

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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7
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 an independent trait,
13 a problem solving ability, does it arise because of links with other behaviors such as neophilia
14 and exploration, or is flexibility the result of an interaction between problem solving ability and
15 other behaviors (see review in Griffin 2016)? There are a variety of ways to measure behavioral
16 flexibility in an experimental context and all involve allowing an individual to learn about a task,
17 which then changes after the individual becomes proficient. Individuals that adapt their behavior
18 to these changing circumstances are considered to exhibit behavioral flexibility. Paradigms
19 testing behavioral flexibility include tasks such as a multi-access box (Auersperg et al., 2011;
20 Manrique, Völter & Call, 2013), water tubes (Logan et al. 2014, Logan 2016a), and episodic-like
21 memory and future planning experiments (Clayton & Dickinson, 1998; Dally, Emery & Clayton,
22 2006; Raby et al., 2007), however the most widely used measure is reversal learning (e.g., Bond
23 et al. 2007, Tebbich et al. 2010, Boogert et al. 2011). Reversal learning involves learning to

24 associate one option with a reward, which subsequently becomes incorrect when the reward is
25 moved to a different option, thus forcing the individual to reverse their preference to consistently
26 obtain the reward. The few studies that have investigated whether behavioral flexibility relates to
27 problem solving ability and speed have found that these traits do not covary in predictable ways
28 (Boogert et al. 2011, Griffin et al. 2013, Isden et al. 2013, Logan 2016a, Bebus et al. 2016). Two
29 studies found that faster learners were slower to reverse their preferences (Griffin et al. 2013,
30 Bebus et al. 2016), suggesting a speed-accuracy trade off that might depend on an individual's
31 ability to inhibit choosing the previously rewarded response (Manrique et al. 2013, Griffin &
32 Guez 2014, Liu et al. 2016, but see Homberg et al. 2007). In contrast, four studies found no
33 correlations between reversal learning speed and problem solving ability or speed (Boogert et al.
34 2011, Isden et al. 2013, Shaw et al. 2015, Logan 2016a), which indicates that increased
35 flexibility did not lead to improvements in problem solving abilities. The latter results suggest
36 that flexibility could be a trait that varies across individuals independently of problem solving
37 ability, and all results considered together suggest that variation in flexibility might correlate
38 with other traits that were not measured in these studies.

39 This leaves an open question of whether behavioral flexibility varies with differences in
40 other behaviors such as exploration, neophobia, risk aversion, persistence, and motor diversity
41 (the number of different motor actions used to attempt to solve a novel problem). There is debate
42 about whether differences in behavior among individuals are linked to suites of correlated
43 behaviors or whether individual behaviors, such as behavioral flexibility, can vary independently
44 (Coppens et al. 2010, Cole et al. 2011, Sih & Del Giudice 2012). Reversal learning is predicted
45 to fall on the fast-slow behavioral type continuum where fast individuals are exploratory, risk
46 seeking, and persistent with poor accuracy because of the speed with which they solve problems,

47 whereas slow individuals are neophobic, risk averse, and more accurately solve problems (Sih &
48 Del Giudice 2012). Accordingly, slow individuals should be more behaviorally flexible because
49 they might be less impulsive, that is, less likely to rush into a situation and persistently try a
50 particular solution, which gives them more time to survey the environment and attend to the
51 relevant features of the situation (Sih & Del Giudice 2012). Individuals that are more neophobic
52 and less exploratory would also have more time to examine a situation before taking action, thus
53 making them more likely to choose correctly when they do take action (Sih & Del Giudice
54 2012).

55 These predictions are at odds with some evidence from the comparative cognition
56 literature. In a multi-access box paradigm, keas (*Nestor notabilis*) were faster to explore and
57 faster to learn more solutions, as well as faster to switch to trying new solutions when previously
58 rewarded solutions stopped working than New Caledonian crows (*Corvus moneduloides*;
59 Auersperg et al. 2011). In this case, a positive correlation between flexibility and exploration led
60 to faster problem solving success, rather than the predicted negative correlation that would result
61 from individuals inhibiting their actions and surveying the task. One reason for this difference
62 could be due to it being an interspecies rather than an intraspecies comparison: differences
63 between species are more likely to be larger and easier to detect than differences between
64 individuals of the same species. Another reason for the disparity between predictions in the
65 comparative cognition and individual differences literatures could come from defining terms
66 differently or not at all. For example, persistence in attempting to solve a task is a measure of
67 impulsivity, however persistence could be defined as the number of attempts directed to all parts
68 of an apparatus or as the number of attempts directed at one part of the apparatus before trying a
69 different part of the apparatus. As such, persistence could involve attention to function or not.

70 The latter might be implied from the individual differences literature, while the former might be
71 implied from the comparative cognition literature. It is unclear whether definitional differences
72 might explain opposite predictions because it is only the recent merging of these two fields that
73 has brought about a need to clarify such definitions. Regardless of potential difficulties arising
74 from differences in definitions, if behavioral flexibility correlates with other behaviors, such
75 correlations could mask whether individuals vary in their behavioral flexibility because this trait
76 is independent or because this variation is caused by a correlated behavior (Herrmann et al. 2010,
77 Thornton & Lukas 2012, Seed et al. 2012).

78 Results from the few studies that investigated the relationship between behavioral
79 flexibility and other behaviors are equivocal. Consistent with predictions, black-capped
80 chickadees (*Poecile atricapillus*) and great tits (*Parus major*) that were more flexible (faster to
81 reverse a previously learned preference) were slower to explore (Verbeek et al. 1994, Guillette et
82 al. 2011), and great tits that were more flexible (reversal learning) were more neophobic
83 (Verbeek et al. 1994). Two studies provided evidence inconsistent with the predictions that
84 behavioral flexibility will positively correlate with neophobia and negatively with exploration:
85 there were no correlations between behavioral flexibility (reversal learning) and neophobia or
86 exploration in Florida scrub jays (*Aphelocoma coerulescens*; Bebus et al. 2016), and also no
87 correlations with activity or boldness in wild cavies (*Cavia aperea*; Guenther et al. 2014a).
88 Given this mixed evidence, it is not yet clear whether behavioral flexibility is part of a suite of
89 correlated traits or a trait that varies independently across individuals.

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

93 2015). Innovativeness, defined as inventing new behaviors to solve novel problems or using
94 existing behaviors in new ways (Griffin & Guez 2014), is distinct from behavioral flexibility. For
95 example, great-tailed grackles exhibit behavioral flexibility in two tests involving reversal
96 learning, showing that they are among the fastest bird species to both learn an initial preference
97 and to reverse this preference (Logan 2016a). However, grackles are not particularly inventive
98 when it comes to creating new behaviors to solve novel problems: they did not successfully
99 innovate string pulling or stick tool use, which are behaviors that many other bird species engage
100 in (Logan 2016b). While it is unknown how motor diversity interacts directly with behavioral
101 flexibility, the prediction is that these traits will positively correlate because increasing the
102 number of motor actions attempted could increase the probability and speed of finding a
103 successful solution to a novel problem (Diquelou et al. 2016).

104 To determine whether behavioral flexibility is related to a variety of behaviors in one
105 species, I investigated great-tailed grackles (*Quiscalus mexicanus*, family Icteridae, hereafter
106 referred to as grackles), a generalist forager (Skutch 1954, Johnson & Peer 2001, Wehtje 2003)
107 that is behaviorally flexible (Logan 2016a). Grackles are a native invasive species (Peer 2011):
108 they have expanded their range north from Central America into North America by over 5500%
109 over the course of 120 years following the expansion of human modified environments, which is
110 their preferred habitat (Wehtje 2003). Behavioral flexibility is hypothesized to be a mechanism
111 involved in successful species invasions (Sol & Lefebvre 2000). Whereas grackles could have
112 expanded their range simply because of an increase in their suitable habitat, species differences
113 in traits that facilitate adapting to environmental change, such as diet, are additionally implicated
114 (Blackburn et al. 2009). Behavioral flexibility is one such trait and a better understanding of how
115 it works could have implications for managing species invasions. To better understand

116 behavioral flexibility, I tested the hypothesis that individual variation in behavioral flexibility
117 correlates with variation in other behaviors on the fast-slow continuum.

118 I predicted that individuals that were more behaviorally flexible would also be the most
119 neophobic and risk averse, the least persistent and exploratory, and use more motor actions. I
120 quantified grackles' activity levels (exploration) when placed in a novel environment and also
121 measured the amount of time spent in the safest sections of the aviary (risk aversion). I measured
122 grackles' neophobic reactions to a novel object next to a food dish in comparison with controls
123 where only a food dish was present. Persistence and motor diversity were measured from videos
124 of a stick tool use experiment (Logan 2016b), where no bird successfully invented stick tool use.
125 Therefore, birds were never rewarded for their actions, which is important when measuring
126 persistence because a food reward could differentially influence persistence across individuals:
127 those who are better at the task would receive more food rewards, which might increase their
128 persistence in future trials.

129

130 **METHODS**

131 **Ethics**

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

138

139 Subjects

140 Eight adult great-tailed grackles (4 females and 4 males) were caught in the wild and held for 2-3
141 months in aviaries before being released back to the wild (see Logan 2016a for full details). Half
142 of the birds were caught in Santa Barbara, California in September 2014 and released in
143 December 2014 (Tequila, Margarita, Cerveza, and Michelada; batch 1) and the other half were
144 caught in January 2015 and released in March 2015 (Refresco, Horchata, Batido, Jugo; batch 2).

145

146 Study Set Up

147 Grackles were housed individually in aviaries (183 cm high by 119 cm wide by 236 cm long) at
148 the University of California Santa Barbara. Grackles had *ad libitum* access to water at all times,
149 and unrestricted amounts of food (Mazuri® Small Bird Food) for a minimum of 20 hrs per day.
150 On testing days, their main diet was removed for up to 4 hrs while they participated in
151 experiments and could eat bread or peanuts if successful. Apparatuses were placed on tables (60
152 cm wide by 39 cm long) and rolled into each aviary for sessions (approximately 20 min per
153 session), which were visually isolated from other grackles and video recorded with a Nikon
154 D5100 camera on a tripod. Experimenters stood just outside the aviary door and in full view of
155 the grackles during the persistence and motor diversity sessions, which did not interfere with
156 behavior (i.e., they readily interacted with the apparatus) because they were habituated to
157 humans in the wild and in the aviary.

158

159 Statistical Analyses

160 Data were analyzed in R 3.2.1 (R Core Team 2015). For those tests that involved p-values, a
161 result was considered statistically significant when $p < 0.05$. When multiple p-values were

162 obtained for one experiment, a Bonferroni-Holm correction was applied to avoid obtaining false
163 positive results simply by conducting many tests on the same data.

164

165 **Data Accessibility**

166 Data are available at the KNB Data Repository (Logan 2016c;
167 https://knb.ecoinformatics.org/#view/corina_logan.18.15). Behavioral flexibility data were
168 previously published and are available at KNB (Logan 2016d).

169

170 **Videos**

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

172

173 **Exploration and Risk Aversion**

174 The exploration session lasted 60 min, starting 30 min after a wild bird's release into the aviary,
175 a novel environment. The grackles' previous experience was always the same: they were
176 trapped, blood was collected, and colored rings put on their legs; they were transported to the
177 aviary in a cat carrier in a car, biometrics were taken, and then they were released into the aviary
178 where they were singly housed, given food and water, and the camera was set up outside their
179 door. The camera was restarted every 20 min, otherwise experimenters were out of visual and
180 auditory contact when recording.

181 Exploration is measured in a number of different ways and I chose two measures for the
182 purposes of this study, which have been used to measure exploration in other species: the amount
183 of activity in a novel environment (exploration; e.g., Verbeek et al. 1994, Fox et al. 2009) and

184 the amount of time spent in the safe areas of the novel environment (risk aversion; e.g., Lynn &
185 Brown 2009, Lerman et al. 2012, Jolles et al. 2014).

186 **Exploration:** Videos were coded by Linnea Palmstrom to determine how often birds
187 moved between sections of the aviary. The aviary was invisibly sectioned into 5 areas with
188 sections 1 and 5 in the upper half of the aviary, where the perches were located, and sections 2-4
189 on the ground (Figure 1). Their exploration score was the number of times they moved from one
190 aviary section to another over the course of the 60 min session, which was an appropriate time
191 period (Montiglio et al. 2010) because an individual's activity level was ranked similarly
192 regardless of whether activity occurred in the first 5 min or over the whole session (Spearman's
193 rank correlation: $S=31.43$, $p=0.10$, $\rho=0.63$, $n=8$).

194 **Risk aversion:** I (invisibly) divided the aviary into safer versus riskier sections (Figure 1)
195 and used the percentage of time spent in sections 1-3 (the safer sections) as a measure of risk
196 aversion. The rear of the aviary was considered less risky because it was the farthest from the
197 door where the camera and other equipment were visible, while the ground and the perches in the
198 front of the aviary were more risky because these sections were next to the door and walking on
199 the ground is more dangerous than flying. Food and water were placed on the ground near the
200 door. The aviary was covered in tarpaulins on three sides (both sides and rear), while the side
201 with the door (front) and the ceiling were wire mesh that the bird could see through.

202

203 **Neophobia**

204 The neophobia sessions began on a grackle's sixth day in the aviary and involved three 10-min
205 trials with trials 1 and 3 serving as a way to quantify food motivation by placing a food bowl
206 alone on the table, while trial 2 had a novel object 2 cm to the right of the food bowl (as in

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

220 Data were analyzed using the latency to land on the table rather than the latency to feed
221 because birds came to the table more often than they ate the food. The data were not normally
222 distributed (Anderson-Darling normality test: GoPro: $A=3.08$, $p<0.001$; stone dropping
223 apparatus: $A=2.76$, $p<0.001$; U-tube: $A=2.46$, $p<0.001$). Therefore, non-parametric paired
224 Wilcoxon signed rank tests with continuity corrections were conducted to determine whether
225 latencies in control trials (averaged) differed from novel object trials. Neophobia scores were
226 obtained for each novel object and summed for an overall score per individual. Scores were
227 calculated by subtracting the latency to land on the table during the novel object trials (trial 2)
228 from the average latency during control trials (trials 1 and 3). Positive scores indicate less
229 neophobia while negative scores indicate more neophobia. Repeatability of individual neophobic

230 responses across contexts was measured using Spearman's rank correlations to determine
231 whether grackles maintained similar neophobia ranks with each of the three novel objects.

232

233 **Persistence and Motor Diversity**

234 Persistence and motor diversity were calculated as in Griffin & Diquelou (2015). Persistence
235 was calculated as the attempt rate: the number of times a bird came to the table or interacted with
236 (touched) the apparatus or stick across 21 trials of a stick tool use experiment (105 min/bird;
237 Logan 2016b). Motor diversity was calculated by counting the number of different motor actions
238 (described in Table 3) performed per individual across the 21 trials of the experiment. Videos
239 were watched from trials 1 to 21 and behaviors from the ethogram (Table 3) were coded at their
240 first observation.

241 The stick tool use experiment involved an apparatus with a wooden base and rear with
242 clear cast acrylic walls providing a narrow gap at the front and top of the apparatus to insert a
243 stick and retrieve a piece of bread (Logan 2016b). Birds were given 21 5 min trials to innovate
244 tool use: first, 3 trials with the stick placed on the table next to the apparatus, then 3 trials with
245 the stick inserted into the apparatus, and finally 15 trials with the stick inserted in the apparatus
246 and tool use demonstrated by the human experimenter.

247

248 **Measure of Behavioral Flexibility**

249 These grackles were previously tested on reversal learning of a color discrimination task
250 consisting of a gold tube and a silver tube placed on the table at the same time with one color
251 containing hidden food and the opportunity to make only one choice per trial (Logan 2016a).
252 Grackles initially learned to search for food hidden in the gold tube and, once proficient, the food

253 was switched to the silver tube and the number of trials required to reach proficiency was
254 assessed. Behavioral flexibility scores were calculated as the number of trials to reverse a color
255 preference minus the number of trials needed to initially learn the color preference (Table 4).
256 Proficiency in the initial discrimination and reversal was demonstrated if individuals chose
257 correctly in at least 17 of the most recent 20 trials with at least 8 or 9 trials correct per set of 10. I
258 then investigated whether relationships between individual variation in behavioral flexibility and
259 exploration, risk aversion, neophobia, persistence, and motor diversity conformed to predictions.

260

261 **General Analyses**

262 I determined whether behavioral flexibility (response variable: behavioral flexibility score)
263 negatively correlated with exploration and persistence while examining whether batch had an
264 effect (explanatory variables) using a Generalized Linear Model (GLM; MCMCglmm function,
265 MCMCglmm package; Hadfield 2014) with a Poisson distribution and log link using 13000
266 iterations with a thinning interval of 10 and a burnin of 3000. The GLM showed acceptable
267 convergence (lag time autocorrelation values were <0.01 ; Hadfield 2010). Risk aversion and
268 motor diversity were excluded from the analysis because they significantly covaried with
269 exploration and persistence, respectively. A Spearman's rank correlation was used to investigate
270 the relationship between behavioral flexibility and neophobia because residuals were not
271 normally distributed.

272 Given the small sample size ($n=7$ for behavioral flexibility scores), I conducted a further
273 analysis to determine whether GLM results were likely to be reliable given the data (Burnham &
274 Anderson 2002). I compared the Akaike weights (range: 0-1, the sum of all model weights
275 equals 1; Akaike 1981) between the test model (above) and a null model (behavioral flexibility

276 score as the response variable and 1 as the explanatory variable) using the dredge function in the
277 MuMIN package (Bates et al. 2011). If the best fitting model has a high Akaike weight (>0.89 ;
278 Burnham & Anderson 2002), then it indicates that the results are likely given the data. The null
279 model was strongly supported with an Akaike weight of 0.92, thus indicating the results are
280 reliable even with a small sample size.

281

282 **Interobserver Reliability**

283 Linnea Palmstrom coded the exploration/risk aversion videos, I coded neophobia videos, and
284 Katherine Lister coded persistence and I coded motor diversity from videos of a tool use
285 experiment (in Logan 2016b). To measure interobserver reliability, I randomly chose 21% of the
286 videos using www.random.org and had a coder who was naïve to the hypotheses (Katharina
287 Brecht) recode their exploration (from which measures of risk aversion are calculated),
288 persistence, and neophobia. I randomly chose 3 of the 8 birds using www.random.org and had
289 Katharina recode their motor diversity (36% of the videos). A higher percentage of motor
290 diversity videos were recoded because agreement determinations were based on the total number
291 of motor actions per bird, which required watching all videos for an individual. There was
292 agreement between Katharina and all other observers for each study: exploration (intraclass
293 correlation coefficient (ICC)=0.998, 95% confidence intervals (CI) =0.98-1.00), neophobia
294 (ICC=0.87, 95% CI=0.67-0.95), persistence (land on table: ICC=0.79, 95% CI=0.49-0.93;
295 interact with apparatus: ICC=1.00, 95% CI=0.999-1.00; interact with stick: ICC=1.00, 95%
296 CI=NA), and motor diversity (ICC=0.71, 95% CI=0.54-0.82; ICCs calculated using R package:
297 irr, function: icc, Gamer et al. 2012).

298

299 **RESULTS**300 **Exploration and Risk Aversion**

301 Exploration and risk aversion were significantly negatively correlated, indicating that these two
302 variables might measure opposite ends of the same behavior or an unmeasured behavior might
303 correlate with both and explain their relationship (Spearman's rank correlation: $S=159.45$,
304 $p=0.002$, $\rho=-0.90$, $n=8$). To eliminate covariance between explanatory variables, I used
305 exploration to represent this behavior in further analyses (see General Analyses section).

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

309 **Risk aversion:** Grackles varied in how much time they spent in the safest sections of the
310 aviary with Batido spending the least time and Refresco the most (Table 1). All grackles (except
311 Refresco) moved through other sections of the aviary and they varied in how much time they
312 spent in sections 4 and 5 (Table 1).

313

314 **Neophobia**

315 There were no significant differences between the latency to land on the table in controls (pre
316 [trial 1] or post [trial 3] novel object trials) versus novel object trials (trial 2) (Wilcoxon tests
317 with Bonferroni-Holm corrected p-values: GoPro: *trials 1-2* $V=21$, $p=1.00$, 95% confidence
318 interval=-283-267, *trials 2-3* $V=8$, $p=1.00$, 90% CI=-427-277.5; stone dropping apparatus: *trials*
319 *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*
320 *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
321 and Margarita were overall less neophobic than the other grackles, and Horchata was the most

322 neophobic (Table 2). There were many trials in which the bird did not come to the table.
323 However, this did not usually appear to be due to neophobia because it happened in many control
324 trials as well as novel object trials, indicating that it might have been due to a lack of motivation
325 to eat or explore the object.

326 There was no individual repeatability of neophobia scores across contexts (Spearman's
327 rank correlation with Bonferroni-Holm corrected p-values: GoPro vs. stone dropping apparatus:
328 $S=79.21$, $p=1.00$, $\rho=-0.41$, GoPro vs. U-tube: $S=56.00$, $p=1.00$, $\rho=0.00$; U-tube vs. stone
329 dropping apparatus: $S=20.68$, $p=0.88$, $\rho=0.63$).

330

331 **Persistence and Motor Diversity**

332 Grackles varied in the number of motor actions they used (1-15) and in how persistent they were
333 (18-4047 total number of times a bird landed on the table, touched the apparatus, or touched the
334 stick; Table 4). A post-hoc analysis indicated that these two variables were significantly
335 positively correlated, indicating that they could have measured the same behavior or have been
336 caused by another, unmeasured variable (Spearman's rank correlation: $S=8.55$, $p=0.002$,
337 $\rho=0.90$, $n=8$). Therefore, only persistence was used in further analyses (see General Analyses
338 section).

339

340 **Does behavioral flexibility positively correlate with motor diversity and risk aversion, and** 341 **negatively with exploration and persistence?**

342 Birds that were more flexible (i.e., faster to reverse a preference: number of trials to reverse a
343 preference minus the number of trials to initially learn the preference) did not have higher
344 exploration scores, they were not more persistent, and there were no batch effects (Figure 2,

345 Supplementary Table S1). There were no significant correlations between flexibility and
346 exploration or persistence, indicating that results did not provide evidence for the predicted
347 negative correlations.

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

354

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

356 Grackles that were more flexible (i.e., faster to reverse a preference) did not have lower
357 neophobia scores, which would indicate more neophobia. There was no significant correlation
358 between behavioral flexibility scores and neophobia (Figure 2; Spearman's rank correlation:
359 $S=92$, $p=0.12$, $\rho=-0.65$).

360

361 **DISCUSSION**

362 **Exploration and Risk Aversion**

363 The exploration and risk aversion scores significantly negatively correlated with each other,
364 indicating they might have measured opposite ends of the same behavior. While risk aversion
365 scores could have been confounded by the placement of food and water in a risky section, which
366 might attract birds to this area, they spent only 0-14% of their time in the section with the food

367 and water (section 4). This indicates that they behaved more according to the prediction that this
368 section would be treated as risky even when an attractor was present.

369 I question whether the measure of exploration actually measured exploration in this
370 species. A bird that is stressed tends to fly back and forth in an aviary, which is not an indicator
371 of exploration, but would be interpreted as such according to the section change measure of
372 exploration. In this study, Jugo mostly flew back and forth between the perches near the top of
373 the aviary while looking up and out of the aviary and not attending to the environment within the
374 aviary. In contrast, Horchata also had many section changes, but she usually walked calmly on
375 the ground, thus perhaps in her case this measure of exploration was appropriate. Therefore, at
376 the species level, activity levels are likely not a good indicator of exploration behavior. Indeed, a
377 distinction is made between forced exploration, where an individual is placed in a novel
378 environment, and voluntary exploration, where an individual in a familiar environment is
379 provided with the opportunity to enter a novel environment (Guenther et al. 2014b). A study on
380 wild guinea pigs (*Cavia aperea*) found that these two variations of exploration measure different
381 behaviors: forced and voluntary exploration activity did not correlate in juveniles or adults
382 (Guenther et al. 2014b).

383 Voluntary exploration would likely be a more accurate measure of actual exploratory
384 behavior in grackles, which could also involve voluntary exploration of a novel object in a
385 familiar environment. Such a measure is also called a neophilia test where a novel object is
386 placed in a familiar aviary in the presence of (but not next to) their regular food source to
387 determine how soon the bird approaches and interacts with the apparatus and for how long (as in
388 Mettke-Hoffman et al. 2002). This kind of test would also likely more directly relate to how
389 grackles have expanded their range so rapidly: rather than exploring novel environments,

390 grackles are more likely to have successfully expanded their range by exploring novel objects.
391 Grackles have not necessarily needed to adapt to novel environments during their range
392 expansion because it coincided with an increase in their suitable (human-managed) habitat
393 (Wehtje 2003). Exploration is more likely to have played a role in exploiting novel objects in
394 their environment because humans throw away products that may be novel to grackles (e.g., egg
395 cartons, yogurt cups) and design new potential food sources (e.g., dumpsters) where food is not
396 necessarily obvious, therefore the objects must be explored to determine whether they contain
397 food.

398

399 **Neophobia**

400 Grackles were not generally neophobic because no significant differences were found between
401 controls and novel object trials in the latency to land on the table. Indeed, the GoPro camera,
402 which was also the smallest of the novel objects, appeared to attract their attention more than the
403 food. Comparing grackles with other species that have been tested using a similar design, it
404 appears that they are less neophobic than starlings (*Sturnus vulgaris*; Boogert et al. 2006), blue
405 tits (*Cyanistes caeruleus*; Herborn et al. 2010), Japanese quail (*Coturnix japonica*; Zimmer et al.
406 2013), Chimango caracaras (*Milvago chimango*; Biondi et al. 2010), European greenfinches
407 (*Carduelis chloris*; Herborn et al. 2011), Indian mynas (Sol et al. 2012, Griffin & Diquelou
408 2015), and mountain chickadees (*Poecile gambeli*; Kozlovsky et al. 2015), and that they have
409 similar levels of neophobia as noisy miners (*Manorina melanocephala*; Griffin & Diquelou
410 2015) and a different group of mountain chickadees (Fox et al. 2009).

411

412 **Persistence and Motor Diversity**

413 The persistence and motor diversity scores significantly correlated with each other, indicating
414 they might have measured the same behavior or have been caused by another, unmeasured
415 variable. This suggests that the longer a bird persists in attempting to solve a task, the more
416 likely it is to use a wider variety of motor actions. Therefore, it is likely that individuals that used
417 few motor actions would likely have used more if they were perhaps more motivated to interact
418 with the task. Measuring persistence and motor diversity in a variety of contexts could address
419 this potential issue and clarify whether these variables actually do covary on a task that all
420 individuals persist on. These results are different from findings using a similar experimental
421 design on Indian mynas and noisy miners where motor diversity differed between species, but
422 persistence did not, thus indicating these were two separate behaviors (Griffin & Diquelou
423 2015). However, birds in Griffin & Diquelou (2015) could receive food rewards from the
424 apparatus if successful (i.e., at the end of each bout of persistence) and such positive
425 reinforcement for persisting could have increased persistence for successful individuals in
426 subsequent trials.

427

428 **Behavioral Flexibility**

429 Contrary to predictions, behavioral flexibility did not correlate with exploration, neophobia, risk
430 aversion, persistence, or motor diversity. The small sample size might have limited my ability to
431 detect significant correlations; however the behavior of the models suggested this was not the
432 case. It is perhaps not surprising that behavioral flexibility did not correlate with neophobia (the
433 only behavior I was able to obtain repeatability measures from) because neophobia was not
434 expressed consistently across contexts. This could indicate a further source of individual
435 variation in grackles or it could result from the inability of the method to accurately measure

436 neophobia in this species. The latter highlights the importance of conducting repeatability tests
437 when attempting to understand how two variables correlate because two unpredictable variables
438 (behavioral flexibility and neophobia) would not likely correlate with each other. These results
439 are similar to results from Florida scrub jays where behavioral flexibility (reversal learning) did
440 not correlate with neophobia or exploration (Bebus et al. 2016). The few studies that investigate
441 the relationship between behavioral flexibility and other behaviors either show relationships
442 opposite to predictions (Verbeek et al. 1994, Guillette et al. 2011) or show no correlations (this
443 study, Bebus et al. 2016). One prediction was supported in only one test: reversal learning speed
444 negatively correlated with neophobia (Verbeek et al. 1994). This accumulating evidence suggests
445 the need to reconsider the basis for hypotheses linking other behaviors with behavioral
446 flexibility.

447

448 **CONCLUSIONS**

449 Traditionally, behavioral flexibility is thought of as a cognitive ability (see review in
450 Shettleworth 2010) and is considered as such in hypotheses linking it with other behaviors (Sih
451 & Del Giudice 2012, Guenther et al. 2013). However, mixed results, with none conforming to
452 predictions, from grackles, keas and New Caledonian crows question this assumption. Grackles
453 lacked correlations between behavioral flexibility and problem solving ability and speed, and
454 individuals that were behaviorally flexible in one type of test were not necessarily flexible in a
455 different type of test (Logan 2016a). The more exploratory keas were more behaviorally flexible
456 on a multi-access box and faster to innovate new solutions to novel problems than New
457 Caledonian crows (Auersperg et al. 2011). These mixed results indicate a need to look beyond
458 cognitive and behavioral measures that might correlate with behavioral flexibility and investigate

459 relationships with factors such as physiology and genetics. For example, grackles that are in
460 better phenotypic condition (e.g., have better immunity) might have the capacity to be more
461 behaviorally flexible than individuals in worse phenotypic condition. Non-behavioral, non-
462 cognitive individual factors have yet to be measured in relation to behavioral flexibility.
463 Considering behavioral flexibility in this more integrated way could allow experimenters to
464 manipulate this elusive trait to understand what it is and how it works.

465 Though the sample size is small, these results provide further support that behavioral
466 flexibility represents a distinct axis of individual variation in behavior. Behaviors that do not
467 correlate with each other are suggested to represent “inherent individual differences” in each of
468 the traits measured (Cole et al. 2011, p. 495). For example, great tit problem solving ability did
469 not correlate with body condition, neophobia, or exploration; therefore problem solving was
470 considered its own behavior that varies across individuals rather than varying due to links with
471 other individual traits (Cole et al. 2011). The methods used to measure neophobia and
472 exploration in grackles might not have accurately represented these behaviors, therefore further
473 investigations using different methods that are validated measures of these behaviors in grackles
474 should be explored before entirely ruling out correlations with behavioral flexibility. Previous
475 research on grackles and other species has shown that behavioral flexibility is independent from
476 innovativeness (Logan 2016b), problem solving ability and speed (Boogert et al. 2011, Isden et
477 al. 2013, Logan 2016a), or that it negatively correlates with problem solving speed (Griffin et al.
478 2013). The majority of evidence so far indicates that individual variation in behavioral flexibility
479 is not confounded with other behaviors, although two alternative hypotheses cannot yet be ruled
480 out: the behaviors might not have been measured with enough consistency across studies to
481 directly compare the results, or the behaviors are not repeatable enough within individuals to

482 reliably covary with each other. Further research is needed to distinguish which hypothesis is
483 supported.

484 It could be adaptive for invasive species, such as the grackle, to maintain many
485 independent axes of individual variation and, in particular, variation in behavioral flexibility.
486 Indeed, Western bluebirds rely on existing intrapopulation variation when expanding their range
487 (Duckworth 2008). While Western bluebirds rely on variation in dispersal strategies, grackles
488 may rely on maintaining individual variation in behavioral flexibility, which could allow them to
489 more quickly adapt to changing or unpredictable environments.

490

491 **FUTURE DIRECTIONS**

492 Future research investigating neophobia, exploration, persistence and motor diversity in this
493 species would benefit from a larger sample size, replicability of results from multiple groups, and
494 finding measures that are repeatable within individuals to determine the reliability of these
495 conclusions. Incorporating the use of a factor analysis would help determine whether correlated
496 explanatory variables measure distinct behaviors or arise from unmeasured correlated variables.
497 Investigating each variable using multiple methods will facilitate an understanding of which
498 methods actually measure the behaviors of interest.

499

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509

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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 safest sections of the aviary; sections 1-3) 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 safest sections of the aviary; sections
 3 1-3) and their exploration score (total number of section changes).

Bird	Aviary Section					Risk Aversion Score (% time in safe sections)	Exploration Score (section changes)
	1	2	3	4	5		
Tequila	94	0.4	0.5	6	0	94	16
Margarita	96	0	0.1	4	0	96	5
Cerveza	95	3	0	2	0	98	8
Michelada	92	0.06	0	6	2	92	19
Horchata	47	35	5	14	0	86	145
Refresco	100	0	0	0	0	100	0
Batido	44	0.6	0	0	55	45	30
Jugo	73	12	2	3	11	86	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).

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

6

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’).

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
16. Step	Places one foot on the apparatus	(or
17. Tips apparatus	Tips apparatus over after standing on top and flying off or by grabbing with bill and pulling over	bill)

3

Table 4(on next page)

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

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Figure 1(on next page)

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).

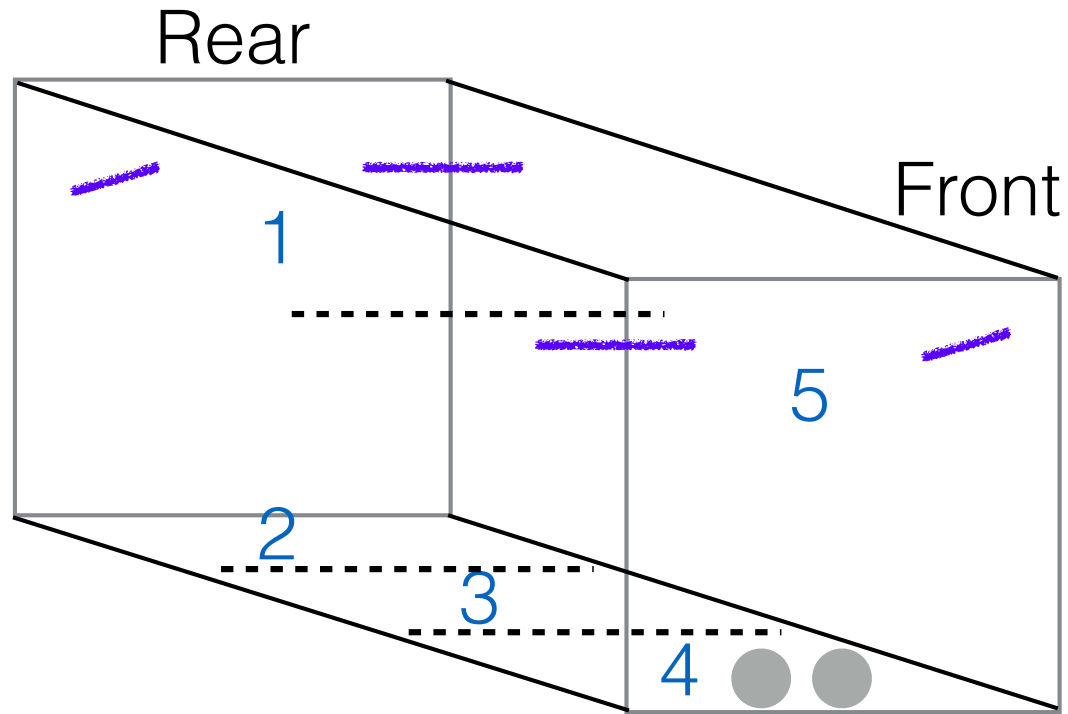


Figure 2 (on next page)

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 safe 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).

