Behavioral flexibility in an invasive bird is independent of other behaviors

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Behavioral flexibility is considered important for a species to adapt to environmental change. Behavioral flexibility relates to problem solving ability and speed in unpredictable ways, which leaves an open question of whether behavioral flexibility instead varies with differences in other behaviors, such as neophobia or exploration. If present, such correlations would mask which behavior causes individuals to vary. I investigated whether behavioral flexibility (reversal learning) performances were linked with other behaviors in great-tailed grackles, an invasive bird. I found that behavioral flexibility did not significantly correlate with neophobia, exploration, risk aversion, persistence, or motor diversity. This suggests that great-tailed grackle performance in behavioral flexibility tasks reflects a distinct source of individual variation. Maintaining multiple distinct sources of individual variation, and particularly variation in behavioral flexibility, may be a mechanism for coping with the diversity of novel elements in their environments and facilitating this species' invasion success.

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8 **BACKGROUND**

9 Behavioral flexibility, defined here as changing preferences according to changing circumstances

10 based on learning (Logan 2016a,b), is considered a key factor involved in a species' ability to

11 adapt to environmental change (Lefebvre et al. 1997, Griffin & Guez 2014, Buckner 2015, Chow

12 et al. 2016). However, it is not known how behavioral flexibility works: is it a problem solving

13 ability or does it arise because of links with other behaviors such as neophilia and exploration

14 (see review in Griffin 2016)? The few studies that have investigated whether behavioral

15 flexibility relates to problem solving ability and speed have found that these traits do not covary

16 in predictable ways (Boogert et al. 2011, Griffin et al. 2013, Isden et al. 2013, Logan 2016a,

17 Bebus et al. 2016). This leaves an open question of whether behavioral flexibility varies with

18 differences in other behaviors such as exploration, neophobia, risk aversion, persistence, and

19 motor diversity (the number of different motor actions used to attempt to solve a novel problem).

20 There is debate about whether differences in behavior among individuals are linked to suites of

21 correlated behaviors or whether individual behaviors, such as behavioral flexibility, can vary

22 independently (Coppens et al. 2010, Cole et al. 2011, Sih & Del Giudice 2012). Reversal

23 learning, a measure of behavioral flexibility, is predicted to fall on the fast-slow behavioral type

24   continuum where fast individuals are exploratory, risk seeking, and persistent with poor accuracy

25   because of the speed with which they solve problems, whereas slow individuals are neophobic,

26   risk averse, and more accurately solve problems (Figure 1; Sih & Del Giudice 2012).

27   Accordingly, slow individuals should be more behaviorally flexible because they might be less

28   impulsive and spend more time sampling the environment (Sih & Del Giudice 2012). If present,

29   these types of behavioral correlations could mask whether differences between individuals in

30   their behavioral flexibility performances are caused by behavioral flexibility or a correlated

31   behavior (Herrmann et al. 2010, Thornton & Lukas 2012, Seed et al. 2012).

32   Results from the few studies that investigated the relationship between behavioral

33   flexibility and other behaviors are equivocal. There are a variety of ways to measure behavioral

34   flexibility in an experimental context and all involve allowing an individual to learn about a task,

35   which then changes after the individual becomes proficient. Individuals that adapt their behavior

36   to these changing circumstances are considered to exhibit behavioral flexibility. Paradigms

37   testing behavioral flexibility include tasks such as a multi-access box (Auersperg et al., 2011;

38   Manrique, Völter & Call, 2013), water tubes (Logan et al. 2014, Logan 2016a), and episodic-like

39   memory and future planning experiments (Clayton & Dickinson, 1998; Dally, Emery & Clayton,

40   2006; Raby et al., 2007), however the most widely used measure is reversal learning (e.g., Bond

41   et al. 2007, Tebbich et al. 2010, Boogert et al. 2011). Reversal learning involves learning to

42   associate one option with a reward, which subsequently becomes incorrect when the reward is

43   moved to a different option, thus forcing the individual to reverse their preference to consistently

44   obtain the reward. Switching preferences is also thought to require inhibition to refrain from

45   choosing the previously rewarded response (Manrique et al. 2013, Griffin & Guez 2014, Liu et

46   al. 2016, but see Homberg et al. 2007), which could be related to a propensity to be more

47   neophobic and less exploratory (Sih & Del Giudice 2012), and/or a propensity to continue to

48   sample the environment (Logan 2016a). Consistent with predictions, black-capped chickadees

49   (*Poecile atricapillus*) and great tits (*Parus major*) that were more flexible (faster to reverse a

50   previously learned preference) were slower to explore (Verbeek et al. 1994, Guillette et al.

51   2011), and great tits that were more flexible (reversal learning) were more neophobic (Verbeek

52   et al. 1994). Two studies provided evidence inconsistent with the predictions that behavioral

53   flexibility will positively correlate with neophobia and negatively with exploration: there were

54   no correlations between behavioral flexibility (reversal learning) and neophobia or exploration in

55   Florida scrub jays (*Aphelocoma coerulescens*; Bebus et al. 2016), and also no correlations with

56   activity or boldness in wild cavies (*Cavia aperea*; Guenther et al. 2014).

57   Innovativeness, considered a subcategory of behavioral flexibility, was linked with the

58   number of motor actions used to try to solve a novel problem, but not with persistence or

59   neophobia in several bird species (Griffin et al. 2014, Diquelou et al. 2016, Griffin & Diquelou

60   2015). Innovativeness, defined as inventing new behaviors to solve novel problems or using

61   existing behaviors in new ways (Griffin & Guez 2014), is distinct from behavioral flexibility. For

62   example, great-tailed grackles exhibit behavioral flexibility in two tests involving reversal

63   learning, showing that they are among the fastest bird species to both learn an initial preference

64   and to reverse this preference (Logan 2016a). However, grackles are not particularly inventive

65   when it comes to creating new behaviors to solve novel problems: they did not successfully

66   innovate string pulling or stick tool use, which are behaviors that many other bird species engage

67   in (Logan 2016b). While it is unknown how motor diversity interacts directly with behavioral

68   flexibility, the prediction is that these traits will positively correlate because increasing the

69   number of motor actions attempted could increase the probability and speed of finding a

70   successful solution to a novel problem (Diquelou et al. 2016).

71   To determine whether behavioral flexibility is related to a variety of behaviors in one

72   species, I investigated great-tailed grackles (*Quiscalus mexicanus*, family Icteridae, hereafter

73   referred to as grackles), a generalist forager (Skutch 1954, Johnson & Peer 2001, Wehtje 2003)

74   that is behaviorally flexible (Logan 2016a). Grackles are a native invasive species (Peer 2011):

75   they have expanded their range north from Central America into North America by over 5500%

76   over the course of 120 years following the expansion of human modified environments, which is

77   their preferred habitat (Wehtje 2003). Behavioral flexibility is hypothesized to be a mechanism

78   involved in successful species invasions (Sol & Lefebvre 2000). While grackles could have

79   expanded their range simply because of an increase in their suitable habitat, species differences

80   in traits that facilitate adapting to environmental change, such as diet, are additionally implicated

81   (Blackburn et al. 2009). Behavioral flexibility is one such trait and a better understanding of how

82   it works could have implications for managing species invasions. To better understand

83   behavioral flexibility, I tested the hypothesis that individual variation in behavioral flexibility

84   correlates with variation in other behaviors on the fast-slow continuum.

85   I predicted that individuals that were more behaviorally flexible would also be the most

86   neophobic and risk averse, the least persistent and exploratory, and use more motor actions. I

87   quantified grackles' activity levels (exploration) when placed in a novel environment and also

88   measured the amount of time spent in the riskiest sections of the aviary (risk aversion). I

89   measured grackles' neophobic reactions to a novel object next to a food dish in comparison with

90   controls where only a food dish was present. Persistence and motor diversity were measured

91   from videos of a stick tool use experiment (Logan 2016b), where no bird successfully invented

92   stick tool use. Therefore, birds were never rewarded for their actions, which is important when

93   measuring persistence because a food reward could differentially influence persistence across

94   individuals: those who are better at the task would receive more food rewards, which might

95   increase their persistence in future trials.

96

97   **METHODS**

98   **Ethics**

99   This research was conducted in accordance with the following permits: U.S. Fish and Wildlife

100   Service (scientific collecting permit number MB76700A-0), U.S. Geological Survey Bird

101   Banding Laboratory (federal bird banding permit number 23872), California Department of Fish

102   and Wildlife (scientific collecting permit number SC-12306), and the Institutional Animal Care

103   and Use Committee at the University of California Santa Barbara (IACUC protocol numbers 860

104   and 860.1).

105

106   **Subjects**

107   Eight adult great-tailed grackles (4 females and 4 males) were caught in the wild and held for 2-3

108   months in aviaries before being released back to the wild (see Logan 2016a for full details). Half

109   of the birds were caught in Santa Barbara, California in September 2014 and released in

110   December 2014 (Tequila, Margarita, Cerveza, and Michelada; batch 1) and the other half were

111   caught in January 2015 and released in March 2015 (Refresco, Horchata, Batido, Jugo; batch 2).

112

113   **Study Set Up**

114   Grackles were housed individually in aviaries (183 cm high by 119 cm wide by 236 cm long) at

115   the University of California Santa Barbara. Grackles had *ad libitum* access to water at all times,

116   and unrestricted amounts of food (Mazuri® Small Bird Food) for a minimum of 20 hrs per day.

117   On testing days, their main diet was removed for up to 4 hrs while they participated in

118   experiments and could eat bread or peanuts if successful. Apparatuses were placed on tables (60

119   cm wide by 39 cm long) and rolled into each aviary for sessions (approximately 20 min per

120   session), which were visually isolated from other grackles and video recorded with a Nikon

121   D5100 camera on a tripod. Experimenters stood just outside the aviary door and in full view of

122   the grackles during the persistence and motor diversity sessions, which did not interfere with

123   behavior (i.e., they readily interacted with the apparatus) because they were habituated to

124   humans in the wild and in the aviary.

125

126   **Statistical Analyses**

127   Data were analyzed in R 3.2.1 (R Core Team 2015). For those tests that involved p-values, a

128   result was considered statistically significant when $p<0.05$. When multiple p-values were

129   obtained for one experiment, a Bonferroni-Holm correction was applied to avoid obtaining false

130   positive results simply by conducting many tests on the same data.

131

132   **Data Accessibility**

133   Data are available at the KNB Data Repository (Logan 2016c;

134   https://knb.ecoinformatics.org/#view/corina_logan.18.13). Behavioral flexibility data were

135   previously published and are available at KNB (Logan 2016d).

136

137 **Videos**

138 Clips of videos from each experiment are available at: https://youtu.be/4efJ2afatus.

139

140 **Exploration and Risk Aversion**

141 The exploration session lasted 60 min, starting 30 min after a wild bird's release into the aviary,

142 a novel environment. The grackles' previous experience was always the same: they were

143 trapped, blood was collected, and colored rings put on their legs; they were transported to the

144 aviary in a cat carrier in a car, biometrics were taken, and then they were released into the aviary

145 where they were singly housed, given food and water, and the camera was set up outside their

146 door. The camera was restarted every 20 min, otherwise experimenters were out of visual and

147 auditory contact when recording.

148 Exploration is measured in a number of different ways and I chose two measures for the

149 purposes of this study, which have been used to measure exploration in other species: the amount

150 of activity in a novel environment (exploration; e.g., Verbeek et al. 1994, Fox et al. 2009) and

151 the amount of time spent in the risky areas of the novel environment (risk aversion; e.g., Lynn &

152 Brown 2009, Lerman et al. 2012, Jolles et al. 2014). It is unclear whether these measure the same

153 behavior because both have not been measured in a single study. Therefore, I conducted a

154 Spearman's rank correlation test to determine whether they are distinct behaviors.

155 *Exploration:* Videos were coded by Linnea Palmstrom to determine how often birds

156 moved between sections of the aviary. The aviary was invisibly sectioned into 5 areas with

157 sections 1 and 5 in the upper half of the aviary, where the perches were located, and sections 2-4

158 on the ground (Figure 2). Their exploration score was the number of times they moved from one

159 aviary section to another over the course of the 60 min session, which was an appropriate time

160 period (Montiglio et al. 2010) because an individual's activity level was ranked similarly

161 regardless of whether activity occurred in the first 5 min or over the whole session (Spearman's

162 rank correlation: S=31.43, p=0.10, rho=0.63, n=8).

163   ***Risk aversion:*** I (invisibly) divided the aviary into safer versus riskier sections (Figure 2)

164 and used the percentage of time spent in sections 4 and 5 as a measure of risk aversion. The rear

165 of the aviary was considered less risky because it was the farthest from the door where the

166 camera and other equipment were visible, while the ground and the perches in the front of the

167 aviary were more risky because these sections were next to the door and walking on the ground

168 is more dangerous than flying. Food and water were placed on the ground near the door. The

169 aviary was covered in tarpaulins on three sides (both sides and rear), while the side with the door

170 (front) and the ceiling were wire mesh that the bird could see through.

171

172 **Neophobia**

173 The neophobia sessions began on a grackle's sixth day in the aviary and involved three 10-min

174 trials with trials 1 and 3 serving as a way to quantify food motivation by placing a food bowl

175 alone on the table, while trial 2 had a novel object 2 cm to the right of the food bowl (as in

176 Boogert et al. 2006). There were 2 min between trials. In all trials, the food bowl contained 1/4

177 of a peanut and the latency to land on the table and to feed was recorded as well as which object

178 was approached first in trial 2 (the food bowl or the novel object). Three novel objects were

179 presented in random order to each bird: a GoPro camera inside its clear waterproof case, a stone

180 dropping training apparatus (see Logan 2016a), and a colored U-tube apparatus (see Logan et al.

181 2016). The stone dropping training apparatus was a clear acrylic box (8.8 cm tall by 18 cm wide

182 by 11 cm deep) with a clear acrylic tube (9 cm tall, outer diameter=5 cm) on top. The colored U-

183   tube apparatus was a box (8cm tall by 40 cm wide by 30 cm deep) with a wooden frame covered

184   in cardboard and a clear acrylic top covered by colored paper. Two clear acrylic tubes (both 17

185   cm tall, one with an outer diameter of 5.1 cm and the other 2.5 cm) protruded from the center of

186   the box and were marked with colored tape at the top. If a grackle did not come to the table

187   within the 10 min period it received a trial duration of 601 seconds. The neophobia tests were

188   conducted on three consecutive days, with one novel object presented to the bird on each day.

189   Data were analyzed using the latency to land on the table rather than the latency to feed

190   because birds came to the table more often than they ate the food. The data were not normally

191   distributed (Anderson-Darling normality test: GoPro: $A=3.08$, $p<0.001$; stone dropping

192   apparatus: $A=2.76$, $p<0.001$; U-tube: $A=2.46$, $p<0.001$). Therefore, non-parametric paired

193   Wilcoxon signed rank tests with continuity corrections were conducted to determine whether

194   latencies in control trials (averaged) differed from novel object trials. Neophobia scores were

195   obtained for each novel object and summed for an overall score per individual. Scores were

196   calculated by subtracting the latency to land on the table during the novel object trials (trial 2)

197   from the average latency during control trials (trials 1 and 3). Positive scores indicate less

198   neophobia while negative scores indicate more neophobia. Repeatability of individual neophobic

199   responses across contexts was measured using Spearman's rank correlations to determine

200   whether grackles maintained similar neophobia ranks with each of the three novel objects.

201

202   **Persistence and Motor Diversity**

203   Persistence and motor diversity were calculated as in Griffin & Diquelou (2015). Persistence

204   was calculated as the attempt rate: the number of times a bird came to the table or interacted with

205   (touched) the apparatus or stick across 21 trials of a stick tool use experiment (105 min/bird).

206 Motor diversity was calculated by counting the number of different motor actions (described in

207 Table 3) performed per individual across the 21 trials of the experiment. Videos were watched

208 from trials 1 to 21 and behaviors from the ethogram (Table 3) were coded at their first

209 observation.

210   The stick tool use experiment involved an apparatus with a wooden base and rear with

211 clear cast acrylic walls providing a narrow gap at the front and top of the apparatus to insert a

212 stick and retrieve a piece of bread. Birds were given 21 5 min trials to innovate tool use: first, 3

213 trials with the stick placed on the table next to the apparatus, then 3 trials with the stick inserted

214 into the apparatus, and finally 15 trials with the stick inserted in the apparatus and tool use

215 demonstrated by the human experimenter.

216

217 **Measure of Behavioral Flexibility**

218 These grackles were previously tested on reversal learning of a color discrimination task

219 consisting of a gold tube and a silver tube placed on the table at the same time with one color

220 containing hidden food and the opportunity to make only one choice per trial (Logan 2016a).

221 Grackles initially learned to search for food hidden in the gold tube and, once proficient, the food

222 was switched to the silver tube and the number of trials required to reach proficiency was

223 assessed. Behavioral flexibility scores were calculated as the number of trials to reverse a color

224 preference minus the number of trials needed to initially learn the color preference (Table 4).

225 Proficiency in the initial discrimination and reversal was demonstrated if individuals chose

226 correctly in at least 17 of the most recent 20 trials with at least 8 or 9 trials correct per set of 10. I

227 then investigated whether relationships between individual variation in behavioral flexibility and

228 exploration, risk aversion, neophobia, persistence, and motor diversity conformed to predictions.

229

General Analyses

231 I determined whether behavioral flexibility (response variable: behavioral flexibility score)

232 negatively correlated with exploration and persistence while examining whether batch had an

233 effect (explanatory variables) using a Generalized Linear Model (GLM; MCMCglmm function,

234 MCMCglmm package; Hadfield 2014) with a Poisson distribution and log link using 13000

235 iterations with a thinning interval of 10 and a burnin of 3000. The GLM showed acceptable

236 convergence (lag time autocorrelation values were <0.01; Hadfield 2010). Risk aversion and

237 motor diversity were excluded from the analysis because they significantly covaried with

238 exploration and persistence, respectively. A Spearman's rank correlation was used to investigate

239 the relationship between behavioral flexibility and neophobia because residuals were not

240 normally distributed.

241   Given the small sample size (n=7 for behavioral flexibility scores), I conducted a further

242 analysis to determine whether GLM results were likely to be reliable given the data (Burnham &

243 Anderson 2002). I compared the Akaike weights (range: 0-1, the sum of all model weights

244 equals 1; Akaike 1981) between the test model (above) and a null model (behavioral flexibility

245 score as the response variable and 1 as the explanatory variable) using the dredge function in the

246 MuMIN package (Bates et al. 2011). If the best fitting model has a high Akaike weight (>0.89;

247 Burnham & Anderson 2002), then it indicates that the results are likely given the data. The null

248 model was strongly supported with an Akaike weight of 0.92, thus indicating the results are

249 reliable even with a small sample size.

250

Interobserver Reliability

252 Linnea Palmstrom coded the exploration/risk aversion videos, I coded neophobia videos, and

253 Katherine Lister coded persistence and I coded motor diversity from videos of a tool use

254 experiment (in Logan 2016b). To measure interobserver reliability, I randomly chose 21% of the

255 videos using www.random.org and had a coder who was naïve to the hypotheses (Katharina

256 Brecht) recode their exploration (from which measures of risk aversion are calculated),

257 persistence, and neophobia. I randomly chose 3 of the 8 birds using www.random.org and had

258 Katharina recode their motor diversity (36% of the videos). A higher percentage of motor

259 diversity videos were recoded because agreement determinations were based on the total number

260 of motor actions per bird, which required watching all videos for an individual. There was

261 agreement between Katharina and all other observers for each study: exploration (intraclass

262 correlation coefficient (ICC)=0.998, 95% confidence intervals (CI) =0.98-1.00), neophobia

263 (ICC=0.87, 95% CI=0.67-0.95), persistence (land on table: ICC=0.79, 95% CI=0.49-0.93;

264 interact with apparatus: ICC=1.00, 95% CI=0.999-1.00; interact with stick: ICC=1.00, 95%

265 CI=NA), and motor diversity (ICC=0.71, 95% CI=0.54-0.82; ICCs calculated using R package:

266 irr, function: icc, Gamer et al. 2012).

267

268 **RESULTS**

269 **Exploration and Risk Aversion**

270 Exploration and risk aversion were significantly positively correlated, indicating that these two

271 variables actually measure the same behavior (Spearman's rank correlation: S=8.55, p=0.002,

272 rho=0.90, n=8). Therefore, I used exploration to represent this behavior in further analyses (see

273 General Analyses section).

274   ***Exploration:*** Grackles varied in how many times they changed sections across the 60

275 min session (0-163), with Refresco having no section changes and Jugo having the most (Table

276 1). They also varied in the total number of sections they visited during the session (1-5; Table 1).

277   ***Risk aversion:*** Grackles varied in how much time they spent in the riskiest sections of the

278 aviary with Batido spending the most time and Refresco the least (Table 1). All grackles (except

279 Refresco) moved through other sections of the aviary and they varied in how much time they

280 spent in sections 4 and 5 (Table 1).

281

282 **Neophobia**

283 There were no significant differences between the latency to land on the table in controls (pre

284 [trial 1] or post [trial 3] novel object trials) versus novel object trials (trial 2) (Wilcoxon tests

285 with Bonferroni-Holm corrected p-values: GoPro: *trials 1-2* V=21, p=1.00, 95% confidence

286 interval=-283-267, *trials 2-3* V=8, p=1.00, 90% CI=-427-277.5; stone dropping apparatus: *trials*

287 *1-2* V=7, p=1.00, 80% CI=-369-338, *trials 2-3* V=0, p=0.54, 80% CI=-455-(-41); U-tube: *trials*

288 *1-2* V=1, p=0.88, 80% CI=-481-(-85), *trials 2-3* V=1, p=0.88, 80% CI=-507-(-190.5)). Refresco

289 and Margarita were overall less neophobic than the other grackles, and Horchata was the most

290 neophobic (Table 2). There were many trials in which the bird did not come to the table.

291 However, this did not usually appear to be due to neophobia because it happened in many control

292 trials as well as novel object trials, indicating that it might have been due to a lack of motivation

293 to eat or explore the object.

294   There was no individual repeatability of neophobia scores across contexts (Spearman's

295 rank correlation with Bonferroni-Holm corrected p-values: GoPro vs. stone dropping apparatus:

296   S=79.21, p=1.00, rho=-0.41, GoPro vs. U-tube: S=56.00, p=1.00, rho=0.00; U-tube vs. stone

297   dropping apparatus: S=20.68, p=0.88, rho=0.63).

298

299   Persistence and Motor Diversity

300   Grackles varied in the number of motor actions they used (1-15) and in how persistent they were

301   (18-4047 total number of times a bird landed on the table, touched the apparatus, or touched the

302   stick; Table 4). A post-hoc analysis indicated that these two variables were significantly

303   positively correlated, and thus both measured the same behavior (Spearman's rank correlation:

304   S=8.55, p=0.002, rho=0.90, n=8). Therefore, only persistence was used in further analyses (see

305   General Analyses section).

306

307   Does behavioral flexibility positively correlate with motor diversity and risk aversion, and

308   negatively with exploration and persistence?

309   Birds that were more flexible (i.e., faster to reverse a preference: number of trials to reverse a

310   preference minus the number of trials to initially learn the preference) did not have higher

311   exploration scores, they were not more persistent, and there were no batch effects (Figure 3,

312   Supplementary Table S1).

313   Risk aversion and motor diversity significantly covaried with exploration and persistence,

314   respectively, and these relationships were investigated further. I confirmed that the relationship

315   between these variables and behavioral flexibility was the same as their collinear variables with

316   an additional GLM. This GLM was the same as above, except the explanatory factors were

317   motor diversity, risk aversion and batch. As above, flexibility did not correlate with risk aversion

318   or motor diversity (Figure 3, Supplementary Table S2).

319

320 **Does behavioral flexibility positively correlate with neophobia?**

321 Grackles that were more flexible (i.e., faster to reverse a preference) did not have lower

322 neophobia scores, which would indicate more neophobia. There was no significant correlation

323 between behavioral flexibility scores and neophobia (Figure 3; Spearman's rank correlation:

324 S=92, p=0.12, rho=-0.65).

325

326 **DISCUSSION**

327 **Exploration and Risk Aversion**

328 The exploration and risk aversion scores significantly correlated with each other, indicating they

329 measured the same behavior. While risk aversion scores could have been confounded by the

330 placement of food and water in a risky section, which might attract birds to this area, they spent

331 only 0-14% of their time in the section with the food and water (section 4). This indicates that

332 they behaved more according to the prediction that this section would be treated as risky even

333 when an attractor was present.

334   I question whether the measure of exploration actually measured exploration in this

335 species. A bird that is stressed tends to fly back and forth in an aviary, which is not an indicator

336 of exploration, but would be interpreted as such according to the section change measure of

337 exploration. In this study, Jugo mostly flew back and forth between the perches near the top of

338 the aviary while looking up and out of the aviary and not attending to the environment within the

339 aviary. In contrast, Horchata also had many section changes, but she usually walked calmly on

340 the ground, thus perhaps in her case this measure of exploration was appropriate. Therefore, at

341 the species level, activity levels are likely not a good indicator of exploration behavior. Indeed, a

342   distinction is made between forced exploration, where an individual is placed in a novel

343   environment, and voluntary exploration, where an individual in a familiar environment is

344   provided with the opportunity to enter a novel environment (Guenther et al. 2014). A study on

345   wild guinea pigs (*Cavia aperea*) found that these two variations of exploration measure different

346   behaviors: forced and voluntary exploration activity did not correlate in juveniles or adults

347   (Guenther et al. 2014).

348   Voluntary exploration would likely be a more accurate measure of actual exploratory

349   behavior in grackles, which could also involve voluntary exploration of a novel object in a

350   familiar environment. Such a measure is also called a neophilia test where a novel object is

351   placed in a familiar aviary in the presence of (but not next to) their regular food source to

352   determine how soon the bird approaches and interacts with the apparatus and for how long (as in

353   Mettke-Hoffman et al. 2002). This kind of test would also likely more directly relate to how

354   grackles have expanded their range so rapidly: rather than exploring novel environments,

355   grackles are more likely to have successfully expanded their range by exploring novel objects.

356   Grackles have not necessarily needed to adapt to novel environments during their range

357   expansion because it coincided with an increase in their suitable (human-managed) habitat

358   (Wehtje 2003). Exploration is more likely to have played a role in exploiting novel objects in

359   their environment because humans throw away products that may be novel to grackles (e.g., egg

360   cartons, yogurt cups) and design new potential food sources (e.g., dumpsters) where food is not

361   necessarily obvious, therefore the objects must be explored to determine whether they contain

362   food.

363

364   **Neophobia**

365   Grackles were not generally neophobic because no significant differences were found between

366   controls and novel object trials in the latency to land on the table. Indeed, the GoPro camera,

367   which was also the smallest of the novel objects, appeared to attract their attention more than the

368   food. Comparing grackles with other species that have been tested using a similar design, it

369   appears that they are less neophobic than starlings (*Sturnus vulgaris*; Boogert et al. 2006), blue

370   tits (*Cyanistes caeruleus*; Herborn et al. 2010), Japanese quail (*Coturnix japonica*; Zimmer et al.

371   2013), Chimango caracaras (*Milvago chimango*; Biondi et al. 2010), European greenfinches

372   (*Carduelis chloris*; Herborn et al. 2011), Indian mynas (Sol et al. 2012, Griffin & Diquelou

373   2015), and mountain chickadees (*Poecile gambeli*; Kozlovsky et al. 2015), and that they have

374   similar levels of neophobia as noisy miners (*Manorina melanocephala*; Griffin & Diquelou

375   2015) and a different group of mountain chickadees (Fox et al. 2009).

376

377   **Persistence and Motor Diversity**

378   The persistence and motor diversity scores significantly correlated with each other, indicating

379   they measured the same behavior. This suggests that the longer a bird persists in attempting to

380   solve a task, the more likely it is to use a wider variety of motor actions. Therefore, it is likely

381   that individuals that used few motor actions would likely have used more if they were perhaps

382   more motivated to interact with the task. Measuring persistence and motor diversity in a variety

383   of contexts could address this potential issue and clarify whether these variables actually do

384   covary on a task that all individuals persist on. These results are different from findings using a

385   similar experimental design on Indian mynas and noisy miners where motor diversity differed

386   between species, but persistence did not, thus indicating these are two separate behaviors (Griffin

387   & Diquelou 2015). However, birds in Griffin & Diquelou (2015) could receive food rewards

388   from the apparatus if successful (i.e., at the end of each bout of persistence) and such positive

389   reinforcement for persisting could have increased persistence for successful individuals in

390   subsequent trials.

391

392   **Behavioral Flexibility**

393   Contrary to predictions, behavioral flexibility did not correlate with exploration, neophobia, risk

394   aversion, persistence, or motor diversity. The small sample size might have limited my ability to

395   detect significant correlations, however the behavior of the models suggested this was not the

396   case. It is perhaps not surprising that behavioral flexibility did not correlate with neophobia (the

397   only behavior I was able to obtain repeatability measures from) because neophobia was not

398   expressed consistently across contexts. This could indicate a further source of individual

399   variation in grackles or it could result from the inability of the method to accurately measure

400   neophobia in this species. The latter highlights the importance of conducting repeatability tests

401   when attempting to understand how two variables correlate because two unpredictable variables

402   (behavioral flexibility and neophobia) would not likely correlate with each other. These results

403   are similar to results from Florida scrub jays where behavioral flexibility (reversal learning) did

404   not correlate with neophobia or exploration (Bebus et al. 2016). The few studies that investigate

405   the relationship between behavioral flexibility and other behaviors either show relationships

406   opposite to predictions (Verbeek et al. 1994, Guillette et al. 2011) or show no correlations (this

407   study, Bebus et al. 2016). One prediction was supported in only one test: reversal learning speed

408   negatively correlated with neophobia (Verbeek et al. 1994). This accumulating evidence suggests

409   the need to reconsider the basis for hypotheses linking other behaviors with behavioral

410   flexibility.

411

CONCLUSIONS

412

413 Traditionally, behavioral flexibility is thought of as a cognitive ability (see review in

414 Shettleworth 2010) and is considered as such in hypotheses linking it with other behaviors (Sih

415 & Del Giudice 2012, Guenther et al. 2013). However, mixed results, with none conforming to

416 predictions, from grackles, keas and New Caledonian crows question this assumption. Grackles

417 lacked correlations between behavioral flexibility and problem solving ability and speed, and

418 individuals that were behaviorally flexible in one type of test were not necessarily flexible in a

419 different type of test (Logan 2016a). The more exploratory keas were more behaviorally flexible

420 on a multi-access box and faster to innovate new solutions to novel problems than New

421 Caledonian crows (Auersperg et al. 2011). These mixed results indicate a need to look beyond

422 cognitive and behavioral measures that might correlate with behavioral flexibility and investigate

423 relationships with factors such as physiology and genetics. For example, grackles that are in

424 better phenotypic condition (e.g., have better immunity) might have the capacity to be more

425 behaviorally flexible than individuals in worse phenotypic condition. Non-behavioral, non-

426 cognitive individual factors have yet to be measured in relation to behavioral flexibility.

427 Considering behavioral flexibility in this more integrated way could allow experimenters to

428 manipulate this elusive trait to understand what it is and how it works.

429 Though the sample size is small, these results provide further support that behavioral

430 flexibility represents a distinct axis of individual variation in behavior. Behaviors that do not

431 correlate with each other are suggested to represent "inherent individual differences" in each of

432 the traits measured (Cole et al. 2011, p. 495). For example, great tit problem solving ability did

433 not correlate with body condition, neophobia, or exploration; therefore problem solving was

434 considered its own behavior that varies across individuals rather than varying due to links with

435 other individual traits (Cole et al. 2011). The methods used to measure neophobia and

436 exploration in grackles might not have accurately represented these behaviors, therefore further

437 investigations using different methods that are validated measures of these behaviors in grackles

438 should be explored before entirely ruling out correlations with behavioral flexibility. Previous

439 research on grackles and other species has shown that behavioral flexibility is independent from

440 innovativeness (Logan 2016b), problem solving ability and speed (Boogert et al. 2011, Isden et

441 al. 2013, Logan 2016a), or that it negatively correlates with problem solving speed (Griffin et al.

442 2013). The majority of evidence so far indicates that individual variation in behavioral flexibility

443 is not confounded with other behaviors, although two alternative hypotheses cannot yet be ruled

444 out: the behaviors might not have been measured with enough consistency across studies to

445 directly compare the results, or the behaviors are not repeatable enough within individuals to

446 reliably covary with each other. Further research is needed to distinguish which hypothesis is

447 supported.

448   It could be adaptive for invasive species, such as the grackle, to maintain many

449 independent axes of individual variation and, in particular, variation in behavioral flexibility.

450 Indeed, Western bluebirds rely on existing intrapopulation variation when expanding their range

451 (Duckworth 2008). While Western bluebirds rely on variation in dispersal strategies, grackles

452 may rely on maintaining individual variation in behavioral flexibility, which could allow them to

453 more quickly adapt to changing or unpredictable environments.

454

455 **FUTURE DIRECTIONS**

456   Future research investigating neophobia, exploration, persistence and motor diversity in this

457   species would benefit from a larger sample size, replicability of results from multiple groups, and

458   finding measures that are repeatable within individuals to determine the reliability of these

459   conclusions. Investigating each variable using multiple methods will facilitate an understanding

460   of which methods actually measure the behaviors of interest.

461

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471

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Exploration and risk aversion results

The percentage of time spent in each aviary section, their risk aversion score (percent time spent in the riskiest sections of the aviary; sections 4 and 5) and their exploration score (total number of section changes).

1   Table 1. Exploration and risk aversion results: the percentage of time spent in each aviary

2   section, their risk aversion score (percent time spent in the riskiest sections of the aviary; sections

3   4 and 5) and their exploration score (total number of section changes).

	Aviary Section					Risk Aversion Score (% time in risky sections)	Exploration Score (section changes)
Bird	**1**	**2**	**3**	**4**	**5**		
Tequila	94	0.4	0.5	6	0	6	16
Margarita	96	0	0.1	4	0	4	5
Cerveza	95	3	0	2	0	2	8
Michelada	92	0.06	0	6	2	8	19
Horchata	47	35	5	14	0	14	145
Refresco	100	0	0	0	0	0	0
Batido	44	0.6	0	0	55	55	30
Jugo	73	12	2	3	11	14	163

Neophobia results

Neophobia scores for each novel object and an overall score for each individual. Neophobia score calculations: the latency to land on the table in controls (trials 1 and 3 averaged) minus the latency in the novel object condition (trial 2) for each object type (GoPro camera, stone dropping apparatus, and U-tube apparatus), and summed across object types for the overall neophobia score (positive=less neophobic [bold text], negative=more neophobic).

1 Table 2. Neophobia scores for each novel object and an overall score for each individual.

2 Neophobia score calculations: the latency to land on the table in controls (trials 1 and 3

3 averaged) minus the latency in the novel object condition (trial 2) for each object type (GoPro

4 camera, stone dropping apparatus, and U-tube apparatus), and summed across object types for

5 the overall neophobia score (positive=less neophobic [bold text], negative=more neophobic).

Bird	GoPro	Stone dropping apparatus	U-tube	Neophobia score
Tequila	7	-444.5	-156.5	-594
Margarita	**20**	0	0	**20**
Cerveza	-182	**167.5**	-42.5	-57
Michelada	0	0	-228	-228
Horchata	-580	-1	-277.5	-858.5
Refresco	**1**	**148.5**	**1**	**150.5**
Batido	**187**	-275.5	-541	-629.5
Jugo	**338**	-227.5	-373.5	-263

Motor diversity ethogram

Description of motor actions used while presented with a stick tool use task (techniques 1, 2, 4, 5, 13 and 14 are from Griffin & Diquelou (2015) who refer to 'gape' as 'lever').

1   Table 3. Description of motor actions used while presented with a stick tool use task (techniques

2   1, 2, 4, 5, 13 and 14 are from Griffin & Diquelou 2015 who refer to 'gape' as 'lever').

Technique	Description	Body part
1. Vertical peck	Pecks vertically to the horizontal surface of the apparatus with beak open or closed	Bill
2. Horizontal peck	Pecks horizontally to the vertical edges of the apparatus with beak open or closed	
3. Upside Down Peck	Pecks horizontally to the vertical edges of the apparatus while standing on top of the apparatus, thus the head is upside down	
4. Vertical push	Makes closed beak contact with the horizontal surfaces of the apparatus and slides beak vertically along the surface	
5. Grab apparatus	The apparatus is held between the two mandibles	
6. Grab stick	The stick is held between the two mandibles	
7. Pull stick	The stick is held between the two mandibles and pulled	
8. Push stick	The stick is held between the two mandibles and pushed	
9. Move stick	The stick is moved from inside to outside of the apparatus	
10. Manipulate Stick	Manipulate stick inside apparatus	
11. Carry stick away	The stick is held in the beak as the bird flies away from the table	
12. Throw stick	The stick is tossed to the side	
13. Gape	The closed beak is placed under the edge, in an opening, or on a surface of the apparatus and then opened	
14. Gape upside-down	Same as gape but the head is upside-down (or at least 45 degrees from complete upside-down position	
15. Stand	Stands on top of the apparatus	Feet (or bill)
16. Step	Places one foot on the apparatus	
17. Tips apparatus	Tips apparatus over after standing on top and flying off or by grabbing with bill and pulling over	

Persistence and motor diversity results, and behavioral flexibility scores

Persistence (the total number of times a bird landed on the table, touched the apparatus, or touched the stick), motor diversity (the total number of motor actions used), and behavioral flexibility scores (number of trials to reverse a preference minus the number of trials to initially learn the preference; from Logan 2016a) per bird (- = did not complete this experiment).

1 Table 4. Persistence (the total number of interactions with the table, apparatus, and stick), motor

2 diversity (the total number of motor actions used), and behavioral flexibility scores (number of

3 trials to reverse a preference minus the number of trials to initially learn the preference; from

4 Logan 2016a) per bird (- = did not complete this experiment).

Bird	Sex	Persistence	Motor diversity	Behavioral flexibility score
Tequila	M	175	6	70
Margarita	F	72	5	70
Cerveza	F	81	2	60
Michelada	F	18	1	30
Horchata	F	145	8	100
Refresco	M	1114	14	50
Batido	M	4047	15	-
Jugo	M	197	6	40

Predictions about how behavioral flexibility will relate to other behaviors

Predictions are adapted from Table 1 in Sih and Del Giudice (2012).

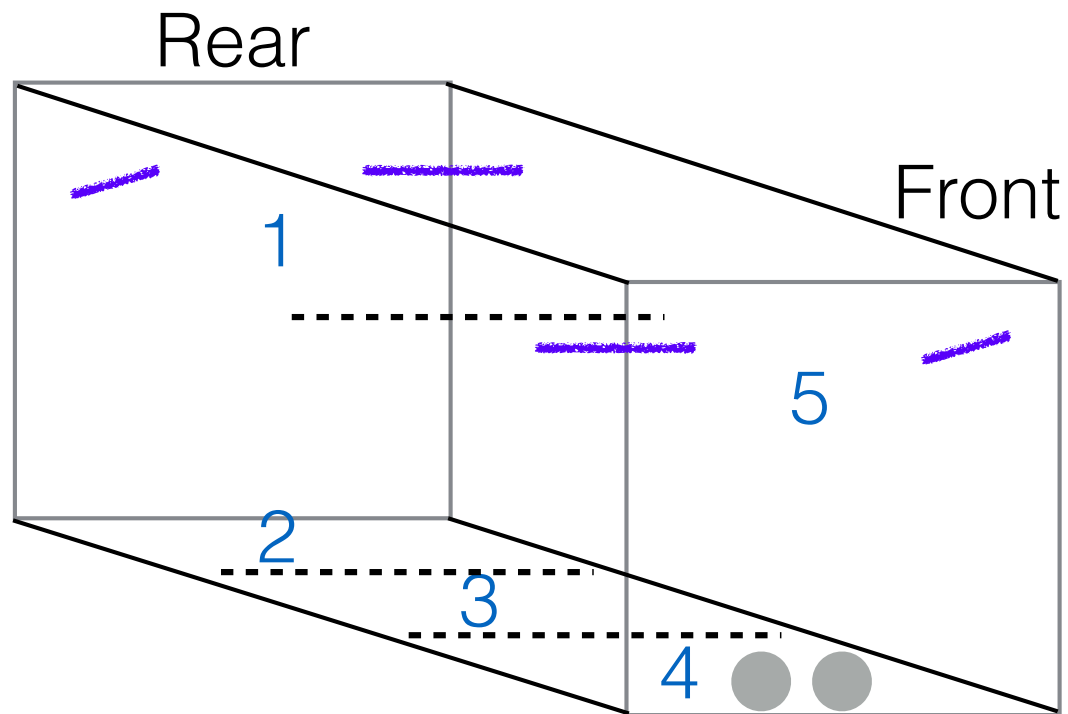
More behaviorally flexible
(fast reversal learning)

Generally low speed-high accuracy
Slow behavioral type
Collects more information
Slower to learn new activities
Faster to learn to avoid
Less impulsive
Risk averse
Slow exploring
Cautious
Rarely exposed to novel environments

Less behaviorally flexible
(slow reversal learning)

Generally high speed-low accuracy
Fast behavioral type
Collects less information
Faster to learn new activities
Slower to learn to avoid
More impulsive
Risk seeking
Fast exploring
Bold
Commonly exposed to novel environments

Aviary diagram

The aviary was invisibly sectioned (dotted lines) from least (1) to most risky (4 and 5). The camera was positioned outside a door at the front of the aviary. Food and water bowls were on the ground at the front of the aviary (grey circles) and perches were located in all upper corners (purple lines).

Behavioral flexibility scores in relation to other behaviors

The relationship between behavioral flexibility scores and exploration (A, total number of aviary section changes), risk aversion (B, percentage of time spent in risky aviary sections), persistence (C, total number of interactions with the table, apparatus, and stick), motor diversity (D, total number of different motor actions used), and neophobia (E, latency to land on table during controls minus latency to land next to a novel object) (n=7 grackles).