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Logan CJ. 2016. Behavioral flexibility in an invasive bird is independent of other behaviors. PeerJ 4:e2215 <https://doi.org/10.7717/peerj.2215>

# **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. Yet behavioral flexibility relates to problem solving ability and speed in unpredictable ways. This leaves an open question of whether behavioral flexibility instead varies with differences in individual behaviors, such as neophobia or exploration. If present, such correlations would mask which behavior causes individual variation. 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 reflect a distinct source of individual variation. Maintaining multiple distinct sources of individual variation, and particularly variation in behavioral flexibility, may be a mechanism for this species' invasion success by permitting populations to cope with the diversity of novel elements in their environments.

1 **Behavioral flexibility in an invasive bird is independent of other behaviors**

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7  
8 **BACKGROUND**

9 Behavioral flexibility, defined here as changing preferences according to changing circumstances  
10 based on learning (Logan 2016a,b, Griffin & Guez 2014), is considered a key factor involved in  
11 a species' ability to adapt to environmental change (Lefebvre et al. 1997, Griffin & Guez 2014,  
12 Buckner 2015, Chow et al. 2016). Yet the few studies that have investigated whether behavioral  
13 flexibility relates to problem solving ability and speed have found that these traits do not covary  
14 in predictable ways (Boogert et al. 2011, Griffin et al. 2013, Isden et al. 2013, Logan 2016a,  
15 Bebus et al. 2016). This leaves an open question of whether behavioral flexibility instead varies  
16 with differences in individual behaviors such as exploration, neophobia, risk aversion,  
17 persistence, and motor diversity (the number of different motor actions used to attempt to solve a  
18 novel problem). There is debate about whether differences in behavior among individuals are  
19 linked to suites of correlated behaviors or whether individual behaviors, such as behavioral  
20 flexibility, can vary independently (Coppens et al. 2010, Cole et al. 2011, Sih & Del Giudice  
21 2012). Behavioral flexibility is predicted to fall on the fast-slow behavioral type continuum  
22 where fast individuals are exploratory, risk seeking, and persistent with poor accuracy because of  
23 the speed with which they solve problems, whereas slow individuals are neophobic, risk averse,

24 and more accurately solve problems (Sih & Del Giudice 2012). Accordingly, slow individuals  
25 should be more behaviorally flexible because they are less impulsive and they spend more time  
26 sampling the environment (Sih & Del Giudice 2012). If present, these types of behavioral  
27 correlations could mask whether differences between individuals in their behavioral flexibility  
28 performances are caused by behavioral flexibility or a correlated behavior (Herrmann et al. 2010,  
29 Thornton & Lukas 2012, Seed et al. 2012).

30 Results from the few studies that investigated the relationship between behavioral  
31 flexibility and individual behaviors are equivocal. Reversal learning is a common measure of  
32 behavioral flexibility and involves learning to associate one option with a reward, which  
33 subsequently becomes incorrect when the reward is moved to a different option, thus forcing the  
34 individual to reverse their preference to consistently obtain the reward (e.g., Bond et al. 2007,  
35 Tebbich et al. 2010, Boogert et al. 2011). Contrary to predictions, black-capped chickadees  
36 (*Poecile atricapillus*) and great tits (*Parus major*) that were more flexible (faster to reverse a  
37 previously learned preference) were slower to explore (Verbeek et al. 1994, Guillette et al.  
38 2011). There were no correlations between behavioral flexibility (reversal learning) and  
39 neophobia or exploration in Florida scrub jays (*Aphelocoma coerulescens*; Bebus et al. 2016),  
40 and also no correlations with activity or boldness in wild cavies (*Cavia aperea*; Guenther et al.  
41 2014). There are two results that are consistent with predictions: great tits that were more flexible  
42 (reversal learning) were more neophobic (Verbeek et al. 1994), and wild cavies that were more  
43 flexible (reversal learning) were less aggressive (Guenther et al. 2014).

44 Innovativeness, considered a subcategory of behavioral flexibility, was linked with the  
45 number of motor actions used to try to solve a novel problem, but not with persistence or  
46 neophobia in several bird species (Griffin et al. 2014, Diquelou et al. 2016, Griffin & Diquelou

47 2015). Innovativeness, defined as inventing new behaviors to solve novel problems or using  
48 existing behaviors in new ways (Griffin & Guez 2014), is distinct from behavioral flexibility. For  
49 example, great-tailed grackles exhibit behavioral flexibility (Logan 2016a), but are not  
50 particularly inventive when it comes to creating new behaviors to solve novel problems (Logan  
51 2016b). While it is unknown how motor diversity interacts directly with behavioral flexibility,  
52 the prediction is that these traits will positively correlate because increasing the number of motor  
53 actions attempted could increase the probability and speed of finding a successful solution to a  
54 novel problem (Diquelou et al. 2016).

55 To determine whether behavioral flexibility is related to a wide variety of behaviors in  
56 one species, I investigated great-tailed grackles (*Quiscalus mexicanus*, family Icteridae, hereafter  
57 referred to as grackles), a behaviorally flexible (Logan 2016a) invasive urban bird (Peer 2011,  
58 Wehtje 2003). I predicted that individuals that were more behaviorally flexible would also be the  
59 most neophobic and risk averse, the least persistent and exploratory, and use more motor actions.

60

## 61 **METHODS**

### 62 **Ethics**

63 This research was conducted in accordance with the following permits: U.S. Fish and Wildlife  
64 Service (scientific collecting permit number MB76700A-0), U.S. Geological Survey Bird  
65 Banding Laboratory (federal bird banding permit number 23872), California Department of Fish  
66 and Wildlife (scientific collecting permit number SC-12306), and the Institutional Animal Care  
67 and Use Committee at the University of California Santa Barbara (IACUC protocol numbers 860  
68 and 860.1).

69

## 70 **Subjects**

71 Eight adult great-tailed grackles (4 females and 4 males) were caught in the wild and held for 2-3  
72 months in aviaries before being released back to the wild (see Logan 2016a for full details).  
73 Birds were caught in Santa Barbara, California in September 2014 and released in December  
74 2014 (Tequila, Margarita, Cerveza, and Michelada; batch 1) and in January 2015 and released in  
75 March 2015 (Refresco, Horchata, Batido, Jugo; batch 2).

76

## 77 **Experimental Set Up**

78 Grackles were housed individually in aviaries (183 cm high by 119 cm wide by 236 cm long) at  
79 the University of California Santa Barbara. Grackles had *ad libitum* access to water at all times  
80 and unrestricted amounts of food (Mazuri Small Bird Food) for a minimum of 20 hrs per day. On  
81 testing days, their main diet was removed for up to 4 hrs while they participated in experiments  
82 and could eat bread or peanuts if successful. Test apparatuses were placed on tables (60cm wide  
83 by 39 cm long) and rolled into each aviary for testing sessions (approximately 20 min per  
84 session), which were visually isolated from other grackles and video recorded with a Nikon  
85 D5100 camera on a tripod. Experimenters stood just outside the aviary door and in full view of  
86 the grackles when testing, which did not interfere with test performance (i.e., they readily  
87 interacted with the apparatuses) because they were habituated to humans in the wild and in the  
88 aviary.

89

## 90 **The Experiments**

91 Experiment 1 quantified grackles' activity levels (exploration) when placed in a novel  
92 environment and also measured the amount of time spent in the riskiest sections of the aviary

93 (risk aversion). Experiment 2 measured grackles' neophobic reactions to a novel object in  
94 comparison with controls. Persistence and motor diversity were measured from videos of a stick  
95 tool use experiment (Logan in review), where no bird successfully invented stick tool use.  
96 Therefore, birds were never rewarded for their actions, which is important when measuring  
97 persistence because a food reward could differentially influence persistence across individuals:  
98 those who are better at the task would receive more food rewards, which might increase their  
99 persistence.

100

### 101 **Statistical Analyses**

102 Data were analyzed in R 3.2.1 (R Core Team 2015). For those tests that involved p-values, a  
103 result was considered statistically significant when  $p < 0.05$ . When multiple p-values were  
104 obtained for one experiment, a Bonferroni-Holm correction was applied to avoid obtaining false  
105 positive results simply by conducting many tests on the same data.

106

### 107 **Interobserver Reliability**

108 Linnea Palmstrom coded the exploration videos and Katherine Lister coded persistence and  
109 motor diversity from videos of a tool use experiment (in Logan in review). I randomly chose 1 of  
110 the 8 birds (using [www.random.org](http://www.random.org); bird: Refresco) and coded their exploration, persistence, and  
111 motor diversity (12.5% of the videos) to measure interobserver reliability. There was almost  
112 complete agreement between video coders for exploration (Cohen's kappa=0.90) and persistence  
113 (intraclass correlation coefficient (ICC)=0.88, 95% confidence intervals (CI)=0.73-0.95 for  
114 persistence to land on the table; ICC=0.98, 95% CI=0.94-0.99 for persistence to interact with the  
115 apparatus; ICC=0.90, 95% CI=0.78-0.96 for persistence to interact with the stick; ICCs

116 calculated using R package: irr, function: icc, Gamer et al. 2012). The Cohen's kappa was used  
117 to analyze interobserver agreement for exploration because Refresco had too few aviary section  
118 changes (n=3 data points) for the ICC analysis. There was poor interobserver agreement for  
119 motor diversity (ICC=0.37, 95% CI=-0.10-0.71; Landis & Koch 1977). Therefore, I calculated  
120 my intraobserver reliability on Refresco's videos (from his last trial to his first trial, which is the  
121 reverse order from the first time I coded his videos to avoid scoring the same events). There was  
122 complete agreement for my intraobserver measurements (ICC=1.00, 95% CI=NA), therefore I  
123 coded all of the grackle motor diversity videos and used these data in the analyses.

124

#### 125 **Data Accessibility**

126 Data are available at the KNB Data Repository (Logan 2016c;  
127 [https://knb.ecoinformatics.org/#view/corina\\_logan.18.4](https://knb.ecoinformatics.org/#view/corina_logan.18.4)). Behavioral flexibility data were  
128 previously published and are available at KNB (Logan 2016d).

129

#### 130 **Video**

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

132

### 133 ***EXPERIMENT 1: EXPLORATION***

#### 134 ***Experiment 1: Methods***

135 The exploration test lasted 60 min, starting 30 min after a wild bird's release into the aviary, a  
136 novel environment. The grackles' previous experience was always the same: they were trapped,  
137 blood was collected, and colored rings put on; they were transported to the aviary in a cat carrier  
138 in a car, biometrics were taken, and then they were released into the aviary where they were



139 singly housed, given food and water, and the camera was set up outside their door. The camera  
140 was restarted every 20 min, otherwise experimenters were out of visual and auditory contact  
141 when recording.

142         Exploration is measured in a number of different ways and I chose two measures for the  
143 purposes of this study, which have been used to measure exploration in other species: the amount  
144 of activity in a novel environment (exploration; e.g., Verbeek et al. 1994, Fox et al. 2009) and  
145 the amount of time spent in the risky areas of the novel environment (risk aversion; e.g., Jolles et  
146 al. 2014). It is unclear whether these measure the same behavior because both have not been  
147 measured in a single study. Therefore, I conducted a Spearman's rank correlation test to  
148 determine whether they are distinct behaviors.

149 **Exploration:** Videos were coded by Linnea Palmstrom to determine how often birds moved  
150 between sections of the aviary (Figure 1). Their exploration score was the number of times they  
151 moved from one aviary section to another over the course of the 60 min test. Analyzing the  
152 number of section changes across the 60 min period was an appropriate time period (Montiglio et  
153 al. 2010) because an individual was ranked similarly regardless of whether activity occurred in  
154 the first 5 min or over the whole test (Spearman's rank correlation:  $S=31.43$ ,  $p=0.10$ ,  $\rho=0.63$ ,  
155  $n=8$ ).

156 **Risk aversion:** I (invisibly) divided the aviary into safer versus riskier sections (Figure 1) and  
157 used the percentage of time spent in sections 4 and 5 as a measure of risk aversion (Jolles et al.  
158 2014). The rear of the aviary was considered less risky because it was the farthest from the door  
159 where the camera and other equipment were visible, while the ground and the perches in the  
160 front of the aviary were more risky because these sections were next to the door and walking on  
161 the ground is more dangerous than flying. Food and water were placed on the ground near the

162 door. The aviary was covered in a white tarp on three sides (both sides and rear), while the side  
163 with the door (front) and the ceiling were wire mesh that the bird could see through.

164

### 165 ***Experiment 1: Results***

166 Exploration and risk aversion were significantly positively correlated, indicating that these two  
167 measures actually measure the same behavior (Spearman's rank correlation:  $S=8.55$ ,  $p=0.002$ ,  
168  $\rho=0.90$ ,  $n=8$ ). Therefore, I used exploration to represent this behavior in further analyses (see  
169 General Analyses section).

170 **Exploration:** Grackles varied in how many times they changed sections across the 60 min test  
171 (0-163), with Refresco having no section changes and Jugo having the most. They also varied in  
172 the total number of sections they visited during the test (1-5).

173 **Risk aversion:** Grackles varied in how much time they spent in the riskiest sections of the aviary  
174 with Batido spending the most time and Refresco the least (Table 1). All grackles (except  
175 Refresco) moved in other sections of the aviary and they varied in how much time they spent in  
176 sections 4 and 5 (Table 1).

177

### 178 ***Experiment 1: Discussion***

179 The exploration and risk aversion scores significantly correlated with each other, indicating they  
180 measured the same behavior. However, I question whether they actually measured exploration in  
181 this species. A bird that is stressed tends to fly back and forth in an aviary, which is not an  
182 indicator of exploration, but would be interpreted as such according to the section change  
183 measure of exploration. In this study, Jugo mostly flew back and forth between the perches near  
184 the top of the aviary while looking up and out of the aviary and not attending to the environment

185 within the aviary. Whereas Horchata had many section changes and usually walked calmly on  
186 the ground, thus perhaps in her case this measure of exploration is appropriate. Therefore, at the  
187 species level, this test is likely not a good indicator of exploration behavior. Indeed, a distinction  
188 is made between forced exploration, where an individual is placed in a novel environment, and  
189 voluntary exploration, where an individual in a familiar environment is provided with the  
190 opportunity to enter a novel environment (Guenther et al. 2014). A study on wild guinea pigs  
191 (*Cavia aperea*) found that these two variations of exploration measure different behaviors:  
192 forced and voluntary exploration activity did not correlate as juveniles or adults (Guenther et al.  
193 2014).

194 Voluntary exploration would likely be a more accurate measure of actual exploratory  
195 behavior in grackles, which could also involve voluntary exploration of a novel object in a  
196 familiar environment. Such a measure is also called a neophilia test where a novel object is  
197 placed in a familiar aviary in the presence of (but not next to) their regular food source to  
198 determine how soon the bird approaches and interacts with the apparatus and for how long (as in  
199 Mettke-Hoffman et al. 2002). This kind of test would also likely more directly relate to how  
200 grackles have expanded their range so rapidly: rather than exploring novel environments,  
201 grackles are more likely to have successfully expanded their range by exploring novel objects.  
202 Grackles have not necessarily needed to adapt to novel environments during their range  
203 expansion because it coincided with an increase in their suitable (human-managed) habitat  
204 (Wehtje 2003). Exploration is more likely to have played a role in exploiting novel objects in  
205 their environment because humans throw away products that may be novel to grackles (e.g., egg  
206 cartons, yogurt cups) and design new potential food sources (e.g., dumpsters) where food is not  
207 necessarily obvious, therefore the objects must be explored to determine whether food is inside.

208

209 ***EXPERIMENT 2: NEOPHOBIA***

210 ***Experiment 2: Methods***

211 The neophobia tests began on a grackle's sixth day in the aviary and involved three 10-min trials  
212 with trials 1 and 3 serving as a way to quantify food motivation by placing a food bowl alone on  
213 the table, while trial 2 had a novel object 2 cm to the right of the food bowl (as in Boogert et al.  
214 2006). There were 2 min between trials. In all trials, the food bowl contained 1/4 of a peanut and  
215 the latency to land on the table and to feed was recorded as well as which object was approached  
216 first in trial 2 (the food bowl or the novel object). Three novel objects were presented in random  
217 order to each bird: a GoPro camera inside its clear waterproof case, a stone dropping training  
218 apparatus (see Logan 2016a), and a colored U-tube apparatus (see Logan et al. 2016). The stone  
219 dropping training apparatus was a clear acrylic box (8.8 cm tall by 18 cm wide by 11 cm deep)  
220 with a clear acrylic tube (9 cm tall, outer diameter=5 cm) on top. The colored U-tube apparatus  
221 was a box (8cm tall by 40 cm wide by 30 cm deep) with a wooden frame covered in cardboard  
222 and a clear acrylic top covered by colored paper. Two clear acrylic tubes (both 17 cm tall, one  
223 with an outer diameter of 5.1 cm and the other 2.5 cm) protruded from the center of the box and  
224 were marked with colored tape at the top. If a grackle did not come to the table within the 10 min  
225 period it received a duration of 601 seconds. The neophobia tests were conducted on three  
226 consecutive days, with one novel object presented to the bird on each day.

227 Data were analyzed using the latency to land on the table rather than the latency to feed  
228 because birds came to the table more often than they ate the food. The data were not normally  
229 distributed (Anderson-Darling normality test: GoPro:  $A=3.08$ ,  $p<0.001$ ; stone dropping  
230 apparatus:  $A=2.76$ ,  $p<0.001$ ; U-tube:  $A=2.46$ ,  $p<0.001$ ). Therefore, non-parametric paired

231 Wilcoxon signed rank tests with continuity corrections were conducted to determine whether  
232 latencies in control trials (averaged) differed from novel object trials. Neophobia scores were  
233 obtained for each novel object and summed for an overall score per individual. Scores were  
234 calculated by subtracting the latency to land on the table during the novel object trials (trial 2)  
235 from the average latency during control trials (trials 1 and 3). Positive scores indicate less  
236 neophobia while negative scores indicate more neophobia. Repeatability of individual neophobic  
237 responses across contexts was measured using Spearman's rank correlations to determine  
238 whether grackles maintained similar neophobia ranks with each of the three novel objects.

239

#### 240 ***Experiment 2: Results***

241 There were no significant differences between the latency to land on the table in controls (pre  
242 [trial 1] or post [trial 3] novel object trials) versus novel object trials (trial 2) (Wilcoxon tests  
243 with Bonferroni-Holm corrected p-values: GoPro: *trials 1-2*  $V=21$ ,  $p=1.00$ , 95% confidence  
244 interval= $-283-267$ , *trials 2-3*  $V=8$ ,  $p=1.00$ , 90% CI= $-427-277.5$ ; stone dropping apparatus: *trials*  
245 *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*  
246 *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  
247 and Margarita were overall less neophobic than the other grackles, and Horchata was the most  
248 neophobic (Table 2). There were many trials in which the bird did not come to the table.  
249 However, this did not usually appear to be due to neophobia because it happened in many control  
250 trials as well as novel object trials, indicating that it might have been due to a lack of motivation  
251 to eat or explore the object.

252 There was no individual repeatability of neophobia scores across contexts (Spearman's  
253 rank correlation with Bonferroni-Holm corrected p-values: GoPro vs. stone dropping apparatus:

254  $S=79.21$ ,  $p=1.00$ ,  $\rho=-0.41$ , GoPro vs. U-tube:  $S=56.00$ ,  $p=1.00$ ,  $\rho=0.00$ ; U-tube vs. stone  
255 dropping apparatus:  $S=20.68$ ,  $p=0.88$ ,  $\rho=0.63$ ).

256

## 257 ***Experiment 2: Discussion***

258 Grackles were not generally neophobic because no significant differences were found between  
259 controls and novel object trials in the latency to land on the table. Indeed, the GoPro camera,  
260 which was also the smallest of the novel objects, appeared to attract their attention more than the  
261 food. Comparing grackles with other species that have been tested using a similar design, it  
262 appears that they are less neophobic than starlings (Boogert et al. 2006), blue tits (Herborn et al.  
263 2010), Japanese quail (Zimmer et al. 2013), Chimango caracaras (Biondi et al. 2010), European  
264 greenfinches (Herborn et al. 2011), common mynas (Sol et al. 2012), Indian mynas (Griffin &  
265 Diquelou 2015), and mountain chickadees (Kozlovsky et al. 2015), and that they have similar  
266 levels of neophobia as noisy miners (Griffin & Diquelou 2015) and a different group of  
267 mountain chickadees (Fox et a. 2009).

268

## 269 ***MEASURES OF PERSISTENCE AND MOTOR DIVERSITY***

### 270 ***Persistence and Motor Diversity: Methods***

271 Persistence and motor diversity were calculated as in Griffin & Diquelou (2015). Persistence  
272 was calculated as the attempt rate: the number of times a bird came to the table or interacted with  
273 (touched) the apparatus or stick across 21 trials of the stick tool use experiment (105 min/bird).  
274 Motor diversity was calculated by counting the number of different motor actions (described in  
275 Table 3) performed per individual across 21 trials of the experiment (105 min/bird). Videos were

276 watched from trials 1 to 21 and behaviors from the ethogram (Table 3) were coded at their first  
277 observation.

278

### 279 ***Persistence and Motor Diversity: Results***

280 Grackles varied in the number of motor actions they used (1-15) and in how persistent they were  
281 (18-4047 interactions; Table 4). A post-hoc analysis indicated that these two variables were  
282 significantly positively correlated, and thus both measured the same behavior (Spearman's rank  
283 correlation:  $S=8.55$ ,  $p=0.002$ ,  $\rho=0.90$ ,  $n=8$ ). Therefore, only persistence was used in further  
284 analyses (see General Analyses section).

285

### 286 ***Persistence and Motor Diversity: Discussion***

287 The persistence and motor diversity scores significantly correlated with each other, indicating  
288 they measured the same behavior. This suggests that the longer a bird persists in attempting to  
289 solve a task, the more likely they are to use a wider variety of motor actions. Therefore, it is  
290 likely that individuals that used few motor actions would likely have used more if they were  
291 perhaps more motivated to interact with a task. Measuring persistence and motor diversity in a  
292 variety of contexts could address this potential issue and clarify whether these variables actually  
293 do covary on a task that all individuals persist on. These results are different from findings using  
294 a similar experimental design on Indian mynas and noisy miners where motor diversity differed  
295 between species, but persistence did not, thus indicating these are two separate behaviors (Griffin  
296 & Diquelou 2015). However, birds in Griffin & Diquelou (2015) could receive food rewards  
297 from the apparatus if successful, which could have influenced their level of persistence.

298

299 ***MEASURE OF BEHAVIORAL FLEXIBILITY***

300 These grackles were previously tested on reversal learning of a color discrimination task (Logan  
301 2016a). Behavioral flexibility scores were calculated as the number of trials to reverse a color  
302 preference minus the number of trials needed to initially learn the color discrimination (Table 4).  
303 Proficiency in each discrimination was demonstrated if individuals chose correctly in at least 17  
304 of the most recent 20 trials with at least 8 or 9 trials correct per set of 10.

305

306 ***GENERAL ANALYSES***

307 I determined whether behavioral flexibility (response variable: behavioral flexibility score)  
308 negatively correlated with exploration and persistence while controlling for batch effects  
309 (explanatory variables) using a Generalized Linear Model (GLM; MCMCglmm function,  
310 MCMCglmm package; Hadfield 2014) with a Poisson distribution and log link using 13000  
311 iterations with a thinning interval of 10 and a burnin of 3000. The GLM showed acceptable  
312 convergence (lag time autocorrelation values were  $<0.01$ ; Hadfield 2010). Risk aversion and  
313 motor diversity were excluded from the analysis because they significantly covaried with  
314 exploration and persistence, respectively. A Spearman's rank correlation was used to investigate  
315 the relationship between behavioral flexibility and neophobia because residuals were not  
316 normally distributed.

317         Given the small sample size ( $n=7$  for behavioral flexibility scores), I conducted a further  
318 analysis to determine whether GLM results were likely to be reliable given the data (Burnham &  
319 Anderson 2002). I compared the Akaike weights (range: 0-1, the sum of all model weights  
320 equals 1; Akaike 1981) between the test model (above) and a null model (behavioral flexibility  
321 score as the response variable and 1 as the explanatory variable) using the dredge function in the



322 MuMIN package (Bates et al. 2011). If the best fitting model has a high Akaike weight ( $>0.89$ ;  
323 Burnham & Anderson 2002), then it indicates that the results are likely given the data. The null  
324 model was strongly supported with an Akaike weight of 0.92, thus indicating the results are  
325 reliable even with a small sample size.

326

327 *Does behavioral flexibility positively correlate with motor diversity and risk aversion, and*  
328 *negatively with exploration and persistence?*

329 Birds that were more flexible did not have higher exploration scores, they were not more  
330 persistent, and there were no batch effects (Figure 2, Supplementary Table S1).

331 Risk aversion and motor diversity significantly covaried with exploration and persistence,  
332 respectively, and these relationships were investigated further. I confirmed that the relationship  
333 between these variables and behavioral flexibility is the same as their collinear variables with an  
334 additional GLM. This GLM was the same as above, except the explanatory factors were motor  
335 diversity, risk aversion and batch. As above, flexibility did not correlate with risk aversion or  
336 motor diversity (Figure 2, Supplementary Table S2).

337

338 *Does behavioral flexibility positively correlate with neophobia?*

339 Grackles that were more flexible did not have lower neophobia scores, which would indicate  
340 more neophobia: there was no significant correlation between behavioral flexibility and  
341 neophobia (Figure 2; Spearman's rank correlation:  $S=92$ ,  $p=0.12$ ,  $\rho=-0.65$ ).

342

343 **DISCUSSION**

344 Contrary to predictions, behavioral flexibility did not correlate with exploration, neophobia, risk  
345 aversion, persistence, or motor diversity. This is perhaps not surprising with regard to neophobia,  
346 the only behavior I was able to obtain repeatability measures from, which was not expressed  
347 consistently across contexts, indicating a further source of individual variation in grackles. Two  
348 unpredictable variables (behavioral flexibility and neophobia) would not likely correlate with  
349 each other. These results are similar to results from Florida scrub jays where behavioral  
350 flexibility (reversal learning) did not correlate with neophobia or exploration (Bebus et al. 2016).  
351 The few studies that investigate the relationship between behavioral flexibility and other  
352 behaviors either show relationships opposite to predictions (Verbeek et al. 1994, Guillette et al.  
353 2011) or show no correlations (this study, Bebus et al. 2016). One prediction was supported in  
354 only one test: reversal learning speed negatively correlated with neophobia (Verbeek et al. 1994).  
355 This accumulating evidence suggests the need to reconsider the basis for hypotheses linking  
356 other behaviors with behavioral flexibility.

357 Traditionally, behavioral flexibility is thought of as a cognitive ability (see review in  
358 Shettleworth 2010) and is considered as such in hypotheses linking it with other behaviors (Sih  
359 & Del Giudice 2012, Guenther et al. 2013). However, the lack of correlations between  
360 behavioral flexibility and problem solving ability and speed question this assumption.  
361 Additionally, individuals that are behaviorally flexible in one type of test are not necessarily  
362 flexible in a different type of test (Logan 2016a). This suggests that behavioral flexibility is  
363 influenced by non-cognitive, non-behavioral factors, which could include factors such as  
364 physiology and genetics. For example, grackles that are in better phenotypic condition (e.g., have  
365 better immunity) might have the capacity to be more behaviorally flexible than individuals in  
366 worse phenotypic condition. Non-behavioral, non-cognitive individual factors have yet to be

367 measured in relation to behavioral flexibility. Considering behavioral flexibility in this more  
368 integrated way could allow experimenters to manipulate this elusive trait to understand what it is  
369 and how it works.

370         These results provide further support that behavioral flexibility represents a distinct  
371 source of individual variation in behavior (Cole et al. 2011). Previous research on grackles and  
372 other species has shown that behavioral flexibility is independent from innovativeness (Logan  
373 2016b), problem solving ability and speed (Boogert et al. 2011, Isden et al. 2013, Logan 2016a).  
374 Taken together, evidence indicates that individual variation in behavioral flexibility is not  
375 confounded with other behaviors.

376         For an invasive species such as the great-tailed grackle, it could be adaptive to maintain  
377 many distinct sources of individual variation and, in particular, behavioral flexibility. Indeed,  
378 Western bluebirds rely on existing intrapopulation variation when expanding their range  
379 (Duckworth 2008). While Western bluebirds rely on variation in dispersal strategies, grackles  
380 may rely on variation in behavioral flexibility when adapting to changing environments.

381

## 382 **ACKNOWLEDGEMENTS**

383 I am grateful to Linnea Palmstrom for coding the exploration videos; Katherine Lister for coding  
384 motor diversity and persistence; Luisa Bergeron, Christin Palmstrom, Linnea Palmstrom, and  
385 Michelle Gertsvolf for trapping and aviary assistance; Steve Rothstein for use of the aviaries; Joe  
386 Jablonski for making the cast acrylic apparatuses; Jill Zachary and Kathy Frye at Santa Barbara  
387 City Parks and Recreation for use of the Andree Clark Bird Refuge and East Beach Park; Estelle  
388 Sandhaus and Chris Briggs at the Santa Barbara Zoo for access to wild grackles; and Dieter  
389 Lukas, Ted Bergstrom, Carl Bergstrom for discussions; and Alecia Carter for analysis and

390 manuscript feedback.

391

## 392 **FUNDERS**

393 I am grateful to my funders: the SAGE Center for the Study of the Mind at the University of  
394 California Santa Barbara and the National Geographic Society/Waitt Grants Program (grant  
395 number W252-12).

396

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**Table 1** (on next page)

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).

<b>Bird</b>	<b>Aviary Section</b>					<b>Risk Aversion Score (% time in risky sections)</b>	<b>Exploration Score (section changes)</b>
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>		
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

4

## **Table 2**(on next page)

### 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).

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

### **Table 3**(on next page)

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’).

<b>Technique</b>	<b>Description</b>	<b>Body part</b>
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	



**Table 4**(on next page)

Persistence and motor diversity results, and behavioral flexibility scores

Persistence (the total number of interactions with the table, apparatus, and 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).

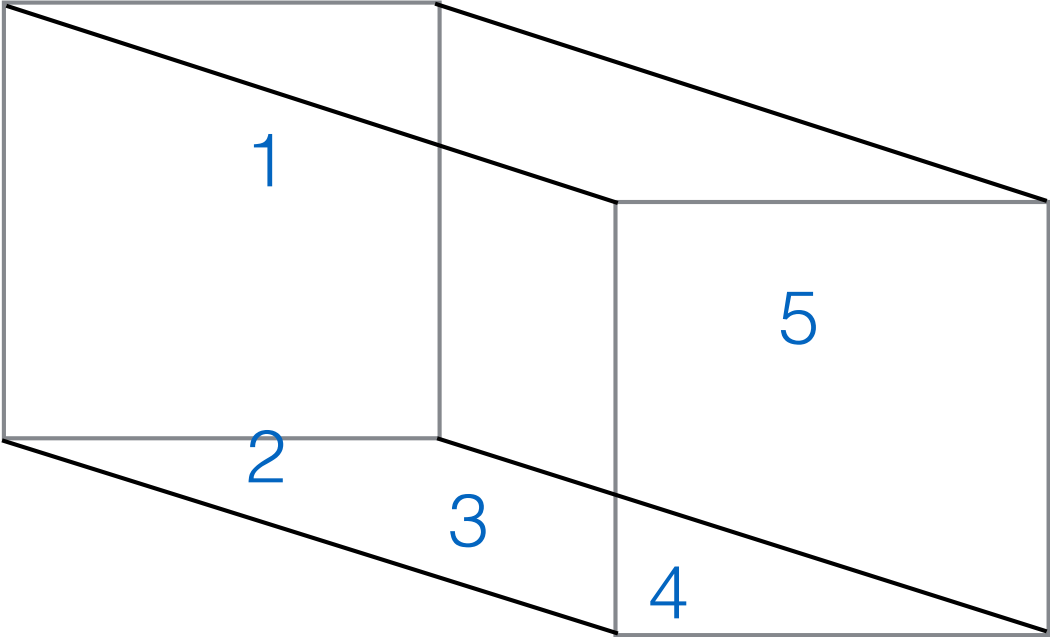
<b>Bird</b>	<b>Sex</b>	<b>Persistence</b>	<b>Motor diversity</b>	<b>Behavioral flexibility score</b>
Tequila	M	175	6	70
Margarita	F	72	5	70
Cerveza	F	81	2	60
Michelada	F	18	1	30
Horchata	F	145	8	100
Refresco	M	1114	14	50
Batido	M	4047	15	-
Jugo	M	197	6	40

**Figure 1**(on next page)

Aviary diagram

The aviary was invisibly sectioned from least (1) to most risky (4 and 5). The camera was positioned outside a door at the front of the aviary.

Rear

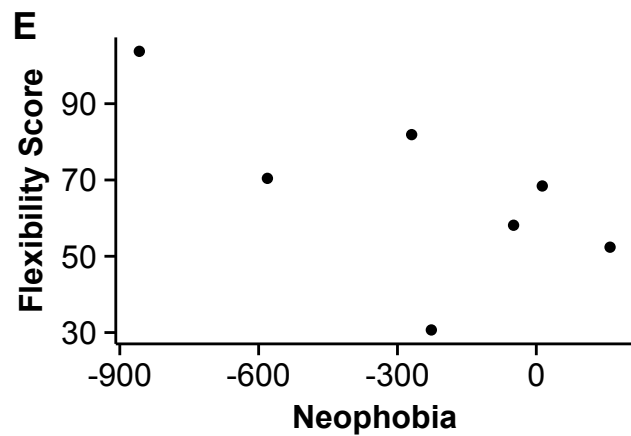
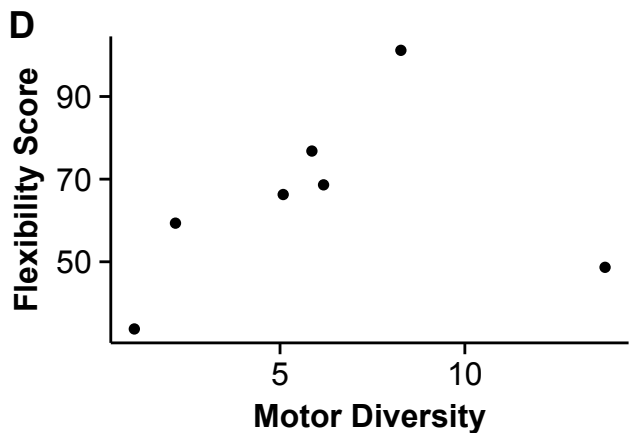
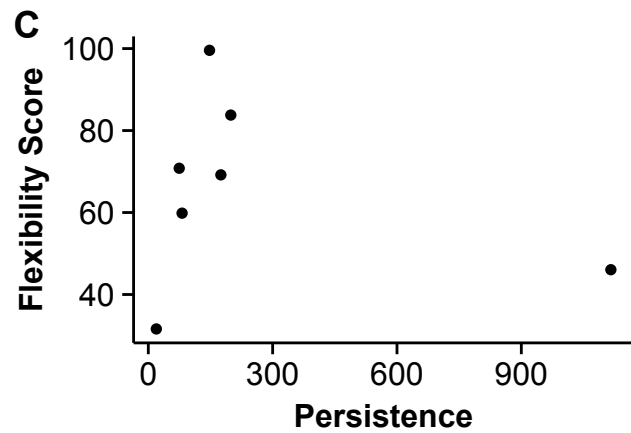
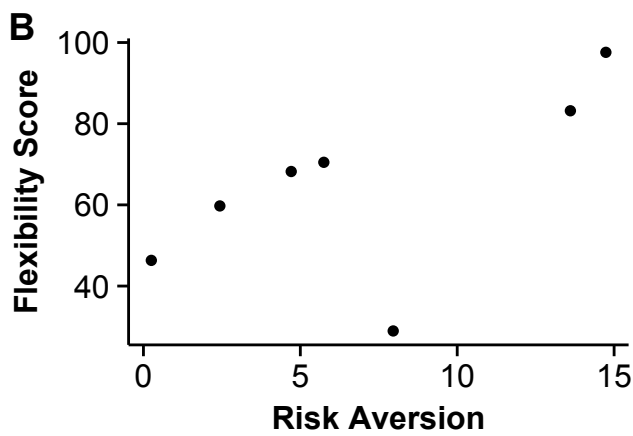
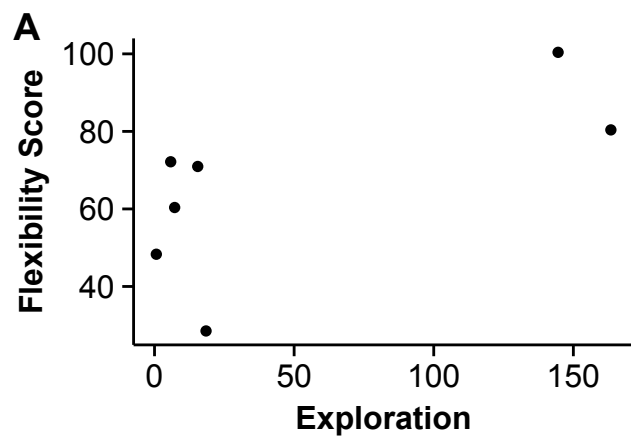


Front

## **Figure 2**(on next page)

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).



**Figure 3**(on next page)

Integrated behavioral flexibility framework

Behavioral flexibility is distinct from how well a task is performed and it can be constrained by task-specific cognitive abilities and also physiology, genetics, and other factors.

