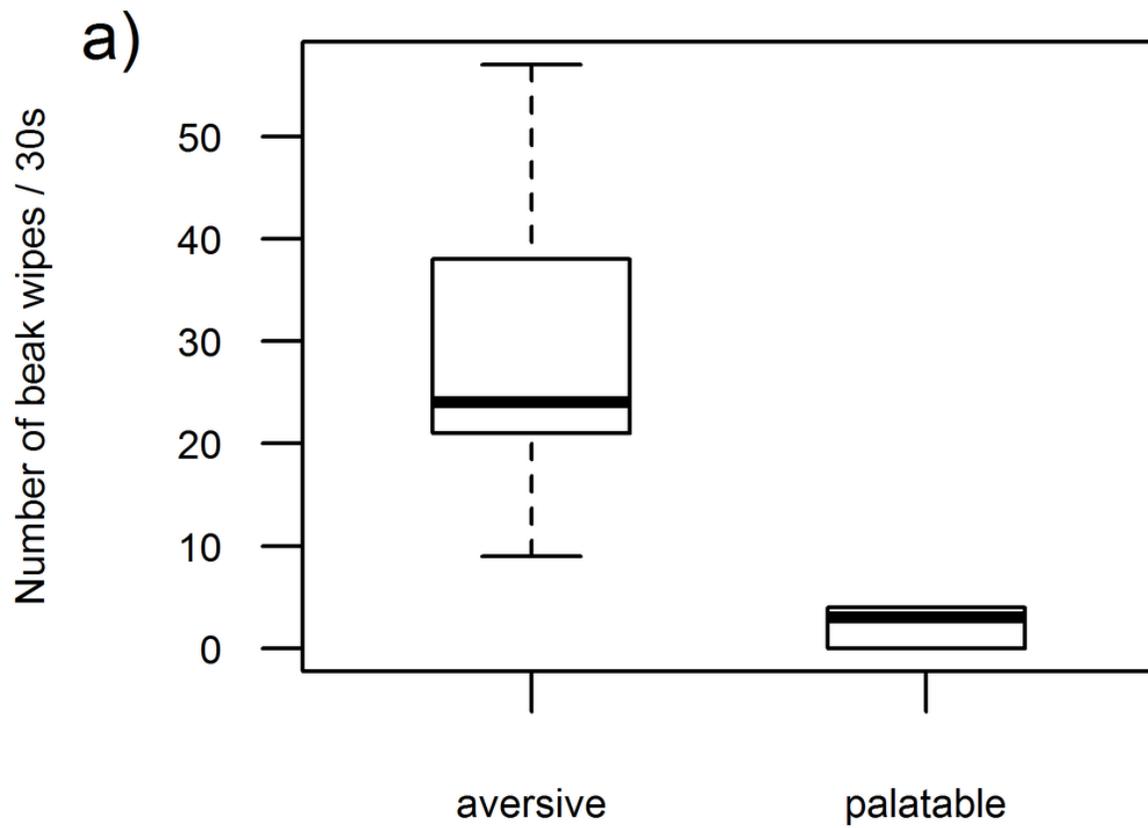



Figure 3

Focal birds' response to video playback.

Mean (± s.e.) proportion of time observers faced the screen (a), and the number of head turns (b) and hops (c) observers performed when they were presented i) an empty cage with a feeding cup before a demonstrator, ii) a demonstrator or iii) an empty cage with a feeding cup after a demonstrator. The time observers faced the screen, and the number of head turns differed between palatable (triangles + solid line) and aversive prey (circles + dashed line).

a)

b)

c)

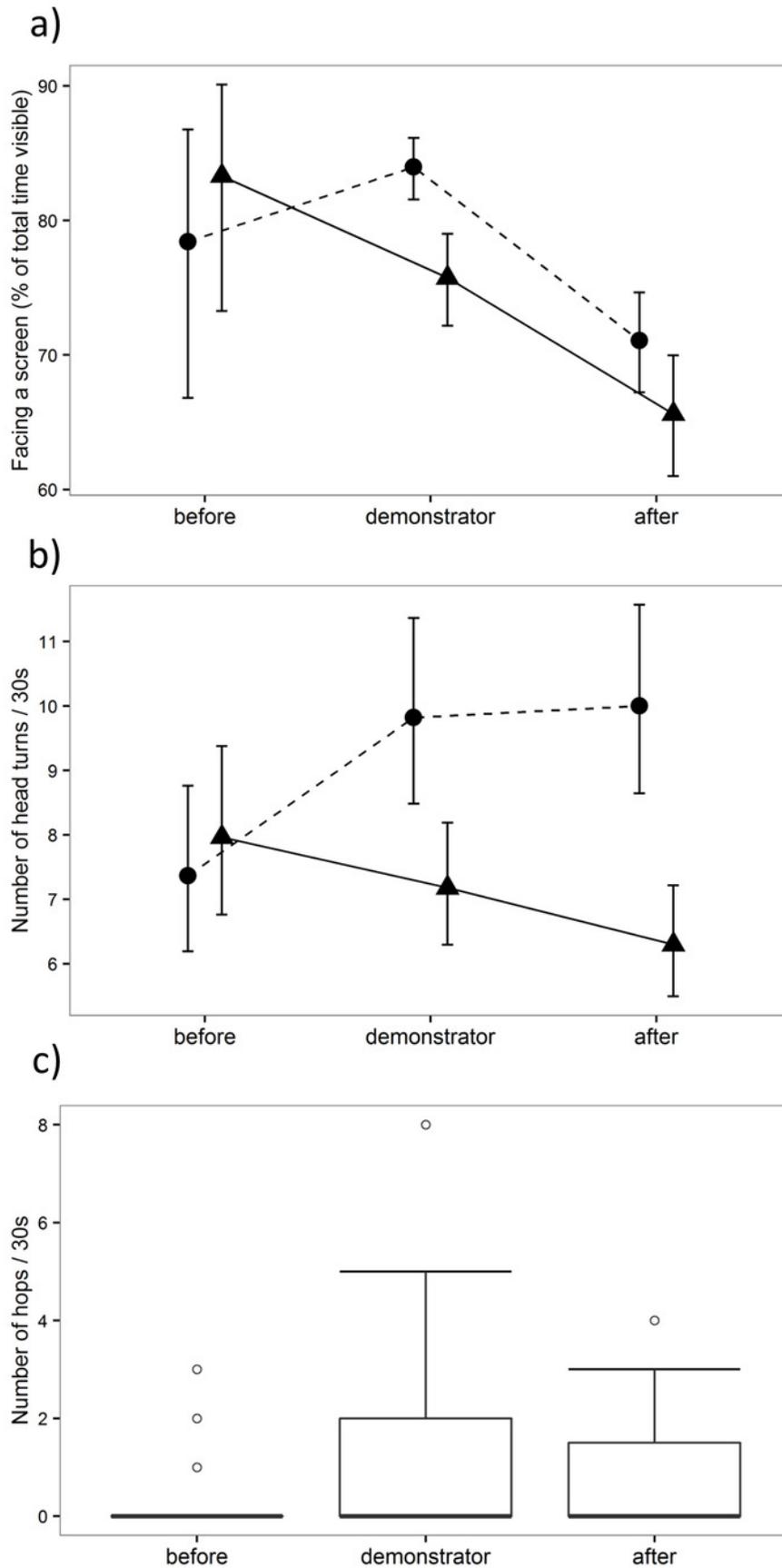



Figure 4

Time before individuals chose a cup in a two-choice test.

Time (sec) before individuals made their cup choice when they i) chose a different cup than predicted (i.e. did not use social information, n = 19), or ii) chose the predicted cup (n = 21). The interaction between prey type and social information use did not have a significant effect on time that it took birds to choose a cup (estimate = 0.218 ± 0.532, Z = 0.410, p = 0.68) so responses are plotted across prey types.