

1 Are the more flexible great-tailed grackles also better at behavioral  
2 inhibition?

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12 See the HTML version because it is easy-to-read, and the reproducible manuscript Rmd version for the code.



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16 **tion?** ([http://corinalogan.com/Preregistrations/g\\_inhibition.html](http://corinalogan.com/Preregistrations/g_inhibition.html)) In principle acceptance by *PCI Ecology*  
17 of the version on 6 Mar 2019 [https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/](https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/g_inhibitionPassedPreStudyPeerReview6Mar2019.pdf)  
18 [g\\_inhibitionPassedPreStudyPeerReview6Mar2019.pdf](https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/g_inhibitionPassedPreStudyPeerReview6Mar2019.pdf).



19  
20 **This preregistration has been pre-study peer reviewed and received an In Principle Recom-**  
21 **mendation by:**

22 Erin Vogel (2019) Adapting to a changing environment: advancing our understanding of the mechanisms  
23 that lead to behavioral flexibility. *Peer Community in Ecology*, 100016. 10.24072/pci.ecology.100016

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## 25 ABSTRACT

26 Behavioral flexibility (hereafter, flexibility) should theoretically be positively related to behavioral inhibition  
27 (hereafter, inhibition) because one should need to inhibit a previously learned behavior to change their  
28 behavior when the task changes (the flexibility component; Manrique et al. 2013; Griffin and Guez 2014; Liu  
29 et al. 2016). However, several investigations show no or mixed support of this hypothesis, which challenges  
30 the assumption that inhibition is involved in making flexible decisions. We aimed to test the hypothesis  
31 that flexibility (measured as reversal learning and solution switching on a multi-access box by Logan et al.  
32 2019) is associated with inhibition by measuring both variables in the same individuals and three inhibition  
33 tests (a go/no go task on a touchscreen, a detour task, and a delay of gratification experiment). We set out  
34 to measure grackle inhibition to determine whether those individuals that are more flexible are also better  
35 at inhibition. Because touchscreen experiments had never been conducted in this species, we additionally  
36 validated that a touchscreen setup is functional for wild-caught grackles who learned to use the touchscreen  
37 and completed the go/no go inhibition task on it. Results showed that only performance on the go/no go  
38 inhibition task correlated with the two flexibility measures: positively with the number of trials to reverse  
39 a preference in the reversal learning experiment, and negatively with the average latency to attempt a new  
40 option on the multi-access box. That is, individuals who were faster to update their behavior in the reversal  
41 experiment were also faster to reach criterion in the go/no go task, but took more time to attempt a new  
42 option in the multi-access box experiment. Performance on the detour inhibition task did not correlate  
43 with either measure of flexibility, suggesting that detour performance and the flexibility experiments may  
44 measure separate traits. We were not able to run the delay of gratification experiment because the grackles  
45 never habituated to the apparatuses. Performance on the go/no go and detour inhibition tests did not  
46 correlate with each other, indicating that they did not measure the same trait. We conclude that flexibility  
47 is associated with certain types of inhibition, but not others, in great-tailed grackles.

48 **Video summary <https://youtu.be/TXFOYqZztf4>**

## 49 INTRODUCTION

50 Individuals who are more behaviorally flexible (the ability to change behaviors in response to a changing  
51 environment, Mikhalevich et al. 2017) are assumed to also be better at inhibiting a prepotent response  
52 (Ghahremani et al. 2009; Manrique et al. 2013; Griffin and Guez 2014; Liu et al. 2016). This is because  
53 one should need to inhibit a previously learned behavior to change their behavior when the task changes.  
54 However, there is mixed support for the hypothesis that behavioral flexibility (hereafter, flexibility) and  
55 behavioral inhibition (hereafter, inhibition) are linked. Many investigations found no correlation between  
56 reversal learning (a measure of flexibility) and detour performance (a measure of inhibition) (Boogert et al.  
57 2011; Shaw et al. 2015; Brucks et al. 2017; Damerius et al. 2017; DuBois et al. 2018; Ducatez et al. 2019),  
58 while others found mixed support that varied by species and experimental design (Deaner et al. 2006).  
59 Investigations using other measures of flexibility and inhibition have also failed to find a connection between  
60 the two (Johnson-Ulrich et al. 2018), and even between different measures of inhibition (e.g., Bray et al. 2014;  
61 Fagnani et al. 2016). Further, causal evidence directly challenges the assumption that flexibility requires  
62 inhibition. For example, Homberg et al. (2007) showed that rats with improved inhibition (due to gene  
63 knockouts) did not perform better in a reversal learning experiment than non-knockout rats. Additionally,  
64 Ghahremani et al. (2009) found in humans that brain regions that are active during reversal learning are  
65 different from those that are active when someone inhibits a prepotent learned association. These results  
66 indicate that inhibition and flexibility are separate traits. The mixed support for a relationship between  
67 detour performance and reversal learning makes it difficult to determine whether inhibition is unrelated to  
68 flexibility or whether the detour or reversal learning tasks are instead inappropriate for some species.

69 It is important to use multiple experimental assays to validate that performance on a task reflects an inherent  
70 trait (Carter et al. 2013). We aimed to determine whether great-tailed grackles that are better at inhibiting  
71 behavioral responses in three experiments (go/no go, detour, delay of gratification) are also more flexible  
72 (measured as reversal learning of a color preference, and the latency to attempt a new solution on a puzzle box  
73 (multi-access) by Logan et al. 2019). The go/no go experiment consisted of two different shapes sequentially

74 presented on a touchscreen where one shape must be pecked to receive a food reward (automatically provided  
75 by a food hopper under the screen) and the other shape must not be pecked or there will be a penalty of  
76 a longer intertrial interval. In the detour task, individuals are assessed on their ability to inhibit the motor  
77 impulse to try to reach a reward through the long side of a transparent cylinder, and instead to detour and  
78 take the reward from an open end (Kabadayi et al. 2018; methods as in MacLean et al. 2014 who call it  
79 the ‘cylinder task’). In the delay of gratification task, grackles must wait longer for higher quality (more  
80 preferred) food or for higher quantities (methods as in Hillemann et al. 2014). The reversal learning of a color  
81 preference task involved one reversal (half the birds) or serial reversals (half the birds) of a light gray and a  
82 dark gray colored tube, one of which contained a food reward (the experiments and data are in Logan et al.  
83 2019). The multi-access box experimental paradigm is modeled after Auersperg et al. (2011) and consists of  
84 four different access options to obtain food where each option requires a different type of action to solve it (the  
85 experiments and data are in Logan et al. 2019). Once a grackle passes criterion for demonstrating proficiency  
86 in solving an option, that option becomes non-functional in all future trials. The measure of flexibility is the  
87 latency to switch to attempting a new option after a proficient option becomes non-functional. Employing  
88 several experimental assays to measure flexibility and inhibition supports a rigorous approach to testing the  
89 hypothesis that they are linked.

90 This investigation adds to current knowledge of flexibility and inhibition in several ways. First, our results  
91 indicate whether flexibility and inhibition are related and whether tests of inhibition measure the same trait  
92 in great-tailed grackles. In addition, touchscreen experiments had never been conducted in this species  
93 before, and it was one of our goals to validate whether this setup is viable for running a inhibition task  
94 on wild-caught adult grackles. Furthermore, when experimenters test subjects on a series of behavioral  
95 tasks, learning from previous tasks can carry over to affect performance on the focal task. Indeed, Horik et  
96 al. (2018) found that previous experience with transparent materials influenced detour performance, while  
97 Isaksson et al. (2018) found no effect. Therefore, we also aimed to examine whether the extensive experience  
98 of obtaining food from tubes in the reversal learning experiment had an influence on a subject’s detour  
99 performance, which also involves a tube with food in it.

## 100 ASSOCIATED PREREGISTRATION

101 Our hypotheses, methods, and analysis plans are described in the peer-reviewed preregistration of this article,  
102 which is included below as the Methods.

## 103 DEVIATIONS FROM THE PREREGISTRATION

### 104 After data collection began and before data analysis:

- 105 1) Jan 2020 reversal performance: we discovered that none of the grackles reached 100% accuracy within  
106 150 trials (at least not at the level of 20 trial blocks), which is consistent with their reversal performance  
107 as well where they usually do not 100% prefer one option, but continue to occasionally explore the  
108 other option. The passing criterion of 100% correct within 150 trials or 85% correct between 150-200  
109 trials could be the reason there was not much individual variation in this test (passing in 160-190 trials  
110 or they did not reach 85% accuracy within 200 trials). All grackles received 150+ trials, therefore we  
111 only measured variation after 150 trials, rather than variation across all trials. We decided to add a  
112 **post-hoc passing criterion** that might be more illustrative of individual differences in inhibition in  
113 grackles: 85% accuracy at the level of the most recent sliding 10 trial block (i.e., the most recent 10  
114 trials, regardless of whether it is an even 20, 30, 40 trials). We added this modified response variable  
115 post hoc to the discussion. We predict this new passing criterion will show more individual variation,  
116 and that it will more accurately represent individual differences in grackle inhibition.
- 117 2) Jul 2020: in the section ‘Independent variables > P1 go/no go > Model 2b’, removed the variable  
118 “flexibility condition” because, by definition, the birds in the manipulated condition were faster to  
119 reverse.

120 3) Sep 2020: Prediction 1 alternative 2 analysis - when we tried to run the code we discovered that the  
121 Cronbach's alpha is not the appropriate test to run on our experimental design to test the internal  
122 validity of the experiment (e.g., does this test actually measure what we think it does). To test internal  
123 validity, we would need to change the experimental design, which was not the goal of our current study.  
124 Therefore, we did not conduct this analysis.

## 125 **RESULTS**

126 A total of 18 grackles participated to varying degrees in the test battery between Sep 2018 and May 2020  
127 (Table 1). Sample sizes vary between the tests due to the extensive amount of time it took most birds to  
128 get through the test battery, in which case several had to be released before they were finished because,  
129 for example, they reached the end of the maximum amount of time we were allowed to temporarily hold  
130 them in the aviaries (see protocol for details). Data are publicly available at the Knowledge Network for  
131 Biocomplexity (Logan et al. 2020). Details on how the grackles were trained to use the touchscreen are in  
132 Seitz et al. (2020).

133 **Table 1.** Summarized results per bird in the go/no go and detour inhibition experiments, and the reversal  
134 and multi-access box (MAB) flexibility experiments (flexibility data from Logan et al. 2019). We used data  
135 from the MAB plastic experiment and the MAB wooden experiment because the wooden and plastic scores  
136 did not correlate with each other (Logan et al. 2019). **Go/no go trials to 85% correct after 150 trials**  
137 requires the bird must achieve 100% correct before trial 150 and if they did not, then they pass after they  
138 achieve 85% correct. **Go/no go trials to 85% correct** is simply the number of trials to reach this criterion  
139 without the 150 trial threshold of needing to get 100% correct. A value of 201 for go/no go indicates that  
140 the bird did not pass criterion within the 200 trial maximum (but note the exception of Taquito who was  
141 tested beyond trial 200 until he passed due to experimenter error). **Detour proportion correct modified**  
142 accounts for the grackle-specific behavior of standing at the opening of the tube where they are about to  
143 reach their head inside the tube to get the food, but they appear frustrated and bite the edge of the plastic  
144 tube. These bites do not count as first touch to the plastic when the bird obtains the food immediately after  
145 the bite (see Results for the Detour task for justification of this coding).

Bird	Go/no go trials to 85% correct after 150 trials	Go/no go trials to 85% correct	Detour propor- tion correct	Detour propor- tion correct modi- fied	Detour pre- or post- reversal	Trials to reverse in first reversal	Trials to reverse in last reversal	Average latency to at- tempt new solution (MAB plastic)	Average latency to at- tempt new solution (MAB log)
Diablo	170	170	0.7	0.7	Post	80	40	25	NA
Burrito	190	190	0.5	0.9	Post	60	23	76	391
Adobo	160	160	0.4	0.6	Pre	100	50	31	79
Chilaquile	170	140	0.6	1.0	Post	40	30	44	170
Yuca	170	60	0.2	0.6	Post	80	80	132	77
Mofongo	201	60	0.8	1.0	Pre	40	40	502	630
Pizza	170	100	NA	NA	Post	60	60	NA	1482
Taquito	201	290	0.8	1.0	Post	160	160	NA	100
Queso	NA	NA	0.9	0.9	Pre	70	70	88	NA
Mole	170	170	0.8	0.9	Post	70	50	356	1173
Tomatillo	NA	NA	0.8	0.8	Post	50	50	317	NA
Tapa	NA	NA	1.0	1.0	Pre	100	100	685	NA
Chalupa	NA	NA	0.9	1.0	Post	90	50	NA	NA
Habanero	NA	NA	1.0	1.0	Post	80	40	28	NA
Pollito	NA	NA	0.9	0.9	Post	60	40	NA	668
Taco	NA	NA	0.2	1.0	Post	80	80	NA	117
Huachinango	NA	NA	0.7	0.7	Post	NA	NA	NA	NA
Pavo	NA	NA	0.8	0.8	Pre	NA	NA	NA	NA

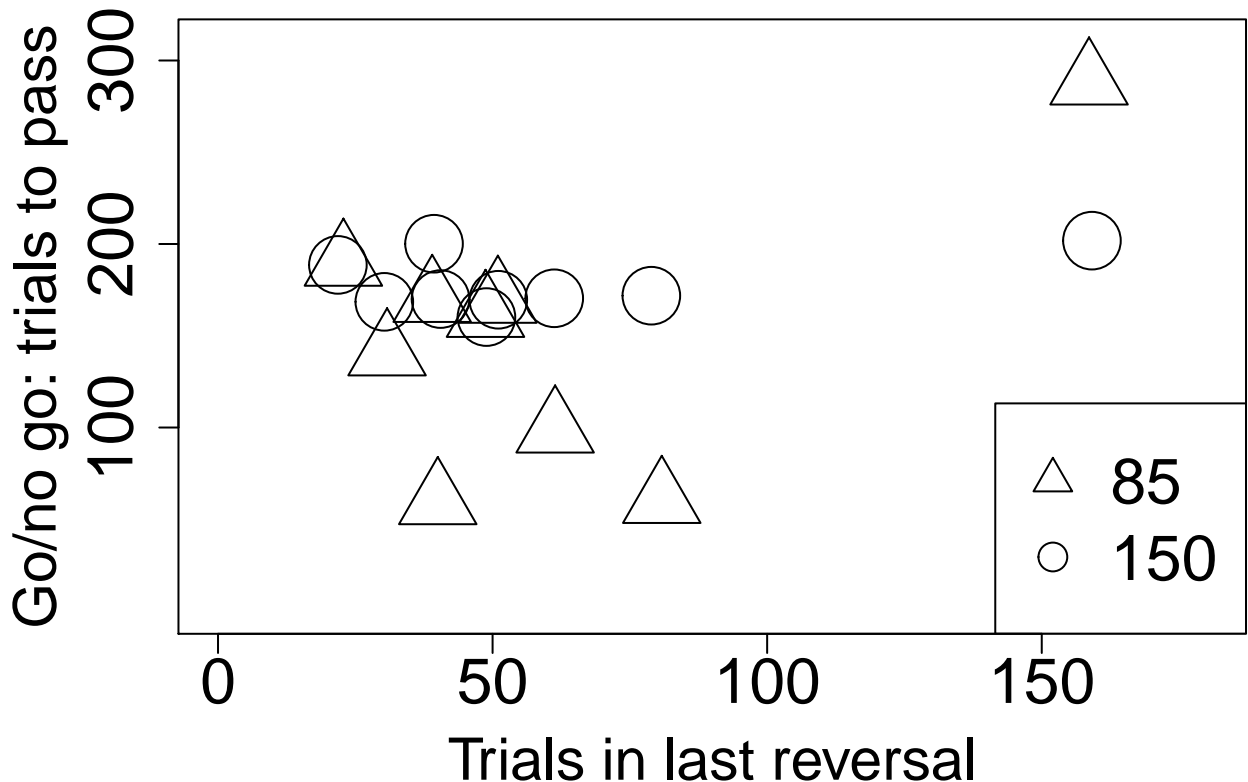
147 **Prediction 1 the more flexible individuals are also better at inhibition: go/no go**

148 **Model 2a: Number of trials to pass criterion in go/no go**

149 ***Flexibility: Reversal learning***

150 There was a positive correlation between the number of trials to pass criterion in the go/no go experiment and  
151 the number of trials to reverse a preference in the colored tube reversal experiment (in their **last reversal**)  
152 when using one of the two go/no go passing criteria: the number of trials to reach 85% correct (measured  
153 in the most recent 20 trial block; Table 2, Figure 1). The other passing criterion of achieving 100% correct  
154 performance by trial 150, and if this is not met then they pass when they reach 85% correct after trial  
155 150 (measured in the most recent 20 trial block) did not correlate with reversal performance. Regardless

156 of criterion type, we capped the number of trials at 200, with the exception of 2 individuals who continued  
 157 trials to 249 (and did not pass) and 290 (and passed).



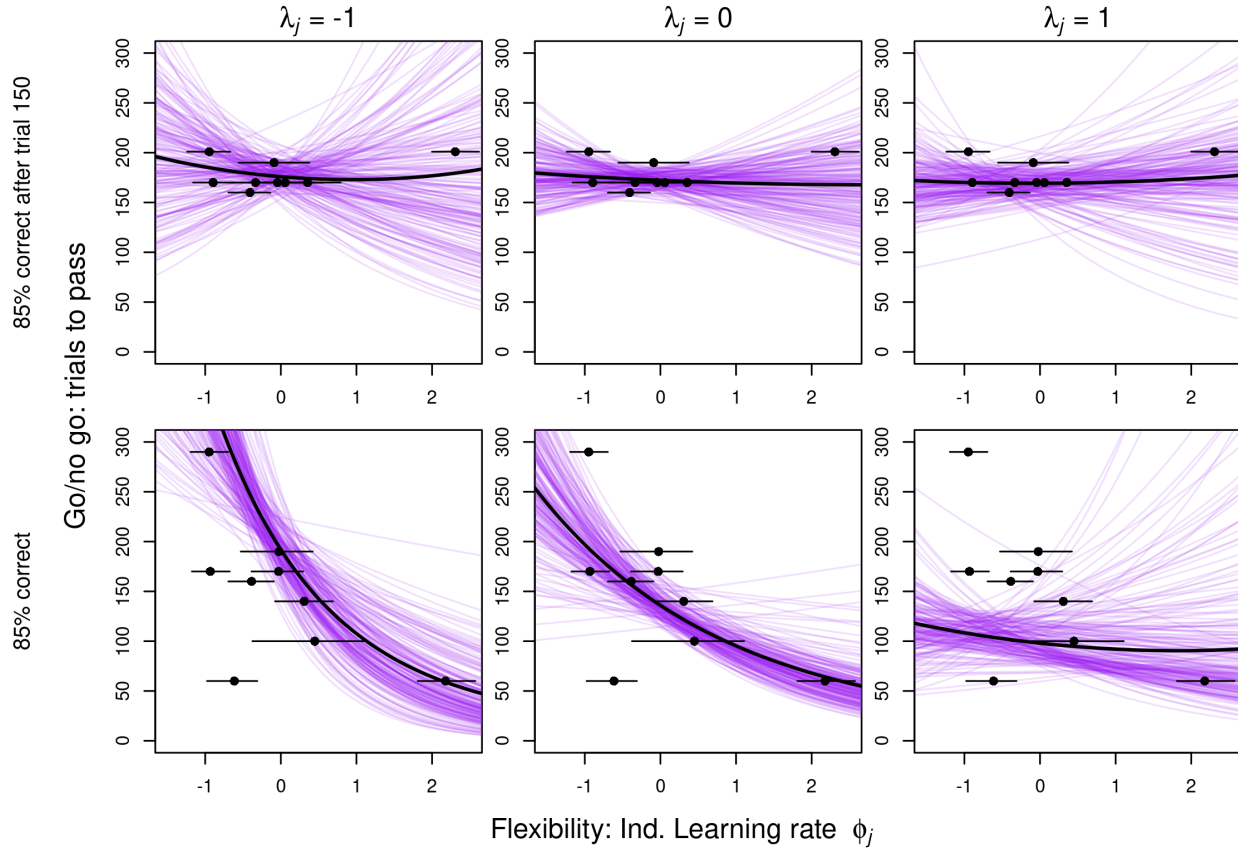
158

159 **Figure 1.** The number of go/no go trials to pass criterion per bird using the 85% correct (triangles) or 85%  
 160 correct after 150 trials (circles) criteria and the number of trials to reverse a color preference in their last  
 161 reversal.

162 These two results were confirmed using a more comprehensive computational measure of reversal learning  
 163 that accounts for all of the choices an individual made as well as the degree of uncertainty exhibited as  
 164 preferences change (flexibility 4 in the Methods). We use multilevel Bayesian reinforcement learning models  
 165 to investigate a bird’s learning rate and random choice rate per reversal (see Methods for more details; results  
 166 presented as posterior means and 89% highest posterior density intervals (HPDI)). With the **85% correct**  
 167 **criterion**, we found a negative relationship between reversal learning rate and the number of go/no go trials  
 168 to pass criterion. This means that birds who are faster to update their behavior in the reversal experiment  
 169 were also faster to reach criterion in the go/no go task ( $\beta_\phi = -0.37$ , HPDI = -0.54 to -0.16). Moreover,  
 170 birds that exhibited a higher random choice rate in the reversal experiment took longer to reach the 85%  
 171 correct criterion compared to birds that were less random in their choices ( $\beta_\lambda = -0.34$ , HPDI = -0.52 to  
 172 -0.12). We also found some evidence for a positive interaction between both learning parameters (reversal  
 173 learning rate and random choice rate;  $\beta_{\phi\lambda} = 0.27$ , HPDI = 0.02 - 0.58), suggesting a buffering effect among  
 174 parameters such that the influence of random choice rate is weaker for individuals that are fast learners. As  
 175 with the other analysis, there was no robust association between either learning rate ( $\beta_\phi = -0.02$ , HPDI  
 176 = -0.15 - 0.12) or random choice rate ( $\beta_\lambda = -0.02$ , HPDI = -0.12 - 0.07) and the number of trials to pass  
 177 the other go/no go criterion (**100% correct by trial 150**). There was no interaction between the learning  
 178 parameters ( $\beta_{\phi\lambda} = 0.01$ , HPDI = -0.23 - 0.19).

179 Figure 2 plots posterior predictions for the effect of learning rate  $\phi_j$  on the number of trials to pass criteria for  
 180 three different levels of the random choice rate  $\lambda_j$ . Focusing on the bottom row (**85% correct criterion**),  
 181 the model, in general, predicts that fast learners in the reversal learning experiment also reach the criterion  
 182 in the go/no go experiment in fewer trials. There appears to be a trade-off between learning parameters,  
 183 such that fast learners who are somewhat exploratory are predicted to perform better than fast learners who  
 184 show very limited randomness in their choices. Lastly, overall individuals who show fewer random choices in

185 the flexibility experiment are predicted to perform better in the go/no go inhibition experiment.



186

187 **Figure 2.** Results from the computational learning model (flexibility 4). Posterior predicted number of trials  
 188 to pass go/no go using the 85% correct after 150 trials (top row) or 85% correct (bottom row) criteria, based  
 189 on estimates for the individual-level learning rates from the reinforcement learning model ( $\phi_j$ ; black dots  
 190 show posterior means, black horizontal lines indicate 89% highest posterior density intervals). Curves are  
 191 plotted for high (left;  $\lambda_j=-1$ ), average (middle;  $\lambda_j=0$ ) and low (right;  $\lambda_j=1$ ) random choice rates. Purple lines  
 192 represent 200 independent draws from the posterior, the black lines show posterior means. Both predictors  
 193 ( $\lambda_j$  and  $\phi_j$ ) were standardized before calculations.

194 The 85% correct passing criterion was more relevant to the grackles, and the one we recommend using  
 195 in the future, because setting an **arbitrary threshold** of needing 100% correct in the first 150 trials to  
 196 pass criterion, which is not generally used in go/no go inhibition tasks, was not ecologically relevant for  
 197 grackles. In reversal learning tests, which are similar to the go/no go experimental design in that they learn  
 198 to discriminate between two shapes, grackles almost always continue to explore their options regardless of  
 199 whether they already have a color preference (e.g., Logan 2016). There was also more individual variation  
 200 using the 85% passing criterion.

201 Nine grackles participated in the go/no go experiment. They passed the 85% criterion in an average of 149  
 202 trials (standard deviation: 71, range: 60-290 trials), and passed the 150 threshold criterion in an average  
 203 of 178 trials (standard deviation: 15, range: 160 trials to not passing before the experiment ended at 200  
 204 trials) (Table 1). The positive correlation between go/no go and reversal performance indicates that those  
 205 individuals that have more inhibition are also faster at changing their preferences when circumstances change.  
 206 We must note that the relationship was likely influenced by Taquito, who was particularly slow at both tests  
 207 and was one of the two birds who was tested beyond the 200-trial cap due to experimenter error. We  
 208 would need a larger sample size to determine to what degree the relationship is perturbed by such individual  
 209 variation.

210 **Unregistered analyses**

211 We additionally analyzed the relationship between go/no go performance and the number of trials to reverse  
 212 a color preference in the **first reversal** to make our results comparable across more species. This is because  
 213 most studies do not conduct serial reversals, but only one reversal. The results remained the same regardless  
 214 of whether the first or last reversal were analyzed: there was a positive correlation between go/no go and  
 215 reversal learning performance when using the 85% go/no go criterion, and no relationship when using the  
 216 100% by 150 trial criterion (Table 2).

217 **Table 2.** Results from the go/no go and reversal learning GLMs: **m1** and **m2** show GLM outputs for the  
 218 last reversal, while **m3** and **m4** show GLM outputs for the first reversal. **m1** and **m3** show results from the  
 219 GLM using the number of trials to reach 85% correct if 100% correct was not achieved within the first 150  
 220 trials in go/no go, while **m2** and **m4** use the number of trials to reach 85% correct without the 150 trial  
 221 threshold. The estimate is presented above the standard error, which is in parentheses; asterisks refer to  
 222 p-value significance.

	m1: 150 last reversal	m2: 85 last reversal	m3: 150 first reversal	m4: 85 first reversal
(Intercept)	5.14 *** (0.05)	4.68 *** (0.05)	5.15 *** (0.06)	4.34 *** (0.07)
TrialsLast	0.00 (0.00)	0.01 *** (0.00)		
TrialsFirst			0.00 (0.00)	0.01 *** (0.00)
N	9	9	9	9
AIC	75.91	278.00	76.96	211.92
BIC	76.30	278.40	77.36	212.31
Pseudo R2	0.15	1.00	0.04	1.00

\*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.

223 **Flexibility: Multi-access box**

224 There was no correlation between the two flexibility experiments: the number of trials to reverse a preference  
 225 in the last reversal and the average number of seconds (latency) to attempt a new option on the multi-access  
 226 box after a different locus has become non-functional because they passed criterion on it (Pearson’s r=0.52  
 227 (95% confidence interval: -0.12-0.85), t=1.83, df=9, p=0.10). Therefore, we conducted a separate analysis  
 228 to determine whether the number of trials to pass criterion in the go/no go experiment correlates with the  
 229 average latency to attempt a new option in the MAB plastic and MAB log experiments (the average latency  
 230 to attempt a new option did not correlate between the plastic and log experiments, which is why they are  
 231 analyzed separately; Logan et al. 2019). Results showed that the average latency to attempt a new option  
 232 on both MAB experiments (plastic and log) negatively correlated with go/no go performance when using  
 233 the 85% go/no go criterion, and there was no correlation when using the 150 trial threshold (Table 3, Figure  
 234 3).

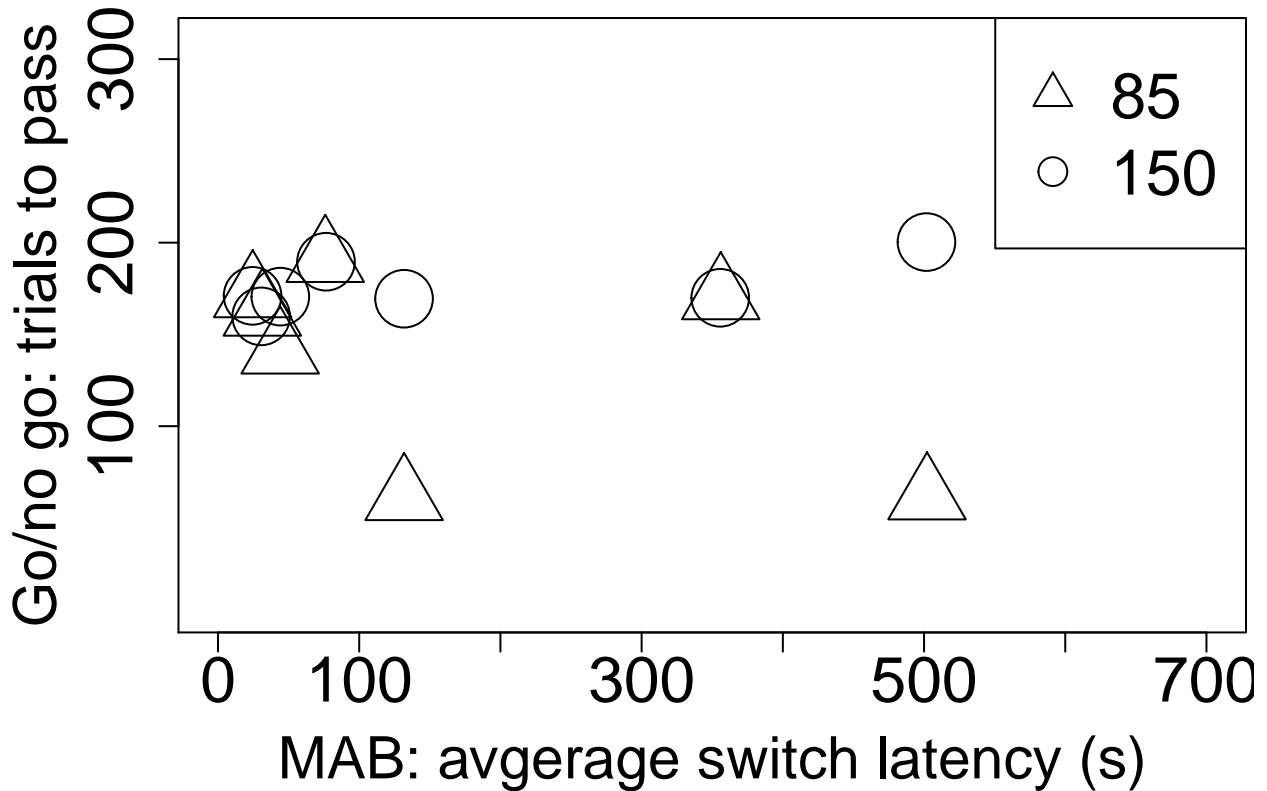
235 **Table 3.** Results from the go/no go and multi-access box GLMs: **m1** and **m3** show results from the GLM  
 236 using the number of trials to reach 85% correct if 100% correct was not achieved within the first 150 trials in



237 go/no go, while **m2** and **m4** use the number of trials to reach 85% correct without the 150 trial threshold.  
 238 **m1** and **m2** show results from the plastic multi-access box, while **m3** and **m4** show results from the log  
 239 multi-access box. The estimate is presented above the standard error, which is in parentheses; asterisks refer  
 240 to p-value significance.

	m1: 150 plastic	m2: 85 plastic	m3: 150 log	m4: 85 log
(Intercept)	5.13 *** (0.04)	5.09 *** (0.04)	5.20 *** (0.04)	5.10 *** (0.04)
AvgLatencyPlastic	0.00 (0.00)	-0.00 *** (0.00)		
AvgLatencyLog			-0.00 (0.00)	-0.00 *** (0.00)
N	7	7	8	8
AIC	57.23	163.75	69.83	315.01
BIC	57.12	163.65	69.99	315.17
Pseudo R2	0.31	0.99	0.02	0.88

\*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.



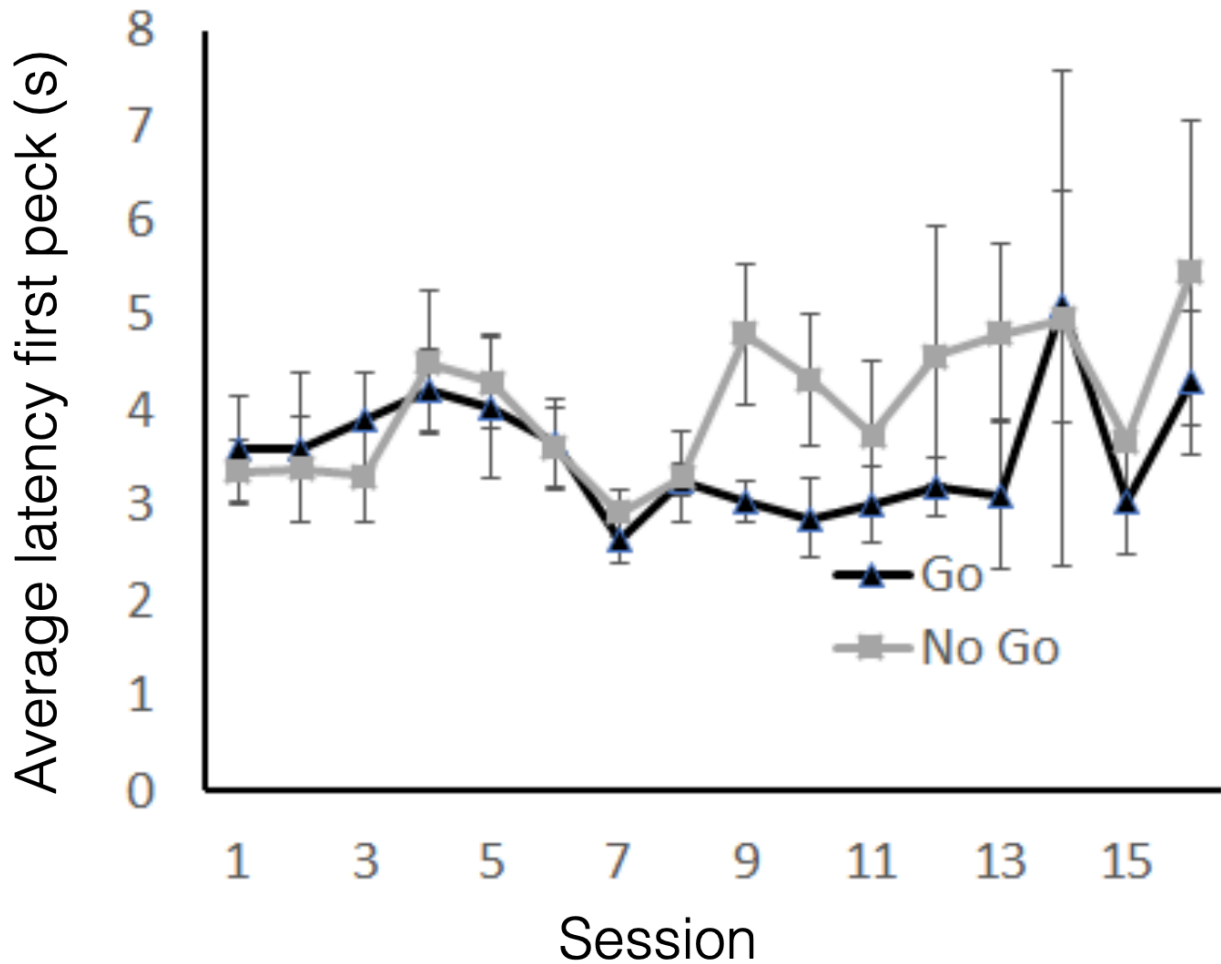
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242 **Figure 3.** The number of go/no go trials to pass criterion per bird using the 85% correct (triangles) or 85%

243 correct after 150 trials (circles) criteria and the average latency to attempt a new locus on the multi-access  
244 box (MAB) plastic.

245 **Model 2b: Latency to peck screen in go/no go**

246 The model that examined whether the latency of the first peck to the screen per trial (response variable) was  
247 associated with the outcome of the trial (correct/incorrect) did not converge. This is probably because the  
248 correct choice on the no go trials was not to peck the screen and so this level of the categorical choice variable  
249 has much less data than the other two levels (incorrect choice and correct choice on the go trials; Figure 4).  
250 Therefore, we cannot include the analysis here or make conclusions based on it. Additionally, there was a  
251 problem matching the latency data across data sheets. Latency data was brought in from the PsychoPy data  
252 sheets, however, the number of trials reported by the experimenter and by PsychoPy sometimes differed for  
253 reasons that are unclear. Therefore, the first latency to peck the screen is not completely accurately matched  
254 between the two data sheets.



255  
256 **Figure 4.** The average latency (seconds) across all birds to first peck the screen in a trial per session  
257 according to whether it was a go trial (when they should peck; black triangles and black regression line) or  
258 a no go trial (when they should not peck; gray squares and gray regression line) (error bars=standard error  
259 of the mean).

260 **Prediction 1 the more flexible individuals are also better at inhibition: detour**

261 *Flexibility: Reversal learning*

262 There was no correlation between the proportion correct on the detour experiment and the number of trials  
263 to reverse their last preference in the reversal learning experiment (Table 3, Figure 5). The same result was  
264 found using the more comprehensive flexibility measure with the Bayesian reinforcement model: we found  
265 no relationship between the learning rate ( $\beta_\phi = 0.12$ , HPDI = -0.13 to 0.38) or random choice rate ( $\beta_\lambda =$   
266  $-0.07$ , HPDI = -0.55 to 0.46) and the proportion of correct choices in the detour experiment. There was  
267 also no interaction among parameters (learning rate and random choice rate;  $\beta_{\phi\chi\lambda} = 0.01$ , HPDI = -0.39  
268 to 0.38). Eighteen grackles completed this experiment and they averaged 71% correct (standard deviation:  
269 25%, range: 20-100%).

## 270 Unregistered analyses

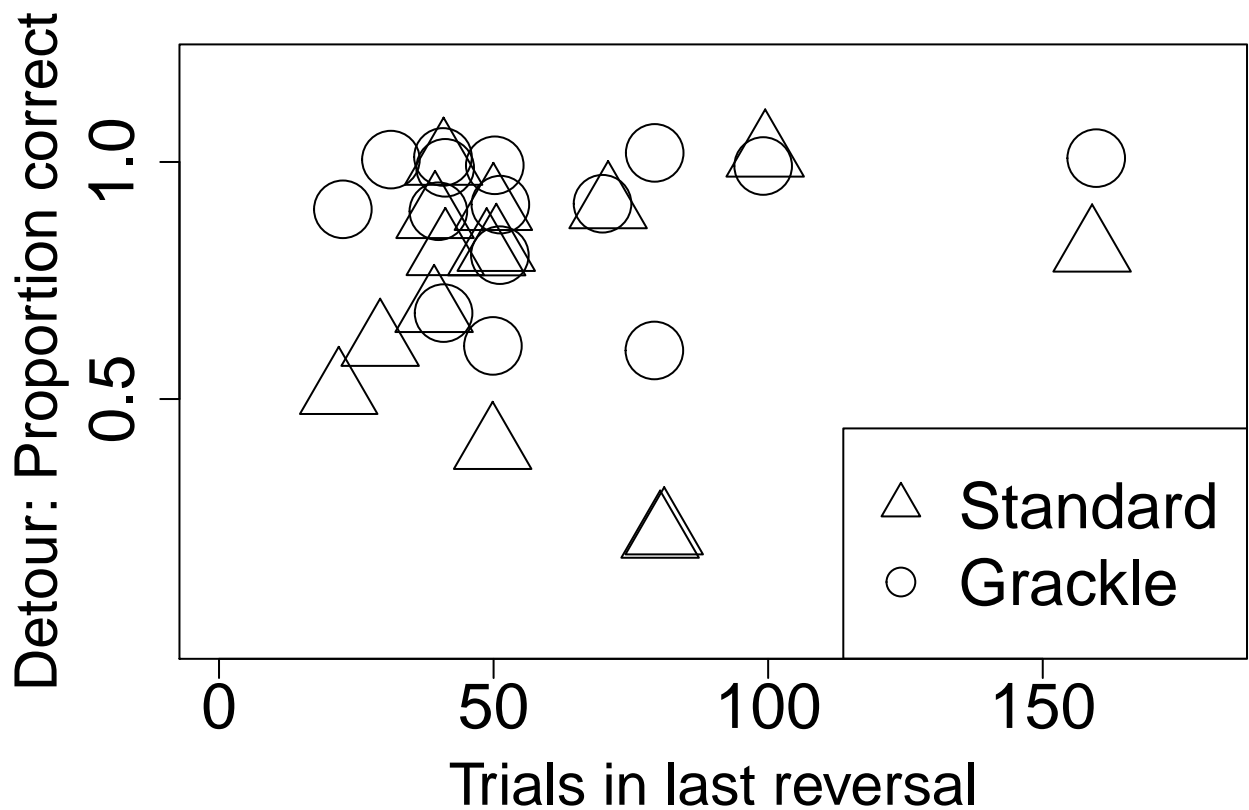
271 We additionally analyzed the relationship between detour performance and the number of trials to reverse a  
272 color preference in the **first reversal** to make our results comparable across more species. This is because  
273 most studies do not conduct serial reversals, but only one reversal. The results remained the same regardless  
274 of whether the first or last reversal were analyzed: there was no relationship between detour and reversal  
275 learning performance (Table 3).

276 As we conducted this experiment, we discovered that scoring whether the grackle made a correct or incorrect  
277 first choice is more complicated than the scoring method used in MacLean et al. (2014). In MacLean et al.  
278 (2014), and most other studies using a detour task, to our knowledge, if the plastic is touched first, then it is  
279 an incorrect choice, whereas if the food is touched first, it is a correct choice. If the plastic is touched first, it  
280 is assumed that the individual touched the plastic on the long side of the tube and not on the rim side where  
281 the opening is because they were trying to reach the food through plastic (which is non-functional). We  
282 found that many grackles have a habit of standing at the tube opening biting the rim of the tube and then  
283 immediately afterwards putting their head in to obtain the food, possibly due to reluctance to put their heads  
284 into the tube. This behavior did not appear to be an attempt to reach the food through the plastic because:  
285 1) it was always followed by immediate food retrieval, and 2) it was distinct from other pecks to plastic on  
286 the long side. For these reasons, we coded an additional variable, the “grackle-specific correct choice”. In  
287 this variable, a bite to the plastic rim does not count as an incorrect choice if they then obtained the food  
288 without having touched the front (non-edge) of the plastic tubing between their bite to the rim and their  
289 obtaining the food. Instead, this counts as a correct choice. We therefore conducted *post hoc* analyses of the  
290 proportion correct on the detour task in relation to their reversal performance (Table 3). The results were  
291 the same as above: there is no correlation between detour performance (using the grackle-specific correct  
292 choice) and the number of trials to reverse their last or first preference. With this scoring method, grackles  
293 averaged 87% correct (standard deviation: 25%, range: 60-100%). Results were also identical to above for  
294 the more comprehensive flexibility measure using the Bayesian model: there was no relationship between  
295 detour performance (using the grackle-specific method) and learning rate ( $\beta_\phi = 0.17$ , HPDI = -0.11 to 0.44)  
296 or random choice rate ( $\beta_\lambda = -0.13$ , HPDI = -0.44 to 0.21) and no interaction ( $\beta_{\phi\chi\lambda} = 0.06$ , HPDI = -0.28  
297 to 0.38).

298 **Table 4.** Results from the detour and reversal learning GLMs: **m1** and **m2** show GLM outputs using the  
299 standard MacLean et al. (2014) method of scoring (std), while **m3** and **m4** show GLM outputs using the  
300 grackle-specific scoring method (grackle). **m1** and **m3** show results using the last reversal (last rev), while  
301 **m2** and **m4** use the first reversal (1st rev).

	m1: std & last rev	m2: std & 1st rev	m3: grackle & last rev	m4: grackle & 1st rev
(Intercept)	0.82	0.73	1.66	0.73
	(1.16)	(1.63)	(1.78)	(1.63)
TrialsLast	0.00		0.01	
	(0.02)		(0.03)	
TrialsFirst		0.00		0.00
		(0.02)		(0.02)
N	15	15	15	15
AIC	21.47	21.52	7.62	21.52
BIC	22.89	22.93	9.03	22.93
Pseudo R2	0.00	-0.00	-0.00	-0.00

\*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.



302

303 **Figure 5.** The proportion of detour trials correct per bird using the standard calculation method (triangles)  
 304 or the grackle-specific calculation method (circles) and the number of trials to reverse a color preference in  
 305 their last reversal.

306 *Flexibility: Multi-access box*

307 We conducted a separate analysis to determine whether the proportion correct in the detour experiment was  
 308 related to the average latency to attempt a new option on the multi-access boxes (plastic and log) and found  
 309 no relationship with detour performance [using the MacLean et al. (2014) method of scoring; Table 5].

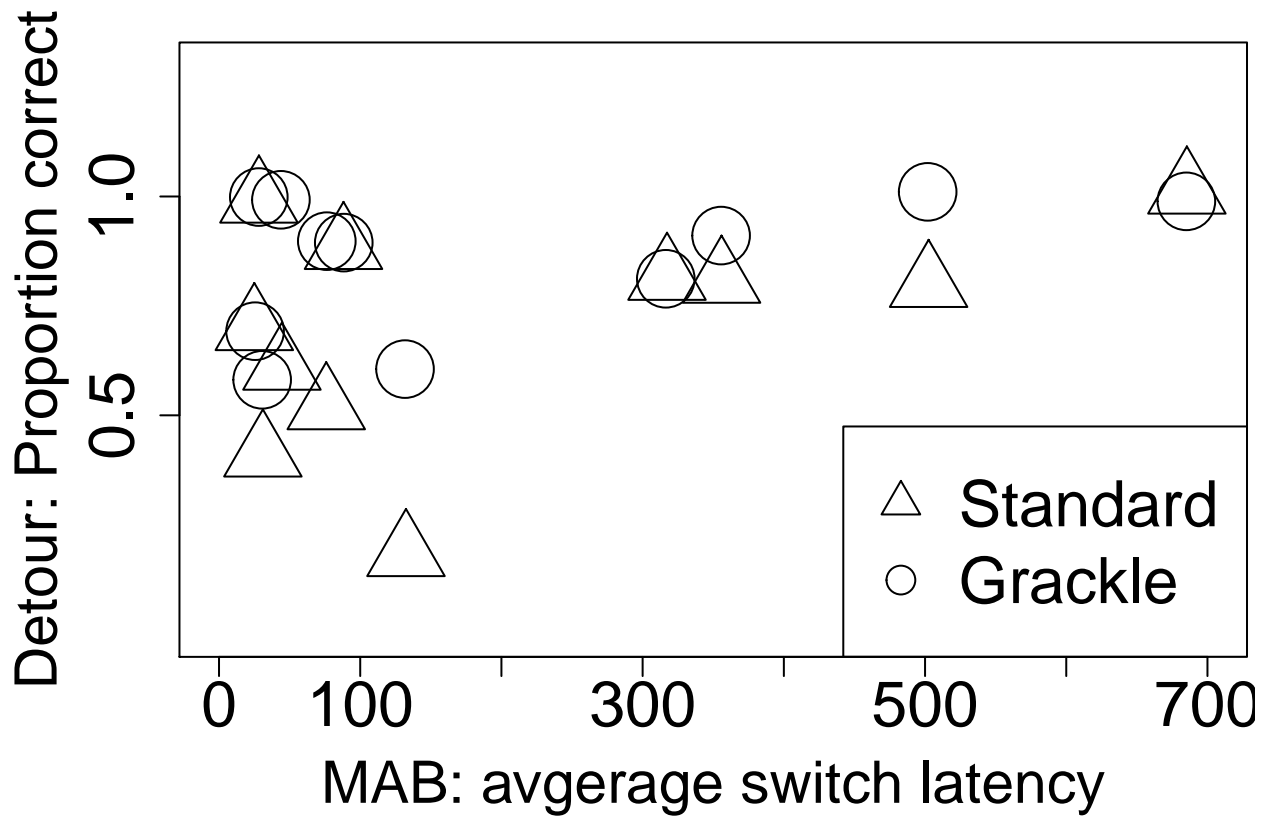
310 **Unregistered analyses**

311 There was no correlation between the proportion correct in the detour experiment using the grackle-specific  
 312 scoring method and the average latency to attempt a new option on either of the multi-access boxes (plastic  
 313 or log; Table 5, Figure 6).

314 **Table 5.** Results from the detour and multi-access box GLMs: **m1** and **m3** show GLM outputs using the  
 315 standard MacLean et al. (2014) method of scoring (std), while **m2** and **m4** show GLM outputs using the  
 316 grackle-specific scoring method (grackle). **m1** and **m2** show results from the MAB plastic experiment, while  
 317 **m3** and **m4** show results from the MAB log experiment.

	m1: std & plastic	m2: grackle & plastic	m3: std & log	m4: grackle & log
(Intercept)	0.33	-0.47	1.27	1.55
	(0.90)	(1.03)	(1.12)	(1.42)
AvgLatencyPlastic	0.00		0.00	
	(0.00)		(0.01)	
AvgLatencyLog		0.00		0.00
		(0.00)		(0.00)
N	11	9	11	9
AIC	15.45	13.84	7.51	6.37
BIC	16.25	14.23	8.31	6.76
Pseudo R2	0.18	0.33	-0.02	-0.01

\*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.



318

319 **Figure 6.** The proportion of detour trials correct per bird using the standard calculation method (triangles)  
 320 or the grackle-specific calculation method (circles) and the average latency to attempt a new locus on the  
 321 multi-access box (MAB) plastic.

322 **Prediction 2: no correlation between inhibition tasks**

323 There was no correlation between the inhibition tasks go/no go and detour. Cronbach's alpha showed low  
 324 reliability equal to zero for all comparisons (go/no go 150 threshold and detour standard=0.03, go/no go 150  
 325 and detour grackle specific=0.03, go/no go 85 and detour standard=0.005, go/no go 85 and detour grackle  
 326 specific=0.003).

327 **Prediction 3: does training improve detour performance?**

328 There was no difference in the proportion correct on the detour task and whether the individual received  
 329 the detour experiment before or after their reversal learning experiment (which also involved obtaining food  
 330 from tubes; Table 4). Seventeen grackles participated in the detour experiment with 5 in the pre-reversal  
 331 condition and 12 in the post-reversal condition.

332 **Unregistered analysis**

333 We conducted a post-hoc analysis using the detour grackle-specific proportion of correct responses (see full  
 334 explanation in P1: detour > Unregistered analyses) and found that the result is the same as above: there is  
 335 no difference in detour performance relative to their experience with reversal tubes (Table 6).

336 **Table 6.** Results from the detour GLMs to determine whether experience with reversal tubes improves  
 337 detour performance: **Detour standard** shows GLM outputs using the MacLean et al. (2014) method of  
 338 scoring, **Detour grackle-specific** shows GLM outputs using the grackle-specific scoring method, Condition  
 339 refers to whether they received the detour test before (pre) or after (post) their reversal experiment.

	Detour standard	Detour grackle-specific
(Intercept)	0.73	1.95 *
	(0.62)	(0.87)
DetourprepostPre	0.53	-0.13
	(1.24)	(1.56)
N	17	17
AIC	22.83	8.71
BIC	24.50	10.38
Pseudo R2	0.00	-0.00

\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ .

340 We were not able to conduct the delay of gratification experiment because the grackles never habituated to  
341 the apparatuses, therefore the inhibition results come only from the go/no go and detour experiments.

## 342 DISCUSSION

343 We found mixed support for the hypothesis that flexibility and inhibition are associated with each other.  
344 Flexibility on the reversal task and on the multi-access boxes were positively and negatively, respectively,  
345 associated with inhibition in one context (go/no go) and not associated with it in another context (detour).  
346 These results confirm previous findings where detour performance was not associated with behavioral flexi-  
347 bility as measured by the multi-access box locus switching performance (Johnson-Ulrich et al. 2018) or by  
348 reversal learning (Boogert et al. 2011; Shaw et al. 2015; Brucks et al. 2017; Damerius et al. 2017; DuBois  
349 et al. 2018; Ducatez et al. 2019). This mixed support could be because the two inhibition tests, go/no go  
350 and detour, might not measure the same trait in great-tailed grackles.

351 There is controversy around how to best assess inhibition given the several experimental paradigms that are  
352 available. Inhibitory control is a multi-level construct and an integral part of executive functioning. One  
353 aspect of inhibition is motor self-regulation (i.e., stopping a prepotent but counterproductive movement;  
354 Diamond 2013), which is usually assessed with the detour task in non-human animals. While another aspect  
355 of inhibitory control is self-control (i.e., the ability to withhold an immediate response towards a present  
356 stimulus in favor of a later stimulus; Nigg 2017). To assess self-control in non-human animals, a task must  
357 crucially involve a component of decision making, such as deciding between obtaining a less preferred reward  
358 now or tolerating a delay for a more valuable outcome in the future (Beran 2015). In non-human animals,  
359 self-control is typically assessed using experimental paradigms, such as the accumulation paradigm, exchange  
360 paradigm, hybrid delay, and intertemporal choice task (for an overview see: Beran 2018; Miller et al. 2019).  
361 A major concern associated with the comparison of performance on inhibition tasks is that measures are not  
362 always consistent when different experimental paradigms are used (Addessi et al. 2013; Brucks et al. 2017;  
363 Horik et al. 2018), which is further confirmed by our findings. This indicates that it is crucial to compare  
364 inhibition paradigms with each other on the same individuals to understand whether and how they relate to  
365 each other and in which contexts. In addition, it may be best to refer to the different inhibition paradigms  
366 with distinct terms to differentiate them (e.g., “motor inhibition” for detour-like tasks and “self-control” for  
367 delay of gratification tasks).

368 Although great-tailed grackles had never experienced touchscreen experiments before, we found that the  
369 grackles were able to learn to use the touchscreen and to complete the go/no go experiment on it. This

370 validates the use of this setup for future experiments in this species, and shows that it could be a viable  
371 option for wild-caught birds from other species as well. However, there are several caveats to the feasibility  
372 of touchscreen tasks for behavioral testing (see Seitz et al. 2020 for details). First, touchscreen hardware  
373 and software can be prone to error. We recommend future studies ensure that the touchscreens accurately  
374 record the target behaviors prior to intensive experimentation. Second, touchscreen experimentation should  
375 be as fully automated as possible; it can be difficult for observers to objectively code bird behaviors as the  
376 birds interact with a touchscreen. Our interobserver reliability was not as reliable as we had hoped, although  
377 it was still acceptable for data analysis, due to some of these issues (see details in Methods).

378 Performance on the detour inhibition test was not affected by extensive experience obtaining hidden food  
379 from tubes in the reversal learning test. Grackles who received the detour experiment before reversal training  
380 did not perform differently from those who received the detour experiment after reversal training. These  
381 two contexts appear to be different enough to solicit independent responses without interference due to a  
382 grackle’s previous test history. The development of our grackle-relevant detour scoring method resulted in  
383 improved performance for 9 out of the 16 grackles we tested. This indicates that cross-species comparisons  
384 on this test that are not attuned to the species under study could underestimate inhibitory ability. This  
385 finding could partially explain why so many of the 36 species in MacLean et al. (2014) performed so poorly  
386 on this task, aside from actually having poor inhibition.

387 Our developments and modifications to these inhibition tests confirm that it is necessary to accommodate  
388 species-relevant behavioral differences in apparatus design and when scoring choices to measure the actual  
389 potential of a given species (e.g., Thornton and Lukas 2012). Such developments are required to deter-  
390 mine what inherent trait inhibition tests measure, whether it is appropriate to categorize different tests as  
391 measuring the same ability, and how inhibition relates to other traits.

392 In conclusion, our results support the idea that behavioral flexibility used in reversal learning and in task  
393 switching on the multi-access box may only be associated with the “self-control” type of inhibition (as  
394 measured by go/no go tasks) and not motor inhibition (as measured by detour tasks) in great-tailed grackles.  
395 We confirm previous findings that suggest inhibition is multiple constructs that are potentially independent,  
396 as has been suggested for humans and dogs (Friedman and Miyake 2004; Brucks et al. 2017). It is possible  
397 that inhibition represents a set of cognitive pathways that is evolutionarily ancient (such that birds and  
398 mammals share types of inhibition from a common ancestor) or that there has been convergent evolution of  
399 these abilities in multiple lineages.

## 400 METHODS

### 401 A. STATE OF THE DATA

402 **Prior to collecting any data:** This preregistration was written.

403 **After data collection had begun (and before any data analysis):** This preregistration was submitted  
404 to PCI Ecology (Oct 2018) for peer review after starting data collection on the detour task for the pre-reversal  
405 subcategory of subjects (for which there was data from one bird). Reviews were received, the preregistration  
406 was revised and resubmitted to PCI Ecology (Jan 2019) at which point there was detour data for six birds,  
407 data on a few training trials for the delay of gratification task for one bird, and no data from the go/no go  
408 experiment. This preregistration passed peer review and was recommended by PCI Ecology in March 2019  
409 (see the review history).

### 410 B. PARTITIONING THE RESULTS

411 We may decide to present the results from different tests in separate papers. NOTE: everything in the  
412 preregistration is included in this one manuscript.



413 C. HYPOTHESIS

414 **If behavioral flexibility requires behavioral inhibition, then individuals that are more behav-**  
415 **iorally flexible (indicated by individuals that are faster at functionally changing their behavior**  
416 **when circumstances change), as measured by reversal learning and switching to a different op-**  
417 **tion after one becomes non-functional on a multi-access box, will also be better at inhibiting**  
418 **their responses in three tasks: delayed gratification, go/no go, and detour (Figure 7).**

419 **P1:** Individuals that are faster to reverse preferences on a reversal learning task and who also have lower  
420 latencies to successfully solve new loci after previously solved loci become unavailable (multi-access box)  
421 (see flexibility preregistration) will perform better in the go/no go task (methods similar to Harding et al.  
422 (2004)) and in the detour task (methods as in MacLean et al. (2014) who call it the “cylinder task”), and  
423 they will wait longer for higher quality (more preferred) food, but not for higher quantities of food (methods  
424 as in Hillemann et al. (2014)). Waiting for higher quality food has been validated as a test of inhibition in  
425 birds, while waiting for a higher quantity of food does not appear to measure inhibition (Hillemann et al.  
426 (2014)).

427 **P1 alternative 1:** If there is no correlation between flexibility measures and performance on the inhibi-  
428 tion tasks, this may indicate that the flexibility tasks may not require much inhibition (particularly if the  
429 inhibition results are reliable - see *P1 alternative 2*).

430 **P1 alternative 2:** If there is no correlation between flexibility measures and performance on the inhibition  
431 tasks, this may indicate that the inhibition tasks had low reliability and were therefore too noisy to correlate  
432 with flexibility.

433 **P2:** If there is no correlation in performance across inhibition tasks, it may indicate that that one or more  
434 of these tasks does not measure inhibition, or that they measure different types of inhibition (see Friedman  
435 and Miyake (2004)).

436 **P2 alternative:** If go/no go task performance strongly correlates with performance on the delayed grat-  
437 ification task, this indicates these two tasks measure the same trait, which therefore validates a inhibition  
438 task using a touchscreen (the go/no go task).

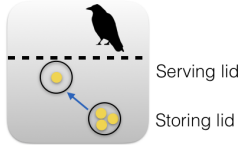
439 **P3:** If individuals perform well on the detour task and with little individual variation, this is potentially  
440 because they will have had extensive experience looking into the sides of opaque tubes during reversal  
441 learning. To determine whether prior experience with opaque tubes in reversal learning contributed to their  
442 detour performance, a subset of individuals will experience the detour task before any reversal learning tests.  
443 If this subset performs the same as the others, then previous experience with tubes does not influence detour  
444 task performance. If the subset performs worse than the others, this indicates that detour task performance  
445 depends on the previous experiences of the individuals tested.

**Inhibition: Delayed gratification task: accumulation**

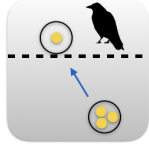
1. Training = b with a as needed

2. Test

a. Demonstration:  
transfer items 1/s



b. Training



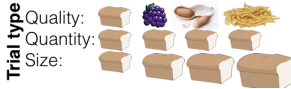
Criterion: obtain >1 item in 3 trials



Items transferred with delay: 2, 5, 10, 20, 40, 60, 80, 160, 320, 640, 1280s

Each delay condition = 4 sessions (6 trials each): 2=quality, 2=quantity

Subject moves to longer delay if wait for 1+ accumulations & take food



**Inhibition: Go no-go task**

1. 20s: peck to start

2a. 10s: peck for food

3. 8s: intertrial



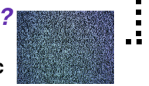
2b. 10s: do not peck

Correct?

2b.2. start intertrial interval

Incorrect?

2b.1. 5s: if peck, static



**Inhibition: Detour task**

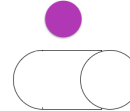
1. Warm-up

2. Test (10 trials) = same as warm up, except transparent tube

a. Move food into cylinder



b. Code first attempt: front (incorrect) or side (correct)



Criterion: obtain food in first attempt in 4/5 consecutive trials

446

447 **Figure 7.** The experimental designs of the three tasks: delayed gratification, go/no go, and detour (see  
 448 protocol for details). In the **delay of gratification** task, individuals learn that food items will be transferred  
 449 by the experimenter from a storing lid (near the experimenter) to a serving lid (near the bird) one at a time,  
 450 and that they have access to the food in the serving lid from which they can eat at any time: they will have  
 451 the opportunity to learn that they will have access to more food if they wait longer for the experimenter to  
 452 transfer food items. Once they pass training (by waiting for more than one food item in three trials), they  
 453 move on to the test where food items are transferred from the serving to the storing lid with delays ranging  
 454 from 2-1280 seconds. Birds will be tested on whether will wait for food items that increase in quality (i.e.,  
 455 are more preferred) or increase in quantity (i.e., the same food type accumulates in the serving lid). In the  
 456 **go/no go** task, after pecking a start key on the touchscreen to show they are attending to a trial, they will  
 457 be presented with either a green circle or a purple circle (the rewarded circle color is counterbalanced across  
 458 birds). Pecking the food key while the rewarded colored circle (green in the figure) is on the screen will  
 459 result in the food hopper rising so the bird can eat food for 2 seconds, after which point the trial ends and  
 460 the screen goes blank for 8 seconds before starting over again. If the non-rewarded colored circle (purple in  
 461 the figure) appears on the screen after the start key is pecked, then the correct response is to refrain from  
 462 pecking the food key for 10 seconds. If the bird succeeds in refraining, the next intertrial interval starts. If  
 463 the bird fails and pecks the food key while the purple circle is on the screen, then it is given an aversive  
 464 stimuli for 5 seconds (TV static screen). In the **detour** task, individuals first receive a warm up with an  
 465 opaque tube where they learn that the experimenter will show them a piece of food and then move that piece  
 466 of food into the tube. Subjects then have the opportunity to approach the tube and eat the food. A correct  
 467 response is when their first approach is to go to the side of the tube to the opening to obtain the food and  
 468 an incorrect response is when they try to access the food by pecking at the front of the tube (which has no  
 469 opening). Once they pass the warm up, by solving correctly in 4 out of 5 consecutive trials, they move on  
 470 to the test, which uses the same setup of tube and food except the tube is transparent. The idea is that  
 471 being able to see the food through the tube wall might entice them to try to go through the wall rather than

472 refrain from a direct approach to the food and instead go around the side through the tube opening.

## 473 **D. METHODS**

### 474 **Open materials**

475 ADDED Sep 2020: Testing protocols: inhibition for the three inhibition experiments: go/no go, detour, and  
476 delay of gratification

477 Testing protocols: flexibility for the experiments: color tube reversal learning and multi-access box

### 478 **Open data**

479 When the study is complete, the data will be published in the Knowledge Network for Biocomplexity's data  
480 repository.

### 481 **Randomization and counterbalancing**

#### 482 **P3**

483 Two individuals from each batch will experience the detour task before participating in the flexibility ma-  
484 nipulation. These individuals will be randomly selected using the random number generator at <https://www.random.org>.  
485

#### 486 **P1-P2**

487 For the rest of the individuals (n=6 per batch), the order of the three inhibition tasks will be counterbalanced  
488 across birds (using <https://www.random.org> to randomly assign individuals to one of three experimental  
489 orders). 1/3 of the individuals will experience:

- 490 1. Delayed gratification task
- 491 2. Go/no go task
- 492 3. Detour

493 1/3 of the individuals will experience:

- 494 1. Go/no go task
- 495 2. Detour
- 496 3. Delayed gratification task

497 1/3 of the individuals will experience:

- 498 1. Detour
- 499 2. Delayed gratification task
- 500 3. Go/no go task

501 NOTE (Sep 2020): the delayed gratification task was not conducted because the grackles never habituated  
502 to the apparatuses. The following birds experienced go/no go first, then detour: Burrito, Chilaquile, Pizza,  
503 Yuca, and Pollito.

### 504 **Delayed gratification**

- 505 • Food preference test: food will be presented in random combinations over six sessions of 12-15 trials.
- 506 • Training trials: The type of demonstration and training trials varied randomly (with more demo  
507 trials near the beginning of training), incorporating trials in which food of the same sort accumulated  
508 (quantity), food of ascending quality accumulated (quality), and trials in which we added increasingly  
509 larger food pieces throughout the trial (size).
- 510 • Test: we will test each food quality (low, mid, high) twice in randomized order in each session.

### 511 **Go/no go**

512 Go and no go trials will be presented randomly with the restriction that no more than four of the same type  
513 will occur in a row. The rewarded color will be counterbalanced across birds.

### 514 **Detour**

515 The side from which the apparatus is baited will be consistent within subjects, but counterbalanced across  
516 subjects.

### 517 **Blinding of conditions during analysis**

518 No blinding is involved in this study. NOTE (Sep 2020): interobserver reliability analyses were conducted  
519 by hypothesis-blind video coders.

### 520 **Dependent variables**

#### 521 *P1: the more flexible individuals are better at inhibition*

522 1) **Delayed gratification:** Number of food pieces waited for (0-3). A successful wait is defined as waiting  
523 for at least one additional piece of food to be added to the serving lid of the three possible additional  
524 food items, and accepting at least one of the reward pieces.

#### 525 2) **Go/no go:**

526 a) The number of trials to reach criterion (85% correct) where correct responses involve pecking when  
527 the rewarded stimulus is displayed and not pecking when the unrewarded stimulus is displayed,  
528 and incorrect responses involve pecking when the unrewarded stimulus is displayed, and not  
529 pecking when the rewarded stimulus is displayed

530 b) The latency to respond (peck the target key)

531 3) **Detour:** First approach (physical contact with bill): Correct (to the tube's side opening) or Incorrect  
532 (to the front closed area of the tube) (methods as in MacLean et al. (2014)).

533 One model will be run per dependent variable.

#### 534 *P3: does training improve detour performance?*

535 1) First approach (physical contact): Correct (to the tube's side opening) or Incorrect (to the front closed  
536 area of the tube) (methods as in MacLean et al. (2014)).

### 537 **Independent variables**

538 ***P1: delayed gratification***

- 539 1) Food quality or quantity (Quality: High, Med, Low; Quantity: Smaller, Medium, Larger)
- 540 2) Trial
- 541 3) Delay (2, 5, 10, 20, 40, 60, or 80 seconds)
- 542 4) Flexibility 1: **Number of trials to reverse** a preference in the last reversal an individual experienced  
543 (reversal learning; an individual is considered to have a preference if it chose the rewarded option at  
544 least 17 out of the most recent 20 trials, with a minimum of 8 or 9 correct choices out of 10 on the two  
545 most recent sets of 10 trials). See behavioral flexibility preregistration.
- 546 5) Flexibility 3: If the number of trials to reverse a preference does not positively correlate with the  
547 latency to attempt or solve new loci on the multi-access box (an additional measure of flexibility),  
548 then the **average latency to solve** and the **average latency to attempt** a new option on the  
549 multi-access box will be additional dependent variables. See behavioral flexibility preregistration.
- 550 6) Flexibility 4: This measure is currently being developed and is intended to be a more accurate repre-  
551 sentation of all of the choices an individual made, as well as accounting for the degree of uncertainty  
552 exhibited by individuals as preferences change. If this measure more effectively represents flexibility  
553 (determined using a modeled dataset and not the actual data), we may decide to solely rely on this  
554 measure and not use flexibility measures 1 through 3. If this ends up being the case, we will modify  
555 the code in the analysis plan below to reflect this change.

556 ***P1: go/no go***

557 Model 2a: number of trials to reach criterion

- 558 1) Flexibility 1: Number of trials to reverse a preference in the last reversal an individual experienced  
559 (reversal learning; as above)
- 560 2) Flexibility 3: If the number of trials to reverse a preference does not positively correlate with the  
561 latency to attempt or solve new loci on the multi-access box, then the **average latency to solve** and  
562 the **average latency to attempt** a new option on the multi-access box will be additional independent  
563 variables (as above).
- 564 3) Flexibility 4: This measure is currently being developed and is intended to be a more accurate repre-  
565 sentation of all the choices an individual made, as well as accounting for the degree of uncertainty  
566 exhibited by individuals as preferences change. If this measure more effectively represents flexibility  
567 (determined using a modeled dataset and not the actual data), we may decide to solely rely on this  
568 measure and not use flexibility measures 1 through 3. If this ends up being the case, we will modify  
569 the code in the analysis plan below to reflect this change.

570 Model 2b: latency to respond

- 571 1) Correct or incorrect response
- 572 2) Trial
- 573 3) Flexibility Condition: control, flexibility manipulation
- 574 4) ID (random effect because multiple measures per bird)

575 NOTE Jul 2020: remove flexibility condition as a variable because, by definition, the birds in the manipulated  
576 group were faster to reverse their preferences.

577 **P1: detour**

578 1) Trial

579 NOTE (Aug 2020): Because the data are analyzed in a GLM, meaning that there is only one row per bird,  
580 trial number is not able to be included because it would need to be conducted on multiple rows per bird.  
581 Therefore, we removed this independent variable from this analysis.

582 2) Flexibility 1: Number of trials to reverse a preference in the last reversal an individual experienced  
583 (reversal learning; as above)

584 3) Flexibility 3: If the number of trials to reverse a preference does not positively correlate with the  
585 latency to attempt or solve new loci on the multi-access box, then the **average latency to solve** and  
586 the **average latency to attempt** a new option on the multi-access box will be additional independent  
587 variables (as above).

588 4) Flexibility 4: This measure is currently being developed and is intended to be a more accurate repre-  
589 sentation of all of the choices an individual made, as well as accounting for the degree of uncertainty  
590 exhibited by individuals as preferences change. If this measure more effectively represents flexibility  
591 (determined using a modeled dataset and not the actual data), we may decide to solely rely on this  
592 measure and not use flexibility measures 1 through 3. If this ends up being the case, we will modify  
593 the code in the analysis plan below to reflect this change.

594 **P3: does training improve detour performance?**

595 1) Condition: pre- or post-reversal learning tests

596 **Unregistered analysis: Interobserver reliability of dependent variables**

597 To determine whether experimenters coded the dependent variables in a repeatable way, hypothesis-blind  
598 video coders, Sophie Kaube (detour) and Brynna Hood (go/no go), were first trained in video coding the  
599 dependent variables (detour and go/no go: whether the bird made the correct choice or not), requiring a  
600 Cohen's unweighted kappa of 0.90 or above to pass training (using the psych package in R Revelle (2017)).  
601 This threshold indicates that the two coders (the experimenter and the video coder) agree with each other  
602 to a high degree (Landis and Koch (1977)). After passing training, the video coders coded 24% (detour)  
603 and 33% (go/no go) of the videos for each experiment and the unweighted Cohen's kappa was calculated  
604 to determine how objective and repeatable scoring was for this variable, while noting that the experimenter  
605 had the advantage over the video coder because watching the videos was not as clear as watching the  
606 bird participate in the trial from the aisle of the aviaries. The unweighted kappa was used because this is a  
607 categorical variable where the distances between the numbers are meaningless (0=incorrect choice, 1=correct  
608 choice, -1=did not participate).

609 **Detour: correct choice**

610 We randomly chose four (Diablo, Queso, Chalupa, and Habanero) of the 11 birds that had participated  
611 in this experiment by Nov 2019 using random.org. First, Kaube analyzed all videos from Habanero and  
612 Diablo, and we analyzed the data using an intraclass correlation coefficient, which is not an appropriate  
613 test for categorical data. After learning this, we switched to using the Cohen's unweighted kappa and  
614 replaced Habanero and Diablo with two new randomly chosen grackles (Mole and Chilaquile). Kaube then  
615 analyzed all videos from Queso and Chalupa for training and passed (Cohen's unweighted kappa=0.91,  
616 confidence boundary=0.75-1.00, n=24 data points). After passing training, Kaube analyzed all videos from  
617 Queso, Chalupa, Mole, and Chilaquile, and highly agreed with the experimenter's data (Cohen's unweighted  
618 kappa=0.91, confidence boundary=0.78-1.00, n=44 data points).

619 **Go/no go: correct choice**

620 We randomly chose three (Diablo, Burrito, and Chilaquile) of the 12 birds that were estimated to complete  
621 this experiment using random.org. Hood then analyzed all videos from Diablo for training and passed  
622 (Cohen’s unweighted kappa=0.91, confidence boundary=0.80-1.00, n=40 data points). Hood then coded the  
623 rest of the videos and had substantial amounts of agreement with the experimenters (Cohen’s unweighted  
624 kappa = 0.82, confidence boundary = 0.78-0.85, n=611 data points).

625 We think the reason for the lower (but still acceptable) interobserver agreement for this variable is due to  
626 the fact that the correct choice data were not as objective to code as we had hoped due to the touchscreen  
627 malfunctioning (not registering touches to the screen), and to the subjective criterion that the bird had to  
628 be within a certain distance of the screen to be considered paying attention and thus be in position to make  
629 a choice or not. This indicates that our touchscreen set up could be greatly improved such that it is actually  
630 automated, rather than needing experimenter intervention for every trial.

### 631 **Go/no go: latency to respond (peck the screen)**

632 Interobserver reliability was not conducted on this variable because we obtained this data from the automat-  
633 ically generated PsychoPy data sheets. However, we must note that when entering the latency to first screen  
634 peck into the main data sheet that the experimenter used to determine whether they made a correct choice  
635 or not, the two data sheets did not always match. This is because: 1) if a session started or ended with  
636 the bird not participating such that a trial was not triggered, this receives a -1 in the experimenter’s data  
637 sheet and is not recorded by the PsychoPy data sheet; and 2) the touchscreen regularly failed to register  
638 screen pecks, which could result in an NA for the PsychoPy data sheet whereas the experimenter’s data  
639 sheet recorded a choice.

## 640 **E. ANALYSIS PLAN**

641 We do not plan to **exclude** any data. When **missing data** occur, the existing data for that individual will  
642 be included in the analyses for the tests they completed. Analyses will be conducted in R (current version  
643 3.6.3; R Core Team (2017)). When there is more than one experimenter within a test, experimenter will be  
644 added as a random effect to account for potential differences between experimenters in conducting the tests.  
645 If there are no differences between models including or excluding experimenter as a random effect, then we  
646 will use the model without this random effect for simplicity.

### 647 **Ability to detect actual effects**

648 To begin to understand what kinds of effect sizes we will be able to detect given our sample size limitations  
649 and our interest in decreasing noise by attempting to measure it, which increases the number of explanatory  
650 variables, we used G\*Power (v.3.1, Faul et al. (2007), Faul et al. (2009)) to conduct power analyses based  
651 on confidence intervals. G\*Power uses pre-set drop down menus and we chose the options that were as close  
652 to our analysis methods as possible (listed in each analysis below). Note that there were no explicit options  
653 for GLMs (though the chosen test in G\*Power appears to align with GLMs) or GLMMs or for the inclusion  
654 of the number of trials per bird (which are generally large in our investigation), thus the power analyses are  
655 only an approximation of the kinds of effect sizes we can detect. We realize that these power analyses are  
656 not fully aligned with our study design and that these kinds of analyses are not appropriate for Bayesian  
657 statistics (e.g., our MCMCglmm below), however we are unaware of better options at this time. Additionally,  
658 it is difficult to run power analyses because it is unclear what kinds of effect sizes we should expect due to  
659 the lack of data on this species for these experiments.

### 660 **Data checking**

661 The data will be visually checked to determine whether they are normally distributed via two methods: 1)  
662 normality is indicated when the histograms of actual data match those with simulated data, and 2) normality  
663 is indicated when the residuals closely fit the dotted line in the Normal Q-Q plot (Zuur et al. 2009). If the  
664 data do not appear normally distributed, visually check the residuals. If they are patternless, then assume a

665 normal distribution (Zuur et al. 2009). Detour data look normal, go/no go data are questionable, and both  
666 have patternless residuals, therefore we presume normality for both variables.

### 667 **P1: delayed gratification**

668 **Assess food preferences:** Conduct preference tests between pairs of different foods. Rank food preferences  
669 into three categories (High, Medium, Low) in the order of the percentage of times a food was chosen.

670 **Analysis:** Generalized Linear Model (GLM; glm function, stats package) with a Poisson distribution and  
671 log link, unless the only choices made were 0 (they didn't wait for food) and 1 (they waited for 1 piece of  
672 food but not for 2 or 3), in which case we will use a binomial distribution with a logit link. We will determine  
673 whether an independent variable had an effect or not using the Estimate in the full model.

674 To determine our ability to detect actual effects, we ran a power analysis in G\*Power with the following  
675 settings: test family=F tests, statistical test=linear multiple regression: Fixed model ( $R^2$  deviation from  
676 zero), type of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and  
677 increased the effect size until the total sample size in the output matched our projected sample size (n=32).  
678 The protocol of the power analysis is here:

679 *Input:*

680 Effect size  $f^2 = 0,41$

681 err prob = 0,05

682 Power (1- err prob) = 0,7

683 Number of predictors = 5

684 *Output:*

685 Noncentrality parameter = 13,1200000

686 Critical F = 2,5867901

687 Numerator df = 5

688 Denominator df = 26

689 Total sample size = 32

690 Actual power = 0,7103096

691 This means that, with our sample size of 32, we have a 71% chance of detecting a large effect (approximated  
692 at  $f^2=0.35$  by Cohen (1988)).

693 These analyses were not conducted because the experiment failed due to the grackles never habituating to  
694 the test apparatuses.

### 695 **P1: go/no go**

696 **Analysis:**

697 **Model 2a: number of trials to reach criterion in the go/no go experiment** Generalized Linear  
698 Model (GLM; glm function, stats package) with a Poisson distribution and a log link. We will determine  
699 whether an independent variable had an effect or not using the Estimate in the full model.

700 To determine our ability to detect actual effects, we ran a power analysis in G\*Power with the following  
701 settings: test family=F tests, statistical test=linear multiple regression: Fixed model ( $R^2$  deviation from  
702 zero), type of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and  
703 increased the effect size until the total sample size in the output matched our projected sample size (n=32).  
704 The protocol of the power analysis is here:

705 *Input:*



706 Effect size  $f^2 = 0,27$   
707 err prob = 0,05  
708 Power (1- err prob) = 0,7  
709 Number of predictors = 2  
710 *Output:*  
711 Noncentrality parameter = 8,6400000  
712 Critical F = 3,3276545  
713 Numerator df = 2  
714 Denominator df = 29  
715 Total sample size = 32  
716 Actual power = 0,7047420

717 This means that, with our sample size of 32, we have a 70% chance of detecting a medium (approximated  
718 at  $f^2=0.15$  by Cohen (1988)) to large effect (approximated at  $f^2=0.35$  by Cohen (1988)).

719 **Flexibility comprehensive:** In addition to the number of trials it took birds to reverse a preference, we  
720 also developed a more mechanistic measure of flexibility that takes into account all choices in the reversal  
721 learning experiment. Specifically, we use multilevel Bayesian reinforcement learning models that, from trial  
722 to trial, update the latent values of different options and use those *attractions* to explain observed choices.

723 There are two basic components:

724 First, we have an updating or learning equation that tells us how attractions to different behavioral options  
725  $A_{i,j,t+1}$  (i.e., how preferable option  $i$  is to the bird  $j$  at time  $t + 1$ ) change over time as a function of previous  
726 attractions  $A_{i,j,t}$  and recently experienced payoffs  $\pi_{i,j,t}$  (i.e., whether they received a reward in a given trial  
727 or not). Attraction scores thus reflect the accumulated learning history up to this point.

$$728 A_{i,j,t+1} = (1 - \phi_j)A_{i,j,t} + \phi_j\pi_{i,j,t}.$$

729 The (bird-specific) parameter  $\phi_j$  describes the weight of recent experience. The higher the value of  $\phi_j$ , the  
730 faster the bird updates their attraction. It thus can be interpreted as the *learning or updating rate of an*  
731 *individual*. This corresponds to the first and third connotation of behavioral flexibility as defined by (Bond  
732 et al. 2007), the ability to rapidly and adaptively change behavior in light of new experiences.

733 The second major part of the model expresses the probability an individual  $j$  chooses option  $i$  in the next  
734 round,  $t + 1$ , based on the latent attractions:

$$735 P(i)_{t+1} = \frac{\exp(\lambda_j A_{i,j,t})}{\sum_{m=1}^2 \exp(\lambda_j A_{m,j,t})}.$$

736 The parameter  $\lambda_j$  represents the *random choice rate* of an individual (also called inverse temperature). It  
737 controls how sensitive choices are to differences in attraction scores. As  $\lambda_j$  gets larger, choices become  
738 more deterministic, as it gets smaller, choices become more exploratory (random choice if  $\lambda_j = 0$ ). This  
739 closely corresponds to the second connotation of internally generated behavioral variation, exploration or  
740 creativity (Bond et al. 2007). To account for potential differences between experimenters, we also included  
741 experimenter ID as a random effect (omitted from previous equations to enhance readability, but available  
742 in the code below).

743 This analysis yields posterior distributions for  $\phi_j$  and  $\lambda_j$  for each individual bird. To use these estimates in  
744 a GLM that predicts their inhibition score, we need to propagate the full *uncertainty* from the reinforcement  
745 learning model, which is achieved by directly passing the variables to the linear model within a single large  
746 *stan* model. We include both parameters ( $\phi_j$  and  $\lambda_j$ ) as predictors and estimate their respective independent  
747 effect on the number of trials to pass criterion in go/no go as well as an interaction term. To model the

748 number of trials to pass criterion, we used a Poisson likelihood and a standard log link function as appropriate  
749 for count data with an unknown maximum.

750 **Model 2b: latency to respond in the go/no go experiment** A Generalized Linear Mixed Model  
751 (GLMM; MCMCglmm function, MCMCglmm package; (Hadfield 2010)) will be used with a Poisson distri-  
752 bution and log link using 13,000 iterations with a thinning interval of 10, a burnin of 3,000, and minimal  
753 priors (V=1, nu=0) (Hadfield 2014). We will ensure the GLMM shows acceptable convergence (lag time  
754 autocorrelation values <0.01 after lag 0; (Hadfield 2010)), and adjust parameters if necessary. We will  
755 determine whether an independent variable had an effect or not using the Estimate in the full model.

756 NOTE (Sep 2020): we changed the distribution to Gaussian (with an identity link) because MCMCglmm  
757 would not run on a Poisson (it kept saying there were negative integers even after we removed them). A  
758 Gaussian distribution also works for this kind of data because the response variable is a latency in seconds.

759 To roughly estimate our ability to detect actual effects (because these power analyses are designed for  
760 frequentist statistics, not Bayesian statistics), we ran a power analysis in G\*Power with the following settings:  
761 test family=F tests, statistical test=linear multiple regression: Fixed model (R<sup>2</sup> deviation from zero), type  
762 of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the  
763 effect size until the total sample size in the output matched our projected sample size (n=32). The number  
764 of predictor variables was restricted to only the fixed effects because this test was not designed for mixed  
765 models. The protocol of the power analysis is here:

766 *Input:*

767 Effect size  $f^2 = 0,32$

768 err prob = 0,05

769 Power (1- err prob) = 0,7

770 Number of predictors = 3

771 *Output:*

772 Noncentrality parameter = 10,2400000

773 Critical F = 2,9466853

774 Numerator df = 3

775 Denominator df = 28

776 Total sample size = 32

777 Actual power = 0,7061592

778 This means that, with our sample size of 32, we have a 71% chance of detecting a large effect (approximated  
779 at  $f^2=0.35$  by Cohen (1988)).

## 780 **P1: detour**

781 **Analysis:** Generalized Linear Model (GLM; glm function, stats package) with a binomial distribution and  
782 a logit link. We will determine whether an independent variable had an effect or not using the Estimate in  
783 the full model.

784 See the protocol for the power analyses for Model 2b above for the rough estimation of our ability to detect  
785 actual effects with this model.

786 **Flexibility comprehensive:** We again repeat the analyses for the detour task with the more comprehensive  
787 computational measure of flexibility that takes into account all choices in the reversal learning experiment.  
788 We include both parameters ( $\phi_j$  and  $\lambda_j$ ) as well as their interaction to predict whether birds make correct  
789 choices in each trial of the detour task. We use a binomial likelihood as the outcome distribution and a logit  
790 link function (see section 2a for full data preparation and analysis script).

791 **P1 alternative 2: are inhibition results reliable?**

792 The reliability of the inhibition tests will be calculated using Cronbach's Alpha (as in Friedman and Miyake  
793 (2004); R package: psy (Falissard 2012), function: cronbach), which is indicated by alpha in the output.

794 NOTE (Sep 2020): when we tried to run this code we discovered that this is not the appropriate test to  
795 run on our experimental design to test the internal validity of the experiment (e.g., does this test actually  
796 measure what we think it does). To test internal validity, we would need to change the experimental design,  
797 which was not the goal of our current study. Therefore, we did not conduct this analysis.

798 **P2: correlation across inhibition tasks**

799 See analysis description for P1 alternative 2.

800 **P3: does training improve detour performance?**

801 **Analysis:** Generalized Linear Model (GLM; glm function, stats package) with a binomial distribution and  
802 a logit link. We will determine whether an independent variable had an effect or not using the Estimate in  
803 the full model.

804 To determine our ability to detect actual effects, we ran a power analysis in G\*Power with the following  
805 settings: test family=F tests, statistical test=linear multiple regression: Fixed model (R<sup>2</sup> deviation from  
806 zero), type of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and  
807 increased the effect size until the total sample size in the output matched our projected sample size (n=32).  
808 The protocol of the power analysis is here:

809 *Input:*

810 Effect size  $f^2 = 0,21$

811 err prob = 0,05

812 Power (1- err prob) = 0,7

813 Number of predictors = 1

814 *Output:*

815 Noncentrality parameter = 6,7200000

816 Critical F = 4,1708768

817 Numerator df = 1

818 Denominator df = 30

819 Total sample size = 32

820 Actual power = 0,7083763

821 This means that, with our sample size of 32, we have a 71% chance of detecting a medium effect (approximated  
822 at  $f^2=0.15$  by Cohen (1988)).

823 **Alternative Analyses**

824 We anticipate that we will want to run additional/different analyses after reading McElreath (2016). We  
825 will revise this preregistration to include these new analyses before conducting the analyses above. See the  
826 State of the Data for a description of the analysis changes we made.

## 827 F. PLANNED SAMPLE

828 Great-tailed grackles are caught in the wild in Tempe, Arizona, USA, for individual identification (colored  
829 leg bands in unique combinations). Some individuals (~32) are brought temporarily into aviaries for testing,  
830 and then they will be released back to the wild. Grackles are individually housed in an aviary (each 244cm  
831 long by 122cm wide by 213cm tall) at Arizona State University for a maximum of three months where they  
832 have ad lib access to water at all times and are fed Mazuri Small Bird maintenance diet ad lib during non-  
833 testing hours (minimum 20h per day), and various other food items (e.g., peanuts, grapes, bread) during  
834 testing (up to 3h per day per bird). Individuals are given three to four days to habituate to the aviaries and  
835 then their test battery begins on the fourth or fifth day (birds are usually tested six days per week, therefore  
836 if their fourth day in the aviaries occurs on a day off, then they are tested on the fifth day instead).

### 837 Sample size rationale

838 We will test as many birds as we can in the approximately three years at this field site given that the  
839 birds only participate in tests in aviaries during the non-breeding season (approximately September through  
840 March). The minimum sample size will be 16, however we expect to be able to test up to 32 grackles.

### 841 Data collection stopping rule

842 We will stop testing birds once we have completed two full aviary seasons (likely in March 2020). NOTE:  
843 the two full aviary seasons concluded in May 2020. NOTE (Sep 2020): data collection stopped after two full  
844 aviary seasons in May 2020.

## 845 G. ETHICS

846 This research is carried out in accordance with permits from the:

- 847 1) US Fish and Wildlife Service (scientific collecting permit number MB76700A-0,1,2)
- 848 2) US Geological Survey Bird Banding Laboratory (federal bird banding permit number 23872)
- 849 3) Arizona Game and Fish Department (scientific collecting license number SP594338 [2017], SP606267  
850 [2018], and SP639866 [2019])
- 851 4) Institutional Animal Care and Use Committee at Arizona State University (protocol number 17-1594R)
- 852 5) University of Cambridge ethical review process (non-regulated use of animals in scientific procedures:  
853 zoo4/17)

## 854 H. AUTHOR CONTRIBUTIONS

855 **Logan:** Hypothesis development, experimental design (go/no go task), data collection, data analysis and  
856 interpretation, write up, revising/editing, materials/funding.

857 **McCune:** Data collection, data interpretation, revising/editing.

858 **MacPherson:** Data collection, data interpretation, revising/editing.

859 **Johnson-Ulrich:** Touchscreen programming for go/no go task, data interpretation, revising/editing.

860 **Rowney:** Data collection, data interpretation, revising/editing.

861 **Seitz:** Experimental design (go/no go task), touchscreen programming (go/no go task), data interpretation,  
862 revising/editing.

863 **Blaisdell:** Experimental design (go/no go task), data interpretation, revising/editing.

864 **Deffner:** Data analysis (Flexibility 4 model), revising/editing.

865 **Wascher:** Hypothesis development, experimental design (delayed gratification and detour tasks), data  
866 analysis and interpretation, write up, revising/editing.

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871 **J. CONFLICT OF INTEREST DISCLOSURE**

872 We, the authors, declare that we have no financial conflicts of interest with the content of this article. Corina  
873 Logan is a Recommender and on the Managing Board at PCI Ecology.

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889 **L. REFERENCES**

- 890 Addessi E, Paglieri F, Beran MJ, Evans TA, Macchitella L, De Petrillo F, Focaroli V. 2013. Delay choice  
891 versus delay maintenance: Different measures of delayed gratification in capuchin monkeys (*cebus apella*).  
892 *Journal of Comparative Psychology*. 127(4):392.
- 893 Auersperg AMI, Bayern AMP von, Gajdon GK, Huber L, Kacelnik A. 2011. Flexibility in problem solving  
894 and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLOS ONE*. 6(6):e20231.  
895 doi:10.1371/journal.pone.0020231. [accessed 2017 May 15]. <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0020231>.
- 897 Beran M. 2018. *Self-control in animals and people*. Academic Press.
- 898 Beran MJ. 2015. The comparative science of ‘self-control’: What are we talking about? *Frontiers in Psy-*  
899 *chology*. 6:51.
- 900 Bond AB, Kamil AC, Balda RP. 2007. Serial reversal learning and the evolution of behavioral flexibility in  
901 three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma*  
902 *californica*). *Journal of Comparative Psychology*. 121(4):372–379. doi:10.1037/0735-7036.121.4.372.
- 903 Boogert NJ, Anderson RC, Peters S, Searcy WA, Nowicki S. 2011. Song repertoire size in male song sparrows  
904 correlates with detour reaching, but not with other cognitive measures. *Animal Behaviour*. 81(6):1209–1216.  
905 doi:10.1016/j.anbehav.2011.03.004. [accessed 2017 May 15]. <http://www.sciencedirect.com/science/article/pii/S0003347211001011>.
- 907 Bray EE, MacLean EL, Hare BA. 2014. Context specificity of inhibitory control in dogs. *Animal Cognition*.  
908 17(1):15–31.

- 909 Brucks D, Marshall-Pescini S, Wallis LJ, Huber L, Range F. 2017. Measures of dogs' inhibitory control  
910 abilities do not correlate across tasks. *Frontiers in Psychology*. 8:849.
- 911 Carter AJ, Feeney WE, Marshall HH, Cowlshaw G, Heinsohn R. 2013. Animal personality: What are  
912 behavioural ecologists measuring? *Biological Reviews*. 88(2):465–475.
- 913 Cohen J. 1988. *Statistical power analysis for the behavioral sciences* 2nd edn.
- 914 Damerius LA, Graber SM, Willems EP, Schaik CP van. 2017. Curiosity boosts orang-utan problem-solving  
915 ability. *Animal Behaviour*. 134:57–70.
- 916 Deaner RO, Schaik CP van, Johnson V. 2006. Do some taxa have better domain-general cognition than  
917 others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology*. 4(1):147470490600400114.  
918 doi:10.1177/147470490600400114. [accessed 2017 May 15]. <http://dx.doi.org/10.1177/147470490600400114>.
- 919 Diamond A. 2013. Executive functions. *Annual review of psychology*. 64:135–168.
- 920 DuBois AL, Nowicki S, Peters S, Rivera-Cáceres KD, Searcy WA. 2018. Song is not a reliable signal of  
921 general cognitive ability in a songbird. *Animal Behaviour*. 137:205–213.
- 922 Ducatez S, Audet J-N, Lefebvre L. 2019. Speed–accuracy trade-off, detour reaching and response to pha in  
923 carib grackles. *Animal cognition*. 22(5):625–633.
- 924 Fagnani J, Barrera G, Carballo F, Bentosela M. 2016. Is previous experience important for inhibitory  
925 control? A comparison between shelter and pet dogs in a-not-b and cylinder tasks. *Animal Cognition*.  
926 19(6):1165–1172.
- 927 Falissard B. 2012. Psy: Various procedures used in psychometry. [https://CRAN.R-project.org/package=](https://CRAN.R-project.org/package=psy)  
928 [psy](https://CRAN.R-project.org/package=psy).
- 929 Faul F, Erdfelder E, Buchner A, Lang A-G. 2009. Statistical power analyses using g\* power 3.1: Tests for  
930 correlation and regression analyses. *Behavior research methods*. 41(4):1149–1160.
- 931 Faul F, Erdfelder E, Lang A-G, Buchner A. 2007. G\* power 3: A flexible statistical power analysis program  
932 for the social, behavioral, and biomedical sciences. *Behavior research methods*. 39(2):175–191.
- 933 Friedman NP, Miyake A. 2004. The relations among inhibition and interference control functions: A latent-  
934 variable analysis. *Journal of experimental psychology: General*. 133(1):101.
- 935 Ghahremani DG, Monterosso J, Jentsch JD, Bilder RM, Poldrack RA. 2009. Neural components underlying  
936 behavioral flexibility in human reversal learning. *Cerebral cortex*. 20(8):1843–1852.
- 937 Griffin AS, Guez D. 2014. Innovation and problem solving: A review of common mechanisms. *Behavioural*  
938 *Processes*. 109:121–134.
- 939 Hadfield J. 2014. MCMCglmm course notes. [http://cran.r-project.org/web/packages/MCMCglmm/](http://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf)  
940 [vignettes/CourseNotes.pdf](http://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf).
- 941 Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm  
942 R package. *Journal of Statistical Software*. 33(2):1–22. <http://www.jstatsoft.org/v33/i02/>.
- 943 Harding EJ, Paul ES, Mendl M. 2004. Animal behaviour: Cognitive bias and affective state. *Nature*.  
944 427(6972):312–312.
- 945 Hillemann F, Bugnyar T, Kotrschal K, Wascher CA. 2014. Waiting for better, not for more: Corvids respond  
946 to quality in two delay maintenance tasks. *Animal behaviour*. 90:1–10.
- 947 Homberg JR, Pattij T, Janssen MC, Ronken E, De Boer SF, Schoffelmeer AN, Cuppen E. 2007. Serotonin  
948 transporter deficiency in rats improves inhibitory control but not behavioural flexibility. *European Journal*  
949 *of Neuroscience*. 26(7):2066–2073.
- 950 Horik JO van, Langley EJ, Whiteside MA, Laker PR, Beardsworth CE, Madden JR. 2018. Do detour  
951 tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences*.  
952 285(1875):20180150.

- 953 Isaksson E, Urhan AU, Brodin A. 2018. High level of self-control ability in a small passerine bird. *Behavioral*  
954 *ecology and sociobiology*. 72(7):118.
- 955 Johnson-Ulrich L, Johnson-Ulrich Z, Holekamp K. 2018. Proactive behavior, but not inhibitory control,  
956 predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition*. 21(3):379–  
957 392.
- 958 Kabadayi C, Bobrowicz K, Osvath M. 2018. The detour paradigm in animal cognition. *Animal cognition*.  
959 21(1):21–35.
- 960 Landis JR, Koch GG. 1977. The measurement of observer agreement for categorical data. *biometrics*:159–  
961 174.
- 962 Liu Y, Day LB, Summers K, Burmeister SS. 2016. Learning to learn: Advanced behavioural flexibility in a  
963 poison frog. *Animal Behaviour*. 111:167–172.
- 964 Logan C. 2016. Behavioral flexibility and problem solving in an invasive bird. *PeerJ*. 4:e1975.
- 965 Logan C, McCune K, MacPherson M, Johnson-Ulrich Z, Rowney C, Seitz B, Blaisdell A, Deffner D, Wascher  
966 C. 2020. Great-tailed grackle inhibition data. Knowledge Network for Biocomplexity. Data package.  
967 doi:10.5063/M043S3.
- 968 Logan CJ, MacPherson M, Rowney C, Bergeron L, Seitz B, Blaisdell A, Folsom M, Johnson-Ulrich Z,  
969 McCune K. 2019. Is behavioral flexibility manipulatable and, if so, does it improve flexibility and problem  
970 solving in a new context? In principle acceptance by PCI Ecology of the version on 26 Mar 2019. [http://](http://corinalogan.com/Preregistrations/g_flexmanip.html)  
971 [corinalogan.com/Preregistrations/g\\_flexmanip.html](http://corinalogan.com/Preregistrations/g_flexmanip.html).
- 972 MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aureli F, Baker JM, Bania AE,  
973 Barnard AM, et al. 2014. The evolution of self-control. *Proceedings of the National Academy of Sciences*.  
974 111(20):E2140–E2148.
- 975 Manrique HM, Völter CJ, Call J. 2013. Repeated innovation in great apes. *Animal Behaviour*. 85(1):195–  
976 202. doi:10.1016/j.anbehav.2012.10.026. [accessed 2017 May 23]. [http://www.sciencedirect.com/science/](http://www.sciencedirect.com/science/article/pii/S0003347212004861)  
977 [article/pii/S0003347212004861](http://www.sciencedirect.com/science/article/pii/S0003347212004861).
- 978 McElreath R. 2016. *Statistical rethinking: A bayesian course with examples in r and stan*. CRC Press.  
979 <http://xcelab.net/rm/statistical-rethinking/>.
- 980 Mikhalevich I, Powell R, Logan C. 2017. Is behavioural flexibility evidence of cognitive complexity? How  
981 evolution can inform comparative cognition. *Interface Focus*. 7(3):20160121. doi:10.1098/rsfs.2016.0121.  
982 [accessed 2017 May 29]. <http://rsfs.royalsocietypublishing.org/lookup/doi/10.1098/rsfs.2016.0121>.
- 983 Miller R, Boeckle M, Jelbert SA, Frohnwieser A, Wascher CA, Clayton NS. 2019. Self-control in crows,  
984 parrots and nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive Science*. 10(6):e1504.
- 985 Nigg JT. 2017. Annual research review: On the relations among self-regulation, self-control, executive  
986 functioning, effortful control, cognitive control, impulsivity, risk-taking, and inhibition for developmental  
987 psychopathology. *Journal of child psychology and psychiatry*. 58(4):361–383.
- 988 R Core Team. 2017. *R: A language and environment for statistical computing*. Vienna, Austria: R  
989 Foundation for Statistical Computing. <https://www.R-project.org>.
- 990 Revelle W. 2017. *Psych: Procedures for psychological, psychometric, and personality research*. Evanston,  
991 Illinois: Northwestern University. <https://CRAN.R-project.org/package=psych>.
- 992 Seitz BM, McCune KB, MacPherson M, Bergeron LM, Blaisdell AP, Logan CJ. 2020. Using touchscreen  
993 equipped operant chambers to study comparative cognition. Benefits, limitations, and advice. *bioRxiv*.  
994 doi:10.1101/2020.10.03.324814. <https://www.biorxiv.org/content/early/2020/10/04/2020.10.03.324814>.
- 995 Shaw RC, Boogert NJ, Clayton NS, Burns KC. 2015. Wild psychometrics: Evidence for ‘general’ cognitive  
996 performance in wild new zealand robins, *petroica longipes*. *Animal Behaviour*. 109:101–111.

997 Thornton A, Lukas D. 2012. Individual variation in cognitive performance: Developmental and  
998 evolutionary perspectives. *Philosophical Transactions of the Royal Society of London B: Biolog-*  
999 *ical Sciences.* 367(1603):2773–2783. doi:10.1098/rstb.2012.0214. [accessed 2017 May 24]. [http:](http://rstb.royalsocietypublishing.org/content/367/1603/2773)  
1000 [//rstb.royalsocietypublishing.org/content/367/1603/2773](http://rstb.royalsocietypublishing.org/content/367/1603/2773).

1001 Zuur AF, Ieno EN, Saveliev AA. 2009. *Mixed effects models and extensions in ecology with r.* Springer.