

1 Behavioral flexibility is manipulatable and it improves flexibility
2 and problem solving in a new context.

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16
17 **This preregistration has been pre-study peer reviewed and received an In Principle Recom-
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22 ABSTRACT

23 Behavioral flexibility, the ability to adapt behavior to new circumstances, is thought to play an important
24 role in a species' ability to successfully adapt to new environments and expand its geographic range. However,
25 flexibility is rarely directly tested in species in a way that would allow us to determine how it works and enable
26 us to make predictions about a species' ability to adapt their behavior to new environments. We use great-
27 tailed grackles (a bird species) as a model to investigate this question because they have rapidly expanded
28 their range into North America over the past 140 years. We attempted to manipulate grackle flexibility using
29 colored tube reversal learning to determine whether flexibility is generalizable across contexts (touchscreen
30 reversal learning and multi-access box), whether it is repeatable within individuals and across contexts, and
31 what learning strategies grackles employ. We found that we were able to manipulate flexibility: birds in the
32 manipulated group reversed a color preference in fewer trials by the end of their serial reversals compared
33 to control birds who had only one reversal. Flexibility was repeatable within individuals (reversal), but not
34 across contexts (from reversal to multi-access box). The touchscreen reversal experiment did not appear to
35 measure what was measured in the reversal learning experiment with the tubes, and we speculate as to why.
36 One third of the grackles in the manipulated reversal learning group switched from one learning strategy
37 (epsilon-decreasing where they have a long exploration period) to a different strategy (epsilon-first where they

38 quickly shift their preference). A separate analysis showed that the grackles did not use a particular strategy
39 earlier or later in their serial reversals. Posthoc analyses using a model that breaks down performance on
40 the reversal learning task into different components showed that learning to be attracted to an option (phi)
41 more consistently correlated with reversal performance than the rate of deviating from learned attractions
42 that were rewarded (lambda). This result held in simulations and in the data from the grackles: learning
43 rates in the manipulated grackles doubled by the end of the manipulation compared to control grackles,
44 while the rate of deviation slightly decreased. Grackles with intermediate rates of deviation in their last
45 reversal solved fewer loci on the plastic and wooden multi-access boxes, and those with intermediate learning
46 rates in their last reversal were faster to attempt a new locus on both multi-access boxes. This investigation
47 allowed us to make causal conclusions, rather than relying only on correlations: we manipulated reversal
48 learning, which caused changes in a different flexibility measure (multi-access box switch times) and in an
49 innovativeness measure (multi-access box loci solved), as well as validating that the manipulation had an
50 effect on the cognitive ability we think of as flexibility. Understanding how behavioral flexibility causally
51 relates to other traits will allow researchers to develop robust theory about what behavioral flexibility is and
52 when to invoke it as a primary driver in a given context, such as a rapid geographic range expansion. Given
53 our results, flexibility manipulations could be useful in training threatened and endangered species in how
54 to be more flexible. If such a flexibility manipulation was successful, it could then change their behavior in
55 this and other domains, giving them a better chance of succeeding in human modified environments.

56 **Video summary**

57 **INTRODUCTION**

58 Behavioral flexibility, the ability to adapt behavior to new circumstances (see Mikhalevich et al. (2017) for
59 the theoretical background on this definition), is thought to play an important role in a species' ability to
60 successfully adapt to new environments and expand its geographic range (e.g., Lefebvre et al., 1997; Sol
61 et al., 2002, 2005, 2007; Sol & Lefebvre, 2000). This research predicts that behavioral flexibility (hereafter
62 referred to as flexibility) should positively relate with innovativeness. However, these predictions are based
63 on species-level data and proxies for flexibility and for innovation when examining such relationships (see
64 Logan et al., 2018). Flexibility is rarely directly tested in species that are rapidly expanding their geographic
65 ranges in a way that would allow us to determine how flexibility works and predict a species' ability to adapt
66 their behavior to new areas. Those investigations that examine the relationship between flexibility and
67 innovation (or problem solving) in species that are expanding their range show mixed results, with these
68 variables correlating positively (e.g., grey squirrels: Chow et al., 2016), negatively (e.g., Indian mynas: Griffin
69 et al., 2013), or not at all (e.g., great-tailed grackles: Logan, 2016). One way to improve our understanding
70 of whether and how flexibility is related to innovativeness is to perform a manipulative experiment on one
71 of the variables to determine whether there is an associated change in the other.

72 We focused our study on great-tailed grackles (*Quiscalus mexicanus*, hereafter grackles), a bird species that
73 is flexible (Logan, 2016) and rapidly expanding its geographic range (Wehtje, 2003). We attempted to
74 manipulate grackle flexibility using serial reversals of a color preference to determine whether their flexibility
75 is generalizable across additional experimental contexts (touchscreen reversal learning and multi-access box
76 solution switching), whether it is repeatable within individuals and across contexts, and what learning
77 strategies grackles employ.

78 If grackle flexibility is manipulatable using serial reversals, this could provide conservation managers with an
79 important tool for managing at-risk populations. If the manipulation works in grackles, it has the potential
80 to be effective in other species as well. This could be particularly useful for endangered species conservation
81 efforts, such as when selecting individuals for captive breeding programs, because individuals that are more
82 flexible might be able to adapt better to new environments. If the flexibility manipulation is not successful,
83 this could indicate either that we did not manipulate the right aspect of flexibility (e.g., perhaps training
84 them to solve a variety of different types of tasks quickly would be more effective) or that grackle flexibility
85 is not a trait that is trainable.

86 **HYPOTHESES**

87 **H1: Behavioral flexibility, as measured by reversal learning using colored tubes, is manipulat-
88 able.** **Prediction 1:** Individuals improve their flexibility on a serial reversal learning task using colored
89 tubes by generally requiring fewer trials to reverse a preference as the number of reversals increases (manip-
90 ulation condition). Their flexibility on this test will have been manipulated relative to control birds who do
91 not undergo serial reversals. Instead, individuals in the control condition will be matched to manipulated
92 birds for experience (they will experience a similar number of trials), but there will be no possibility of a
93 functional tube preference because both tubes will be the same color and both will contain food, therefore
94 either choice will be correct.

95 **P1 alternative 1:** If the number of trials to reverse a preference does not correlate with or positively
96 correlates with reversal number, which would account for all potential correlation outcomes, this suggests
97 that some individuals may prefer to rely on information acquired previously (i.e., they are slow to reverse)
98 rather than relying on current cues (e.g., the food is in a new location) (Griffin & Guez, 2014; Liu et al.,
99 2016; e.g., Manrique et al., 2013; but see Homberg et al., 2007).

100 **H2: Manipulating behavioral flexibility (improving reversal learning speed through serial re-
101 versals using colored tubes) improves flexibility (rule learning and/or switching) and problem
102 solving in a new context (two distinct multi-access boxes and serial reversals on a touchscreen).**

103 **P2:** Individuals that have improved their flexibility on a serial reversal learning task using colored tubes (re-
104quiring fewer trials to reverse a preference as the number of reversals increases) are faster to switch between
105 new methods of solving (latency to solve or attempt to solve a new way of accessing the food [locus]), and
106 learn more new loci (higher total number of solved loci) on multi-access box flexibility tasks, and are faster
107 to reverse preferences in a serial reversal task using a touchscreen than individuals in the control group where
108 flexibility has not been manipulated. The positive correlation between reversal learning performance using
109 colored tubes and a touchscreen (faster birds have fewer trials) and the multi-access boxes (faster birds have
110 lower latencies) indicates that all three tests measure the same ability even though the multi-access boxes
111 require inventing new rules to solve new loci (while potentially learning a rule about switching: “when an
112 option becomes non-functional, try a different option”) while reversal learning requires switching between
113 two rules (“choose light gray” or “choose dark gray”) or learning the rule to “switch when the previously
114 rewarded option no longer contains a reward.” Serial reversals eliminate the confounds of exploration, inhib-
115 ition, and persistence in explaining reversal learning speed because, after multiple reversals, what is being
116 measured is the ability to learn one or more rules. If the manipulation works, this indicates that flexibility
117 can be influenced by previous experience and might indicate that any individual has the potential to move
118 into new environments (see relevant hypotheses in preregistrations on [genetics](#) (R1) and [expansion](#) (H1)).

119 **P2 alternative 1:** If the manipulation does not work in that those individuals in the experimental condition
120 do not decrease their reversal speeds more than control individuals, then this experiment will elucidate
121 whether general individual variation in flexibility relates to flexibility in new contexts (two distinct multi-
122 access boxes and serial reversals on a touchscreen) as well as problem solving ability (multi-access boxes).
123 The prediction is the same in P2, but in this case variation in flexibility is constrained by traits inherent to
124 the individual (some of which will be tested in McCune et al., 2019), which suggests that certain individuals
125 will be more likely to move into new environments.

126 **P2 alternative 2:** If there is no correlation between reversal learning speed (colored tubes) and the latency
127 to solve/attempt a new locus on the multi-access boxes, this could be because the latency to solve not only
128 measures flexibility but also innovativeness. In this case, an additional analysis will be run with the latency
129 to solve as the response variable, to determine whether the fit of the model (as determined by the lower
130 AIC value) with reversal learning as an explanatory variable is improved if motor diversity (the number of
131 different motor actions used when attempting to solve the multi-access box) is included as an explanatory
132 variable (see Diquelou et al., 2015; Griffin et al., 2016). If the inclusion of motor diversity improves the
133 model fit, then this indicates that the latency to solve a new locus on the multi-access box is influenced by
134 flexibility (reversal learning speed) and innovation (motor diversity).

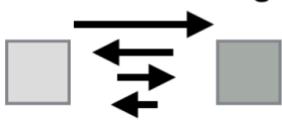
135 **P2 alternative 3:** If there is a negative correlation or no correlation between reversal learning speed on



136 colored tubes and reversal learning speed on the touchscreen, then this indicates that it may be difficult
137 for individuals to perceive and/or understand images on the touchscreen in contrast with physical objects
138 (colored tubes) (e.g., O'Hara et al., 2015).

A. Is flexibility manipulatable?

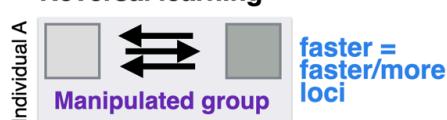
Reversal learning



fewer trials to reverse a preference with each reversal

B. Does manipulating flexibility improve it, and problem solving, in a new context?

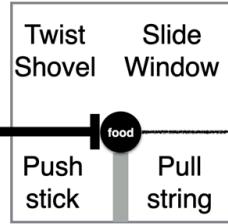
Reversal learning



faster = faster/more loci

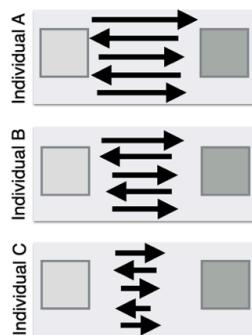
slower = slower/fewer loci

Multi-access box



C1. Repeatable within individuals?

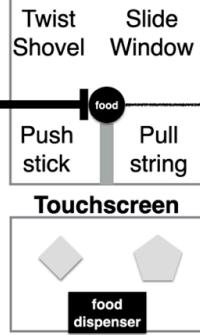
Reversal learning



slower individuals = slower to switch loci

C2. Repeatable across contexts?

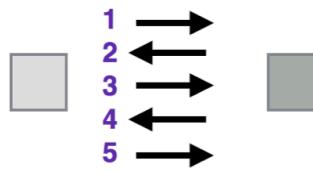
Multi-access box



faster individuals = faster to switch loci

D. Do individuals converge on one learning strategy?

2+ learning strategies



1 learning strategy

139

140 **Figure 1.** A visual illustration of Hypothesis 1 (A), Hypothesis 2 (B), Hypothesis 3 (C1 and C2), and
141 Hypothesis 4 (D). Longer black arrows indicate slower reversal times, the two yellow circles represent
142 experience with the two yellow tubes that both contained food for the control group.

143 **H3a: Behavioral flexibility within a context is repeatable within individuals.** Repeatability of
144 behavioral flexibility is defined as the number of trials to reverse a color preference being strongly negatively
145 correlated within individuals with the number of reversals.

146 **P3a:** Individuals that are faster to reverse a color preference in the first reversal will also be faster to reverse
147 a color preference in the second, etc. reversal due to natural individual variation.

148 **P3a alternative:** There is no repeatability in behavioral flexibility within individuals, which could indicate
149 that performance is state dependent (e.g., it depends on their fluctuating motivation, hunger levels, etc.).
150 We will determine whether performance on colored tube reversal learning related to motivation by examining
151 whether the latency to make a choice influenced the results. We will also determine whether performance was
152 related to hunger levels by examining whether the number of minutes since the removal of their maintenance
153 diet from their aviary plus the number of food rewards they received since then influenced the results.

154 **H3b: The consistency of behavioral flexibility in individuals across contexts (context 1=reversal learning
155 on colored tubes, context 2=multi-access boxes, context 3=reversal learning
156 on touchscreen) indicates their ability to generalize across contexts.** Individual consistency of
157 behavioral flexibility is defined as the number of trials to reverse a color preference being strongly positively
158 correlated within individuals with the latency to solve new loci on each of the multi-access boxes and with
159 the number of trials to reverse a color preference on a touchscreen (total number of touchscreen reversals =
160 5 per bird).

161 If P3a is supported (repeatability of flexibility within individuals)...

162 **P3b:** ...and flexibility is correlated across contexts, then the more flexible individuals are better at generalizing across contexts.

164 **P3b alternative 1:** ...and flexibility is not correlated across contexts, then there is something that influences
165 an individual's ability to discount cues in a given context. This could be the individual's reinforcement history
166 (tested in P3a alternative), their reliance on particular learning strategies (one alternative is tested in H4),
167 or their motivation (tested in P3a alternative) to engage with a particular task (e.g., difficulty level of the
168 task).

169 **H4: Individuals should converge on an epsilon-first learning strategy (learn the correct choice**
170 **after one trial) as they progress through serial reversals. P4:** Individuals will prefer a mixture
171 of learning strategies in the first serial reversals (an *epsilon-decreasing* strategy where individuals explore
172 both options extensively before learning to prefer the rewarded option, and an *epsilon-first* strategy where
173 the correct choice is consistently made after the first trial), and then move toward the epsilon-first learning
174 strategy. The epsilon-first strategy works better later in the serial reversals where the reward is all or
175 nothing because individuals will have learned the environment is changing in predictable ways (Bergstrom
176 & Lachmann, 2004): only one option is consistently rewarded, and if the reward isn't in the previously
177 rewarded option, it must be in the other option.

178 **P4 alternative 1:** Individuals will continue to prefer a mixture of learning strategies, and/or they do
179 not converge on the more functional epsilon-first learning strategy, regardless of how many reversals they
180 participate in. This pattern could suggest that the grackles do not attend to functional meta-strategies, that
181 is, they do not learn the overarching rule (once food is found in the non-preferred tube, one must switch to
182 preferring that tube color), but rather they learn each preference change as if it was new.

183 ASSOCIATED PREREGISTRATION

184 Our methods and analysis plans are described in the peer-reviewed preregistration of this article that received
185 in principle recommendation from PCI Ecology, which is included below as the **Methods**. We moved the
186 hypotheses from the preregistration to the section above to improve flow for the reader.

187 DEVIATIONS FROM THE PREREGISTRATION

188 In the middle of data collection

189 1) 10 April 2019: We discontinued the reversal learning experiment on the touchscreen because it appears
190 to measure something other than what we intended to test and it requires a huge time investment for
191 each bird (which consequently reduces the number of other tests they are available to participate in).
192 This is not necessarily surprising because this is the first time touchscreen tests have been conducted
193 in this species, and also the first time (to our knowledge) this particular reversal experiment has been
194 conducted on a touchscreen with birds. We based this decision on data from four grackles (2 in the
195 flexibility manipulation group and 2 in the flexibility control group; 3 males and 1 female). All four of
196 these individuals showed highly inconsistent learning curves and required hundreds more trials to form
197 each preference when compared to the performance of these individuals on the colored tube reversal
198 experiment. It appears that there is a confounding variable with the touchscreen such that they are
199 extremely slow to learn a preference as indicated by passing our criterion of 17 correct trials out of
200 the most recent 20. We will not include the data from this experiment when conducting the cross-test
201 comparisons in the Analysis Plan section of the preregistration. Instead, in the Results section, we
202 provide summary results for this experiment and, in the Discussion, qualitatively compare it with
203 performance on the colored tube reversal test to explain what might have confounded the touchscreen
204 experiment.

205 2) 16 April 2019: Because we discontinued the touchscreen reversal learning experiment, we added an
206 additional but distinct multi-access box task, which allowed us to continue to measure flexibility across
207 three different experiments. There are two main differences between the first multi-access box, which is

made of plastic, and the new multi-access box, which is made of wood. First, the wooden multi-access box is a natural log in which we carved out 4 compartments. As a result, the apparatus and solving options are more comparable to what grackles experience in the wild, though each compartment is covered by a transparent plastic door that requires different behaviors to open. Furthermore, there is only one food item available in the plastic multi-access box and the bird could use any of 4 loci to reach it. In contrast, the wooden multi-access box has a piece of food in each of the 4 separate compartments.

Post data collection, pre-data analysis

- 3) We completed our simulation to explore the lower boundary of a minimum sample size and determined that **our sample size for the Arizona study site is above the minimum** (see details and code in [Ability to detect actual effects](#); 17 April 2020).
- 4) Please see our [Alternative Analyses](#) section where we describe how we **changed the analysis for P2** and that we are replacing this analysis with the new models in the [Ability to detect actual effects](#) section (14 May 2020). We also describe here that we realized that Condition (manipulated or control) does not need to be a variable in our models because the manipulated birds have, by definition, faster reversal speeds.
- 5) We originally planned on testing only **adults** to have a better understanding of what the species is capable of, assuming the abilities we are testing are at their optimal levels in adulthood, and so we could increase our statistical power by eliminating the need to include age as an independent variable in the models. Because the grackles in Arizona were extremely difficult to catch, we ended up testing two juveniles: Taco and Chilaquile. We did not conduct the full test battery with Taco or put him in the flexibility manipulation or control groups (he received 1 reversal and then moved on to the next test) because he was the first juvenile and we wanted to see whether his performance was different from adult performances. His performances were similar to the adults, therefore we decided to put Chilaquile in the full test battery. Chilaquile's performances were also similar to the adults, therefore we decided not to add age as an independent variable in the models to avoid reducing our statistical power.

Post data collection, mid-data analysis

- 6) We **log transformed** the response variable and changed the GLMM distribution from Poisson to Gaussian in the [P3a analysis](#) (24 Aug 2021).
- 7) The original model for P2 (Table 5: Model 1) included the covariate aviary batch, however this ended up confounding the analysis because control and manipulated individuals, while randomly assigned to these conditions, ended up in particular batches as a result of their willingness to participate in tests offered during their time in the aviary (Table 5: Model 3). Several grackles never passed habituation or training such that their first experiment could begin, therefore we replaced these grackles in the aviaries with others who were willing to participate. This means that batch did not indicate a particular temporal period. Therefore, we removed batch from the model.

RESULTS

- Data are publicly [available](#) at the Knowledge Network for Biocomplexity (Logan, Bergeron, et al., 2021). Please see the data sheet titled `g_flexmanip_data_AllGrackleExpOrder` at KNB for an overview of all color marked grackles at the Arizona field site (2018-2021), which of the aviary experiments they participated in and whether data for the variables that were collected in the wild are present.
- Although 22 grackles completed their initial colored tube discrimination, only 20 grackles participated in one or more reversals (Table 1). The rest of the tests began only after a bird's reversal experiment was complete (see the order of tests for each bird at the data sheet titled `g_flexmanip_data_AllGrackleExpOrder` at KNB). Interobserver reliability analyses (unregistered) showed that the reversal learning and multi-access box (plastic and wooden) experiments were highly repeatable across live coders and video coders (see details in Analysis Plan > Interobserver reliability).

256 **Table 1.** Summarized results per bird in the reversal learning (tube and touchscreen) and multi-access box
 257 (plastic and wooden) experiments. Reversals to pass indicates how many serial reversals it took a bird to
 258 pass criterion if they were in the flexibility manipulation condition. Note: Tapa did not finish the MAB
 259 log experiment; Marisco's MAB log experiment ended too early due to experimenter error (timed out on
 260 2 consecutive sessions, not 3); Mole and Habanero: do not count MAB plastic number of options solved
 261 because they were given the box fully put together for habituation due to experimenter error; Taco was the
 262 first juvenile we tested and we did not put him in the flexibility experiment: he received 1 reversal and moved
 263 on to his next test, therefore he was essentially a control bird without the matched yellow tube experience.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = F, sep = ",",
  stringsAsFactors = F)

d <- data.frame(d)
colnames(d) <- c("Bird", "Batch", "Sex", "Trials to learn (tube)", "Trials to first reversal (tube)",
  "Trials to last reversal (tube)", "Reversals to pass", "Total loci solved (MAB plastic)",
  "Total loci solved (MAB wooden)", "Average latency to attempt new locus (MAB plastic)",
  "Average latency to attempt new locus (MAB wooden)", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "Motor actions (MAB plastic)",
  "Motor actions (MAB wooden)")

library(kableExtra)
knitr::kable(d) %>%
  kable_styling(full_width = T, position = "left")
```

264

Bird	Batch	Sex	Trials to learn (tube)	Trials first (tube)	Trials last (tube)	Trials pass (tube)	Reversals solved (MAB)	Total loci solved (MAB)	Average latency to solve (MAB)	Average latency to solve (plastic)	Trials to learn (touch-reverse)	Trials first (touch-reverse)	Motor actions (MAB)	Motor actions (plastic)
Tomatillo	M	M	40	50	50	Control	3	NA	317	NA	NA	NA	13	NA
Queso 1	M	M	50	70	70	Control	1	NA	88	NA	330	460	8	NA
Tapa 1	F	F	30	100	100	Control	4	NA	685	NA	450	(629+)	13	NA
Yuca 3	F	F	40	80	80	Control	4	4	132	77	NA	NA	13	11
Marisc3	M	M	40	50	50	Control	1	2	NA	208	NA	NA	4	7
Pizza 3	M	M	50	60	60	Control	0	1	NA	1482	NA	NA	0	8
Mofongo	M	M	20	40	40	Control	3	4	502	630	NA	NA	13	14
Taquito4	M	M	90	160	160	Control	0	4	NA	100	NA	NA	11	10
Chalupa	F	F	50	90	50	8	0	NA	NA	NA	NA	NA	6	NA
Mole 1	M	M	30	70	50	7	4	4	356	1173	431	307	14	15
Habanero	M	M	50	80	40	6	4	NA	28	NA	350	290	15	NA
Diablo 3	M	M	20	80	40	8	2	1	25	NA	NA	NA	10	2
Burrito3	M	M	40	60	23	8	3	4	76	391	NA	NA	17	18
Adobo 3	M	M	50	100	50	6	4	4	31	79	NA	NA	16	18
Chilaquile	JM	JM	30	40	30	6	4	4	44	170	NA	NA	19	11
Pollito 4	M	M	40	60	40	8	0	3	NA	668	NA	NA	0	11
Taco 3a	JM	JM	50	80	80	(Control)	1	4	NA	117	NA	NA	3	19
Memela	F	F	50	60	80	X	NA	NA	NA	NA	NA	NA	NA	NA
						(11+)								
Fideo 2	M	M	60	70	70	Control	NA	NA	NA	NA	NA	NA	NA	NA
Avocado	F	F	50	100	100	Control	NA	NA	NA	NA	NA	NA	NA	NA
Huachinago	M	M	70	NA	NA	Control	NA	NA	NA	NA	NA	NA	NA	NA
Guacamole	M	M	30	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

265 Because the wooden multi-access box was added after in principle recommendation, we conducted an un-
 266 registered analysis to determine whether the plastic and wooden multi-access box results correlated with
 267 each other, which would indicate that these tests are interchangeable. We found that they did not corre-
 268 late with each other on either variable measured: the average latency to attempt a new locus (switching;
 269 Pearson's $r=0.74$, 95% CI=-0.19-0.97, $t=2.18$, $df=4$, $p=0.09$) or the total number of loci solved (problem
 270 solving; Pearson's $r=0.51$, 95% CI=-0.09-0.84, $t=1.86$, $df=10$, $p=0.09$). Therefore, these two tests are not
 271 interchangeable and we analyzed them separately.

272 P1: reversal speed gets faster with serial reversals

273 There was a significant negative correlation between the number of trials to reverse (average=71 trials, stan-
 274 dard deviation (sd)=28) and the reversal number for those grackles in the flexibility manipulation condition
 275 ($n=9$, which included Memela who did not pass the manipulation condition; Figure 2). When this model
 276 was compared with the null model, where there was no explanatory variable, the null model had a higher
 277 Akaike weight, however it was not high enough to indicate the two models were reliably different from each
 278 other (Table 2). Therefore, we conclude that there was no effect of a linear relationship between the number
 279 of trials to reverse and reversal number.

280 **Unregistered analysis:** While there may not be an effect when one examines all reversals, there was a

281 difference between manipulated and control reversal speeds when comparing their last reversals (Figure 3;
 282 for the control birds, their last reversal was their first reversal): the Akaike weight of the full model was 0.94,
 283 which means that including condition in the model explains the bulk of the variation in the number of trials
 284 to reverse in the last reversal (Table 3). This analysis includes 19 grackles (8 manipulated condition - only
 285 those who actually passed the manipulation, 11 control condition) who had an overall average of 62 trials in
 286 their last reversal ($sd=32$).

287 **Table 2.** The number of trials to reverse does not linearly decrease with increasing reversal number more
 288 than would be expected by chance. The Akaike weight of null model was higher than that of the full model,
 289 though not >0.89 , which indicates that neither model is more reliable than the other.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"))
  header = T, sep = ",",
  stringsAsFactors = F)
d <- d[!d$ID == "Fajita" & !d$ID == "Empanada", ] #remove Fajita because she was a pilot bird

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d[["TrialsToReverse"]])))
d <- subset(d, !(is.na(d[["ReverseNumber"]])))

# include only those birds in the reversal tubes experiment and only
# those in the manipulation condition bc only these will have more
# than one reversal (and thus something to correlate)
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
       ]

# factor variables
d$Batch <- as.factor(d$Batch)
d$ID <- as.factor(d$ID)

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0)), G = list(G1 = list(V = 1,
  nu = 0), G2 = list(V = 1, nu = 0)))
serial <- MCMCglmm(TrialsToReverse ~ ReverseNumber, random = ~ID + Batch,
  family = "poisson", data = d, verbose = F, prior = prior, nitt = 3e+05,
  thin = 500, burnin = 90000)
# reverse number significantly negatively correlates with trials to
# reverse, as expected due to the manipulation summary(serial) Did
# fixed effects converge (<0.1)? Yes autocorr(serial$Sol) Did random
# effects converge (<0.1)? Yes except for 2 values: 0.11 and 0.12
# autocorr(serial$VCV)

# AIC calculation
library(MuMIn)
options(na.action = "na.fail")
base <- dredge(MCMCglmm(TrialsToReverse ~ ReverseNumber, random = ~ID +
  Batch, family = "poisson", data = d, verbose = F, prior = prior, nitt = 3e+05,
  thin = 500, burnin = 90000))

library(kableExtra)
knitr::kable(base) %>%
  column_spec(column = 1:7, width = "6em") %>%
  scroll_box(width = "100%")
```

(Intercept)	ReverseNumber	df	logLik	AICc	delta	weight
4.202876	NA	4	-239.3302	487.2954	0.000000	0.836164
4.445506	-0.0574845	5	-239.7938	490.5553	3.259918	0.163836

290 # UNREGISTERED ANALYSIS: compare control vs manipulated group
reversal speeds using only last reversals prior = list(R = list(R1
= list(V = 1, nu = 0)), G = list(G1 = list(V = 1, \t nu = 0), G2 =
list(V = 1, nu = 0))) serial <- MCMCglmm(TrialsToReverse ~
ReverseNumber, random = ~ID+Batch, \t family = 'poisson', data = d,
verbose = F, prior = prior, \t nitt = 300000, thin = 500, burnin =
90000) reverse number significantly negatively correlates with
trials to reverse, as expected due to the manipulation
summary(serial) Did fixed effects converge (<0.1)? Yes
autocorr(serial\$Sol) Did random effects converge (<0.1)? Yes except
for 2 values: 0.11 and 0.12 autocorr(serial\$VCV)

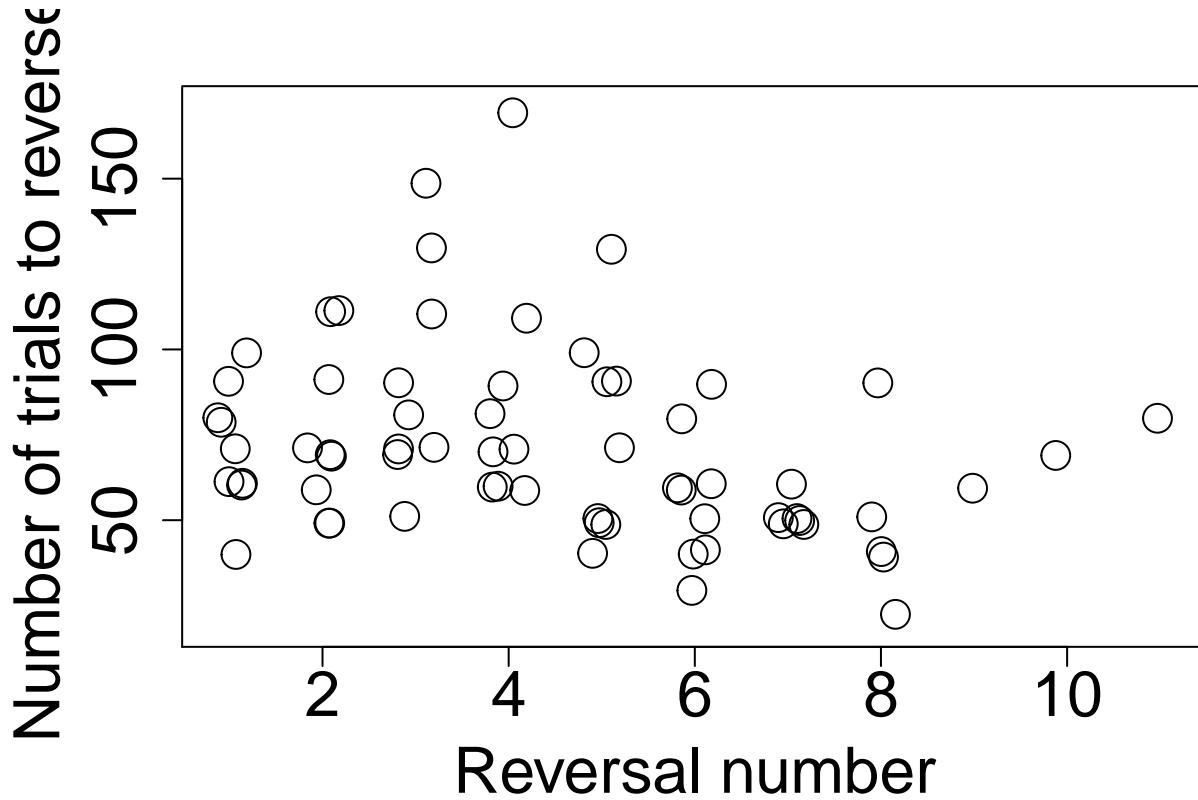
```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"))
  header = T, sep = ",",
  stringsAsFactors = F)
d <- d[!d$ID == "Fajita" & !d$ID == "Empanada", ] #remove Fajita because she was a pilot bird

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d["TrialsToReverse"])))
d <- subset(d, !(is.na(d["ReverseNumber"])))

# include only those birds in the reversal tubes experiment and only
# those in the manipulation condition bc only these will have more
# than one reversal (and thus something to correlate)
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
      ]

# n, mean, sd length(levels(d$ID)) #9 mean(d$TrialsToReverse) #71
# sd(d$TrialsToReverse) #28

# figure
op <- par(mfrow = c(1, 1), mar = c(5.9, 4.9, 2, 0.9))
plot(jitter(d$TrialsToReverse) ~ jitter(d$ReverseNumber), xlab = "Reversal number",
     ylab = "Number of trials to reverse", xlim = c(0.9, 11.1), ylim = c(19,
     171), cex.lab = 2, cex.axis = 2, cex = 2)
```



291

```
par(op)
```

292 **Figure 2.** Individuals in the manipulated condition (who received serial reversals) did not linearly decrease
 293 their reversal passing speeds with increasing reversal number (n=9 grackles).

294 **Table 3.** Individuals in the manipulated condition pass their last reversal in fewer trials than control
 295 individuals. The Akaike weight of the full model was >0.89, indicating that it is more reliable than the null
 296 model.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = F, sep = ",",
  stringsAsFactors = F)

d <- data.frame(d)
colnames(d) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
  "TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
d <- subset(d, !(is.na(d["TrialsLastReversal"])))

# exclude the bird who didn't pass serial
d <- d[!d$Bird == "Memela", ]

# make ReversalsToPass a factor that has only 2 levels: level 1 =
# control, level 2 = manipulated
d$ReversalsToPass <- as.factor(d$ReversalsToPass)
levels(d$ReversalsToPass)[c(1, 2, 3, 4)] <- c("Control", "Manipulated",
  "Manipulated", "Manipulated")
```

```
# UNREGISTERED ANALYSIS: compare control vs manipulated group
# reversal speeds using only last reversals
```

```
last <- glm(d$TrialsLastReversal ~ d$ReversalsToPass)
# manipulated group has significantly fewer trials to reverse in last
# reversal, as expected due to the manipulation summary(last)
```

```
# AIC calculation
```

```
library(MuMIn)
options(na.action = "na.fail")
aw <- dredge(glm(d$TrialsLastReversal ~ d$ReversalsToPass))
```

```
library(kableExtra)
```

```
knitr:::kable(aw) %>%
  column_spec(column = 1:7, width = "6em") %>%
  scroll_box(width = "100%")
```

297

	(Intercept)	d\$ReversalsToPass	df	logLik	AICc	delta	we
2	78.18182	+	3	-88.09966	183.7993	0.000000	0.94218
1	62.26316	NA	2	-92.31561	189.3812	5.581888	0.0578

```
# the full model has an Akaike weight >0.9 so it is reliable. This
# means that condition explains differences in the number of trials
# to pass the last reversal, with the manipulated group being faster
# than the control group
```

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",", stringsAsFactors = F)
```

```
d <- data.frame(d)
```

```
colnames(d) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
  "TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")
```

```
# Remove NAs
```

```
d <- subset(d, !(is.na(d["TrialsLastReversal"])))
```

```
# exclude the bird who didn't pass serial
```

```
d <- d[!d$Bird == "Memela", ]
```

```
# n, mean, and sd length(d$TrialsLastReversal) #19
```

```
# mean(d$TrialsLastReversal) #62 sd(d$TrialsLastReversal) #32
```

```
# make ReversalsToPass a factor that has only 2 levels: level 1 =
```

```
# control, level 2 = manipulated
```

```
d$ReversalsToPass <- as.factor(d$ReversalsToPass)
```

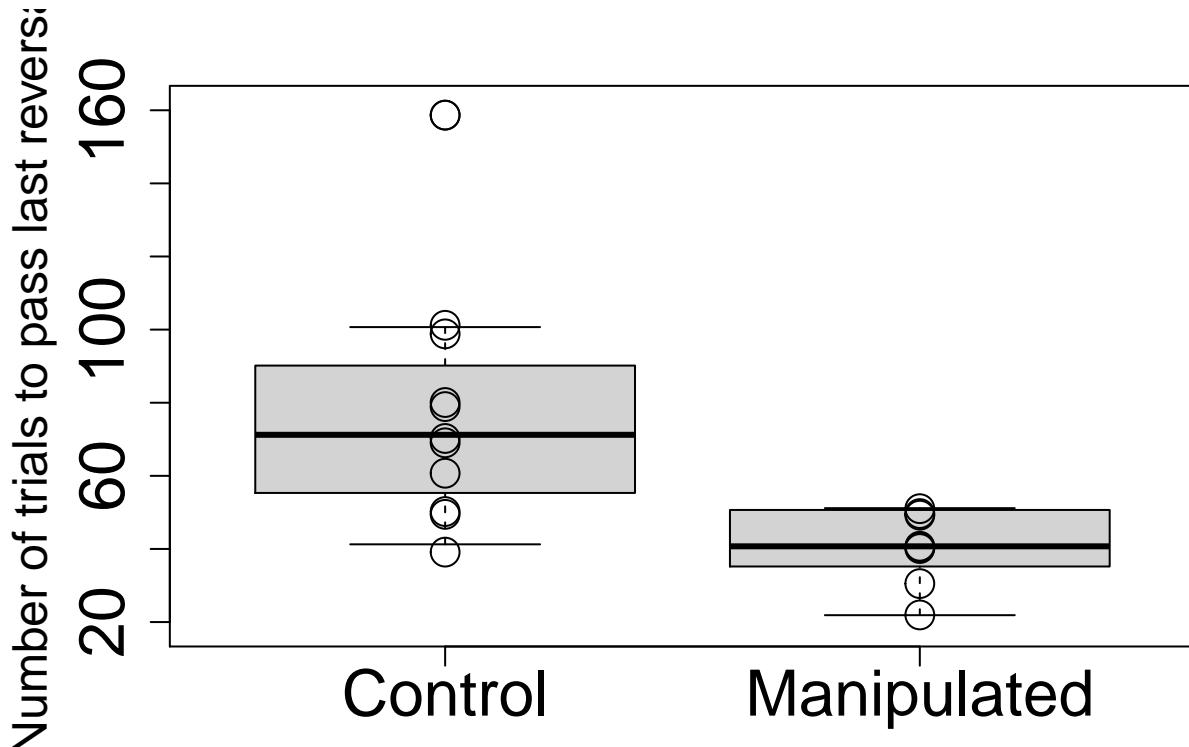
```
levels(d$ReversalsToPass)[c(1, 2, 3, 4)] <- c("Control", "Manipulated",
  "Manipulated", "Manipulated")
```

```
# figure
```

```
op <- par(mfrow = c(1, 1), mar = c(5.9, 4.9, 2, 0.9))
```

```
plot(jitter(d$TrialsLastReversal) ~ d$ReversalsToPass, xlab = "", ylab = "Number of trials to pass last
  ylim = c(19, 161), cex.lab = 1.5, cex.axis = 2, cex = 2)
```

```
points(jitter(d$TrialsLastReversal) ~ d$ReversalsToPass, cex = 2)
```



298

```
par(op)
```

299

Figure 3. Individuals in the manipulated condition (who received serial reversals) passed their last reversal 300 in fewer trials than individuals in the control condition (who only received 1 reversal). n=19 grackles: 301 11=control, 8=manipulated.

302

P2: serial reversals improve rule switching and problem solving on the MAB

303

To determine whether the serial reversal manipulation affected flexibility generally, we compared performance 304 (the number of trials to reverse a preference in the first and last color reversal, performance of the manipulated 305 group relative to control group) to speed of solution switching on two multi-access boxes. Furthermore, we 306 assessed whether flexibility measured through these serial reversals related to innovativeness by comparing 307 performance to the number of loci solved on two multi-access boxes. The results for each of these comparisons 308 are described in detail below and an overview is provided in Figure 4.



P2: How does flexibility, measured via performance on serial reversals, relate to flexibility in another context and innovativeness?

Flexibility (number of trials to pass in serial reversals)



		First Reversal	Last Reversal	Manipulated relative to Control
Flexibility in a new context (latency to switch loci)		+	+	+
		-	0	0
Innovativeness (number of loci solved)		0	+	0
		0	0*	+

309

310 **Figure 4.** Overview of the results from the P2 analyses with the multi-access boxes (plastic and wooden).
311 A plus sign (+) indicates a positive correlation, a minus sign (-) indicates a negative correlation, and a
312 0 indicates no correlation between the two variables. The asterisks (*) indicate that a small sample size
313 decreases the reliability of this result

314 **Rule switching: latency to attempt a new locus on the multi-access box (plastic) ~ trials to
315 reverse** Grackles that were faster to reverse a preference in their **last reversal** (average 52 trials, $sd=23$)
316 were also faster to attempt to solve a new locus on the plastic multi-access box (after just having passed
317 criterion on a different locus; average=208 seconds, $sd=226$; Figure 5a; Table 4: Model 9; $n=11$ grackles:
318 6 in manipulated condition, 5 in control condition; 6 subjects completed this experiment but did not solve
319 enough loci to have switching times (i.e., solved 0 loci or 1 locus)). We also found that individuals in the
320 flexibility manipulation had faster switch latencies than those in the control condition (Table 4: Model 10).
321 There was a positive correlation between the number of trials to reverse in the **first reversal** (average=70
322 trials, $sd=21$) and the average switch latency on the multi-access box (Table 4: Model 11; unregistered
323 analysis).

```
library(rethinking)
library(rstan)
library(formatR)
```

```
# LOAD the data and column names
```

```

d3 <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration")
  header = F, sep = ",", stringsAsFactors = F)

d3 <- data.frame(d3)
colnames(d3) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
  "TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
d3 <- subset(d3, !(is.na(d3["AverageLatencyAttemptNewLocusMABplastic"])) &
  !(is.na(d3["TrialsLastReversal"])))

# n=11: 5 in manipulated group, 6 in control group
# length(d3$AverageLatencyAttemptNewLocusMABplastic)

# make Batch a factor
d3$Batch <- as.factor(d3$Batch)

# look at the data hist(d3$AverageLatencyAttemptNewLocusMABplastic)
# mean(d3$AverageLatencyAttemptNewLocusMABplastic) #208
# sd(d3$AverageLatencyAttemptNewLocusMABplastic) #226
# mean(d3$TrialsLastReversal) #52 sd(d3$TrialsLastReversal) #23
# mean(d3$TrialsFirstReversal) #70 sd(d3$TrialsFirstReversal) #21

# translating the actual data (rather than the simulated data) into
# effect sizes (see equation below in 'translated the simulation
# output into effect sizes')
# sd(d3$AverageLatencyAttemptNewLocusMABplastic)/sd(d3$TrialsLastReversal)
# #=9.9
# cor.test(d3$AverageLatencyAttemptNewLocusMABplastic, d3$TrialsLastReversal, alternative=c('two.sided'),
#   # = c('pearson'), conf.level = 0.95) corr = r = 0.52 solve equation
# for beta:
# 0.52/(sd(d3$AverageLatencyAttemptNewLocusMABplastic)/sd(d3$TrialsLastReversal))
# #0.05 = beta

# RUN MODELS on the actual data
library("Rcpp")
library("rstan")
library(rethinking)
library(ggplot2)

# MODEL 9: batch was excluded because of what was learned in the
# previous sections
dl <- list(trials = standardize(as.numeric(d3$TrialsLastReversal)), latency = as.integer(d3$AverageLatencyAttemptNewLocusMABplastic),
  batch = as.integer(d3$Batch))

mplat1 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a +
  b * trials, a ~ dnorm(1, 1), b ~ dnorm(0, 1), phi ~ dexp(1)), data = dl,
  chains = 4, log_lik = TRUE, messages = FALSE)
# This causes KM's R session to crash every time

```

```

precis(mplat1, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a 4.93 0.30 4.45 5.41 1235 1.01 b
# 0.46 0.29 0.00 0.92 1363 1.00 phi 0.93 0.35 0.44 1.55 1476 1.00 the
# confidence interval for b (the slope) touches 0 but does not cross
# it (which would be indicated by a sign change), which indicates
# that there is likely a positive correlation between MAB switch
# latency and trials to reverse

# check posterior for p to look at the distribution of probabilities
# that are probable
postmplat1 <- extract.samples(mplat1)
p3 <- exp(postmplat1$a) #convert from log to number of seconds
dens(p3, adj = 0.1)
HPDI(p3) #76-209
median(p3) #139, narrower and shifted left than the curve from the simulations
# result: The posterior: the mean y axis point where the intercept is
# is 139 (meaning they switch on average at a latency of 139
# seconds), which means this is when trials to reverse is at the
# average. The actual median is smaller than what we estimated the
# mean would be in the simulations (300s)

# model details: 2000 samples from 4 chains show(mplat1) no
# correlation pairs(mplat1) check the chain - fuzzy caterpillars =
# looks good traceplot(mplat1) check the chain a different way -
# 'histograms overlap and stay within the same range' looks good
# (p.285 Rethinking) trankplot(mplat1)

# MODEL 10: see whether the flexibility manipulation actually had an
# effect on MAB performance by replacing batch with condition
# (control, manipulated) and REMOVING trials
# mean(d2$TrialsFirstReversal) #73.6 sd(d2$TrialsFirstReversal) #34.1

# make ReversalsToPass a factor that has only 2 levels: level 1 =
# manipulated, level 2 = control
d3$ReversalsToPass <- as.factor(d3$ReversalsToPass)
levels(d3$ReversalsToPass)[c(1, 2, 3)] <- c("Manipulated", "Manipulated",
                                             "Manipulated")

dl2 <- list(latency = as.integer(d3$AverageLatencyAttemptNewLocusMABplastic),
            condition = as.integer(d3$ReversalsToPass))

mplat2 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a[condition],
                      a[condition] ~ dnorm(1, 1), phi ~ dexp(1)), data = dl2, chains = 4,
                      log_lik = TRUE, messages = FALSE)

precis(mplat2, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a[1] 4.07 0.39 3.46 4.68 1027 1.00
# a[2] 5.18 0.39 4.50 5.76 1006 1.00 phi 0.91 0.41 0.37 1.63 925 1.01
# Condition correlates with performance on the MAB bc neither a[] CI
# crosses zero, a1 manipulated has a lower mean than a2 control

# contrasts between conditions: the log odds differences in solving a

```

```

# locus between batches. Value = log odds of solving a locus (p.331 &
# 341 Rethinking)
postmplat2 <- extract.samples(mplat2)
diffmplat2 <- postmplat2$a[, 1] - postmplat2$a[, 2]
labsdif2 <- c("Manipulated-Control")
plot(precis(diffmplat2), xlim = c(-2, 0.5), labels = labsdif2)
# contrasts between conditions on the outcome scale (p.341
# Rethinking)
precis(diffmplat2)
# conditons are different from each other in their average latency to
# switch because CI does not cross zero. This means that the
# manipulated individuals are faster to switch than control
# individuals. This suggests that the experience involved in the
# flexibility manipulation had a direct effect on mab performance

# MODEL 11: see whether the flexibility manipulation actually had an
# effect on MAB performance by replacing trials to LAST reversal with
# trials to FIRST reversal
d13 <- list(locisolved = d3$AverageLatencyAttemptNewLocusMABplastic, trials = standardize(d3$TrialsFirst

mplat3 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a +
  b * trials, a ~ dnorm(1, 1), b ~ dnorm(0, 1), phi ~ dexp(1)), data = dl,
  chains = 4, log_lik = TRUE, messages = FALSE)

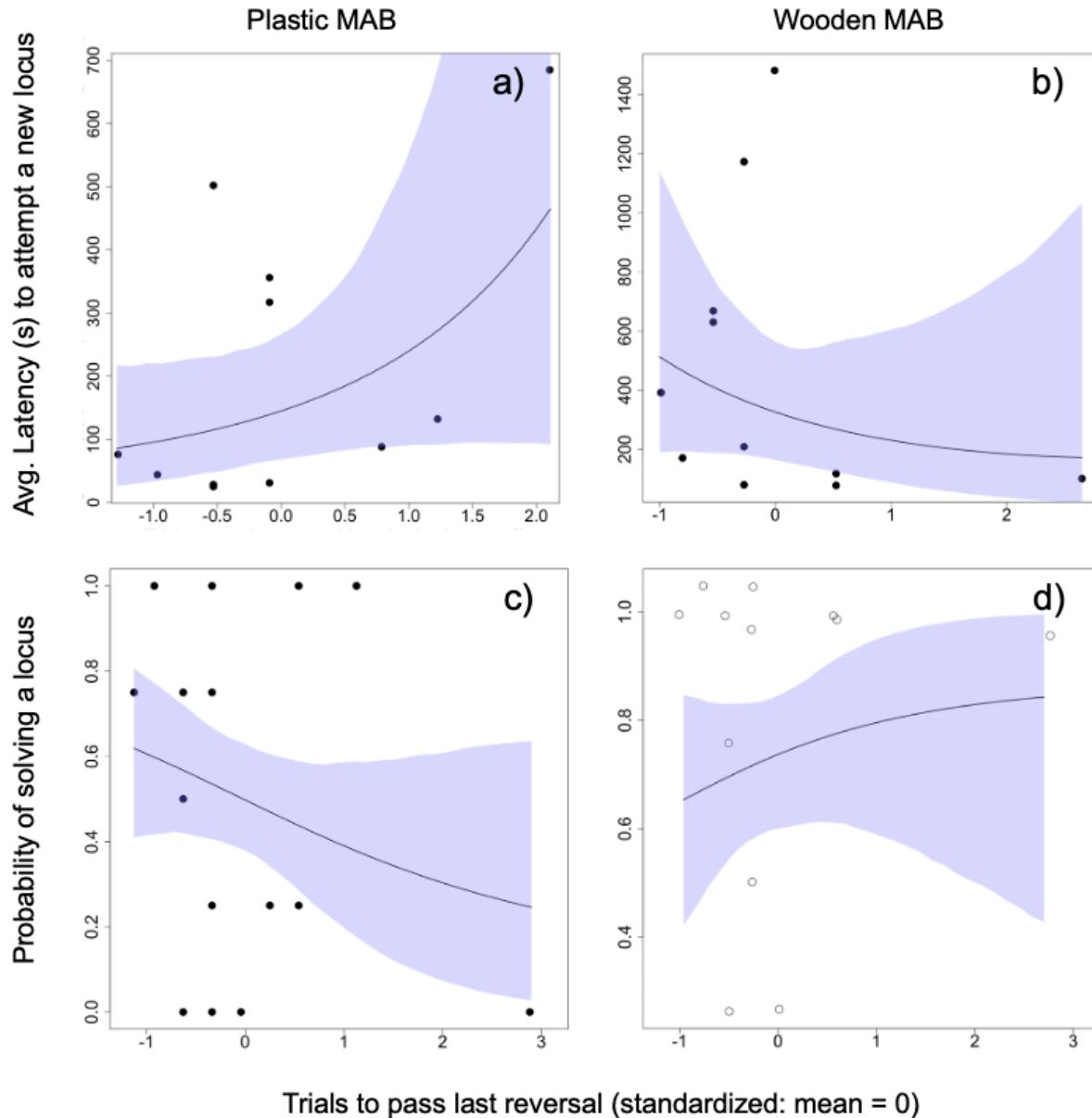
precis(mplat3, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a 4.93 0.29 4.46 5.39 1488 1 b 0.46
# 0.28 0.02 0.93 1211 1 phi 0.94 0.36 0.44 1.60 1447 1 b does not
# cross zero so there is a positive correlation between average
# switch latencies and number of trials to reverse on the first
# reversal. This means that reversal in general correlates with MAB
# loci and that the flexibility manipulation is not needed to enhance
# or make this relationship

# VISUALIZE: plot trials to pass last reversal against number of loci
# solved on the mwobatch model (p249 Rethinking panel on the left)
# figure out xlim: -1.28 - 2.10 range(dl$trials)

# draw 50 lines from the prior
trials_p_seq <- seq(from = -1.29, to = 2.11, length.out = 30)

op <- par(mfrow = c(1, 1), mar = c(5.9, 4.9, 2, 0.9))
plot(dl$latency ~ dl$trials, pch = 16, col = "black", xlab = "Trials to pass last reversal (standardized",
  ylab = "Avg latency (s) to attempt new locus on multi-access box (plastic)",
  xlim = c(-1.2, 2.05), cex.lab = 2, cex.axis = 2, cex = 2)
mu <- link(mplat1, data = data.frame(trials = trials_p_seq))
mu_mean <- apply(mu, 2, mean)
mu_ci <- apply(mu, 2, PI, prob = 0.97)
lines(trials_p_seq, mu_mean, lwd = 2)
shade(mu_ci, trials_p_seq, col = col.alpha(rangi2, 0.3))
par(op)

```



324

325 **Figure 5.** The average latency (seconds) to solve a different locus after having previously
326 successfully solved a locus on a) the plastic multi-access box (MAB) is positively correlated with the number
327 of trials to pass their last reversal ($n = 11$ grackles), but on b) the wooden MAB it is not correlated with
328 the number of trials to pass their last reversal ($n = 11$ grackles). Additionally, the probability of solving a
329 locus on c) the plastic MAB is negatively correlated with the number of trials to pass their last reversal (n
330 = 15 grackles), but on d) the wooden MAB it is not correlated with the number of trials to pass their last
331 reversal ($n = 12$ grackles, estimate of slope includes zero). Shading represents the 97% prediction intervals.

332 **Rule switching: latency to attempt a new locus on the multi-access box (wooden) ~ trials**
333 **to reverse** There was no correlation between the number of trials to reverse a preference in their last
334 **reversal** (average 60 trials, $sd=38$) and the latency to attempt to solve a new locus on the wooden multi-
335 access box (after just having passed criterion on a different locus; average=463 seconds, $sd=481$; Figure 5b;
336 Table 4: Model 12; $n=11$ grackles: 5 in manipulated condition, 6 in control condition; Diablo also completed
337 this experiment and solved 1 locus, but did not attempt another locus after that, thus he does not have any

338 switching times to analyze). We additionally found that there was no difference in average latency to switch
 339 between individuals in the flexibility manipulation and those in the control condition (Table 4: Model 13).
 340 There was a negative correlation between the number of trials to reverse in the **first reversal** (average=73
 341 trials, $sd=34$) and the average switch latency on the multi-access box (Table 4: Model 14; unregistered
 342 analysis). A correlation was determined to be present if the prediction interval for the slope (b) in the model
 343 output did not cross zero (Table 4). This criterion was used throughout the analyses for P2.

```

library(rethinking)
library(rstan)
library(formatR)
library("Rcpp")
library("rstan")
library(ggplot2)

# LOAD the data and column names
d4 <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))
  header = F, sep = ",",
  stringsAsFactors = F)

d4 <- data.frame(d4)
colnames(d4) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
  "TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
d4 <- subset(d4, !(is.na(d4["AverageLatencyAttemptNewLocusMABwooden"])) &
  !(is.na(d4["TrialsLastReversal"])))

# n=11: 5 in manipulated group, 6 in control group
# length(d4$AverageLatencyAttemptNewLocusMABwooden)

# make Batch a factor (assigned Taco to batch 3 because 3a doesn't
# work with the model)
d4$Batch <- as.factor(d4$Batch)
levels(d4$Batch)[c(3)] <- c("3")

# look at the data hist(d4$AverageLatencyAttemptNewLocusMABwooden)
# mean(d4$AverageLatencyAttemptNewLocusMABwooden) #463
# sd(d4$AverageLatencyAttemptNewLocusMABwooden) #481
# mean(d4$TrialsLastReversal) #60 sd(d4$TrialsLastReversal) #38
# mean(d4$TrialsFirstReversal) #73 sd(d4$TrialsFirstReversal) #34

# translating the actual data (rather than the simulated data) into
# effect sizes (see equation below in 'translated the simulation
# output into effect sizes')
# sd(d4$AverageLatencyAttemptNewLocusMABwooden)/sd(d4$TrialsLastReversal)
# #=12.8
# cor.test(d4$AverageLatencyAttemptNewLocusMABwooden, d4$TrialsLastReversal, alternative=c('two.sided'), m
# = c('pearson'), conf.level = 0.95) corr = r = -0.26 solve equation
# for beta:
# #-0.26/(sd(d4$AverageLatencyAttemptNewLocusMABwooden)/sd(d4$TrialsLastReversal)) #0.02 = beta
# looking at table 2 for beta=0 and using the 'Range of MAB loci
# solved' as 0-4 because they were able to solve all 4, the

```

```

# regression coefficient is 0.43.

# RUN MODELS on the actual data

# MODEL 12: batch was excluded because of what was learned in the
# previous sections
dlw <- list(trials = standardize(as.numeric(d4$TrialsLastReversal)), latency = as.integer(d4$AverageLatency))

mwlat1 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a +
  b * trials, a ~ dnorm(1, 1), b ~ dnorm(0, 1), phi ~ dexp(1)), data = dlw,
  chains = 4, log_lik = TRUE, messages = FALSE)

precis(mwlat1, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a 5.75 0.28 5.28 6.18 1049 1.00 b
# -0.41 0.32 -0.86 0.15 1281 1.01 phi 1.04 0.42 0.48 1.77 1456 1.00
# the confidence interval for b (the slope) crosses zero, indicating
# that there is no correlation between MAB switch latency and trials
# to reverse

# check posterior for p to look at the distribution of probabilities
# that are probable
postmwplat1 <- extract.samples(mwlat1)
# p4 <- exp(postmwplat1$a) #convert from log to number of seconds
# dens(p4,adj=0.1) HPDI(p4) #193-469 median(p4) #315, as expected
# from the simulations result: The posterior: the mean y axis point
# where the intercept is is 315 (meaning they switch on average at a
# latency of 315 seconds), which means this is when trials to reverse
# is at the average. The actual median is the same as what we
# estimated the mean would be in the simulations (300s)

# model details: 2000 samples from 4 chains show(mwlat1) no
# correlation pairs(mwlat1) check the chain - fuzzy caterpillars =
# looks good traceplot(mwlat1) check the chain a different way -
# 'histograms overlap and stay within the same range' looks good
# (p.285 Rethinking) trunkplot(mwlat1)

# MODEL 13: see whether the flexibility manipulation actually had an
# effect on MAB performance by replacing batch with condition
# (control, manipulated) and REMOVING trials
# mean(d2$TrialsFirstReversal) #73.6 sd(d2$TrialsFirstReversal) #34.1

# make ReversalsToPass a factor that has only 2 levels: level 1 =
# control, level 2 = manipulated
d4$ReversalsToPass <- as.factor(d4$ReversalsToPass)
levels(d4$ReversalsToPass)[c(1, 2, 3, 4)] <- c("Control", "Manipulated",
  "Manipulated", "Manipulated")

dl3 <- list(latency = as.integer(d4$AverageLatencyAttemptNewLocusMABwooden),
  condition = as.integer(d4$ReversalsToPass))

mwlat2 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a[condition],
  a[condition] ~ dnorm(1, 1), phi ~ dexp(1)), data = dl3, chains = 4,
  
```

```

log_lik = TRUE, messages = FALSE)

precis(mwlat2, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a[1] 5.31 0.42 4.61 5.95 701 1.00
# a[2] 5.34 0.44 4.61 6.00 620 1.01 phi 0.66 0.32 0.25 1.25 806 1.00
# Condition correlates with performance on the MAB bc neither a[] CI
# crosses zero, a1 control and a2 manipulated have similar means

# contrasts between conditions: the log odds differences in solving a
# locus between batches. Value = log odds of solving a locus (p.331 &
# 341 Rethinking)
postmwlat2 <- extract.samples(mwlat2)
diffmwlat2 <- postmwlat2$a[, 1] - postmwlat2$a[, 2]
labsdif3 <- c("Control-Manipulated")
plot(precis(diffmwlat2), xlim = c(-1, 1), labels = labsdif3)
# contrasts between conditions on the outcome scale (p.341
# Rethinking)
precis(diffmwlat2)
# conditons are not different from each other in their average
# latency to switch because CI crosses zero. Same interpretation as
# for MAB plastic loci solved

# MODEL 14: see whether the flexibility manipulation actually had an
# effect on MAB performance by replacing trials to LAST reversal with
# trials to FIRST reversal
dl4 <- list(latency = d4$AverageLatencyAttemptNewLocusMABwooden, trials = standardize(d4$TrialsFirstRev

mwlat3 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a +
  b * trials, a ~ dnorm(1, 1), b ~ dnorm(0, 1), phi ~ dexp(1)), data = dl4,
  chains = 4, log_lik = TRUE, messages = FALSE)

precis(mwlat3, depth = 2)
# mean sd 5.5% 94.5% n_eff Rhat4 a 5.71 0.26 5.28 6.12 1109 1 b -0.50
# 0.28 -0.89 -0.01 1308 1 phi 1.08 0.41 0.53 1.80 1347 1 b does not
# cross zero so there is a negative correlation between average
# switch latencies and number of trials to reverse on the first
# reversal. This means that reversal in general correlates with MAB
# loci and that the flexibility manipulation is not needed to enhance
# or make this relationship

# VISUALIZE: plot trials to pass last reversal against number of loci
# solved on the mwobatch model (p249 Rethinking panel on the left)
# figure out xlim: -1 - 2.65 range(dl4$trials)

# draw 50 lines from the prior
trials_w_seq <- seq(from = -1, to = 2.65, length.out = 30)

op <- par(mfrow = c(1, 1), mar = c(5.9, 4.9, 3, 0.9))
plot(dl4$latency ~ dl4$trials, pch = 16, col = "black", xlab = "Trials to pass last reversal (standardized",
  ylab = "Avg latency (s) to attempt new locus on multi-access box (wooden)",
  xlim = c(-1, 2.65), cex.lab = 2, cex.axis = 2, cex = 2)

```

```

mu <- link(mwlat1, data = data.frame(trials = trialsw_seq))
mu_mean <- apply(mu, 2, mean)
mu_ci <- apply(mu, 2, PI, prob = 0.97)
lines(trialsw_seq, mu_mean, lwd = 2)
shade(mu_ci, trialsw_seq, col = col.alpha(rangi2, 0.3))
par(op)
  
```

344 **Innovativeness: number of loci solved on the multi-access box (plastic) ~ trials to reverse**
 345 Grackles that were faster to reverse a preference in their **last reversal** (average 62 trials, sd=34), where
 346 grackles in the control condition received only one reversal which served as their first and last reversal,
 347 solved more loci on the plastic multi-access box (average=2 loci, sd=1.6; Figure 5c; Table 4: Model 2; n=15
 348 grackles: 6 in manipulated condition, 9 in control condition; this number excludes Mole and Habanero who
 349 were, due to experimenter error, given the fully put together box during habituation and could have learned
 350 how to solve the loci at that time). There was no correlation between the number of loci solved and which
 351 reversal condition a grackle was randomly assigned to (Table 4: Model 4). There was also no correlation
 352 between the number of trials to reverse in the **first reversal** (average=75 trials, sd=31) and the number of
 353 loci solved on the multi-access box (Table 4: Model 5; unregistered analysis).

```

library(rethinking)
library(rstan)
library(formatR)

# LOAD the data and column names
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"))

d <- data.frame(d)
colnames(d) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal", "TrialsLastReversal", "ReversalOrder")

# Exclude Mole and Habanero from this analysis because they were given the put together plastic box during habituation
d <- d[!d$Bird=="Mole" & !d$Bird=="Habanero",]

# Remove NAs
d <- subset(d,!is.na(d["TotalLociSolvedMABplastic"])) & !(is.na(d["TrialsLastReversal"]))

# n=15: 6 in manipulated group, 9 in control group
#length(d$TotalLociSolvedMABplastic)

# make Batch a factor (assigned Taco to batch 3 because 3a doesn't work with the model)
d$Batch <- as.factor(d$Batch)
levels(d$Batch)[c(3)] <- c("3")

# look at the data
#hist(d$TotalLociSolvedMABplastic)
#mean(d$TotalLociSolvedMABplastic) #2
#sd(d$TotalLociSolvedMABplastic) #1.6
#hist(d$TrialsLastReversal)
#mean(d$TrialsLastReversal) #61.5
#sd(d$TrialsLastReversal) #34.2

#translating the actual data (rather than the simulated data) into effect sizes (see equation below in
#sd(d$TotalLociSolvedMABplastic)/sd(d$TrialsLastReversal) #=.5
#cor.test(d$TotalLociSolvedMABplastic, d$TrialsLastReversal, alternative=c("two.sided"), method = c("pearson"))
#corr = r =-.24
  
```

```

#solve equation for beta:
#-0.24/(sd(d$TotalLociSolvedMABplastic)/sd(d$TrialsLastReversal)) #-4.98 = beta

# RUN MODELS on the actual data
dat <- list(locisolved = d$TotalLociSolvedMABplastic,
            trials = standardize(d$TrialsLastReversal),
            batch = d$Batch
            )

# MODEL 1: includes batch
m1 <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[batch] + b*trials , #batch=random effect, standardize trials so 0=mean
  a[batch] ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive, and
) , data=dat , chains=4 , log_lik=TRUE )

#precis(m1,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
#a[1]  0.04 0.46 -0.70  0.78  2304     1
#a[2]  0.29 0.36 -0.30  0.87  2456     1
#a[3] -0.78 0.55 -1.65  0.08  2510     1
#b    -0.22 0.25 -0.63  0.18  2364     1
#mean loci solved varies by batch, b=slope for correlation between number of loci solved and number of trials
#Result: total number of loci solved is not associated with the number of trials to pass criterion on trials

#model details: 2000 samples from 4 chains
#show(m1)
#no correlations between variables across batches
#pairs(m1)
#check the chain - fuzzy caterpillars = looks good
#traceplot(m1)
#check the chain a different way - "histograms overlap and stay within the same range" looks good (p.2)
#trankplot(m1)

# plot the results on the outcome scale (p.330 Rethinking). V1-3 = batch 1-3, value = probability of solving a locus
#postm1 <- extract.samples(m1)
#p_batch <- inv_logit( postm1$a )
#plot( precis( as.data.frame(p_batch) ) , xlim=c(0,1) )

# contrasts between batches: the log odds differences in solving a locus between batches. Value = log odds difference
#diffsm1 <- list(
#  b13 = postm1$a[,1] - postm1$a[,2],
#  b14 = postm1$a[,1] - postm1$a[,3],
#  b34 = postm1$a[,2] - postm1$a[,3] )
#labsdif <- c("Batch 1-3","Batch 1-4","Batch 3-4")
#plot( precis(diffsm1) , xlim=c(-3,3) , labels=labsdif)

# contrasts between batches on the outcome scale (p.341 Rethinking). Value = difference in number of loci solved
diffsm1c <- list(
  diff_b13 <- inv_logit( postm1$a[,1]) - inv_logit( postm1$a[,2]),
  diff_b14 <- inv_logit( postm1$a[,1]) - inv_logit( postm1$a[,3]),
  diff_b34 <- inv_logit( postm1$a[,2]) - inv_logit( postm1$a[32]) )

```

```

#precis( list( diff_b13 , diff_b14 , diff_b34 ) )

#check posterior for p to look at the distribution of probabilities that are probable
#p <- inv_logit(postm1$a) #convert from logit to actual probability
#dens(p,adj=0.1)
#HPDI(p) #most mass is below 0.5
#median(p) #0.49
#result: the prior was a normal curve that peaked at 0.5. The posterior: the mean y axis point where th

# MODEL 2: check to see if including batch has an influence on the estimate of b by removing batch
mwobatch <- ulam( alist(
  locisolved ~ dbinom(4,p) ,
  logit(p) <- a + b*trials, #standardize trials so 0=mean
  a ~ dnorm(0,0.5) ,
  b ~ dnorm(0,2)
) , data=dat , chains=4 , log_lik=TRUE )

precis(mwobatch,depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
#a -0.02 0.24 -0.40  0.35  1466     1
#b -0.46 0.31 -0.97 -0.01  1383     1
#the confidence interval does NOT cross 0, which indicates batch differ in their composition of control

#check posterior for p to look at the distribution of probabilities that are probable
postmwobatch <- extract.samples(mwobatch)
#p2 <- inv_logit(postmwobatch$a) #convert from logit to actual probability
#dens(p2,adj=0.1)
#HPDI(p2)
#median(p2) #0.50, narrower than prior & m1
#result: The posterior: the mean y axis point where the intercept is is 0.50 (meaning they solve on ave

# MODEL 3: see whether the confound of batch in m1 is an issue of the composition of control and manipu
#trialsbatch <- ulam( alist(
#  trials ~ normal(mu,sigma),
#  mu <- a[batch],
#  a[batch] ~ dnorm(0,0.5) ,
#  sigma ~ dexp(1)
#) , data=dat , chains=4 , log_lik=TRUE )
#precis(trialsbatch,depth=2)
#batches differ, which suggests that this is a confound in m1: can't accurately estimate the relationshi

# MODEL 4: see whether the flexibility manipulation actually had an effect on MAB performance by replac
#mean(d$TrialsFirstReversal) #74.7
#sd(d$TrialsFirstReversal) #30.7

# make ReversalsToPass a factor that has only 2 levels: level 1 = control, level 2 = manipulated
#d$ReversalsToPass <- as.factor(d$ReversalsToPass)
#levels(d$ReversalsToPass)[c(1,2,3)] <- c("Control","Manipulated","Manipulated")

#dat2 <- list(locisolved = d$TotalLociSolvedMABplastic,

```

```

#           trials = standardize(d$TrialsFirstReversal),
#           condition = d$ReversalsToPass
#           )

mcondition <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[condition] , #condition=random effect, standardize trials so 0=mean
  a[condition] ~ dnorm(0,1) #each condition gets its own intercept
), data=dat2 , chains=4 , log_lik=TRUE )
#precis(mcondition, depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
#a[1] -0.11 0.32 -0.62   0.4  1311      1
#a[2]  0.15 0.39 -0.46   0.8  1222      1

# contrasts between conditions: the log odds differences in solving a locus between batches. Value = log
postmcondition <- extract.samples(mcondition)
diffsmcondition <- postmcondition$a[,1] - postmcondition$a[,2]
#labsdifc <- c("Control-Manipulated")
#plot( precis(diffsmcondition), xlim=c(-1.5,1), labels=labsdifc)
# contrasts between conditions on the outcome scale (p.341 Rethinking)
#precis( diffsmcondition )
#Both of these results show that the conditions are actually not different from each other in how many loci solved

# MODEL 5: see whether the flexibility manipulation actually had an effect on MAB performance by replacing ReversalsToPass with a factor that has only 2 levels: level 1 = control, level 2 = manipulated
#dat3 <- list(locisolved = d$TotalLociSolvedMABplastic,
#           trials = standardize(d$TrialsFirstReversal),
#           batch = d$Batch
#           )

#mwobatch2 <- ulam( alist(
#  locisolved ~ dbinom(4,p) ,
#  logit(p) <- a + b*trials , #standardize trials so 0=mean
#  a ~ dnorm(0,0.5) ,
#  b ~ dnorm(0,2)
#), data=dat , chains=4 , log_lik=TRUE )

#precis(mwobatch2, depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
#a  0.00 0.24 -0.37  0.39  1208      1
#b -0.44 0.30 -0.94  0.02  1273      1
#b crosses zero so there is no correlation between number of loci solved and number of trials to reversals

# VISUALIZE: plot trials to pass last reversal against number of loci solved on the mwobatch model (p24)
# figure out xlim: -0.96 - 2.65
#range(dat$trials)

# dat$locisolved is on the outcome scale, but the model output is on the logit scale so transform dat$locisolved
dat$locisolvedp <- (dat$locisolved/4)

```

```
# draw 50 lines from the prior
trials_seq <- seq( from=-1.13 , to=2.9 , length.out=30 )

op <- par(mfrow=c(1,1), mar=c(5.9,4.9,2,0.9))
plot(dat$locisolvedp ~ dat$trials , pch=16 , col="black" ,
     xlab="Trials to pass last reversal (standardized: mean=0)" , ylab="Probability of solving a locus or"
mu <- link( mwobatch , data=data.frame( trials=trials_seq ) )
mu_mean <- apply( mu , 2 , mean )
mu_ci <- apply( mu , 2 , PI , prob=0.97 )
lines( trials_seq , mu_mean , lwd=2 )
shade( mu_ci , trials_seq , col=col.alpha(rangi2,0.3) )
par(op)

# contrasts between batches on the outcome scale (p.341 Rethinking). Value = difference in number of loci solved
labsdif1 <- c("m1: Batch 1-3","m1: Batch 1-4","m1: Batch 3-4")
labsdif2 <- c("m4: Control-Manipulated")
op <- par(mfrow=c(2,1), mar=c(4,4,2,0.2))
plot( precis(diffsm1c, diffsmcondition) , xlim=c(-0.5,0.5) , xlab="Difference in number of loci solved" , ylab="Mean" )
plot( precis(diffsmcondition) , xlim=c(-1.5,0.5) , xlab="Difference in number of loci solved" , labels=labsdif2 )
par(op)
```

354 **Table 4.** Model outputs for the number of loci solved and latency to switch loci after passing criterion
 355 on a different locus on the plastic (models 1-5) and wooden (models 6-8) multi-access boxes. SD=standard
 356 deviation, the 89% prediction intervals are shown, n_eff=effective sample size, Rhat4=an indicator of model
 357 convergence (1 is ideal), b=the slope of the relationship between loci solved or average switch latency and
 358 number of trials to pass reversal.

```
table <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration/"))
  header = T, sep = "," , stringsAsFactors = F)

table <- data.frame(table)
colnames(table) <- c("", "Mean", "SD", "5.5%", "94.5%", "n_eff", "Rhat4")

library(kableExtra)
knitr::kable(table) %>%
  kable_styling(full_width = T, position = "left")
```

	Mean	SD	5.5%	94.5%	n_eff	Rhat4
MODEL 1 (last reversal): loci solved ~ $a[batch] + b^*trials$	NA	NA	NA	NA	NA	NA
$a[1]$	0.04	0.46	-0.70	0.78	2304	1.00
$a[2]$	0.29	0.36	-0.30	0.87	2456	1.00
$a[3]$	-0.78	0.55	-1.65	0.08	2510	1.00
b	-0.22	0.25	-0.63	0.18	2364	1.00
MODEL 2 (last reversal): loci solved ~ $a + b^*trials$	NA	NA	NA	NA	NA	NA
a	-0.02	0.24	-0.40	0.35	1466	1.00
b	-0.46	0.31	-0.97	-0.01	1383	1.00
MODEL 3 (last reversal): trials ~ $a[batch]$	NA	NA	NA	NA	NA	NA
$a[1]$	0.09	0.37	-0.48	0.69	2095	1.00
$a[2]$	-0.21	0.29	-0.68	0.25	1715	1.00
$a[3]$	0.25	0.39	-0.38	0.86	2161	1.00
σ	1.03	0.21	0.75	1.39	2049	1.00
MODEL 4: loci solved ~ $a[condition]$	NA	NA	NA	NA	NA	NA
$a[1]$ control	-0.11	0.32	-0.62	0.40	1311	1.00
$a[2]$ manipulated	0.15	0.39	-0.46	0.80	1222	1.00
MODEL 5 (first reversal): loci solved ~ $a + b^*trials$	NA	NA	NA	NA	NA	NA
a	0.00	0.24	-0.37	0.39	1208	1.00
b	-0.44	0.30	-0.94	0.02	1273	1.00
MODEL 6 (last reversal): loci solved ~ $a + b^*trials$	NA	NA	NA	NA	NA	NA
a	1.06	0.27	0.63	1.50	1255	1.00
b	0.41	0.43	-0.21	1.13	1107	1.00
MODEL 7: loci solved ~ $a[condition]$	NA	NA	NA	NA	NA	NA
$a[1]$ control	-0.45	0.40	-1.10	0.18	1161	1.00
$a[2]$ manipulated	0.77	0.41	0.13	1.44	1302	1.00
MODEL 8 (first reversal): loci solved ~ $a + b^*trials$	NA	NA	NA	NA	NA	NA
a	0.11	0.26	-0.30	0.52	1221	1.00

360 **Innovativeness: number of loci solved on the multi-access box (wooden) ~ trials to reverse**
 361 The prediction interval for the estimate for the association between the number of loci solved on the wooden
 362 multi-access box (average=3.2, sd=1.3) and the number of trials to reverse a preference in their last reversal
 363 (average=59 trials, sd=38) crossed zero (Figure 5d; Model 6, Table 4; n=12 grackles: 6 in manipulated
 364 condition, 6 in control condition). This could mean that there is no association, however our simulations
 365 showed that we would not be able to reliably distinguish whether a small effect is different from zero with
 366 our sample size (correlation test suggests effect size of 0.2; Table M2). Aviary batch was excluded because
 367 of what we learned in the previous section. We did find a correlation between the number of loci solved and
 368 which reversal condition a grackle was randomly assigned to, indicating the reversal manipulation appears
 369 to have affected performance on the wooden multi-access box. The model estimates that manipulated birds
 370 solved on average 1.2 loci more than birds in the control condition (Table 4: Model 7, wooden; 89% prediction
 371 intervals=0.34-2.14; n=12 grackles: 6 in manipulated condition, 6 in control condition). However, there is
 372 no association between the number of trials to reverse in the first reversal (average=74 trials, sd=34) and
 373 the number of loci solved on the multi-access box (Table 4: Model 8, wooden; unregistered analysis).

```

library(rethinking)
library(rstan)
library(formatR)

# LOAD the data and column names
d2 <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))

d2 <- data.frame(d2)
colnames(d2) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal", "TrialsLastReversal", "Re

# Remove NAs
d2 <- subset(d2,!is.na(d2["TotalLociSolvedMABwooden"])) & !is.na(d2["TrialsLastReversal"]))

# n=12: 6 in manipulated group, 6 in control group
#length(d2$TotalLociSolvedMABwooden)

# make Batch numeric (assigned Taco to batch 3 because 3a doesn't work with the model)
d2$Batch <- as.factor(d2$Batch)
levels(d2$Batch)[c(2)] <- c("3")

# look at the data
#hist(d2$TotalLociSolvedMABwooden)
#mean(d2$TotalLociSolvedMABwooden) #3.2
#sd(d2$TotalLociSolvedMABwooden) #1.3
#mean(d2$TrialsLastReversal) #59.4
#sd(d2$TrialsLastReversal) #38.0

#translating the actual data (rather than the simulated data) into effect sizes (see equation below in
#sd(d2$TotalLociSolvedMABwooden)/sd(d2$TrialsLastReversal) #=.03
#cor.test(d2$TotalLociSolvedMABwooden, d2$TrialsLastReversal, alternative=c("two.sided"), method = c("pear
#corr = r = .20 = this is the effect size!!!
#solve equation for beta:
#0.20/(sd(d2$TotalLociSolvedMABwooden)/sd(d2$TrialsLastReversal)) #6.08 = beta, which is larger than th

# RUN MODELS on the actual data
datw <- list(locisolved = d2$TotalLociSolvedMABwooden,
              trials = standardize(d2$TrialsLastReversal),
              batch = d2$Batch
            )
  
```

```

# MODEL 6: same as model 2 in previous section
m6 <- ulam( alist(
  locisolved ~ dbinom(4,p) ,
  logit(p) <- a + b*trials, #standardize trials so 0=mean
  a ~ dnorm(0,0.5) ,
  b ~ dnorm(0,2)
) , data=datw , chains=4 , log_lik=TRUE )

precis(m6,depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
#a 1.04 0.28  0.61  1.48  1423     1
#b 0.39 0.41 -0.24  1.09  1517     1
#the confidence interval for b (the slope) crosses 0, which indicates that there is no correlation between a and b

#In case you rerun the model and want to add the new estimates for a and b to the table (Table 4 referred to in the paper)
# This will go to the respective columns 2-7 that have the output information, in lines 21 and 22 which are commented out
#table[21,2:7]<-round(precis(m6,depth=2)[1,],2)
#table[22,2:7]<-round(precis(m6,depth=2)[2,],2)
# For the number of effective samples, we actually want no decimal places, so we can adjust that at the end
#table$n_eff<-round(table$n_eff,0)
# You can save the changed table as
# write.csv(table,file="g_flexmanip_table_modeloutputs.csv")

#check posterior for p to look at the distribution of probabilities that are probable
postm6 <- extract.samples(m6)
#p2 <- inv_logit(postm6$a) #convert from logit to actual probability
#dens(p2,adj=0.1)
#HPDI(p2)
#median(p2) #0.72, narrower than prior & m1, shifted to the right
#result: The posterior: the mean y axis point where the intercept is is 0.72 (meaning they solve on average 72% of the time)

#model details: 2000 samples from 4 chains
#show(m1)
#no correlations between variables across batches
#pairs(m6)
#check the chain - fuzzy caterpillars = looks good
#traceplot(m6)
#check the chain a different way - "histograms overlap and stay within the same range" looks good (p.2)
#trankplot(m6)

# MODEL 7: see whether the flexibility manipulation actually had an effect on MAB performance by replacing the control group with manipulated group
#mean(d2$TrialsFirstReversal) #73.6
#sd(d2$TrialsFirstReversal) #34.1

# make ReversalsToPass a factor that has only 2 levels: level 1 = control, level 2 = manipulated
d2$ReversalsToPass <- as.factor(d2$ReversalsToPass)
levels(d2$ReversalsToPass)[c(1,2,3)] <- c("Control","Manipulated","Manipulated")

dat2 <- list(locisolved = d2$TotalLociSolvedMABplastic,
              trials = standardize(d2$TrialsFirstReversal),
              condition = d2$ReversalsToPass
            )

```

```

m7 <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[condition] , #condition=random effect, standardize trials so 0=mean
  a[condition] ~ dnorm(0,1) #each condition gets its own intercept
) , data=dat2 , chains=4 , log_lik=TRUE )
#precis(m7,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
#a[1] -0.45 0.40 -1.10  0.18 1161     1
#a[2]  0.77 0.41  0.13  1.44 1302     1
#Condition does not correlate with performance on the MAB bc both CIs cross zero

# contrasts between conditions: the log odds differences in solving a locus between batches. Value = log
postm7 <- extract.samples(m7)
diffsm7 <- postm7$a[,1] - postm7$a[,2]
labsdifc <- c("Control-Manipulated")
plot( precis(diffsm7), xlim=c(-1.5,1), labels=labsdifc)
# contrasts between conditions on the outcome scale (p.341 Rethinking)
precis( diffsm7 )
#conditons are actually not different from each other in how many loci they solved because CIs cross zero

# MODEL 8: see whether the flexibility manipulation actually had an effect on MAB performance by replacing
dat3 <- list(locisolved = d2$TotalLociSolvedMABplastic,
              trials = standardize(d2$TrialsFirstReversal),
              batch = d2$Batch
            )

m8 <- ulam( alist(
  locisolved ~ dbinom(4,p) ,
  logit(p) <- a + b*trials , #standardize trials so 0=mean
  a ~ dnorm(0,0.5) ,
  b ~ dnorm(0,2)
) , data=dat3 , chains=4 , log_lik=TRUE )

precis(m8,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
#a  0.11 0.26 -0.30  0.52 1221     1
#b -0.50 0.35 -1.09  0.04 1234     1
#b crosses zero so there is no correlation between number of loci solved and number of trials to reversal

# VISUALIZE: plot trials to pass last reversal against number of loci solved on the mwobatch model (p24)
# figure out xlim: -0.96 - 2.65
#range(datw$trials)

# datw$locisolved is on the outcome scale, but the model output is on the logit scale so transform datw
datw$locisolvedp <- (datw$locisolved/4)

# draw 50 lines from the prior
trials_w_seq <- seq( from=-0.96 , to=2.7 , length.out=30 )

# the plot will automatically be turned into a png file so we need to set the working directory to where
library(rstudioapi)

```

```

setwd(dirname(rstudioapi::getActiveDocumentContext()$path))
# if this does not work, in RStudio click Session > Set working directory > To source file location

op <- par(mfrow=c(1,1), mar=c(5.9,4.9,2,0.9))
#png("g_flexmanip_figp2mablog.png")
plot(jitter(datw$locisolvedp) ~ jitter(datw$trials) , pch=1 , col="black" ,
      xlab="Trials to pass last reversal (standardized: mean=0)" , ylab="Probability of solving a locus"
mu <- link( m6 , data=data.frame( trials=trials_w_seq ) )
mu_mean <- apply( mu , 2 , mean )
mu_ci <- apply( mu , 2 , PI , prob=0.97 )
lines( trials_w_seq , mu_mean , lwd=2 )
shade( mu_ci , trials_w_seq , col=col.alpha(rangi2,0.3) )
#dev.off()
par(op)
#but the png doesn't look good so I will make the png by hand again

```

374 **Reversal learning experiments: discriminating shapes on the touchscreen compared with color**
 375 **using tubes** In the tube experiment, it took four grackles an average of 40 trials ($sd=12$) in the initial
 376 discrimination phase to learn to prefer a color, while it took the same individuals an average of 390 trials
 377 ($sd=59$) to learn to prefer a shape using the touchscreen (Queso, Mole, Habanero, and Tapa). The two
 378 individuals who were faster to learn in the tube experiment were slower to learn in the touchscreen experiment.
 379 For the reversal, it took three of these individuals (Queso, Mole, and Habanero) an average of 80 trials
 380 ($sd=14$) to reverse their colored tube preference, and an average of 362 trials ($sd=111$) to reverse their shape
 381 preference on the touchscreen (Tapa had to be released back to the wild before finishing the experiment, but
 382 was on trial 629 in reversal one of the touchscreen experiment at the time of release. In the tube experiment,
 383 she was also the slowest of the four to reverse at 100 trials). All three individuals were about equally fast at
 384 the reversal in the tube experiment, while their reversal learning speeds differed on the touchscreen.

```

dts <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration.csv"))
  header = F, sep = "," , stringsAsFactors = F)

dts <- data.frame(dts)
colnames(dts) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLocisolvedMABplastic",
  "TotalLocisolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
dts <- subset(dts, !(is.na(dts["TrialsToLearnTouchscreen"])) & !(is.na(dts["TrialsFirstReversal"])))

# Touchscreen initial discrimination n=4: 2 in manipulated group, 2
# in control group length(dts$TrialsToLearnTouchscreen)
mean(dts$TrialsToLearnTouchscreen) #390 trials
sd(dts$TrialsToLearnTouchscreen) #59 trials

# Tube initial discrimination
mean(dts$TrialsToLearn) #40 trials
sd(dts$TrialsToLearn) #12 trials

# Touchscreen 1st reversal (n=3)
mean(c(490, 307, 290)) #362 trials TrialsFirstReversalTouchscreen
sd(c(490, 307, 290)) #111 trials TrialsFirstReversalTouchscreen

```

```
# Tube 1st reversal (n=3)
mean(dts$TrialsFirstReversal) #80 trials
sd(dts$TrialsFirstReversal) #14 trials
```

385 **P2 alternative 2 (additional analysis): latency and motor diversity**

386 Because there was no correlation between the number of trials to reverse in the last reversal and the latency to
 387 attempt a different locus on the wooden multi-access box, we conducted this additional analysis to determine
 388 whether the model fit was improved when adding the number of motor actions as an explanatory variable.
 389 Adding the number of motor actions (wooden: average=13, sd=4) did not improve the model fit when
 390 examining the relationship between the latency to switch loci on the wooden multi-access box (wooden:
 391 average=463, sd=481) and the number of trials to reverse in the last reversal (wooden: average=60, sd=38)
 392 because the Akaike weights were similar for both models (wooden: n=11 grackles: 5 in the manipulated
 393 group, 6 in the control group; Table 5).

394 **Table 5.** GLM output for the average latency to attempt a new option on the wooden multi-access box
 395 with and without motor diversity as an explanatory variable.

```
# WOODEN MULTI-ACCESS BOX (W)
dw <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations/W.csv"),
               header = F, sep = ",",
               stringsAsFactors = F)

dw <- data.frame(dw)
colnames(dw) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
                  "TrialsLastReversal", "ReversalsToPass", "TotalLocisSolvedMABplastic",
                  "TotalLocisSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
                  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
                  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
dw <- subset(dw, !(is.na(dw["MotorActionsWooden"])) & !(is.na(dw["TrialsLastReversal"])) &
               !(is.na(dw["AverageLatencyAttemptNewLocusMABwooden"])))

# n=11: 5 in manipulated group, 6 in control group
# length(dw$AverageLatencyAttemptNewLocusMABwooden)

# look at the data hist(dw$AverageLatencyAttemptNewLocusMABwooden)
# mean(dw$AverageLatencyAttemptNewLocusMABwooden) #463
# sd(dw$AverageLatencyAttemptNewLocusMABwooden) #481

# hist(dw$MotorActionsWooden) mean(dw$MotorActionsWooden) #13
# sd(dw$MotorActionsWooden) #4

# mean(dw$TrialsLastReversal) #60 sd(dw$TrialsLastReversal) #38

# GLM
motw <- glm(dw$AverageLatencyAttemptNewLocusMABwooden ~ dw$TrialsLastReversal +
             dw$MotorActionsWooden)

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
dredgemw <- dredge(glm(dw$AverageLatencyAttemptNewLocusMABwooden ~ dw$TrialsLastReversal +
                         dw$MotorActionsWooden))
```

Table 1:

	(Intercept)	dw\$MotorActionsWooden	dw\$TrialsLastReversal	df	logLik	AICc	delta	weight
1	463.1818	NA	NA	2	-83.02521	171.5504	0.000000	0.70712147
3	665.8320	NA	-3.362220	3	-82.63113	174.6908	3.140406	0.14708333
2	783.9748	-24.85016	NA	3	-82.76565	174.9599	3.409451	0.12857047
4	1136.8430	-32.86188	-4.138591	4	-82.15674	178.9801	7.429713	0.01722472

```

library(knitr)
kable(dredgemw, caption = "")

# Akaike weights = 0.71 null and <0.15 for the rest, therefore the
# models with or without motor actions are essentially the same

```

396 **P3a: reversal is repeatable within individuals within a context**

397 Performance was repeatable within individuals within the context of reversal learning. We obtained a
 398 repeatability value of 0.13, which is significantly greater than that expected if birds are performing randomly
 399 in each reversal ($p=0.001$; see analysis details in the R code for Analysis Plan > P3a). Consequently, and
 400 as preregistered, we did not need to conduct the analysis for P3a alternative to determine whether a lack of
 401 repeatability was due to motivation or hunger.

402 **P3b: repeatable across contexts**

403 There was no consistency of flexibility in individuals across contexts: the latency to attempt a different
 404 locus on both multi-access boxes did not correlate within individuals with the number of trials to reverse
 405 a preference in each reversal (Table 6; $n=8$ grackles: only those in the manipulated condition because only
 406 they experienced more than one reversal; Memela was not included because she did not complete the reversal
 407 experiment and therefore was not offered the multi-access box experiments).

408 **Table 6.** No repeatability across contexts. MCMCglmm output for the multi-access box plastic and wooden
 409 models.

```

d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = T, sep = ",",
  stringsAsFactors = F)

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d[["TrialsToReverse"]])))
d <- subset(d, !(is.na(d[["ReverseNumber"]])))

# include only those birds in the reversal tubes experiment
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
  ]

# factor variable
d$ID <- as.factor(d$ID)

# remove pilot birds (Fajita and Empanada) and Memela who did not
# pass the reversal experiment and therefore was not offered the MAB
# experiments
d <- d[!d$ID == "Fajita" & !d$ID == "Empanada" & !d$ID == "Memela", ]

# n=8 length(unique(d$ID))

```

```

# GLMM color reversal tubes compared with multi-access box
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
            G = list(G1 = list(V = 1, nu = 0)))

# plastic
rm <- MCMCglmm(LatencyMABplastic ~ ReverseNumber * TrialsToReverse, random = ~ID,
                 family = "poisson", data = d, verbose = F, prior = prior, nitt = 130000,
                 thin = 1000, burnin = 30000)
# summary(rm) post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept)
# 2.08708 -4.45451 11.67734 100 0.66 ReverseNumber 1.01476 -2.75484
# 5.49974 100 0.42 TrialsToReverse 0.01693 -0.09999 0.11593 100 0.58
# ReverseNumber:TrialsToReverse -0.01159 -0.07061 0.03283 100 0.42
# nothing significant so no consistent individual differences across
# contexts on MAB plastic and trials to reverse

# wooden
rmw <- MCMCglmm(LatencyMABwooden ~ ReverseNumber * TrialsToReverse, random = ~ID,
                  family = "poisson", data = d, verbose = F, prior = prior, nitt = 130000,
                  thin = 1000, burnin = 30000)
# summary(rmw) post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept)
# 3.622381 0.148743 7.810863 159.0 0.08 . ReverseNumber 0.211605
# -1.843271 2.126334 100.0 0.88 TrialsToReverse 0.032183 -0.019718
# 0.076067 147.9 0.14 ReverseNumber:TrialsToReverse -0.004685
# -0.037464 0.014299 100.0 0.62 nothing significant so no consistent
# individual differences across contexts on MAB wooden and trials to
# reverse

# Make a table with the outputs from both models (following
# https://gkhajduk.github.io/2017-10-25-cleanMCMCglmm/)
library(dplyr)

# for 1 model
clean.MCMC <- function(x) {
  sols <- summary(x)$solutions ## pull out relevant info from model summary
  Gcovs <- summary(x)$Gcovariances
  Rcovs <- summary(x)$Rcovariances
  fixed <- data.frame(row.names(sols), sols, row.names = NULL) ## convert to dataframes with the row
  random <- data.frame(row.names(Gcovs), Gcovs, row.names = NULL)
  residual <- data.frame(row.names(Rcovs), Rcovs, row.names = NULL)
  names(fixed)[names(fixed) == "row.names.sols."] <- "variable" ## change the columns names to variable
  names(random)[names(random) == "row.names.Gcovs."] <- "variable"
  names(residual)[names(residual) == "row.names.Rcovs."] <- "variable"
  fixed$effect <- "fixed" ## add ID column for type of effect (fixed, random, residual)
  random$effect <- "random"
  residual$effect <- "residual"
  modelTerms <- as.data.frame(bind_rows(fixed, random, residual)) # merge it all together
}

# check for one model - it works oneModel <- clean.MCMC(rmw) # get
# all the info from summary(modelName) oneModel$modelName <-
# getName.MCMC(rmw) # add the model's name in a new column oneModel #

```

```

# check out the created dataframe

# check for multiple models - it works
dataList <- list(rm, rmw)
dataListNames <- list("Plastic", "Wooden")
readyList <- mapply(cbind, lapply(dataList, clean.MCMC), modelName = dataListNames,
  SIMPLIFY = F)
mcmcOutputs <- as.data.frame(do.call(rbind, readyList), stringsAsFactors = FALSE)

# NOTE: change to type='html' when preparing the html output and to
# type='latex' when preparing the pdf output
# (https://stackoverflow.com/questions/14670299/using-stargazer-with-rstudio-and-knitr
# , stargazer cheatsheet:
# https://www.jakeruss.com/cheatsheets/stargazer/#html-formatting)
library(stargazer)
stargazer(mcmcOutputs, summary = FALSE, header = FALSE, type = "html",
  digits = 1)
  
```

```

410 variable
411 post.mean
412 1.95..CI
413 u.95..CI
414 eff.samp
415 pMCMC
416 effect
417 modelName
418 1
419 (Intercept)
420 2.5
421 -3.8
422 8.5
423 186.7
424 0.4
425 fixed
426 Plastic
427 2
428 ReverseNumber
429 0.7
430 -2.8
431 3.6
432 162.8
433 0.6
  
```

```
434 fixed
435 Plastic
436 3
437 TrialsToReverse
438 0.01
439 -0.1
440 0.1
441 193.1
442 0.7
443 fixed
444 Plastic
445 4
446 ReverseNumber:TrialsToReverse
447 -0.01
448 -0.05
449 0.03
450 184.1
451 0.7
452 fixed
453 Plastic
454 5
455 ID
456 0.04
457 0
458 0.1
459 42.5
460 random
461 Plastic
462 6
463 units
464 1.9
465 0.8
466 3.8
467 100
468 residual
469 Plastic
```

470 7
471 (Intercept)
472 5.1
473 1.3
474 13.7
475 41.0
476 0.02
477 fixed
478 Wooden
479 8
480 ReverseNumber
481 -0.6
482 -4.3
483 1.7
484 37.1
485 0.9
486 fixed
487 Wooden
488 9
489 TrialsToReverse
490 0.02
491 -0.1
492 0.1
493 44.5
494 0.4
495 fixed
496 Wooden
497 10
498 ReverseNumber:Tria lsToReverse
499 0.004
500 -0.02
501 0.1
502 41.0
503 1
504 fixed
505 Wooden

506 11

507 ID

508 1.1

509 0

510 3.3

511 100

512 random

513 Wooden

514 12

515 units

516 0.6

517 0.1

518 2.0

519 46.7

520 residual

521 Wooden

522 P4: serial reversal learning strategy

523 Three out of nine grackles switched from an epsilon-decreasing to an epsilon-first strategy in their last reversal
 524 (Diablo reversal 8, Burrito reversal 8, and Chilaquile reversal 6; Figure 6). The rest continued to rely on an
 525 epsilon-decreasing strategy throughout their reversals.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = T, sep = ",",
  stringsAsFactors = F)
d$Trial = as.numeric(d$Trial)

# Include only the manipulated birds because they received serial
# reversals
d <- d[d$ID == "Chalupa" | d$ID == "Mole" | d$ID == "Habanero" | d$ID ==
  "Diablo" | d$ID == "Burrito" | d$ID == "Adobo" | d$ID == "Chilaquile" |
  d$ID == "Pollito" | d$ID == "Memela", ]

# Exclude reversal 0 because this was the initial discrimination
d <- d[!d$Reversal == 0, ]
d$Reversal = factor(d$Reversal, levels = c("1", "2", "3", "4", "5", "6",
  "7", "8", "9", "10", "11"))

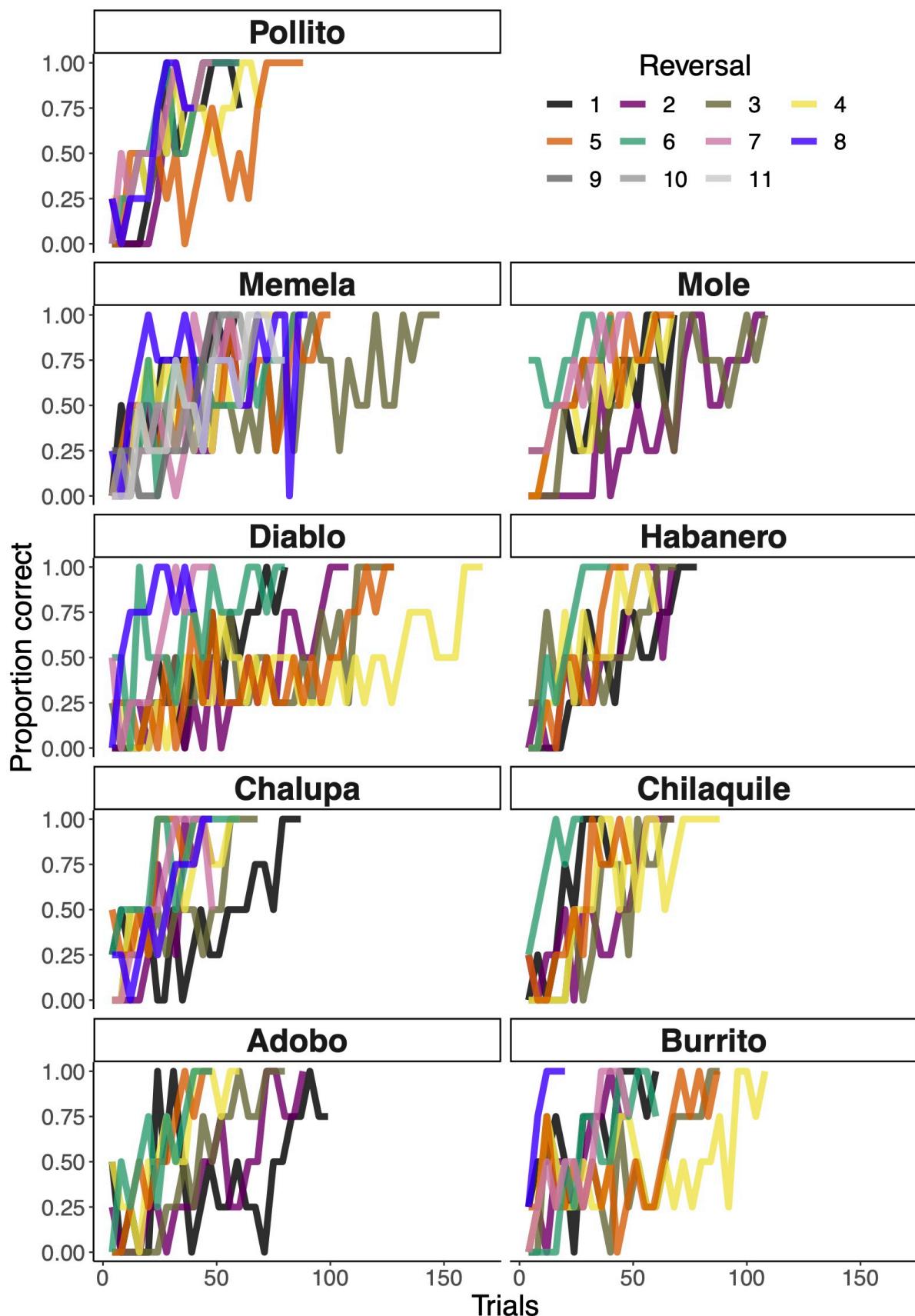
# Factor ID so I can make plots for each bird
d$ID <- factor(d$ID)
# levels(d$ID) #n=9 grackles in manipulated group, including Memela
# who did not complete the experiment make a palette to distinguish
# the data from each reversal that is color blind friendly with 11
# distinct colors
Palette <- c("#000000", "#660066", "#666633", "#FOE442", "#D55E00", "#009E73",
  "#CC79A7", "#3300FF", "#666666", "#999999", "#CCCCCC")
```

```
library(ggplot2)
library(cowplot)

all <- ggplot(d[which(!is.na(d$NonOverlappingWindow4TrialBins)), ], aes(Trial,
  NonOverlappingWindow4TrialBins, color = Reversal)) + geom_line(size = 2,
  alpha = 0.8, position = position_jitter(w = 0.02, h = 0)) + facet_wrap(. ~
  ID, ncol = 2, as.table = F) + scale_colour_manual(values = Palette) +
  guides(col = guide_legend(nrow = 3, byrow = TRUE)) + theme_classic() +
  theme(legend.key.size = unit(0.7, "cm"), legend.key.height = unit(0.5,
    "cm"), legend.title = element_text(size = 18), legend.text = element_text(size = 14),
  legend.title.align = 0.5, axis.title = element_text(size = 18),
  axis.text = element_text(size = 14), strip.text = element_text(size = 20,
    face = "bold")) + xlab("Trials") + ylab("Proportion correct")

b <- get_legend(all)

ggdraw(all + theme(legend.position = "none")) + draw_plot(b, 0.75, 0.91,
  0, 0)
```



527 **Figure 6.** The proportion of trials correct by trial number and reversal for each bird.

528 We additionally quantitatively determined to what degree each bird used the exploration versus exploitation
 529 strategy using methods in (Fedderspiel et al., 2017) by calculating the number of 10-trial blocks where birds
 530 were choosing “randomly” (2-9 correct choices; called sampling blocks; akin to the exploration strategy)
 531 divided by the total number of blocks to reach criterion per bird. This ratio was also calculated for “ac-
 532 quisition” blocks where birds made primarily correct choices (9-10 correct choices; akin to the exploitation
 533 strategy). There was no correlation between exploration (sampling ratio) or exploitation (acquisition ratio)
 534 and reversal number (sampling: reversal estimate=-0.09, SE=0.11, z=-0.86, p=0.39; acquisition: reversal
 535 estimate=0.00, SE=0.00, z=-0, p=1.00), indicating that the grackles did not use a particular strategy earlier
 536 or later in their serial reversals.

537 DISCUSSION

538 The flexibility manipulation worked

539 Although animal behavior can affect conservation outcomes (Greggor et al., 2016), behavioral manipulations
 540 other than predator recognition training have rarely been attempted (Jolly et al., 2018; Moseby et al., 2012;
 541 Ross et al., 2019; West et al., 2018; see review in Tetzlaff et al., 2019). Here, we conducted a controlled
 542 experiment to evaluate whether serial reversal learning affected behavioral flexibility. We found that while
 543 the number of trials to reverse did not linearly decrease with increasing reversal number, when examining
 544 last reversals, there was a difference between the manipulated and control groups. This indicates that the
 545 flexibility manipulation was effective in that it manipulated reversal learning speeds. This result is a novel
 546 and important contribution because manipulating flexibility, which is thought of as a generalizable cognitive
 547 ability, has the potential to change not only the behavior that was trained, but to allow trained individuals
 548 to change other behaviors related to this general cognitive ability.

549 Post-hoc, unregistered exploratory analyses to investigate the effect the flexibility manipula- 550 tion had on performance

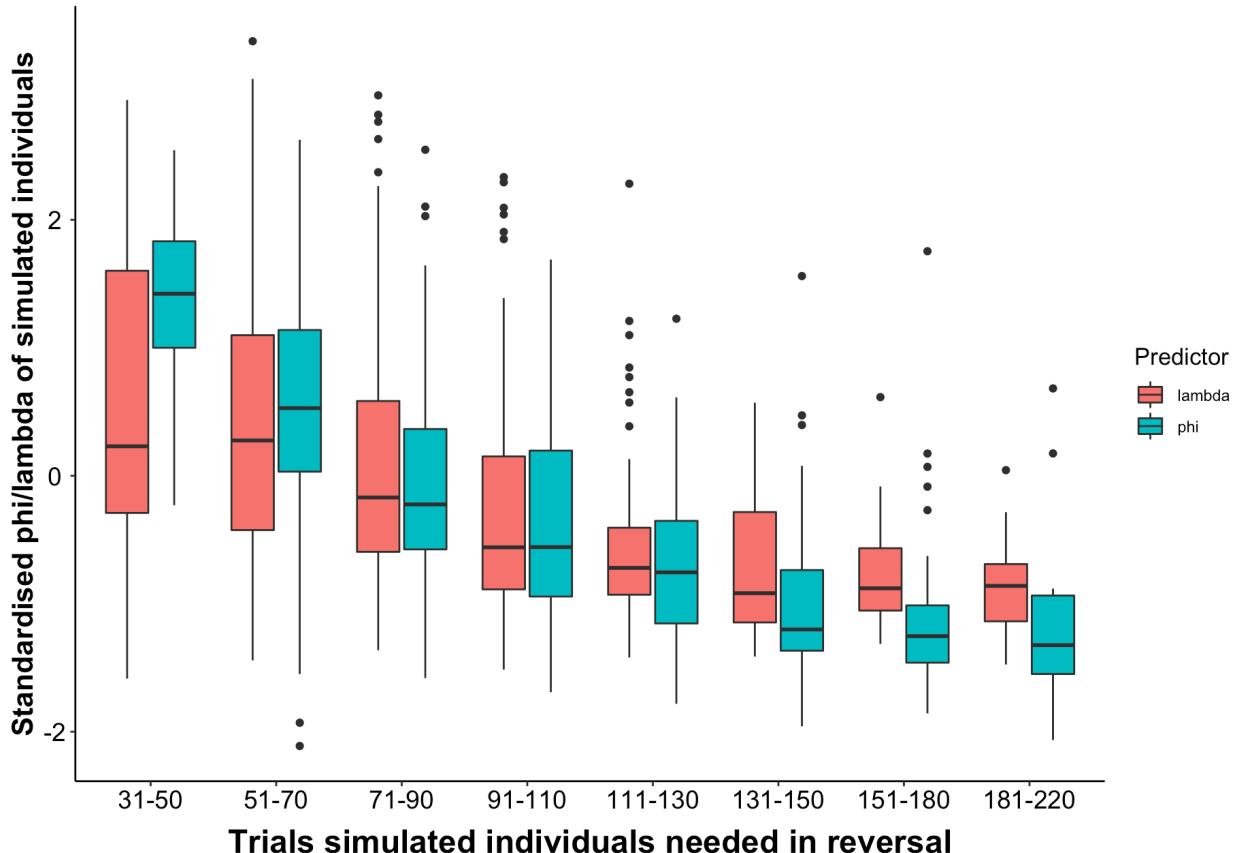
551 Furthermore, in addition to the planned analyses, we conducted post-hoc exploratory analyses on the serial
 552 reversal learning data to better understand the effect the flexibility manipulation had on performance. We
 553 used the version of the Bayesian model that was developed by A. Blaisdell et al. (2021) and modified
 554 by Logan CJ et al. (2020, see Analysis Plan > Flexibility analysis in 2020 for model specifications and
 555 validation). This model uses data from every trial of reversal learning (rather than only using the total
 556 number of trials to pass criterion) and represents behavioral flexibility using two parameters: the learning
 557 rate of attraction to either option (ϕ) and the rate of deviating from learned attractions (λ).

558 **Using simulations to check models estimating potential factors underlying performance in
 559 reversal tests** We first ran the Bayesian model on simulated data to better understand how the two
 560 parameters might lead to differences in performance and whether we could detect meaningful differences
 561 between control and manipulated birds. The settings for the simulations were based on the previous analysis
 562 of data from grackles in a different population (Santa Barbara, A. Blaisdell et al. (2021)). When we used
 563 only the choices simulated individuals made during their one reversal, the estimated ϕ and λ values did not
 564 match those the individuals had been assigned. We realized that ϕ and λ values were consistently shifted in
 565 a correlated way. When estimating these values from only a single reversal, there was equifinality: multiple
 566 combinations of the two parameters ϕ and λ can potentially explain the performance of birds during this
 567 reversal, and the estimation adjusts both learning parameters towards the mean. However, when we combined
 568 data from across at least one switch in the color of the rewarded option, combining initial discrimination
 569 learning with the first reversal, the model accurately recovered the ϕ and λ values that simulated individuals
 570 had been assigned.

571 In terms of the influence of the two parameters ϕ and λ on the number of trials birds needed to reverse
 572 an association, the ϕ values assigned to simulated individuals have a stronger influence than the λ values
 573 (estimated association of number of trials with standardized values of ϕ : -21, 89% prediction interval (PI):-22
 574 to -19; with standardized values of λ -14, 89% PI: -16 to -13). In particular, low numbers of trials to reverse



575 can be observed across the full range of λ values, though when λ is smaller than 8, simulated birds might
576 need 150 or more trials to reverse a preference (Figure 7). In contrast, there is a more linear relationship
577 between ϕ and the number of trials to reverse, with birds needing fewer trials the larger their ϕ .



578 **Figure 7.** In the simulations, the ϕ values assigned to individuals (green) have a clearer influence on the
579 number of trials these individuals needed in their reversal than their λ values (red). Phi and λ values are
580 standardised for direct comparison. In general, individuals need fewer trials to reverse if they have larger
581 ϕ and λ values. However, relatively small λ values can be found across the range of reversal performances,
582 whereas there is a more clear distinction with ϕ values.

```
#####
##### Load #####
#####
##### previous #####
#####
##### simulation #####
#####
##### data #####
#####
##### from #####
#####
##### xpop #####
#####
# These two are the sets we decided on, with initial attractions at
# 0.1 and eight different phi and four different lambda combinations
simulatedreversaldata_attractionscores_1 <- read.csv(url("https://raw.githubusercontent.com/corinalogan"))
  header = T, sep = ",", stringsAsFactors = F)

simulatedreversaldata_attractionscores_2 <- read.csv(url("https://raw.githubusercontent.com/corinalogan"))
  header = T, sep = ",", stringsAsFactors = F)

# In both simulations, sites were counted from 1-16; for the second
# simulation we change this to 17-32
```

```

simulatedreversaldata_attractionscores_2$Site <- simulatedreversaldata_attractionscores_2$Site +
  16

# In both simulations, individuals were counted from 1-320; for the
# second population we change the ids to start at 321
simulatedreversaldata_attractionscores_2$Bird_ID <- simulatedreversaldata_attractionscores_2$Bird_ID +
  320

# We combine the two data sets for the further analyses
library(dplyr)
simulatedreversaldata_attractionscores <- bind_rows(simulatedreversaldata_attractionscores_1,
  simulatedreversaldata_attractionscores_2)

#####
# In the simulations, trials were counted continuously for each bird.
# We now want to change this so that it restarts counting trials from
# 1 upward once a bird switches to reversal.

for (birds in 1:length(unique(simulatedreversaldata_attractionscores$Bird_ID))) {
  currentbird <- unique(simulatedreversaldata_attractionscores$Bird_ID)[birds]
  maximuminitial <- max(simulatedreversaldata_attractionscores[simulatedreversaldata_attractionscores ==
    currentbird & simulatedreversaldata_attractionscores$Reversal ==
    "initial", ]$Trial)
  simulatedreversaldata_attractionscores[simulatedreversaldata_attractionscores$Bird_ID ==
    currentbird & simulatedreversaldata_attractionscores$Reversal ==
    "reversal", ]$Trial <- simulatedreversaldata_attractionscores[simulatedreversaldata_attractionscores ==
    currentbird & simulatedreversaldata_attractionscores$Reversal ==
    "reversal", ]$Trial - maximuminitial
}

# We need to adjust the coding during the reversal learning so that
# 'correct' now matches whether it is correct or not.
simulatedreversaldata_attractionscores[simulatedreversaldata_attractionscores$Choice ==
  0, ]$Choice <- 2

# To use the model to estimate the phi and lambda parameters, we
# first need to change the column names to match these to the
# specifications in the model: change Bird_ID to id; change Reversal
# to Choice, change CorrectChoice to Correct, change Site to Expid

colnames(simulatedreversaldata_attractionscores) <- c("counter", "id",
  "Session", "Trial", "Reversal", "Choice", "Correct", "Phi_mean", "Lambda_mean",
  "Site", "Phi_sd", "Lambda_sd", "ThisBirdsPhi", "ThisBirdsLambda", "Attraction1",
  "Attraction2")

# There are several simulated individuals who never reached the
# criterion during the initial learning phase. We need to remove
# these from the dataset

birdswithreversal <- as.data.frame(simulatedreversaldata_attractionscores %>%
  group_by(id) %>%

```

```

    summarise(experiments = length(unique(Reversal))))
birdswithreversal <- birdswithreversal[birdswithreversal$experiments ==
  2, ]
simulatedreversaldata_attractionscores <- simulatedreversaldata_attractionscores[simulatedreversaldata_-
  reversaldata_attractionscores$id, ]

# Next, we need to change the ids of the birds to be continuous again
# so the STAN model will include them all
simulatedreversaldata_attractionscores$id <- as.integer(as.factor(simulatedreversaldata_attractionscores$id))

# We first focus only on the performance in the reversal trials
simulatedreversaldata_attractionscores_reversalphase <- simulatedreversaldata_attractionscores[simulatedreversaldata_-
  "reversal", ]

# Let's start with 30 individuals for comparison
firstreversal_simulated <- simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attr-
  actionscores_reversalphase$id == 1]
c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300,
  320, 340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560,
  580, 600, 620), ]

firstreversal_simulated$id <- as.numeric(as.factor(firstreversal_simulated$id))

# We can now extract the relevant data from the first reversal for
# the STAN model to estimate phi and lambda at the beginning
datfirstsimulated <- as.list(firstreversal_simulated)
datfirstsimulated$N <- nrow(firstreversal_simulated)
datfirstsimulated$N_id <- length(unique(firstreversal_simulated$id))

# Next, we also look at the estimation of the phi and lambda values
# based on their performance in the initial association learning
# phase

# We first focus only on the performance in the reversal trials
simulatedreversaldata_attractionscores_learningphase <- simulatedreversaldata_attractionscores[simulatedreversaldata_-
  "initial", ]

# Let's start with 30 individuals for comparison
initiallearning_simulated <- simulatedreversaldata_attractionscores_learningphase[simulatedreversaldata_attr-
  actionscores_learningphase$id == 1]
c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300,
  320, 340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560,
  580, 600, 620), ]

initiallearning_simulated$id <- as.numeric(as.factor(initiallearning_simulated$id))

# We can now extract the relevant data from the first reversal for
# the STAN model to estimate phi and lambda at the beginning
datinitialsimulated <- as.list(initiallearning_simulated)
datinitialsimulated$N <- nrow(initiallearning_simulated)
datinitialsimulated$N_id <- length(unique(initiallearning_simulated$id))

# The STAN model is set up to have the initial attraction for each

```

```

# option set to 0.1, and that individuals only learn the reward of
# the option they chose in a given trial.
reinforcement_model_nonzeroattraction <- "


data{
  int N;
  int N_id;
  int id[N];
  int Trial[N];
  int Choice[N];
  int Correct[N];
}

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual
  matrix[2,N_id] z_ID;
  vector<lower=0>[2] sigma_ID;          //SD of parameters among individuals
  cholesky_factor_corr[2] Rho_ID;
}

transformed parameters{
matrix[N_id,2] v_ID; // varying effects on stuff
v_ID = ( diag_pre_multiply( sigma_ID , Rho_ID ) * z_ID )';
}

model{
matrix[N_id,2] A; // attraction matrix

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(z_ID) ~ normal(0,1);
sigma_ID ~ exponential(1);
Rho_ID ~ lkj_corr_cholesky(4);

// initialize attraction scores

for ( i in 1:N_id ) {
A[i,1] = 0.1; A[i,2] = 0.1';
}

// loop over Choices

for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;
}

```

```

// first, what is log-prob of observed choice

L = exp(log_L + v_ID[id[i],1]);
p = softmax(L*A[id[i],1:2]');
Choice[i] ~ categorical( p );

// second, update attractions conditional on observed choice

phi = inv_logit(logit_phi + v_ID[id[i],2]);
pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ id[i] , Choice[i] ] = ( (1-phi)*(A[ id[i] , Choice[i] ]) + phi*pay[Choice[i]])';

}//i
}

"

# We run this model for the first reversal
m_firstsimulated <- stan(model_code = reinforcement_model_nonzeroattraction,
  data = datfirstsimulated, iter = 5000, cores = 4, chains = 4, control = list(adapt_delta = 0.9,
  max_treedepth = 12))

sfirstrsimulated <- extract.samples(m_firstsimulated)
firstreversal_simulatedlambda <- sapply(1:datfirstsimulated$N_id, function(x) exp(mean(sfirstrsimulated$mean(sfirstrsimulated$v_ID[, x, 1]))))
firstreversal_simulatedphi <- sapply(1:datfirstsimulated$N_id, function(x) inv_logit(mean(sfirstrsimulated$mean(sfirstrsimulated$v_ID[, x, 2]))))

# alternative using cmdstan
library(cmdstanr)
currentlocation <- getwd()
cmdstanlocation <- cmdstan_path()
setwd(cmdstanlocation)

# access the output file created by the model running the
# reinforcement model
write(reinforcement_model_nonzeroattraction, file = "myowntrial.stan")
file <- file.path(cmdstan_path(), "myowntrial.stan")
mod <- cmdstan_model(file)
options(mc.cores = 4)

datfirstsimulated$Reversal <- as.numeric(as.factor(datfirstsimulated$Reversal))

# RUN the model
fit <- mod$sample(data = datfirstsimulated, seed = 123, chains = 4, parallel_chains = 4,
  refresh = 500)
# Extract relevant variables
outcome <- data.frame(fit$summary())
rownames(outcome) <- outcome$variable

# Show the 90% compatibility intervals for the association between
# latency to switch loci on the plastic multi-access box and lambda

```

```

# and phi, and the interaction between lambda and phi from the
# reinforcement learning model
library(posterior)
library(rethinking)
drawsarray <- fit$draws()
drawsdataframe <- as_draws_df(drawsarray)
drawsdataframe <- data.frame(drawsdataframe)
initialandreversal_lambda <- sapply(1:datfirstsimulated$N_id, function(x) exp(mean(drawsdataframe$log_L
  mean(drawsdataframe[, x + 3])))
initialandreversal_phi <- sapply(1:datfirstsimulated$N_id, function(x) inv_logit(mean(drawsdataframe$log_phi
  mean(drawsdataframe[, x + 33])))

# Remove the stan command line file we created for this particular
# model from your computer
fn <- "myowntrial"
file.remove(fn)

# Reset your working directory to what it was before we ran the model
setwd(currentlocation)

# And we run this model for the initial learning phase
m_initialsimulated <- stan(model_code = reinforcement_model_nonzeroattraction,
  data = datinitialsimulated, iter = 5000, cores = 4, chains = 4, control = list(adapt_delta = 0.9,
  max_treedepth = 12))

sinitialsimulated <- extract.samples(m_initialsimulated)
initiallearning_simulatedlambda <- sapply(1:datinitialsimulated$N_id, function(x) exp(mean(sinitialsimulated
  mean(sinitialsimulated$v_ID[, x, 1])))
initiallearning_simulatedphi <- sapply(1:datinitialsimulated$N_id, function(x) inv_logit(mean(sinitialsimulated
  mean(sinitialsimulated$v_ID[, x, 2])))

# We now can get back the phi and lambda values 30 individuals were
# assigned at the beginning of the simulation
simulatedphis <- unique(simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attractionscores_reversalphase])
c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300,
  320, 340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560,
  580, 600, 620), ]$ThisBirdsPhi)
simulatedlambdas <- unique(simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attractionscores_reversalphase])
c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300,
  320, 340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560,
  580, 600, 620), ]$ThisBirdsLambda)

# Some of the phi values estimated from the performance during the
# initial learning are estimated as higher than what the individuals
# had during the simulation.
plot(initiallearning_simulatedphi ~ simulatedphis, xlim = c(0, 0.08), ylim = c(0,
  0.08))
abline(a = 0, b = 1)

# In contrast, some of the lambda values estimated from the

```

```

# performance during the initial learning are estimated as lower than
# what the individuals had during the simulation
plot(initiallearning_simulatedlambda ~ simulatedlambdas)
abline(a = 0, b = 1)

# The issue likely arises because the STAN model assumes that the phi
# and lambda values are correlated - whereas in the simulations they
# were allowed to vary independently from each other
plot(initiallearning_simulatedphi ~ initiallearning_simulatedlambda)
plot(simulatedphis ~ simulatedlambdas)

# In the simulation, we set some high lambda values and low phi
# values - because of the assumed correlation, the STAN model
# estimates higher phi values than simulated in cases when lambda was
# high, and lower lambda values than simulated when phi was low

plot(initiallearning_simulatedphi[simulatedlambdas < 5] ~ simulatedphis[simulatedlambdas <
  5], xlim = c(0, 0.08), ylim = c(0, 0.08))
points(initiallearning_simulatedphi[simulatedlambdas > 5] ~ simulatedphis[simulatedlambdas >
  5], xlim = c(0, 0.08), ylim = c(0, 0.08), col = "red")
abline(a = 0, b = 1)

# The phi values for the first reversal are systematically
# underestimated. This likely results from the model assuming that
# the attraction scores for both options are initially equal, while
# in reality there will be a skewed attraction towards the option
# that was rewarded during the initial learning. According, the birds
# seem to change their behaviour very slowly (because in the
# estimation they do not have to overcome their initially biased
# attraction) leading to the model estimating much lower phi values
# than those that the birds really had.
plot(firstreversal_simulatedphi ~ simulatedphis, xlim = c(0, 0.06), ylim = c(0,
  0.06))
abline(a = 0, b = 1)

# We can see how skewed the attraction scores were in the simulation
# at the beginning of the first reversal learning trial and use these
# values as priors in the STAN model (instead of the current setup
# where both attraction scores are set to be 0.1)
median(simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attractionscores_rever-
  1, ]$Attraction1/simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attract-
  1, ]$Attraction2)

median(simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attractionscores_rever-
  1, ]$Attraction1)

median(simulatedreversaldata_attractionscores_reversalphase[simulatedreversaldata_attractionscores_rever-
  1, ]$Attraction2)
# Based on this we want to set it to 0.1 and 0.7

# Try different priors to reduce the correlation between estimated

```

```

# phis and lambdas

reinforcement_model_nonzeroattraction_alternativepriors <- "


data{
  int N;
  int N_id;
  int id[N];
  int Trial[N];
  int Choice[N];
  int Correct[N];
}

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual
  matrix[N_id,2] v_ID;
}

model{
matrix[N_id,2] A; // attraction matrix

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(v_ID) ~ normal(0,1);

// initialize attraction scores

for ( i in 1:N_id ) {
A[i,1] = 0.1; A[i,2] = 0.1';
}

// loop over Choices

for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;

// first, what is log-prob of observed choice

L = exp(log_L + v_ID[id[i],1]);
p = softmax(L*A[id[i],1:2]');
Choice[i] ~ categorical( p );

// second, update attractions conditional on observed choice

phi = inv_logit(logit_phi + v_ID[id[i],2]);
}

```

```

pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ id[i] , Choice[i] ] = ( (1-phi)*(A[ id[i] , Choice[i] ]) + phi*pay[Choice[i]] )';

} // i
}
"

m_initialsimulated_alternativepriors <- stan(model_code = reinforcement_model_nonzeroattraction_alternativeprioratraction,
  data = datinitialsimulated, iter = 5000, cores = 4, chains = 4, control = list(adapt_delta = 0.9,
  max_treedepth = 12))

sinitialsimulatedalternativepriors <- extract.samples(m_initialsimulated_alternativepriors)
initiallearning_simulatedlambda_alternativepriors <- sapply(1:datinitialsimulated$N_id,
  function(x) exp(mean(sinitialsimulatedalternativepriors$log_L) + mean(sinitialsimulatedalternativepriors$x, 1)))
initiallearning_simulatedphi_alternativepriors <- sapply(1:datinitialsimulated$N_id,
  function(x) inv_logit(mean(sinitialsimulatedalternativepriors$logit_phi) +
  mean(sinitialsimulatedalternativepriors$v_ID[, x, 2])))

# Need to change the priors for the attraction scores 0.1 and 0.7

# Based on this information, we can now modify the STAN model to have
# the prior for the attraction for option set 1 (the option rewarded
# during the initial learning) to 0.7 and for option 2 set to 0.1,
# and that individuals only learn the reward of the option they chose
# in a given trial.
reinforcement_model_nonzeroattraction_skewedpriorattraction <- "


data{
  int N;
  int N_id;
  int id[N];
  int Trial[N];
  int Choice[N];
  int Correct[N];
}

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual
  matrix[2,N_id] z_ID;
  vector<lower=0>[2] sigma_ID;           //SD of parameters among individuals
  cholesky_factor_corr[2] Rho_ID;
}

transformed parameters{
matrix[N_id,2] v_ID; // varying effects on stuff
v_ID = ( diag_pre_multiply( sigma_ID , Rho_ID ) * z_ID )';
}

```

```

model{
matrix[N_id,2] A; // attraction matrix

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(z_ID) ~ normal(0,1);
sigma_ID ~ exponential(1);
Rho_ID ~ lkj_corr_cholesky(4);

// initialize attraction scores

for ( i in 1:N_id ) {
A[i,1] = 0.7; A[i,2] = 0.1';
}

// loop over Choices

for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;

// first, what is log-prob of observed choice

L = exp(log_L + v_ID[id[i],1]);
p = softmax(L*A[id[i],1:2]');
Choice[i] ~ categorical( p );

// second, update attractions conditional on observed choice

phi = inv_logit(logit_phi + v_ID[id[i],2]);
pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ id[i] , Choice[i] ] = ( (1-phi)*(A[ id[i] , Choice[i] ]) + phi*pay[Choice[i]])';

}//i
}
"

# We run this model for the first reversal
m_firstsimulated_skewedpriorattraction <- stan(model_code = reinforcement_model_nonzeroattraction_skewed,
       data = datfirstsimulated, iter = 5000, cores = 4, chains = 4, control = list(adapt_delta = 0.9,
       max_treedepth = 12))

sfirrstsimulatedskewedpriorattraction <- extract.samples(m_firstsimulated_skewedpriorattraction)
firstreversalsimulated_lambda_skewedpriorattraction <- sapply(1:datfirstsimulated$N_id,
      function(x) exp(mean(sfirrstsimulatedskewedpriorattraction$log_L) +
      mean(sfirrstsimulatedskewedpriorattraction$v_ID[, x, 1])))
firstreversalsimulated_phi_skewedpriorattraction <- sapply(1:datfirstsimulated$N_id,
      function(x) inv_logit(mean(sfirrstsimulatedskewedpriorattraction$logit_phi) +

```

```

mean(sfirstrsimulatedskewedpriorattraction$v_ID[, x, 2])))

plot(firstreversalsimulated_phi_skewedpriorattraction ~ simulatedphis,
      xlim = c(0, 0.06), ylim = c(0, 0.06))

# In these estimations based on the performance during single setups
# (either just the initial learning or the first reversal learning)
# the model always estimates that lambda and phi are correlated. This
# likely reflects equifinality - individuals can achieve the same
# performance with a range of phis and lambdas, and the model will
# slide to the middle along the line for each individual:

plot(x = "lambda", y = "phi", xlim = c(0, 10), ylim = c(0, 0.1))
# Individuals who needed a long time to learn the association will be
# in the bottom left corner
abline(a = 0.04, b = -0.01, lty = 2)
abline(a = 0.06, b = -0.01, lty = 2)
abline(a = 0.08, b = -0.01, lty = 2)
# Individuals who needed a short time to learn the association will
# be in the top right corner
abline(a = 0.1, b = -0.01, lty = 2)
abline(a = 0.12, b = -0.01, lty = 2)
abline(a = 0.14, b = -0.01, lty = 2)

points(x = 1, y = 0.03, cex = 2)
points(x = 2, y = 0.04, cex = 2)
points(x = 3, y = 0.05, cex = 2)
points(x = 4, y = 0.06, cex = 2)
points(x = 5, y = 0.07, cex = 2)
points(x = 6, y = 0.08, cex = 2)
abline(a = 0.02, b = 0.01, col = "red", lwd = 1.5)
points(initiallearning_simulatedphi ~ initiallearning_simulatedlambda,
      pch = 2)

# Maybe the model can better separate the lambda and phi values when
# combining data from multiple runs - in the case of the simulations
# that means combining the data from the initial learning with the
# data of the first reversal
simulatedreversaldata_attractionscores_reversalphase <- simulatedreversaldata_attractionscores[simulated
  "reversal", ]

# Let's start with 30 individuals for comparison
initialandreversal_simulated <- simulatedreversaldata_attractionscores[simulatedreversaldata_attractionscores
  c(20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 220, 240, 260, 300,
    320, 340, 360, 380, 400, 420, 440, 460, 480, 500, 520, 540, 560,
    580, 600, 620), ]

initialandreversal_simulated$id <- as.numeric(as.factor(initialandreversal_simulated$id))

# We can now extract the relevant data from the first reversal for

```

```

# the STAN model to estimate phi and lambda at the beginning
datinitialandreversalsimulated <- as.list(initialandreversal_simulated)
datinitialandreversalsimulated$N <- nrow(initialandreversal_simulated)
datinitialandreversalsimulated$N_id <- length(unique(initialandreversal_simulated$id))

m_initialandreversal <- stan(model_code = reinforcement_model_nonzeroattraction,
  data = datinitialandreversalsimulated, iter = 5000, cores = 4, chains = 4,
  control = list(adapt_delta = 0.9, max_treedepth = 12))

sinitialandreversal <- extract.samples(m_initialandreversal)
initialandreversal_lambda <- sapply(1:datinitialandreversalsimulated$N_id,
  function(x) exp(mean(sinitialandreversal$log_L) + mean(sinitialandreversal$v_ID[, 
    x, 1])))
initialandreversal_phi <- sapply(1:datinitialandreversalsimulated$N_id,
  function(x) inv_logit(mean(sinitialandreversal$logit_phi) + mean(sinitialandreversal$v_ID[, 
    x, 2])))

plot(initialandreversal_phi ~ simulatedphis)
abline(a = 0, b = 1)
plot(initialandreversal_lambda ~ simulatedlambdas)
abline(a = 0, b = 1)

plot(initialandreversal_phi ~ initialandreversal_lambda)

currentlocation <- getwd()
cmdstanlocation <- cmdstan_path()
setwd(cmdstanlocation)

# access the output file created by the model running the
# reinforcement model
write(reinforcement_model_nonzeroattraction_alternativepriors, file = "myowntrial.stan")
file <- file.path(cmdstan_path(), "myowntrial.stan")
mod <- cmdstan_model(file)
options(mc.cores = 4)

# RUN the model
fit <- mod$sample(data = datinitialandreversalsimulated, seed = 123, chains = 4,
  parallel_chains = 4, refresh = 500)
# Extract relevant variables
outcome <- data.frame(fit$summary())
rownames(outcome) <- outcome$variable

# Show the 90% compatibility intervals for the association between
# latency to switch loci on the plastic multi-access box and lambda
# and phi, and the interaction between lambda and phi from the
# reinforcement learning model
drawsarray <- fit$draws()
drawsdataframe <- as_draws_df(drawsarray)
drawsdataframe <- data.frame(drawsdataframe)
initialandreversal_lambda <- sapply(1:datinitialandreversalsimulated$N_id,
  function(x) exp(mean(drawsdataframe$log_L) + mean(drawsdataframe[, 
    x + 3])))

```

```

initialandreversal_phi <- sapply(1:datinitialandreversalsimulated$N_id,
  function(x) inv_logit(mean(drawsdataframe$logit_phi) + mean(drawsdataframe[,,
  x + 33])))

# Remove the stan command line file we created for this particular
# model from your computer
fn <- "myowntrial"
file.remove(fn)

# Reset your working directory to what it was before we ran the model
setwd(currentlocation)

simulatedphi <- initialandreversal_simulated %>%
  group_by(id) %>%
  summarise(mean(Phi_mean))
simulatedphi <- as.data.frame(simulatedphi)
simulatedphis <- simulatedphi[, 2]

# OPEN QUESTIONS: How did you decide that the manipulation worked?
# two consecutive reversals passed in 50 or less trials Can check
# what phi/lambda has to be so that they pass in 50 or less trials in
# the simulation Is it easier to change phi or lambda to get at 50 or
# fewer trials?

# We might want to compare first 20 trials to last 20 trials, both
# for the simulated data, and for the observed data look at the first
# and last 20 trials for each the first and the last reversal

summarysimulateddata <- matrix(nrow = length(unique(simulatedreversaldata_attractionscores$id)),
  ncol = 5)
summarysimulateddata <- as.data.frame(summarysimulateddata)
colnames(summarysimulateddata) <- c("id", "ThisBirdsPhi", "ThisBirdsLambda",
  "TrialsInitial", "TrialsReversal")

summarysimulateddata$id <- unique(simulatedreversaldata_attractionscores$id)

for (i in 1:nrow(summarysimulateddata)) {
  summarysimulateddata[i, ]$TrialsInitial <- max(filter(simulatedreversaldata_attractionscores,
    id == unique(simulatedreversaldata_attractionscores$id)[i], Reversal ==
    "initial")$Trial)
}

for (i in 1:nrow(summarysimulateddata)) {
  summarysimulateddata[i, ]$TrialsReversal <- max(filter(simulatedreversaldata_attractionscores,
    id == unique(simulatedreversaldata_attractionscores$id)[i], Reversal ==
    "reversal")$Trial)
}

for (i in 1:nrow(summarysimulateddata)) {
  summarysimulateddata[i, ]$ThisBirdsPhi <- max(filter(simulatedreversaldata_attractionscores,
    id == unique(simulatedreversaldata_attractionscores$id)[i])$ThisBirdsPhi)
}

```

```

for (i in 1:nrow(summarysimulateddata)) {
  summarysimulateddata[i, ]$ThisBirdsLambda <- max(filter(simulatedreversaldata_attractionscores,
    id == unique(simulatedreversaldata_attractionscores$id))[i])$ThisBirdsLambda
}

plot(summarysimulateddata$TrialsReversal ~ summarysimulateddata$ThisBirdsPhi)

plot(summarysimulateddata$TrialsReversal ~ summarysimulateddata$ThisBirdsLambda)

dat_trialsphiandlambda <- list(Trials = (summarysimulateddata$TrialsReversal),
  bird = c(as.numeric(as.factor(summarysimulateddata$id))), phi = standardize(c(summarysimulateddata$lambda = standardize(c(summarysimulateddata$ThisBirdsLambda)))))

trials.phiandlambda <- ulam(alist(Trials ~ normal(mu, sigma), mu <- a +
  b * phi + c * lambda, a ~ normal(70, 40), b ~ normal(0, 20), c ~ normal(0,
  20), sigma ~ exponential(1)), data = dat_trialsphiandlambda, chains = 4,
  cores = 4, iter = 10000)

precis(trials.phiandlambda, depth = 2)

# mean sd 5.5% 94.5% n_eff Rhat4 a 92.33 0.94 90.84 93.83 24367 1 b
# -20.62 0.94 -22.12 -19.11 25492 1 c -14.25 0.94 -15.74 -12.75 24876
# 1 sigma 23.38 0.64 22.37 24.43 24251 1

summarysimulateddata_forplotting <- matrix(ncol = 3, nrow = 2 * nrow(summarysimulateddata))
summarysimulateddata_forplotting <- as.data.frame(summarysimulateddata_forplotting)
colnames(summarysimulateddata_forplotting) <- c("TrialsReversal", "Predictor",
  "Value")
summarysimulateddata_forplotting$TrialsReversal <- c(summarysimulateddata$TrialsReversal,
  summarysimulateddata$TrialsReversal)
summarysimulateddata_forplotting$Predictor <- c(rep("phi", nrow(summarysimulateddata)),
  rep("lambda", nrow(summarysimulateddata)))
summarysimulateddata_forplotting$Value <- c(standardize(summarysimulateddata$ThisBirdsPhi),
  standardize(summarysimulateddata$ThisBirdsLambda))

summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  181, ]$TrialsReversal <- 8
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  151, ]$TrialsReversal <- 7
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  131, ]$TrialsReversal <- 6
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  111, ]$TrialsReversal <- 5
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  91, ]$TrialsReversal <- 4
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  71, ]$TrialsReversal <- 3
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  51, ]$TrialsReversal <- 2
summarysimulateddata_forplotting[summarysimulateddata_forplotting$TrialsReversal >
  31, ]$TrialsReversal <- 1
summarysimulateddata_forplotting$TrialsReversal <- as.factor(summarysimulateddata_forplotting$TrialsReversal)
  
```

```

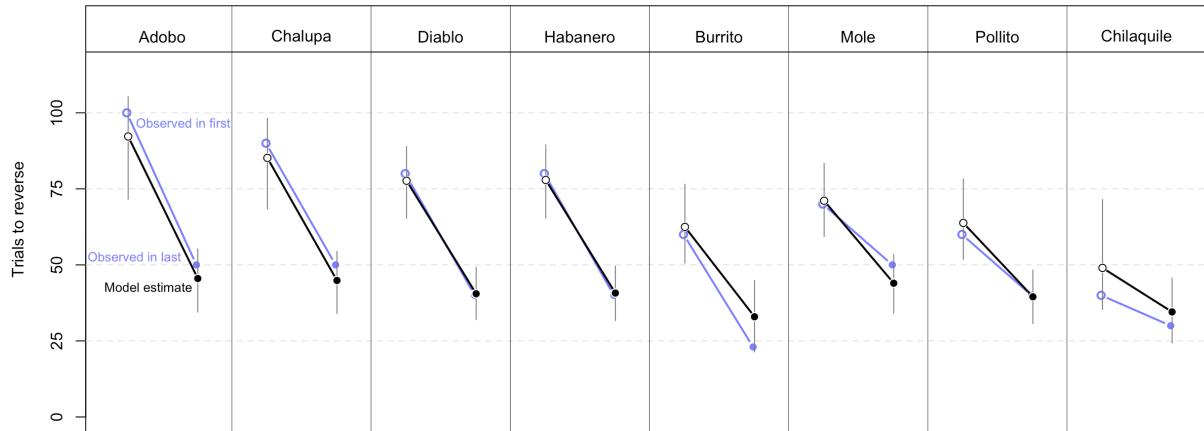
library(ggplot2)

ggplot(summariesimulateddata_forplotting, aes(x = TrialsReversal, y = Value,
  fill = Predictor)) + geom_boxplot() + xlab("Trials simulated individuals needed in reversal") +
  scale_y_continuous(name = "Standardised phi/lambda of simulated individuals") +
  theme_classic() + scale_x_discrete(name = "Trials simulated individuals needed in reversal",
  breaks = 1:8, labels = c("31-50", "51-70", "71-90", "91-110", "111-130",
  "131-150", "151-180", "181-220")) + theme(axis.text.x = element_text(size = 14,
  colour = "black", hjust = 0.5, angle = 0)) + theme(axis.title.x = element_text(size = 18,
  colour = "black", face = "bold", hjust = 0.5, vjust = -0.5, angle = 0)) +
  theme(axis.text.y = element_text(size = 14, colour = "black", hjust = 0.5,
  angle = 0)) + theme(axis.title.y = element_text(size = 16, colour = "black",
  face = "bold", hjust = 0.5, angle = 90)) + theme(legend.title = element_text(size = 13))
  
```

584 With this Bayesian estimation of the parameters ϕ and λ which underlie the performance in the reversal
 585 learning task, we wanted to address the following questions: 1) What did the manipulation change? Can
 586 we determine what mechanisms of flexibility the birds in the manipulated group who were already fast at
 587 reversing rely on? We predicted that birds that were already faster at reversing would have similar deviation
 588 rates from the learned attractions between the first and last reversals and lower learning rates than slower
 589 birds, which would allow them to change their preference more quickly because the attraction would be
 590 weaker and easier to reverse. 2) Do the manipulations shift birds beyond what is naturally observed and
 591 does it make them more similar? In the analyses in the Results section, it was unclear how there was an effect
 592 on innovation and flexibility in the multi-access box experiments when, in some cases, there was no difference
 593 between the control and manipulated conditions. Therefore, for both the control and manipulated groups,
 594 we investigated whether the learning rate and rate of deviating from learned attractions differed between a
 595 bird's first 10 trials of the first and last reversals and whether what we observe among the manipulated birds
 596 at the end might already naturally be present in some birds in the control group. In addition, we wanted to
 597 know whether the manipulations affected all birds equally or if we could still detect variation. 3) Are ϕ or λ ,
 598 the two components of flexibility in reversal learning, associated with performance on the multi-access boxes
 599 across control and manipulated birds? In the analyses in the Results section, we detected some associations
 600 between a bird's performance in the reversal learning task and on the multi-access boxes. Examining the
 601 two parameters, ϕ and λ , separately might offer a more detailed understanding of potential abilities that
 602 might influence performance in the different tasks.

603 **1) Observed effects of manipulation on reversal performance, ϕ , and λ** The birds in the manip-
 604 ulated group required a similar number of trials during their first reversal (R1 median=75 trials) than the
 605 birds in the control group needed during their first and only reversal (R1 median=70 trials). The manip-
 606 ulated birds improved during the reversal manipulation to needing a median of 40 trials in their last reversal.
 607 A pooled model estimates that birds can expect to improve by about 30 trials (89% prediction interval (PI):
 608 25-36) (Figure 8) after completing the serial reversals. While all manipulated birds improved, those birds
 609 that were already fast to reverse in their first reversal improved less than the birds that required many trials
 610 to reverse in their first reversal (posterior peak indicates a correlation of +0.22 between the first reversal
 611 value and the improvement achieved by the last reversal). However, the birds who performed worse in the
 612 first reversal do not become as fast at reversing as those who were already fast in the first reversal by the
 613 end of their manipulation: those who were the fastest in the first reversal, were also the fastest in the last
 614 reversal. But the difference between the slower and faster reversers is reduced in the last reversal. The pass-
 615 ing criterion for the manipulated grackles (reversing in 50 trials or fewer in their last two reversals) resulted
 616 in the number of trials in the last reversal equaling roughly $(\text{trials first reversal})^2 / 200$. This means that,
 617 also among the manipulated birds, we still detect variation in their performance, and this variation in per-
 618 formance appears to be specific to the individual across the whole manipulation. This, again, indicates that
 619 there is repeatability of individual performance within the serial reversal learning task. Their performance
 620 in the last reversal and how much they improved is not linked to how many reversals they needed to reach
 621 criterion. Most grackles performed worse in the middle of the manipulation (e.g., reversals 2 through their

622 third to last reversal) before improving and reaching criterion.



623

624 **Figure 8.** All eight manipulated birds need fewer trials to reverse in their last reversal than in their first.
 625 Their improvement depends on their starting value, with steeper slopes for those birds that needed more
 626 trials to reverse in the first reversal (blue colours for observed values and changes, black colours for model
 627 estimates). However, birds who needed more trials in the first reversal do not completely catch up, such that
 628 the birds that needed more trials in their first reversal also needed more trials in their last reversal relative
 629 to other grackles.

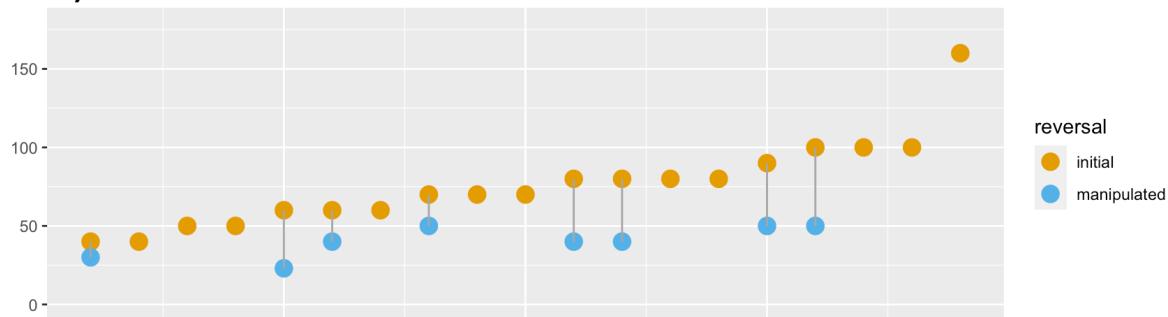
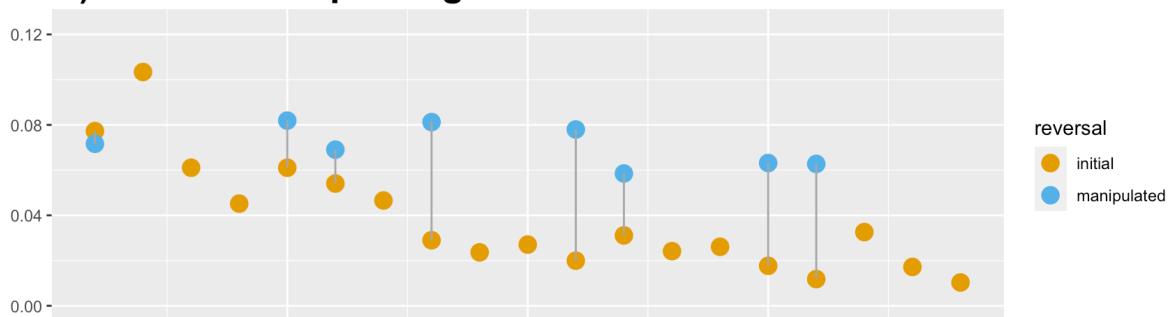
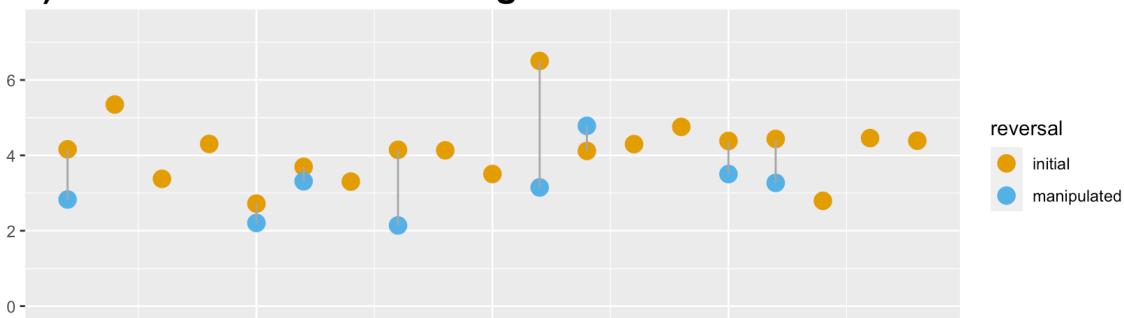
630 The findings from the simulated data indicated that λ and ϕ can only be estimated accurately when calcu-
 631 lating them across at least one switch (initial discrimination plus first reversal or final two reversals). For
 632 the manipulated birds, the estimated ϕ more than doubled from 0.03 in their first reversal (control grackles:
 633 0.03) to 0.07 in their last reversal (model estimate of expected average change: +0.02 to +0.05), while their
 634 λ went slightly down from 4.2 (control grackles: 4.3) to 3.2 (model estimate of average change -1.63 to -0.56).
 635 For ϕ , this pattern fits with the observations in the simulations: larger ϕ values are associated with fewer
 636 trials to reverse. However, in the simulations we saw a negative correlation between λ and the number of
 637 trials to reverse, whereas, for the birds here, λ in the last reversal when birds needed fewer trials is smaller
 638 than their λ for the first reversal. This fits with the observation that λ seems to be a constraint rather than
 639 a direct linear influence on the number of trials to reverse, and that, in combination with the correct ϕ value,
 640 birds only need few trials to reverse even if they have a smaller λ (see also below).

641 For the ϕ values, we also observe a correlation between the ϕ estimated from an individual's performance in
 642 the first reversal and how much their ϕ changed toward the value for their performance in the last reversal
 643 (-0.4; 50% highest posterior density intervals (HPDI) all negative), while there is no such obvious relationship
 644 for λ (-0.15; 50% HPDI crosses zero). For both ϕ and λ , unlike for the number of trials to reverse, we do
 645 not see that the individuals who had the largest values during the first reversal also always had the largest
 646 value during the last reversal. The manipulation changed both phi and λ , such that, across all birds, there
 647 is a negative correlation between ϕ and λ . In addition, for the manipulated birds, there is also a clear
 648 negative correlation between the phis and lambdas estimated from their last reversals. The decrease in
 649 λ from the first to the last reversal might indicate that individuals learned a meta-rule about the serial
 650 reversal experiment, that this is an environment that frequently changes so that they should deviate from
 651 their previous attractions as soon as the reward changes, whereas the increase in ϕ is linked to the learning
 652 whenever the environment changes.

653 **2) Variation in reversal performance, phi, and lambda** The values for the number of trials to reverse,
654 ϕ , and λ that we observed after the manipulation in the last reversal, fall within the range of variation we
655 observed among the control birds in their first and only reversal. This means that the manipulation did not
656 push birds to new levels, but changed them within the boundaries of their natural environment. This fits
657 with the observation that, for the correlations with performance on the multi-access box, there was generally
658 no difference between the control and the manipulated birds. Instead, their performance in the last reversal
659 before they attempted other tasks (first reversal for control birds, last reversal for manipulated birds) was
660 associated with some of their other behaviors.

661 Across both manipulated and control birds, ϕ was more consistently associated with the number of trials
662 individuals needed to reverse, and ϕ changed more than λ for the manipulated birds (Figure 9). However,
663 changes in ϕ and λ independently explain changes in the improvement in performance of the manipulated
664 birds from the first to the last reversal (association of change in number of trials from first to last trial with
665 standardized change in ϕ : 11, 89% PI: 6-15 and with standardized λ : 6, 89% PI: 1-10).

666 As mentioned above, birds who needed fewer trials than other birds during the first reversal also needed
667 fewer trials during the last reversal. Combining all of these relationships into a single model suggests that
668 the ϕ the initial learning and first reversal determines the number of trials individuals need during the first
669 reversal, which, in turn, explains how many trials they need during their last reversal. The ϕ for the last
670 reversal does not appear to provide any additional information about the number of trials in the last reversal,
671 and λ is not associated with the number of trials birds need to reverse.

a) Trials to reach association criterion

b) Phi: rate of updating learned attractions

c) Lambda: rate of deviating from learned attractions


672

673 **Figure 9.** Comparisons of the different measures of performance in the reversal task for each of the 19
 674 birds. The figure shows the trials to reach the association criterion after the reversal (a, top) during the
 675 initial (first) reversal (for all birds, orange) and the last reversal (for manipulated birds, blue); the ϕ values
 676 reflecting the updating of their information about the two options during those trials and during the trials
 677 before (initial = initial discrimination plus first reversal; manipulated = last two reversals) (b, middle); and
 678 the λ values reflecting their rate of deviation from the two options during those trials (c, bottom). Individual
 679 birds have the same position along the x-axis in all three panels. Birds that needed fewer trials to reverse
 680 their preference generally had higher ϕ values, whereas λ appears to reflect more whether any choices of
 681 the unrewarded tube occurred throughout the trials or only at the beginning. The values do not align
 682 perfectly because the ϕ and λ values are estimated across two rather than just the one reversal (e.g. bird
 683 2, Mofongo, has a very high ϕ because he only needed 20 trials during the initial discrimination). For the
 684 manipulated birds, their ϕ values changed more consistently than their λ values, and the ϕ values of the
 685 manipulated individuals were generally higher than those observed in the control individuals, while their λ

686 values remained within the range also observed in the control group.

Code below copied from Blaisdell et al. 2021

Using OBSERVED not simulated data

We want to estimate lambda and phi differently. For the initial
values, we combine the data from the first association learning
with the first reversal.

```
dflex <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrat
  header = T, sep = ",", stringsAsFactors = F)

library(rstan)
library(rethinking)
library(cmdstanr)
library(posterior)

# If you have cmdstan installed, use the following:
# set_ulam_cmdstan(TRUE)

### Code below copied from Blaisdell et al. 2021

# PREPARE reversal learning data exclude yellow tube trials for
# control birds because we are only interested in reversal data
dflex <- subset(dflex, dflex$Reversal != "Control: Yellow Tube" & dflex$ID !=
  "Memela")
# include only those trials where the bird made a choice (0 or 1)
dflex <- subset(dflex, dflex$CorrectChoice != -1)
# reverse number. 0=initial discrimination
dflex$Reversal <- as.integer(dflex$Reversal)

dflex$Correct <- as.integer(dflex$CorrectChoice)
dflex$Trial <- as.integer(dflex$Trial)
# exclude NAs from the CorrectChoice column
dflex <- subset(dflex, is.na(dflex$Correct) == FALSE)

# Want data ONLY from initial learning and first reversal to
# determine phi and lambda at the beginning. This is for all birds,
# including those that did not experience the reversal manipulation
# experiment
reduceddata <- matrix(ncol = ncol(dflex), nrow = 0)
reduceddata <- data.frame(reduceddata)
for (i in 1:length(unique(dflex$ID))) {
  thisbird <- unique(dflex$ID)[i]
  thisbirddata <- dflex[dflex$ID == thisbird, ]
  thisbirdslastreversal <- thisbirddata[thisbirddata$Reversal %in% c(0,
    1), ]
  reduceddata <- rbind(reduceddata, thisbirdslastreversal)
}
dflex_beginning <- reduceddata

# We want to remove the birds who did not go through at least the
```

```

# first reversal trial
birdscompletedreversal <- unique(dflex_beginning[dflex_beginning$Reversal ==
  1, ]$ID)

dflex_beginning <- dflex_beginning[dflex_beginning$ID %in% birdscompletedreversal,
  ]

length(unique(dflex_beginning$ID)) #21 birds

# Construct Choice variable
dflex_beginning$Choice <- NA
for (i in 1:nrow(dflex_beginning)) {
  if (dflex_beginning$Reversal[i] %in% seq(0, max(unique(dflex_beginning$Reversal)),
    by = 2)) {

    if (dflex_beginning$Correct[i] == 1) {
      dflex_beginning$Choice[i] <- 1
    } else {
      dflex_beginning$Choice[i] <- 2
    }
  } else {
    if (dflex_beginning$Correct[i] == 1) {
      dflex_beginning$Choice[i] <- 2
    } else {
      dflex_beginning$Choice[i] <- 1
    }
  }
}
dflex_beginning <- dflex_beginning[with(dflex_beginning, order(dflex_beginning$ID)),
  ]

colnames(dflex_beginning)[4] <- "id"

# Sort birds alphabetically
dflex_beginning <- dflex_beginning[with(dflex_beginning, order(dflex_beginning$id)),
  ]
birdnames <- unique(dflex_beginning$id)

# Convert bird names into numeric ids
dflex_beginning$id <- as.numeric(as.factor(dflex_beginning$id))

datinitialandfirstreversal <- as.list(dflex_beginning)
datinitialandfirstreversal$N <- nrow(dflex_beginning)
datinitialandfirstreversal$N_id <- length(unique(dflex_beginning$id))

# The STAN model is set up to have the initial attraction for each
# option set to 0.1, and that individuals only learn the reward of
# the option they chose in a given trial.
reinforcement_model_nonzeroattraction <- "
data{

```

```

int N;
int N_id;
int id[N];
int Trial[N];
int Choice[N];
int Correct[N];
}

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual
  matrix[2,N_id] z_ID;
  vector<lower=0>[2] sigma_ID;      //SD of parameters among individuals
  cholesky_factor_corr[2] Rho_ID;
}

transformed parameters{
matrix[N_id,2] v_ID; // varying effects on stuff
v_ID = ( diag_pre_multiply( sigma_ID , Rho_ID ) * z_ID )';
}

model{
matrix[N_id,2] A; // attraction matrix

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(z_ID) ~ normal(0,1);
sigma_ID ~ exponential(1);
Rho_ID ~ lkj_corr_cholesky(4);

// initialize attraction scores

for ( i in 1:N_id ) {
A[i,1] = 0.1; A[i,2] = 0.1';
}

// loop over Choices

for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;

// first, what is log-prob of observed choice

L = exp(log_L + v_ID[id[i],1]);
p = softmax(L*A[id[i],1:2]');
Choice[i] ~ categorical( p );
}

```

```

// second, update attractions conditional on observed choice

phi = inv_logit(logit_phi + v_ID[id[i],2]);
pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ id[i] , Choice[i] ] = ( (1-phi)*(A[ id[i] , Choice[i] ]) + phi*pay[Choice[i]])';

}//i
}
"
m_initialandreversal <- stan(model_code = reinforcement_model_nonzeroattraction,
  data = datinitialandfirstreversal, iter = 5000, cores = 4, chains = 4,
  control = list(adapt_delta = 0.9, max_treedepth = 12))

sinitialandreversal <- extract.samples(m_initialandreversal)
initialandreversal_lambda <- sapply(1:datinitialandfirstreversal$N_id,
  function(x) exp(mean(sinitialandreversal$log_L) + mean(sinitialandreversal$v_ID[, x, 1])))
initialandreversal_phi <- sapply(1:datinitialandfirstreversal$N_id, function(x) inv_logit(mean(sinitialandreversal$v_ID[, x, 2])))

plot(initialandreversal_phi ~ initialandreversal_lambda)

# Next, for comparison, want data ONLY from last two reversal trials
# to determine phi and lambda at the end. This is for the manipulated
# birds only because the control group only went through a single
# reversal.

# Need to do the analysis for the last two reversals with the skewed
# priors for the attraction values for the manipulated birds.

# link manipulatedbirdids to birdnames

dflex_last_manipulated <- dflex[dflex$ID == "Chalupa" | dflex$ID == "Mole" |
  dflex$ID == "Habanero" | dflex$ID == "Diablo" | dflex$ID == "Burrito" |
  dflex$ID == "Adobo" | dflex$ID == "Chilaquile" | dflex$ID == "Pollito" |
  dflex$ID == "Memela", ]

colnames(dflex_last_manipulated)[4] <- "id"

# Sort birds alphabetically
dflex_last_manipulated <- dflex_last_manipulated[with(dflex_last_manipulated,
  order(dflex_last_manipulated$id)), ]
birdnames_manipulated <- unique(dflex_last_manipulated$id)

# Convert bird names into numeric ids
dflex_last_manipulated$id <- as.numeric(as.factor(dflex_last_manipulated$id))

length(unique(dflex_last_manipulated$id)) #8 birds

# Construct Choice variable

```

```

dflex_last_manipulated$Choice <- NA
for (i in 1:nrow(dflex_last_manipulated)) {
  if (dflex_last_manipulated$Reversal[i] %in% seq(0, max(unique(dflex_last_manipulated$Reversal)), by = 2)) {

    if (dflex_last_manipulated$Correct[i] == 1) {
      dflex_last_manipulated$Choice[i] <- 1
    } else {
      dflex_last_manipulated$Choice[i] <- 2
    }
  } else {
    if (dflex_last_manipulated$Correct[i] == 1) {
      dflex_last_manipulated$Choice[i] <- 2
    } else {
      dflex_last_manipulated$Choice[i] <- 1
    }
  }
}

# Want data ONLY from last two reversals to determine phi and lambda
# at the beginning. This is for all birds, including those that did
# not experience the reversal manipulation experiment
reduceddata <- matrix(ncol = ncol(dflex), nrow = 0)
reduceddata <- data.frame(reduceddata)
for (i in 1:length(unique(dflex_last_manipulated$id))) {
  thisbird <- unique(dflex_last_manipulated$id)[i]
  thisbirddata <- dflex_last_manipulated[dflex_last_manipulated$id ==
    thisbird, ]
  thisbirdslastreversal <- thisbirddata[thisbirddata$Reversal %in% c(max(thisbirddata$Reversal) -
    1, max(thisbirddata$Reversal)), ]
  reduceddata <- rbind(reduceddata, thisbirdslastreversal)
}
dflex_last_manipulated <- reduceddata

datlasterversalsskewed <- as.list(dflex_last_manipulated)
datlasterversalsskewed$N <- nrow(dflex_last_manipulated)
datlasterversalsskewed$N_id <- length(unique(dflex_last_manipulated$id))

# The STAN model is set up to have theattraction for the previously
# rewarded option set to 0.7 and the unrewarded option set to 0.1
# when birds start with their final reversals, and that individuals
# only learn the reward of the option they chose in a given trial.
reinforcement_model_nonzeroattraction_skewedpriorattraction <- ""

data{
  int N;
  int N_id;
  int id[N];
  int Trial[N];
  int Choice[N];
  int Correct[N];
}

```

```

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual
  matrix[2,N_id] z_ID;
  vector<lower=0>[2] sigma_ID;          //SD of parameters among individuals
  cholesky_factor_corr[2] Rho_ID;
}

transformed parameters{
matrix[N_id,2] v_ID; // varying effects on stuff
v_ID = ( diag_pre_multiply( sigma_ID , Rho_ID ) * z_ID )';
}

model{
matrix[N_id,2] A; // attraction matrix

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(z_ID) ~ normal(0,1);
sigma_ID ~ exponential(1);
Rho_ID ~ lkj_corr_cholesky(4);

// initialize attraction scores

for ( i in 1:N_id ) {
A[i,1] = 0.7; A[i,2] = 0.1';
}

// loop over Choices

for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;

// first, what is log-prob of observed choice

L = exp(log_L + v_ID[id[i],1]);
p = softmax(L*A[id[i],1:2]');
Choice[i] ~ categorical( p );

// second, update attractions conditional on observed choice

phi = inv_logit(logit_phi + v_ID[id[i],2]);
pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ id[i] , Choice[i] ] = ( (1-phi)*(A[ id[i] , Choice[i] ]) + phi*pay[Choice[i]])';
}

```

```

} // i
}

m_lastreversals_skewed <- stan(model_code = reinforcement_model_nonzeroattraction_skewedpriorattraction
  data = datlasterversalsskewed, iter = 5000, cores = 4, chains = 4,
  control = list(adapt_delta = 0.9, max_treedepth = 12))

slastreversals_skewed <- extract.samples(m_lastreversals_skewed)
lastreversals_lambda_skewed <- sapply(1:datlasterversalsskewed$N_id, function(x) exp(mean(slastreversals_skewed$lambda[, x, 1])))
lastreversals_phi_skewed <- sapply(1:datlasterversalsskewed$N_id, function(x) inv_logit(mean(slastreversals_skewed$phi[, x, 2])))

# We can now combine the information on the estimated phis and
# lambdas for the initial performance of all birds and the last
# performance of the manipulated birds into a single table
eachbirdslearningparameters <- matrix(nrow = datinitialandfirstreversal$N_id,
  ncol = 8)
eachbirdslearningparameters <- data.frame(eachbirdslearningparameters)
colnames(eachbirdslearningparameters) <- c("Bird", "Number", "beginningphi",
  "beginninglambda", "manipulatedphi", "manipulatedlambda", "lastphi",
  "lastlambda")
eachbirdslearningparameters[, 1] <- birdnames
eachbirdslearningparameters[, 2] <- unique(dflex_beginning$id)
eachbirdslearningparameters[, 3] <- initialandreversal_phi
eachbirdslearningparameters[, 4] <- initialandreversal_lambda
eachbirdslearningparameters[eachbirdslearningparameters$Bird %in% birdnames_manipulated,
  5] <- lastreversals_phi_skewed
eachbirdslearningparameters[eachbirdslearningparameters$Bird %in% birdnames_manipulated,
  6] <- lastreversals_lambda_skewed
for (i in 1:nrow(eachbirdslearningparameters)) {
  if (is.na(eachbirdslearningparameters[i, ]$manipulatedphi) == T) {
    eachbirdslearningparameters[i, ]$lastphi <- eachbirdslearningparameters[i,
      ]$beginningphi
    eachbirdslearningparameters[i, ]$lastlambda <- eachbirdslearningparameters[i,
      ]$beginninglambda
  }
  if (is.na(eachbirdslearningparameters[i, ]$manipulatedphi) == F) {
    eachbirdslearningparameters[i, ]$lastphi <- eachbirdslearningparameters[i,
      ]$manipulatedphi
    eachbirdslearningparameters[i, ]$lastlambda <- eachbirdslearningparameters[i,
      ]$manipulatedlambda
  }
}
write.csv(eachbirdslearningparameters, file = "g_flexmanip_ArizonaBirds_EstimatedPhiLambdaReversalLearn")

##### Is there a linear improvement?

performanceimprovement <- matrix(ncol = 10, nrow = length(unique(dflex$ID)))
performanceimprovement <- as.data.frame(performanceimprovement)

```

```

colnames(performanceimprovement) <- c("Bird", "initialassociation", "reversal1",
  "reversal2", "reversal3", "reversal4", "reversal5", "reversal6", "reversal7",
  "reversal8")

for (i in 1:length(unique(dflex$ID))) {
  thisbird <- unique(dflex$ID)[i]
  thisbirddata <- dflex[dflex$ID == thisbird, ]
  for (k in 1:length(unique(thisbirddata$Reversal))) {
    thisbirdcurrentreversal <- thisbirddata[thisbirddata$Reversal %in%
      unique(thisbirddata$Reversal)][k], ]
    performanceimprovement[i, 1] <- thisbird
    performanceimprovement[i, k + 1] <- max(thisbirdcurrentreversal$Trial)
  }
}

colourstoplot <- c("red", "blue", "red", "black", "yellow", "red", "red",
  "black", "blue", "red", "red", "red", "red", "yellow", "red", "blue",
  rep("red", 6))
plot(NULL, xlim = c(1, 9), ylim = c(0, 200), xlab = "Reversal", ylab = "Trials",
  xaxt = "n", yaxt = "n")
for (j in 1:nrow(performanceimprovement)) {
  lines(c(1:9), performanceimprovement[j, 2:10], lwd = 2, col = colourstoplot[j])
}

manipulatedperformanceimprovement <- performanceimprovement[is.na(performanceimprovement$reversal2) ==
  F, ]
manipulatedperformanceimprovement <- mutate(manipulatedperformanceimprovement,
  maximumreversal = pmax(reversal1, reversal2, reversal3, reversal4,
  reversal5, reversal6, reversal7, reversal8, na.rm = T))

smallimprovementdata <- select(improvementdata, Bird, lastphi, lastlambda,
  beginningphi, beginninglambda)
largecombined <- left_join(manipulatedperformanceimprovement, smallimprovementdata,
  by = "Bird")

# first\last\max 40\t 30\t 90 60\t 23\t 110 60\t 40\t 90 70\t 50\t
# 110 80\t 40\t 80 80\t 40\t 170 90\t 50\t 90 100\t 50\t 100

# # # # # #

# What did the manipulation change? Determine what mechanisms of flexibility the birds in the manipulation

# Questions:
# 1) Effect of manipulation
# Say that manipulation reduces number of trials birds needed to reverse (trials ~ reversal) - on average
# 1a) Did manipulation change phi and lambda? (phi ~ reversal (first vs last); lambda ~ reversal)
# 1b) Does extent of change depend on how the birds started? Expect that birds that were already good improved more

# 2) Is improvement in performance mainly due to change in phi or in lambda?
# 2a) (model improvement: trialimprovement ~ lambda_improvement + phi_improvement)
# 2b) cafe waiting model for trials to reverse, with morning/afternoon as first/last, and slope depends on reversal
# 2c) Can we estimate all changes simultaneously? mallchanges, maybe run with just phi and just lambda

```

```

library(rethinking)

# if you have cmdstan installed, use the following:
# set_ulam_cmdstan(TRUE)

d3 <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))

d3 <- data.frame(d3)
colnames(d3) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal", "TrialsLastReversal", "Re

# n=11: 5 in manipulated group, 6 in control group
#length(d3$AverageLatencyAttemptNewLocusMABplastic)

# make Batch a factor
d3$Batch <- as.factor(d3$Batch)

# Need to fix spelling mistake in a bird name to match it to the other data
d3[d3$Bird=="Huachinago",]$Bird<-"Huachinango"

d3_match<- subset(d3, d3$Bird != "Memela")
d3_match <- d3_match[with(d3_match, order(d3_match$Bird)), ]

eachbirdslearningparameters<-read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/EachbirdLearningParameters"))

library(dplyr)
combinedreversaldata<-left_join(d3_match, eachbirdslearningparameters, by="Bird")

# Sort birds alphabetically, so the birds are always in the same order in both data sets and the model
combinedreversaldata <- combinedreversaldata[with(combinedreversaldata, order(combinedreversaldata$Bird))]

# Store the bird names in case we want to link their data from here back to other datasets
birdnames<-unique(combinedreversaldata$Bird)

plot(TrialsFirstReversal~beginningphi, data=combinedreversaldata[is.na(combinedreversaldata$lastlambda)==T])
points(TrialsLastReversal~lastphi, data=combinedreversaldata[is.na(combinedreversaldata$manipulatedlambda)==T])

plot(TrialsFirstReversal~beginninglambda, data=combinedreversaldata[is.na(combinedreversaldata$lastlambda)==T])
points(TrialsLastReversal~lastlambda, data=combinedreversaldata[is.na(combinedreversaldata$manipulatedlambda)==T])

# Filter the dataset to only include those birds that experienced the reversal manipulation
improvementdata<-combinedreversaldata[is.na(combinedreversaldata$manipulatedphi)==F,]

# For these birds, we can calculate how much they changed from beginning to end
improvementdata$phiimprovement<-improvementdata$lastphi-improvementdata$beginningphi
improvementdata$lambdaimprovement<-improvementdata$lastlambda-improvementdata$beginninglambda
improvementdata$performanceimprovement<-improvementdata$TrialsFirstReversal -improvementdata$TrialsLastReversal

# Filter the dataset a second time to only include the control birds
singlereversaldata<-combinedreversaldata[is.na(combinedreversaldata$manipulatedphi)==T,]
singlereversaldata<-singlereversaldata[is.na(singlereversaldata$TrialsFirstReversal)==F,]

```

```

# How much did birds change that experienced the manipulation?

median(improvementdata$beginningphi)
# 0.03
median(improvementdata$manipulatedphi)
# 0.07
median(improvementdata$beginninglambda)
# 4.2
median(improvementdata$manipulatedlambda)
# 3.2

median(singlereversaldata$beginningphi)
# 0.03
median(singlereversaldata$beginninglambda)
# 4.3

median(improvementdata$TrialsFirstReversal)
# 75
median(improvementdata$TrialsLastReversal)
# 40
median(singlereversaldata$TrialsFirstReversal)
# 70

# 1) First, we want to model the changes that happened during the manipulations

# How did the number of trials change - is there a difference between first and last reversal and how many
dat_change_trials <- list(
  trials = c(improvementdata$TrialsFirstReversal, improvementdata$TrialsLastReversal),
  bird = c(as.factor(improvementdata$Bird), as.factor(improvementdata$Bird)),
  reversal = c(rep(0, nrow(improvementdata)), rep(1, nrow(improvementdata)))
)

mchangetrialspool <- ulam(alist(
  trials ~ dnorm(mu, sigma),
  mu <- a[bird]+b[bird]*reversal,
  a[bird] ~ dnorm(100, 50),
  b[bird] ~ dnorm(b_bar, sigma_bar),
  b_bar ~ dnorm(30, 20),
  sigma ~ dexp(1),
  sigma_bar ~ dexp(1)
), data = dat_change_trials, chains=4, log_lik = TRUE, messages = FALSE)
precis(mchangetrialspool, depth=2)

# The relevant estimate here is for b_bar, showing that birds on average improve by between 25-36 trials

#          mean    sd   5.5%  94.5% n_eff Rhat4
# a[1]      91.62  5.80  82.51 100.10    33  1.14
# a[2]      57.85  4.98  49.48  65.18   739  1.01
# a[3]      85.83  5.14  77.61  94.23   184  1.03
# a[4]      48.63  6.66  36.69  58.57    26  1.19
# a[5]      76.55  5.32  67.81  85.57    66  1.07

```

```

# a[6]      75.77 5.14  68.18  83.18   100  1.04
# a[7]      74.20 5.59  66.82  83.56   108  1.05
# a[8]      64.34 5.46  56.13  73.21    85  1.06
# b[1]     -32.76 6.84 -49.77 -24.93    11  1.55
# b[2]     -31.16 4.13 -37.24 -24.74    33  1.15
# b[3]     -31.56 4.65 -40.11 -24.73    20  1.23
# b[4]     -27.79 6.96 -35.22 -10.13    10  1.67
# b[5]     -31.53 4.68 -40.12 -24.74    20  1.23
# b[6]     -31.49 4.65 -39.90 -24.53    21  1.22
# b[7]     -29.00 4.78 -35.47 -19.93    16  1.31
# b[8]     -29.01 4.71 -35.34 -20.07    16  1.31
# b_bar    -30.30 3.51 -35.65 -24.65   109  1.06
# sigma     6.54 2.42  0.23   9.41    10  1.60
# sigma_bar 2.13 2.93  0.17   9.77     9  1.73

# We might expect that birds who took many trials during their first reversal had to improve more to reach the reversal point.

dat_change_trials_noncentered <- list(
  trials = standardize(c(improvementdata$TrialsFirstReversal, improvementdata$TrialsLastReversal)),
  bird = c(as.factor(improvementdata$Bird), as.factor(improvementdata$Bird)),
  reversal = c(rep(1, nrow(improvementdata)), rep(2, nrow(improvementdata)))
)

mchangetrialnoncentered <- ulam(
  alist(
    trials ~ normal(mu, sigma),
    mu <- a_reversal[reversal] + b_reversal[bird, reversal],
    # adaptive priors - non-centered
    transpars > matrix[bird, 2]:b_reversal <-
      compose_noncentered( sigma_reversal , L_Rho_reversal , z_reversal ),
    matrix[2,bird]:z_reversal ~ normal( 0 , 1 ),
    # fixed priors
    a_reversal[reversal] ~ normal(0, 20),
    sigma ~ exponential(1),
    vector[2]:sigma_reversal ~ dexp(1),
    cholesky_factor_corr[2]:L_Rho_reversal ~ lkj_corr_cholesky( 2 ),
    # compute ordinary correlation matrixes from Cholesky factors
    gq > matrix[2,2]:Rho_actor <<- Chol_to_Corr(L_Rho_reversal)
  ) , data=dat_change_trials_noncentered , chains=4 , cores=4 , log_lik=TRUE )

precis(mchangetrialnoncentered, depth=4)

# Is there a correlation between the initial trials to reverse and how much they improve? Yes, it appears there is.

post <- extract.samples(mchangetrialnoncentered)
dens( post$Rho[,1,2] , xlim=c(-1,1) ) # posterior
R <- rlkjcorr( 1e4 , K=2 , eta=2 )      # prior
dens( R[,1,2] , add=TRUE , lty=2 )

PI(post$Rho[,1,2], 0.10)

# We can plot the observed and estimated changes for each bird with the following block of code. This section is omitted for brevity.

```

```

# compute mean for each bird in each treatment
pl <- by( c(improvementdata$TrialsFirstReversal,improvementdata$TrialsLastReversal) , list( c(as.factor
pl<-pl[c(1,3,5,6,2,7,8,4),]
# generate posterior predictions using link
datp <- list(
  bird=rep(1:8,each=2) ,
  reversal=rep(1:2,times=8) )
p_post <- link( mchangetrialnoncentered , data=datp )
p_mu <- apply( p_post , 2 , mean )
p_mu<-p_mu[c(1,2,5,6,9,10,11,12,3,4,13,14,15,16,7,8)]
p_ci <- apply( p_post , 2 , PI )
p_ci<-p_ci[,c(1,2,5,6,9,10,11,12,3,4,13,14,15,16,7,8)]
# set up plot
plot( NULL , xlim=c(1,16) , ylim=c(0,130) , xlab="" ,
      ylab="Trials to reverse" , xaxt="n" , yaxt="n" )
axis( 2 , at=c(0,25,50,75,100) , labels=c(0,25,50,75,100) )
abline( h=25 , lty=2, col="grey90" )
abline( h=50 , lty=2, col="grey90" )
abline( h=75 , lty=2, col="grey90" )
abline( h=100 , lty=2, col="grey90" )
abline( h=120 , lty=1 )
for ( j in 1:8 ) abline( v=(j*2+0.5) , lwd=0.5 )
improvementdatabirds<-improvementdata[c(1,3,5,6,2,7,8,4),]$Bird
for ( j in 1:8 ) text( (j-1)*2+1.5 , 125 , improvementdatabirds[j] , xpd=TRUE )
xo <- 0.01 # offset distance to stagger raw data and predictions
# raw data
for ( j in (1:8) ) {
  lines( (j-1)*2+c(1,2)-xo , pl[j,c(1,2)] , lwd=2 , col=rangi2 )
}
points( 1:16-xo , t(pl) , pch=16 , col="white" , cex=1.7 )
points( 1:16-xo , t(pl) , pch=c(1,16,1,16) , col=rangi2 , lwd=2 )
yoff <- 12
text( 1+0.8 , pl[1,1]+1 , "Observed in first" , pos=1 , cex=0.8, col=rangi2 )
text( 2-0.9 , pl[1,2]-2 , "Observed in last" , pos=3 , cex=0.8 , col=rangi2)
text( 2-0.7 , pl[1,2]-12 , "Model estimate" , pos=3 , cex=0.8 , col="black")

# posterior predictions
for ( j in (1:8) ) {
  lines( (j-1)*2+c(1,2)+xo , p_mu[(j-1)*2+c(1,2)]*sd(c(improvementdata$TrialsFirstReversal,improvementdata$TrialsLastReversal))+
}
for ( i in 1:16 ) lines( c(i,i)+xo , p_ci[,i]*sd(c(improvementdata$TrialsFirstReversal,improvementdata$TrialsLastReversal))+
points( 1:16+xo , p_mu*sd(c(improvementdata$TrialsFirstReversal,improvementdata$TrialsLastReversal))+mean(p_ci[,1]) )
points( 1:16+xo , p_mu*sd(c(improvementdata$TrialsFirstReversal,improvementdata$TrialsLastReversal))+mean(p_ci[,2]) )

# We can similarly check whether phi and lambda changed between the first and the last reversal, and agree with our model estimates
# Phi increases for the manipulated birds by +0.02 - +0.05, whereas lambda decreases by -1.63 - -0.56. For the raw data, the changes are much smaller
dat_change_phi <- list(
  phi = c(improvementdata$beginningphi,improvementdata$manipulatedphi),
  bird = c(as.integer(as.factor(improvementdata$Bird)),as.integer(as.factor(improvementdata$Bird)))
  reversal = c(rep(1,nrow(improvementdata)),rep(2,nrow(improvementdata)))
)

```

```

)
mchangephi <- ulam(
  alist(
    phi ~ normal( mu , sigma ),
    mu <- a_bird[bird] + b_bird[bird]*reversal,
    c(a_bird,b_bird)[bird] ~ multi_normal( c(a,b) , Rho , sigma_bird ),
    a ~ normal(5,2),
    b ~ normal(-1,0.5),
    sigma_bird ~ exponential(1),
    sigma ~ exponential(1),
    Rho ~ lkj_corr(2)
  ) , data=dat_change_phi , chains=4 , cores=4,iter=10000 )
precis(mchangephi,depth=4)

post <- extract.samples(mchangephi)
dens( post$Rho[,1,2] , xlim=c(-1,1) ) # posterior
R <- rlkjcorr( 1e4 , K=2 , eta=2 )      # prior
dens( R[,1,2] , add=TRUE , lty=2 )

HPDI( post$Rho[,1,2],0.5 )

# The phis of the individuals from their first reversal are not correlated with the phis from their last
dat_phi_correlated<-list(
  phifirst = improvementdata$beginningph,
  philast = standardize(improvementdata$manipulatedphi)
)

mchangephi_correlated <- ulam(
  alist(
    phifirst ~ normal( mu , sigma ),
    mu <- a*philast,
    a ~ normal(0,1),
    sigma ~ exponential(1)
  ) , data=dat_phi_correlated , chains=4 , cores=4,iter=10000,cmdstan=T )

precis(mchangephi_correlated)
#      mean   sd  5.5% 94.5% n_eff Rhat4
#a     0.01 0.02 -0.03  0.04  7519      1
#sigma 0.06 0.02  0.03  0.09  6230      1

dat_change_lambda <- list(
  lambda = c(improvementdata$beginninglambda,improvementdata$manipulatedlambda),
  bird = c(as.integer(as.factor(improvementdata$Bird)),as.integer(as.factor(improvementdata$Bird))),
  reversal = c(rep(1,nrow(improvementdata)),rep(2,nrow(improvementdata)))
)

```

```

mchangelambda <- ulam(
  alist(
    lambda ~ normal( mu , sigma ),
    mu <- a_bird[bird] + b_bird[bird]*reversal,
    c(a_bird,b_bird)[bird] ~ multi_normal( c(a,b) , Rho , sigma_bird ),
    a ~ normal(5,2),
    b ~ normal(-1,0.5),
    sigma_bird ~ exponential(1),
    sigma ~ exponential(1),
    Rho ~ lkj_corr(2)
  ) , data=dat_change_lambda , chains=4 , cores=4 )

precis(mchangelambda,depth=2)

post <- extract.samples(mchangelambda)
dens( post$Rho[,1,2] , xlim=c(-1,1) ) # posterior
R <- rlkjcorr( 1e4 , K=2 , eta=2 ) # prior
dens( R[,1,2] , add=TRUE , lty=2 )
HPDI(post$Rho[,1,2],0.5)

# Both phi and lambda change during the manipulation. Is there a systematic change in how birds attempt
# We can see that the manipulation changes both phi and lambda, so that across all values there is a ne

dat_change_phi_correlated_lambda <- list(
  lambda = c(improvementdata$beginninglambda,improvementdata$manipulatedlambda,singlereversaldata$b
  reversal = c(rep(1,nrow(improvementdata)),rep(2,nrow(improvementdata)),rep(3,nrow(singlereversalda
  phi = standardize(c(improvementdata$beginningphi,improvementdata$manipulatedphi,singlereversaldata
  )

mchangelambda <- ulam(
  alist(
    lambda ~ normal( mu , sigma ),
    mu <- a[reversal]+b[reversal]*phi ,
    a[reversal] ~ normal(5,2),
    b[reversal] ~ normal(0,5),
    sigma ~ exponential(1)
  ) , data=dat_change_phi_correlated_lambda , chains=4 , cores=4 )

precis(mchangelambda,depth=2)
#               mean   sd  5.5% 94.5% n_eff Rhat4
# a[manipulated first] 4.04 0.30  3.57  4.54  1515     1
# a[manipulated last]  4.96 0.74  3.82  6.14   893     1
# a[control]           4.14 0.24  3.76  4.50  1535     1
# b[manipulated first] -0.62 0.32 -1.13 -0.12  1159     1
# b[manipulated last] -2.01 0.78 -3.28 -0.77   835     1
# b[control]            0.18 0.24 -0.20  0.57  1716     1
# sigma                 0.77 0.12  0.61  0.97  1275     1

# 2a) is improvement in trials to reverse linked to improvement in
# phi and/or lambda?

```

```

improvementdata$performanceimprovement <- improvementdata$TrialsFirstReversal -
  improvementdata$TrialsLastReversal

dat_improvement <- list(lambdaimprovement = standardize(as.numeric(improvementdata$lambdaimprovement)),
  phiimprovement = standardize(as.numeric(improvementdata$phiimprovement)),
  performanceimprovement = as.integer(improvementdata$performanceimprovement))

mimprovementboth <- ulam(alist(performanceimprovement ~ dnorm(mu, sigma),
  mu <- a + b * phiimprovement + c * lambdaimprovement, a ~ dnorm(40,
  10), b ~ dnorm(0, 10), c ~ dnorm(0, 10), sigma ~ dexp(1)), data = dat_improvement,
  chains = 4, log_lik = TRUE, messages = FALSE)
precis(mimprovementboth, depth = 2)

# Changes in both phi (11, 6-15) and lambda (6, 1-10) appear
# associated with the changes in the number of trials needed to
# reverse a preference. The estimate for phi is however twice as high
# as the estimate for lambda (both are standardized)

# Before we saw that how much a bird improves depends on where they
# started off from - birds that needed more trials in the first
# reversal improved more than birds that needed fewer trials
# initially. However, it appeared that the birds that needed more
# trials initially did not fully catch up. So we want to see whether
# there are consistent individual differences, where the starting
# point of a bird influences where they end up, both potentially
# influenced by their phi and lambda. We can now try to bring it all
# together in one model.

# This model shows that trials needed in the last reversal is
# influenced by trials in the first reversal and trials in the first
# reversals are influenced by the initial phi of an bird. No other
# links appear.

dat_allchanges <- list(TrialsLast = standardize(improvementdata$TrialsLastReversal),
  TrialsFirst = standardize(improvementdata$TrialsFirstReversal), philast = standardize(improvementdata$beginningphi),
  lambdalast = standardize(improvementdata$lastlambda), phifirst = standardize(improvementdata$beginningphi),
  lambdafirst = standardize(improvementdata$beginninglambda))

mallchanges <- ulam(alist(TrialsLast ~ dnorm(mutrialslast, sigmaltrialslast),
  mutrialslast <- x * TrialsFirst + a * philast + b * lambdalast, TrialsFirst ~
  dnorm(mutrialsfirst, sigmatrialsfirst), mutrialsfirst <- c * phifirst +
  d * lambdafirst, philast ~ dnorm(muphilast, sigmaphilast), muphilast <- e *
  phifirst, lambdalast ~ dnorm(mulambda, sigmalambda), mulambda <- f *
  lambdafirst, x ~ dnorm(0, 1), a ~ dnorm(0, 1), b ~ dnorm(0, 1),
  c ~ dnorm(0, 1), d ~ dnorm(0, 1), e ~ dnorm(0, 1), f ~ dnorm(0, 1),
  sigmaltrialslast ~ dexp(1), sigmatrialsfirst ~ dexp(1), sigmaphilast ~
  dexp(1), sigmalambda ~ dexp(1)), data = dat_allchanges, chains = 4,
  log_lik = TRUE, messages = FALSE)

precis(mallchanges, depth = 2)

# mean sd 5.5% 94.5% n_eff Rhat4 x 0.62 0.36 0.04 1.17 1166 1 a -0.28

```

```

# 0.51 -1.07 0.54 1095 1 b -0.22 0.48 -0.98 0.55 1278 1 c -1.04 0.15
# -1.26 -0.80 1059 1 d -0.18 0.16 -0.41 0.06 890 1 e 0.29 0.37 -0.31
# 0.86 1696 1 f 0.19 0.38 -0.41 0.79 1806 1 sigmaltrialslast 0.85
# 0.28 0.52 1.33 1185 1 sigmatrialsfirst 0.33 0.13 0.19 0.52 778 1
# sigmaphilast 1.03 0.29 0.67 1.56 1283 1 sigmalambdalast 1.06 0.29
# 0.70 1.59 1824 1

# We now want to know whether the number of trials a bird needed in
# either the initial or the last reversal is influenced more by phi
# or more by lambda. The results indicate that phi is more related to
# the number of trials - lambda is more related to when birds make
# 'mistakes', whether at the beginning (high lambda) or throughout
# (low lambda). So the manipulation makes birds less fixated on small
# differences (smaller lambda) because they now quickly vote one
# option up or down (larger phi)

dat_trialsphiandlambda <- list(Trials = c(improvementdata$TrialsFirstReversal,
    improvementdata$TrialsLastReversal, singlereversaldata$TrialsFirstReversal),
    bird = c(as.numeric(as.factor(improvementdata$Bird)), as.numeric(as.factor(improvementdata$Bird)),
        9:19), phi = standardize(c(improvementdata$beginningphi, improvementdata$lastphi,
        singlereversaldata$beginningphi)), lambda = standardize(c(improvementdata$beginninglambda,
        improvementdata$lastlambda, singlereversaldata$beginninglambda)))

trials.phiandlambda <- ulam(alist(Trials ~ normal(mu, sigma), mu <- a +
    b * phi + c * lambda, a ~ normal(70, 40), b ~ normal(0, 20), c ~ normal(0,
    20), sigma ~ exponential(1)), data = dat_trialsphiandlambda, chains = 4,
    cores = 4, iter = 10000)

precis(trials.phiandlambda, depth = 2)

# mean sd 5.5% 94.5% n_eff Rhat4 a 65.34 2.69 61.04 69.60 19803 1 b
# -23.38 2.98 -28.15 -18.62 18077 1 c -0.04 2.98 -4.83 4.75 19159 1
# sigma 13.88 1.53 11.66 16.51 19522 1

# Given that phi and lambda are negatively correlated, bird with
# intermediate values might do best on other tasks

# For plotting

combinedreversaldata$TrialsLastButOneReversal <- NA
for (i in 1:length(unique(combinedreversaldata$Bird))) {
    combinedreversaldata[combinedreversaldata$Bird == unique(combinedreversaldata$Bird)[i],
        ]$TrialsLastButOneReversal <- max((filter(dflex, ID == unique(combinedreversaldata$Bird)[i],
            Reversal == max(dflex[dflex$ID == unique(combinedreversaldata$Bird)[i],
                ]$Reversal) - 1))$Trial)
}

improvementdata <- combinedreversaldata[is.na(combinedreversaldata$manipulatedphi) ==
    F, ]

improvementdata$phiimprovement <- improvementdata$lastphi - improvementdata$beginningphi

```

```

improvementdata$lambda_improvement <- improvementdata$last_lambda - improvementdata$beginning_lambda
improvementdata$performance_improvement <- improvementdata$TrialsFirstReversal -
  improvementdata$TrialsLastReversal

singlereversaldata <- combinedreversaldata[is.na(combinedreversaldata$manipulated_phi) ==
  T, ]
singlereversaldata <- singlereversaldata[is.na(singlereversaldata$TrialsFirstReversal) ==
  F, ]

library(cowplot)

## Plotting trials across a switch (initial = initial association
## learning plus first reversal; manipulated = last two reversals) -
## with this the phi and lambda match more closely the performance
## but the changes are not as clearly visible
dat_for_plotting_reversals <- list(trials = c(singlereversaldata$TrialsFirstReversal +
  singlereversaldata$"Trials to learn", improvementdata$TrialsFirstReversal +
  improvementdata$"Trials to learn", improvementdata$TrialsLastReversal +
  improvementdata$TrialsLastButOneReversal), bird = c(as.integer(as.factor(singlereversaldata$Bird)) +
  max(as.integer(as.factor(improvementdata$Bird))), as.integer(as.factor(improvementdata$Bird)),
  as.integer(as.factor(improvementdata$Bird))), reversal = c(rep("initial",
  nrow(singlereversaldata)), rep("initial", nrow(improvementdata)), rep("manipulated",
  nrow(improvementdata)), reversal_for_sorting = c(singlereversaldata$TrialsFirstReversal +
  singlereversaldata$"Trials to learn", improvementdata$TrialsFirstReversal +
  improvementdata$"Trials to learn", improvementdata$TrialsFirstReversal +
  improvementdata$"Trials to learn"))

dat_for_plotting_reversals <- as.data.frame(dat_for_plotting_reversals)
dat_for_plotting_reversals <- arrange(dat_for_plotting_reversals, reversal_for_sorting,
  bird)
dat_for_plotting_reversals$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_reversals)) {
  if (dat_for_plotting_reversals[i, ]$reversal == "initial") {
    count <- count + 1
  }
  dat_for_plotting_reversals[i, ]$plotid <- count
}

trialsplot <- dat_for_plotting_reversals %>%
  ggplot(aes(plotid, trials)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 280) + scale_colour_manual(values = c("#
  "#56B4E9")) + theme(axis.line = element_blank(), axis.text.x = element_blank(),
  axis.title.x = element_blank(), axis.title.y = element_blank()) + theme(plot.margin = unit(c(2,
  1, 2, 2), "lines"))

dat_for_plotting_phi <- list(phi = c(singlereversaldata$beginning_phi, improvementdata$beginning_phi,
  improvementdata$manipulated_phi), bird = c(as.integer(as.factor(singlereversaldata$Bird)) +
  max(as.integer(as.factor(improvementdata$Bird))), as.integer(as.factor(improvementdata$Bird)),
  as.integer(as.factor(improvementdata$Bird))), reversal = c(rep("initial",
  nrow(singlereversaldata)), rep("initial", nrow(improvementdata)), rep("manipulated",
  nrow(improvementdata)), reversal_for_sorting = c(singlereversaldata$TrialsFirstReversal +

```

```

singlereversaldata$"Trials to learn", improvementdata$TrialsFirstReversal +
improvementdata$"Trials to learn", improvementdata$TrialsFirstReversal +
improvementdata$"Trials to learn"))

dat_for_plotting_phi <- as.data.frame(dat_for_plotting_phi)
dat_for_plotting_phi <- arrange(dat_for_plotting_phi, reversalforsorting,
                                bird)
dat_for_plotting_phi$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_phi)) {
  if (dat_for_plotting_phi[i, ]$reversal == "initial") {
    count <- count + 1
  }
  dat_for_plotting_phi[i, ]$plotid <- count
}

phiplot <- dat_for_plotting_phi %>%
  ggplot(aes(plotid, phi)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 0.125) +
  scale_colour_manual(values = c("#E69F00", "#56B4E9")) + theme(axis.line = element_blank(),
  axis.text.x = element_blank(), axis.title.x = element_blank(), axis.title.y = element_blank()) +
  theme(plot.margin = unit(c(2, 1, 2, 2), "lines"))

dat_for_plotting_lambda <- list(lambda = c(singlereversaldata$beginninglambda,
                                             improvementdata$beginninglambda, improvementdata$manipulatedlambda),
                                  bird = c(as.integer(as.factor(singlereversaldata$Bird)) + max(as.integer(as.factor(improvementdata$Bird)),
                                             as.integer(as.factor(improvementdata$Bird))), as.integer(as.factor(improvementdata$Bird))),
                                  reversal = c(rep("initial", nrow(singlereversaldata)), rep("initial",
                                             nrow(improvementdata)), rep("manipulated", nrow(improvementdata))),
                                  reversalforsorting = c(singlereversaldata$TrialsFirstReversal + singlereversaldata$"Trials to learn",
                                             improvementdata$TrialsFirstReversal + improvementdata$"Trials to learn",
                                             improvementdata$TrialsFirstReversal + improvementdata$"Trials to learn"))

dat_for_plotting_lambda <- as.data.frame(dat_for_plotting_lambda)
dat_for_plotting_lambda <- arrange(dat_for_plotting_lambda, reversalforsorting,
                                    bird)
dat_for_plotting_lambda$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_lambda)) {
  if (dat_for_plotting_lambda[i, ]$reversal == "initial") {
    count <- count + 1
  }
  dat_for_plotting_lambda[i, ]$plotid <- count
}

lambdaplot <- dat_for_plotting_lambda %>%
  ggplot(aes(plotid, lambda)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 7.5) + scale_colour_manual(values = c("#
  "#56B4E9")) + theme(axis.line = element_blank(), axis.text.x = element_blank(),
  axis.title.x = element_blank(), axis.title.y = element_blank()) + theme(plot.margin = unit(c(2,
  1, 2, 3.5), "lines"))

```

```

plot_grid(trialsplot, phiplot, lambdaplot, labels = c("a) Trials to reverse",
  "b) Estimated phi", "c) Estimated lambda"), label_x = 0.31, label_size = 20,
  hjust = -0.05, ncol = 1, rel_heights = c(1, 1, 1))

## Plotting trials only for first reversal (initial) or for last
## reversal (manipulated) - with this the phi and lambda might not
## fully reflect the performance but the changes are more clearly
## visible.
dat_for_plotting_reversals <- list(trials = c(singlereversaldata$TrialsFirstReversal,
  improvementdata$TrialsFirstReversal, improvementdata$TrialsLastReversal),
  bird = c(as.integer(as.factor(singlereversaldata$Bird)) + max(as.integer(as.factor(improvementdata$Bird))),
  as.integer(as.factor(improvementdata$Bird)), as.integer(as.factor(improvementdata$Bird))),
  reversal = c(rep("initial", nrow(singlereversaldata)), rep("initial",
  nrow(improvementdata)), rep("manipulated", nrow(improvementdata))),
  reversalforsorting = c(singlereversaldata$TrialsFirstReversal, improvementdata$TrialsFirstReversal,
  improvementdata$TrialsFirstReversal))

dat_for_plotting_reversals <- as.data.frame(dat_for_plotting_reversals)
dat_for_plotting_reversals <- arrange(dat_for_plotting_reversals, reversalforsorting,
  bird)
dat_for_plotting_reversals$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_reversals)) {
  if (dat_for_plotting_reversals[i, ]$reversal == "initial") {
    count <- count + 1
  }
  dat_for_plotting_reversals[i, ]$plotid <- count
}

trialsplot <- dat_for_plotting_reversals %>%
  ggplot(aes(plotid, trials)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 180) + scale_colour_manual(values = c("#
  "#56B4E9")) + theme(axis.line = element_blank(), axis.text.x = element_blank(),
  axis.title.x = element_blank(), axis.title.y = element_blank()) + theme(plot.margin = unit(c(2,
  1, 2, 2), "lines"))

dat_for_plotting_phi <- list(phi = c(singlereversaldata$beginningphi, improvementdata$beginningphi,
  improvementdata$manipulatedphi), bird = c(as.integer(as.factor(singlereversaldata$Bird)) +
  max(as.integer(as.factor(improvementdata$Bird))), as.integer(as.factor(improvementdata$Bird)),
  as.integer(as.factor(improvementdata$Bird))), reversal = c(rep("initial",
  nrow(singlereversaldata)), rep("initial", nrow(improvementdata)), rep("manipulated",
  nrow(improvementdata))), reversalforsorting = c(singlereversaldata$TrialsFirstReversal,
  improvementdata$TrialsFirstReversal, improvementdata$TrialsFirstReversal))

dat_for_plotting_phi <- as.data.frame(dat_for_plotting_phi)
dat_for_plotting_phi <- arrange(dat_for_plotting_phi, reversalforsorting,
  bird)
dat_for_plotting_phi$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_phi)) {
  if (dat_for_plotting_phi[i, ]$reversal == "initial") {

```

```

    count <- count + 1
  }
  dat_for_plotting_phi[i, ]$plotid <- count
}

phiplot <- dat_for_plotting_phi %>%
  ggplot(aes(plotid, phi)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 0.125) +
  scale_colour_manual(values = c("#E69F00", "#56B4E9")) + theme(axis.line = element_blank(),
  axis.text.x = element_blank(), axis.title.x = element_blank(), axis.title.y = element_blank()) +
  theme(plot.margin = unit(c(2, 1, 2, 2), "lines"))

# NOTE: take inverse of lambda to make it rate of deviation. With
# inverse, larger values means you deviate more from the learned
# associations.

dat_for_plotting_lambda <- list(lambda = c(singlereversaldata$beginninglambda,
  improvementdata$beginninglambda, improvementdata$manipulatedlambda),
  bird = c(as.integer(as.factor(singlereversaldata$Bird)) + max(as.integer(as.factor(improvementdata$Bird)),
    as.integer(as.factor(improvementdata$Bird))), as.integer(as.factor(improvementdata$Bird))),
  reversal = c(rep("initial", nrow(singlereversaldata)), rep("initial",
    nrow(improvementdata)), rep("manipulated", nrow(improvementdata))),
  reversalforsorting = c(singlereversaldata$TrialsFirstReversal, improvementdata$TrialsFirstReversal,
  improvementdata$TrialsFirstReversal))

dat_for_plotting_lambda <- as.data.frame(dat_for_plotting_lambda)
dat_for_plotting_lambda <- arrange(dat_for_plotting_lambda, reversalforsorting,
  bird)
dat_for_plotting_lambda$plotid <- NA
count <- 0
for (i in 1:nrow(dat_for_plotting_lambda)) {
  if (dat_for_plotting_lambda[i, ]$reversal == "initial") {
    count <- count + 1
  }
  dat_for_plotting_lambda[i, ]$plotid <- count
}

lambdaplot <- dat_for_plotting_lambda %>%
  ggplot(aes(plotid, lambda)) + geom_point(aes(color = reversal), size = 4) +
  geom_line(aes(group = bird), color = "darkgrey") + ylim(0, 7.5) + scale_colour_manual(values = c("#
  "#56B4E9")) + theme(axis.line = element_blank(), axis.text.x = element_blank(),
  axis.title.x = element_blank(), axis.title.y = element_blank()) + theme(plot.margin = unit(c(2,
  1, 2, 3.5), "lines"))

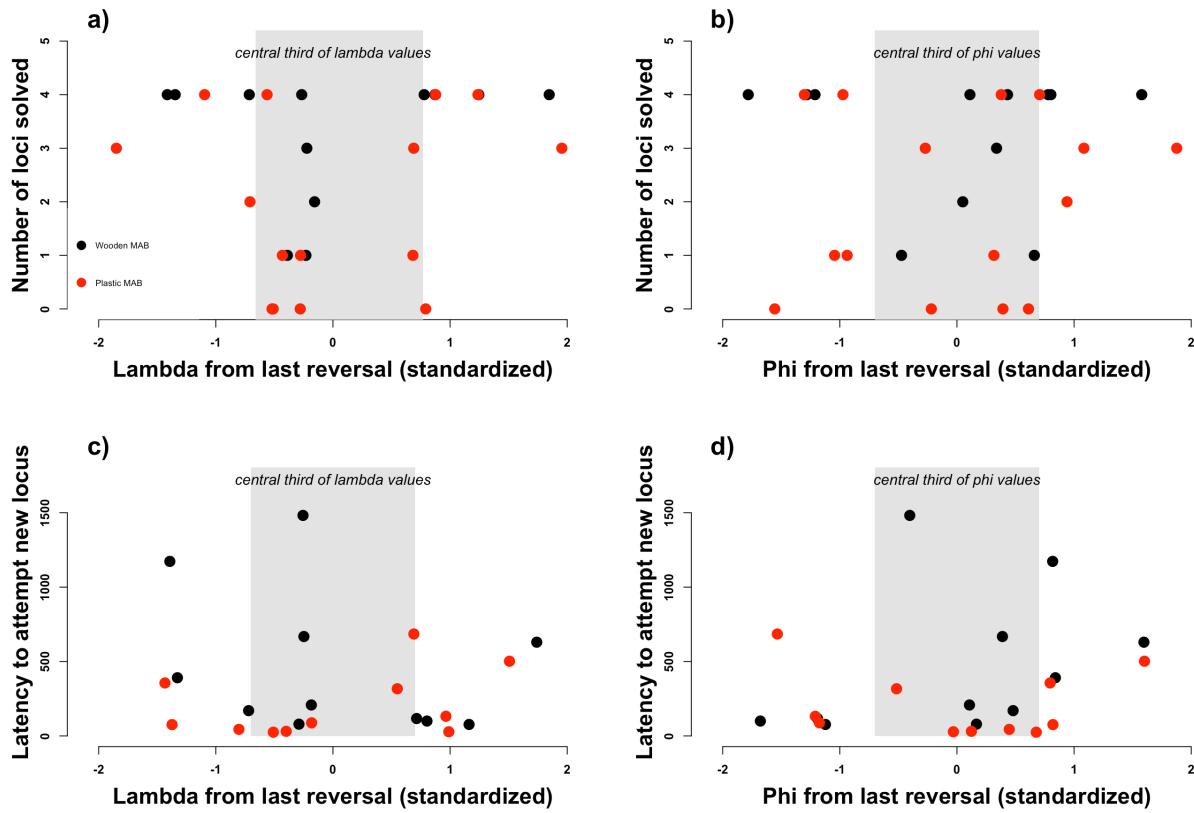
plot_grid(trialsplot, phiplot, lambdaplot, labels = c("a) Trials to reach association criterion",
  "b) Phi: rate of updating learned attractions", "c) Lambda: rate of deviating from learned attractions"),
  label_x = 0.05, label_size = 20, hjust = -0.05, ncol = 1, rel_heights = c(1,
  1, 1))

```

687 3) Association between ϕ and λ with performance on the multi-access boxes We modified the
 688 analyses from the Results section that assessed potential links between reversal learning and performance
 689 on the multi-access boxes by replacing the number of trials it took individuals to reverse with ϕ (rate of

690 updating previous attractions) and λ (rate of deviation from learned attractions) estimated from the reversal
691 performances. The modified analyses aligned only with one of the three previously detected correlations
692 between reversal learning and the performance on the two multi-access boxes and they indicated no additional
693 correlations. The latency to attempt a new locus on the wooden multi-access box was positively correlated
694 with ϕ in the last reversal, indicating that individuals who were faster to update their associations in reversal
695 learning (higher ϕ , therefore need fewer trials in their last reversal) take more time to attempt a new locus.
696 As mentioned above, we are not sure what the latency to attempt a new locus reflects. Even though ϕ
697 is closely associated with the number of trials a bird needs to reach the reversal criterion, we presumably
698 could not recover the other two correlations (latency to attempt a locus on the plastic multi-access box;
699 number of loci solved on the plastic multi-access box) because of our small sample sizes. In addition, we
700 estimated ϕ and λ across at least one reversal (initial discrimination plus first reversal or last two reversals
701 for manipulated birds), whereas the previous analyses using the number of trials to reverse were based on a
702 single reversal (first or last reversal).

703 For the manipulated birds, we found that during their last reversal there was a negative correlation between
704 ϕ and λ , with individuals with higher ϕ values also showing higher λ values. If birds can reach a solution on
705 the multi-access boxes with either of these abilities, we might expect that it will be birds with intermediate
706 values who perform worse. We might also expect that birds with intermediate values potentially perform
707 worse on the multi-access boxes because in this scenario: birds can learn that a previous option is no longer
708 rewarded while exploring new options. Therefore, birds that either quickly devalue options or are likely to
709 deviate from previous attractions might be more likely to attempt a new locus faster. Our data shows that,
710 for the number of loci solved on both the plastic and the wooden multi-access boxes, there is a U-shaped
711 association, particularly with λ values in the last reversal (Figure 10), with birds with intermediate values
712 of λ solving fewer loci on the plastic and the wooden multi-access boxes. For the latency to attempt a new
713 locus, there is also a U-shaped association, particularly with ϕ , with birds with intermediate phis showing
714 shorter latencies to attempt a new locus. Given that there is a positive correlation between number of loci
715 solved and the latency to attempt a new locus, there might be a trade off, where birds with extreme phis and
716 lambdas solve more loci, but need more time, whereas birds with intermediate values have shorter latencies,
717 but solve fewer loci.



718

719 **Figure 10.** Relationships between phi and lambda from the last reversal and performance on the wooden
 720 (black dots) and plastic (red dots) multi-access boxes. Birds with intermediate λ values during their last
 721 reversal (a) are less likely to solve all four loci on the multi-access boxes than birds with either high or low
 722 λ values. Birds who solved two or fewer loci on either box all fall within the central third of the λ values
 723 observed for the last reversal, while 12 of the 14 birds who solved all four loci fall outside this central range. λ
 724 values do not perfectly match between the two boxes (wooden [black dots] and plastic [red dots] multi-access
 725 boxes [MAB]) because not all individuals were tested on both boxes, which lead to slight shifts during the
 726 standardization of the λ values. There are no clear relationships between lambda and (b) the latency to
 727 attempt a locus, or between phi and either (c) the number of loci solved or (d) the latency to attempt a new
 728 locus.

```

library(rstan)
library(rethinking)
library(cmdstanr)
library(posterior)
library("Rcpp")
library(ggplot2)

# if you have cmdstan installed, use the following:
# set_ufam_cmdstan(TRUE)

### Now we can link the phi and lambda values we extracted for each bird to the various parameters that

# First, we link it to the latency to switch loci on the plastic multi-access box

d3 <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))
  
```

```

d3 <- data.frame(d3)
colnames(d3) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal", "TrialsLastReversal", "Re

# n=11: 5 in manipulated group, 6 in control group
#length(d3$AverageLatencyAttemptNewLocusMABplastic)

# make Batch a factor
d3$Batch <- as.factor(d3$Batch)

# Need to fix spelling mistake in a bird name to match it to the other data
d3[d3$Bird=="Huachinago",]$Bird<-"Huachinango"

d3_match<- subset(d3, d3$Bird != "Memela")
d3_match <- d3_match[with(d3_match, order(d3_match$Bird)), ]

eachbirdslearningparameters<-read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/eachbird

library(dplyr)
combinedreversaldata<-left_join(d3_match,eachbirdslearningparameters,by="Bird")

# Sort birds alphabetically, so the birds are always in the same order in both data sets and the model
combinedreversaldata <- combinedreversaldata[with(combinedreversaldata, order(combinedreversaldata$Bird))

# Store the bird names in case we want to link their data from here back to other datasets
birdnames<-unique(combinedreversaldata$Bird)

# MODEL phi lat plastic:
# First, we link the latency to attempt a new locus on the plastic multi-access box to phi (updating of

# Keep only birds who finished the task
inputdata_philatencyplastic <- subset(combinedreversaldata,!is.na(combinedreversaldata["AverageLatency

# Based on last reversal

dl_phi <- list(learningphi = standardize(as.numeric(inputdata_philatencyplastic$lastphi)),
               latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic)
               )

mplat1alternative1 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat1alternative1,depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a    4.99 0.31  4.51  5.48  1354     1
# b   -0.07 0.24 -0.45  0.31  1769     1
# phi  0.80 0.31  0.39  1.34  1527     1

```

```

# The parameter b estimates the association between phi and the latency. It's compatibility in

dl_lambda <- list(learninglambda = standardize(as.numeric(inputdata_philatencyplastic$lastlambda),
                                              latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic),
                                              batch = as.integer(inputdata_philatencyplastic$Batch)
                                              )

mplat1alternative2 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat1alternative2, depth=2)

#      mean   sd 5.5% 94.5% n_eff Rhat4
# a    4.97 0.30  4.5  5.46  1547     1
# b    0.32 0.27 -0.1  0.74  1260     1
# phi 0.87 0.34  0.4  1.46  1425     1

# The parameter b estimates the association between lambda and the latency. It's compatibility in

dl_lambda_phi <- list(learninglambda = standardize(as.numeric(inputdata_philatencyplastic$lastlambda),
                                                 learningphi = standardize(as.numeric(inputdata_philatencyplastic$lastphi)),
                                                 latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic),
                                                 batch = as.integer(inputdata_philatencyplastic$Batch)
                                                 )

mplat1alternative3 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda + c * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  c ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat1alternative3, depth=2)

#      mean   sd 5.5% 94.5% n_eff Rhat4
# a    4.99 0.31  4.52  5.46  1183     1
# b    0.33 0.27 -0.09  0.76  1736     1
# c    -0.01 0.26 -0.41  0.42  1556     1
# phi 0.83 0.32  0.39  1.42  1321     1

dl_lambda_phi <- list(learninglambda = standardize(as.numeric(inputdata_philatencyplastic$lastlambda),
                                                 learningphi = standardize(as.numeric(inputdata_philatencyplastic$lastphi)),
                                                 latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic),
                                                 batch = as.integer(inputdata_philatencyplastic$Batch)
                                                 )
  
```

```

mplat1alternative4 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat1alternative4, depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  5.02 0.31  4.51  5.49   886     1
# b  0.07 0.21 -0.25  0.42  1256     1
# phi 0.80 0.30  0.39  1.33  1493     1

# Is there a U-shaped association with birds with intermediate values performing differently?
dl_lambda_phi_U <- list(learninglambda = abs(stdize(as.numeric(inputdata_philatencyplastic$lambda)),
                           learningphi = abs(stdize(as.numeric(inputdata_philatencyplastic$lastphi)),
                                              latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic),
                                              batch = as.integer(inputdata_philatencyplastic$Batch)
                           )
)

mplat1alternative5 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda + c * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  c ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi_U, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat1alternative5, depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  3.07 0.52  2.29  3.91  1210  1.01
# b  0.82 0.53 -0.02  1.68  1353  1.00
# c  1.49 0.47  0.76  2.27  1226  1.00
# phi 1.27 0.48  0.61  2.12  1456  1.00

# Based on first reversal

dl_phi <- list(learningphi = stdize(as.numeric(inputdata_philatencyplastic$beginningphi)),
                latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic)
               )

mplat2alternative1 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1)
))

```

```

    b ~ dnorm(0, 1),
    phi ~ dexp(1)
  ), data = dl_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat2alternative1,depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  4.97 0.30  4.49  5.44  1105     1
# b  0.16 0.26 -0.24  0.60  1376     1
# phi 0.80 0.30  0.39  1.32  1218     1

dl_lambda <- list(learninglambda = standardize(as.numeric(inputdata_philatencyplastic$beginninglatency),
                                                latency = as.integer(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic),
                                                batch = as.integer(inputdata_philatencyplastic$Batch)
                                              )

mplat2alternative2 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda, chains=4, log_lik = TRUE, messages = FALSE)

precis(mplat2alternative2,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  4.95 0.34  4.40  5.47  1284     1
# b  0.20 0.44 -0.53  0.88  1334     1
# phi 0.80 0.34  0.36  1.41  1614     1

# MODEL phi lat wooden:
# Second, we link the latency to attempt a new locus on the wooden multi-access box to phi (updating of

inputdata_philatencywooden<-combinedreversaldata[is.na(combinedreversaldata$AverageLatencyAttemptNewLocusMABwooden),
                                                 c("AverageLatencyAttemptNewLocusMABwooden", "latency")]

# Based on last reversal

dl_phi <- list(learningphi = standardize(as.numeric(inputdata_philatencywooden$lastphi)),
               latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden),
               batch = as.integer(inputdata_philatencywooden$Batch)
             )

mwood1alternative1 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood1alternative1,depth=2)

```

```

#      mean   sd 5.5% 94.5% n_eff Rhat4
# a    5.73 0.28 5.27  6.15  1064     1
# b    0.47 0.30 0.00  0.94  1144     1
# phi 1.06 0.44 0.48  1.86  1364     1
# The parameter b estimates the association between phi and the latency. It's compatibility int

dl_lambda <- list(learninglambda = standardize(as.numeric(inputdata_philatencywooden$lastlambda),
                                                latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden),
                                                batch = as.integer(inputdata_philatencywooden$Batch)
                                               )

mwood1alternative2 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood1alternative2, depth=2)

      mean   sd 5.5% 94.5% n_eff Rhat4
#      mean   sd 5.5% 94.5% n_eff Rhat4
# a    5.76 0.30 5.28  6.21  1373     1
# b   -0.25 0.25 -0.63  0.16  1415     1
# phi  0.96 0.37 0.45  1.62  1532     1

# The parameter b estimates the association between lambda and the latency. It's compatibility int

dl_lambda_phi <- list(learninglambda = standardize(as.numeric(inputdata_philatencywooden$lastlambda),
                                                    learningphi = standardize(as.numeric(inputdata_philatencywooden$lastphi)),
                                                    latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden),
                                                    batch = as.integer(inputdata_philatencywooden$Batch)
                                                   )

mwood1alternative3 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda + c * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  c ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood1alternative3, depth=2)

      mean   sd 5.5% 94.5% n_eff Rhat4
# a    5.72 0.28 5.27  6.16  1174     1
# b   -0.29 0.28 -0.73  0.15  1712     1
# c    0.47 0.29 0.01  0.93  1642     1
# phi  1.07 0.45 0.49  1.89  1642     1

```



```
dl_lambda_phi <- list(learninglambda = standardize(as.numeric(inputdata_philatencywooden$lastlambda)),
                      learningphi = standardize(as.numeric(inputdata_philatencywooden$lastphi)),
                      latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwood),
                      batch = as.integer(inputdata_philatencywooden$Batch)
                     )

mwood1alternative4 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood1alternative4, depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a    5.80  0.30  5.31  6.23  1259     1
# b    0.15  0.24 -0.22  0.56  1448     1
# phi  0.92  0.35  0.44  1.54  1342     1

# Again, we might expect a U-shaped relationship

dl_lambda_phi_U <- list(learninglambda = abs(standardize(as.numeric(inputdata_philatencywooden$lastlambda)),
                           learningphi = abs(standardize(as.numeric(inputdata_philatencywooden$lastphi))),
                           latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwood),
                           batch = as.integer(inputdata_philatencywooden$Batch)
                          )

mwood1alternative5 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda + c * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  c ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda_phi_U, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood1alternative5, depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a    5.07  0.53  4.20  5.90  739     1
# b    0.68  0.59 -0.23  1.68  867     1
# c    0.39  0.77 -0.81  1.62  931     1
# phi  0.78  0.34  0.34  1.42  932     1

# Based on first reversal

dl_phi <- list(learningphi = standardize(as.numeric(inputdata_philatencywooden$beginningphi)),
                latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwood),
                batch = as.integer(inputdata_philatencywooden$Batch)
               )
```

```

mwood2alternative1 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learningphi,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_phi, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood2alternative1, depth=2)

#      mean   sd  5.5% 94.5% n_eff Rhat4
# a    5.75 0.30  5.27  6.22  1172     1
# b    0.30 0.33 -0.22  0.82  1467     1
# phi  0.95 0.40  0.43  1.65  1216     1

dl_lambda <- list(beginninglambda = standardize(as.numeric(inputdata_philatencywooden$beginninglambda),
                                                 latency = as.integer(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden),
                                                 batch = as.integer(inputdata_philatencywooden$Batch)
                                               )

mwood2alternative2 <- ulam(alist(
  latency ~ dgampois(lambda, phi),
  log(lambda) <- a + b * learninglambda,
  a ~ dnorm(1, 1),
  b ~ dnorm(0, 1),
  phi ~ dexp(1)
), data = dl_lambda, chains=4, log_lik = TRUE, messages = FALSE)

precis(mwood2alternative2, depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
# a    5.76 0.30  5.28  6.21  1250     1
# b   -0.21 0.26 -0.60  0.21  1233     1
# phi  0.94 0.37  0.45  1.59  1537     1

# MODEL phi loci plastic:
# Third, we link the number of loci solved on the plastic multi-access box to phi (updating of attracti

inputdata_philociplastic<-combinedreversaldata[is.na(combinedreversaldata$TotalLociSolvedMABplastic),
                                               

# Exclude Mole and Habanero from this analysis because they were given the put together plastic
inputdata_philociplastic <- inputdata_philociplastic[!inputdata_philociplastic$Bird=="Mole" & !inputdata_philociplastic$Bird=="Habanero"]

# Remove NAs
inputdata_philociplastic <- subset(inputdata_philociplastic,!is.na(inputdata_philociplastic["TotalLociSolvedMABplastic"]))

# n=15

dat <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMABplastic),
            learninglambda = standardize(as.numeric(inputdata_philociplastic$beginninglambda))
          )

```

```

m1plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learninglambda , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m1plasticloci,depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
# a  0.01  0.26 -0.41  0.42  1346      1
# b  0.29  0.23 -0.08  0.66  1536      1


dat <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMABplastic),
            learningphi = standardize(as.numeric(inputdata_philociplastic$beginningphi))
            )
m2plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) ,
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m2plasticloci,depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
# a  0.02  0.26 -0.41  0.42  1313      1
# b  0.20  0.22 -0.16  0.54  1624      1


dat <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMABplastic),
            learninglambda = standardize(as.numeric(inputdata_philociplastic$lastlambda))
            )
m3plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learninglambda , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m3plasticloci,depth=2)
#   mean   sd  5.5% 94.5% n_eff Rhat4
# a  0.00  0.25 -0.40  0.41  1369      1
# b  0.14  0.22 -0.21  0.49  1200      1


dat <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMABplastic),
            learningphi = standardize(as.numeric(inputdata_philociplastic$lastphi))
            )
m4plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept

```

```

    b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m4plasticloci,depth=2)
# mean sd 5.5% 94.5% n_eff Rhat4
# a 0.02 0.30 -0.45 0.50 1153     1
# b 0.24 0.26 -0.16 0.65 1463     1

dat_loci_plastic_both <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMAB),
                                learningphi = standardize(as.numeric(inputdata_philociplastic$lastphi)),
                                learninglambda = standardize(as.numeric(inputdata_philociplastic$lastlambda))
)
m5plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi*learninglambda , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat_loci_plastic_both , chains=4 )

precis(m5plasticloci,depth=2)

# MODEL phi loci wooden:
# Fourth, we link the number of loci solved on the wooden multi-access box to phi (updating of attracti

inputdata_philociwooden<-combinedreversaldata[is.na(combinedreversaldata$TotalLociSolvedMABwooden),
                                               ]
# Remove NAs
inputdata_philociwooden <- subset(inputdata_philociwooden,!is.na(inputdata_philociwooden["TotalLociSolvedMABwooden"]))

# n=12

dat <- list(locisolved = as.numeric(inputdata_philociwooden$TotalLociSolvedMABwooden),
            learninglambda = standardize(as.numeric(inputdata_philociwooden$beginninglambda))
)
miwoodenloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learninglambda , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(miwoodenloci,depth=2)
# mean sd 5.5% 94.5% n_eff Rhat4
#a 1.34 0.33 0.82 1.88 1283     1
#b -0.11 0.27 -0.52 0.32 1111     1

dat <- list(locisolved = as.numeric(inputdata_philociwooden$TotalLociSolvedMABwooden),
            learningphi = standardize(as.numeric(inputdata_philociwooden$beginningphi)))
)

```

```

m2woodenloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m2woodenloci,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  1.34  0.34  0.82  1.91  1259     1
# b  0.05  0.28 -0.37  0.48  1434     1

dat <- list(locisolved = as.numeric(inputdata_philocewooden$TotalLociSolvedMABwooden),
            learninglambda = standardize(as.numeric(inputdata_philocewooden$lastlambda)))
            )

m3woodenloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learninglambda , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m3woodenloci,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  1.34  0.33  0.83  1.87  1566     1
# b  0.20  0.27 -0.24  0.63  1444     1

dat <- list(locisolved = as.numeric(inputdata_philocewooden$TotalLociSolvedMABwooden),
            learningphi = standardize(as.numeric(inputdata_philocewooden$lastphi)))
            )

m4woodenloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

precis(m4woodenloci,depth=2)
#      mean   sd  5.5% 94.5% n_eff Rhat4
# a  1.35  0.34  0.83  1.90  1329     1
# b -0.08  0.27 -0.52  0.37  1268     1

# Phi and lambda are negatively correlated, so we could expect that birds with intermediate values

dat_loci_wooden_both <- list(locisolved = as.numeric(inputdata_philocewooden$TotalLociSolvedMABwooden),
                               learningphi = abs(standardize(as.numeric(inputdata_philocewooden$lastphi))),
                               learninglambda = abs(standardize(as.numeric(inputdata_philocewooden$lastlambda)))
                               )

m6plasticloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a+ b*learningphi , #batch=random effect, standardize trials so 0=mean
  a ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive
) , data=dat , chains=4 )

```

```

logit(p) <- a + b*learningphi+c*learninglambda , #batch=random effect, standardize trials so 0
a ~ dnorm(0,1) , #each batch gets its own intercept
b ~ dnorm(0,0.4),#our prior expectation for b is that it is around 0, can be negative or positive
c ~ dnorm(0,0.4)
) , data=dat_loci_wooden_both , chains=4 )

precis(m6plasticloci,depth=2)

# Create a plot that shows the U-shaped relationship

dat_loci_wooden_both <- list(locisolved = as.numeric(inputdata_philocewooden$TotalLociSolvedMABwooden),
                             learningphi = (standardize(as.numeric(inputdata_philocewooden$lastphi))),
                             learninglambda = (standardize(as.numeric(inputdata_philocewooden$lastlambda)))
                             )

dat_loci_plastic_both <- list(locisolved = as.numeric(inputdata_philociplastic$TotalLociSolvedMABplastic),
                               learningphi = (standardize(as.numeric(inputdata_philociplastic$lastphi))),
                               learninglambda = (standardize(as.numeric(inputdata_philociplastic$lastlambda)))
                               )

par(mfrow=c(2,2))

plot( NULL , xlim=c(-2.1,2.1) , ylim=c(0,5) , cex=2,cex.lab=1.5,font=2 , bty="n",ylab="",xlab="" )
rect(xleft=-0.66,ybottom=-0.5,xright=0.77,ytop=5.5,col="grey90",border="NA")

points(dat_loci_wooden_both$locisolved~dat_loci_wooden_both$learninglambda,col="black",pch=16,cex=2)
points(dat_loci_plastic_both$locisolved~dat_loci_plastic_both$learninglambda,col="red",pch=16,cex=2)

legend(x="bottomleft", legend=c(pch16="Wooden MAB", pch16="Plastic MAB"), pch=c(16,16), col=c("black","red"))

mtext("central third of lambda values", side=3,line=-2,font=3)
mtext("a)", side=3,line=0,font=2,at=-2,cex=1.7)
mtext("Number of loci solved" , side=2,font=2,cex=1.5,line=2.4)
mtext("Lambda from last reversal (standardized)",side=1,font=2,cex=1.5,line=3)

plot( NULL , xlim=c(-2.1,2.1) , ylim=c(0,5) , cex=2,cex.lab=1.5,font=2 , bty="n",ylab="",xlab="" )
rect(xleft=-0.7,ybottom=-0.5,xright=0.7,ytop=5.5,col="grey90",border="NA")

points(dat_loci_wooden_both$locisolved~dat_loci_wooden_both$learningphi,col="black",pch=16,cex=2)
points(dat_loci_plastic_both$locisolved~dat_loci_plastic_both$learningphi,col="red",pch=16,cex=2)

mtext("central third of phi values", side=3,line=-2,font=3)
mtext("b)", side=3,line=0,font=2,at=-2,cex=1.7)
mtext("Number of loci solved" , side=2,font=2,cex=1.5,line=2.4)
mtext("Phi from last reversal (standardized)",side=1,font=2,cex=1.5,line=3)

plot( NULL , xlim=c(-2.1,2.1) , ylim=c(0,1800) , cex=2,cex.lab=1.5,font=2 , bty="n",ylab="",xlab="" )
rect(xleft=-0.7,ybottom=-0.5,xright=0.7,ytop=1805.5,col="grey90",border="NA")

```

```

points(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden~standardize(inputdata_philatencywooden))
points(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic~standardize(inputdata_philatencyplastic))

mtext("central third of lambda values", side=3, line=-2, font=3)
mtext("c)", side=3, line=0, font=2, at=-2, cex=1.7)
mtext("Latency to attempt new locus", side=2, font=2, cex=1.5, line=2.4)
mtext("Lambda from last reversal (standardized)", side=1, font=2, cex=1.5, line=3)

plot( NULL , xlim=c(-2.1,2.1) , ylim=c(0,1800) , cex=2, cex.lab=1.5, font=2 , bty="n", ylab="", xlab="" )
rect(xleft=-0.7,ybottom=-0.5,xright=0.7,ytop=1805.5,col="grey90",border="NA")

points(inputdata_philatencywooden$AverageLatencyAttemptNewLocusMABwooden~standardize(inputdata_philatencywooden))
points(inputdata_philatencyplastic$AverageLatencyAttemptNewLocusMABplastic~standardize(inputdata_philatencyplastic))

mtext("central third of phi values", side=3, line=-2, font=3)
mtext("d)", side=3, line=0, font=2, at=-2, cex=1.7)
mtext("Latency to attempt new locus", side=2, font=2, cex=1.5, line=2.4)
mtext("Phi from last reversal (standardized)", side=1, font=2, cex=1.5, line=3)

### Below is an alternative approach where phi and lambda are
### estimated in the same STAN model in which their association with
### other parameters is assessed.

### Code below copied from Blaisdell et al. 2021

dflex <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = T, sep = ",", stringsAsFactors = F)
dmabp <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",", stringsAsFactors = F)

# PREPARE reversal learning data exclude yellow tube trials for
# control birds because we are only interested in reversal data
dflex <- subset(dflex, dflex$Reversal != "Control: Yellow Tube" & dflex$ID != "Memela")
# include only those trials where the bird made a choice (0 or 1)
dflex <- subset(dflex, dflex$CorrectChoice != -1)
# reverse number. 0=initial discrimination
dflex$Reversal <- as.integer(dflex$Reversal)
# exclude reversal=0 because this was the initial discrimination and
# not a reversal
dflex <- subset(dflex, dflex$Reversal != 0)
dflex$Correct <- as.integer(dflex$CorrectChoice)
dflex$Trial <- as.integer(dflex$Trial)
# exclude NAs from the CorrectChoice column
dflex <- subset(dflex, is.na(dflex$Correct) == FALSE)

# Want data ONLY from LAST TWO reversals to compare with main results
# from the other model in the Results section (which were from the
# last reversal)
reduceddata <- matrix(ncol = ncol(dflex), nrow = 0)
reduceddata <- data.frame(reduceddata)
for (i in 1:length(unique(dflex$ID))) {
  thisbird <- unique(dflex$ID)[i]

```

```

thisbirddata <- dflex[dflex$ID == thisbird, ]
thisbirdslastreversal <- thisbirddata[thisbirddata$Reversal %in% c((max(thisbirddata$Reversal) - 1), max(thisbirddata$Reversal)), ]
reduceddata <- rbind(reduceddata, thisbirdslastreversal)
}
dflex <- reduceddata
length(unique(dflex$ID)) #21 birds

# Construct Choice variable
dflex$Choice <- NA
for (i in 1:nrow(dflex)) {
  if (dflex$Reversal[i] %in% seq(0, max(unique(dflex$Reversal)), by = 2)) {

    if (dflex$Correct[i] == 1) {
      dflex$Choice[i] <- 1
    } else {
      dflex$Choice[i] <- 2
    }
  } else {
    if (dflex$Correct[i] == 1) {
      dflex$Choice[i] <- 2
    } else {
      dflex$Choice[i] <- 1
    }
  }
}
dflex <- dflex[with(dflex, order(dflex$ID)), ]

# PREPARE MAB data for models
dmabp <- data.frame(dmabp)
colnames(dmabp) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
"TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
"TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
"AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
"Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Keep only birds who finished the task
dmabp <- subset(dmabp, is.na(dmabp$AverageLatencyAttemptNewLocusMABplastic) ==
FALSE)

# Flexibility data for birds with inhibition score
d <- subset(dflex, dflex$ID %in% dmabp$ID)

# Sort birds alphabetically, so the birds are always in the same
# order in both data sets and the model can attribute the right data
# to the right birds
d <- d[with(d, order(d$ID)), ]
dmabp <- dmabp[with(dmabp, order(dmabp$ID)), ]

# Store the bird names in case we want to link their data from here
# back to other datasets
birdnames <- unique(d$ID)

```

```

# Convert bird names into numeric ids
d$ID <- as.numeric(as.factor(d$ID))
dmabp$ID <- as.numeric(as.factor(dmabp$ID))

# Keep only the columns we are going to analyze
d <- subset(d, select = c(ID, Choice, Correct))

### The STAN model. Code below copied from Logan et al. 2020
### http://corinalogan.com/Preregistrations/gxpopbehaviorhabitat.html
### and modified to obtain phi and lambda from reversal learning
### (explanatory variables) and MAB plastic latency to switch
### (response variable)

# PREPARE the data for the STAN model
dat_full <- as.list(d)
dat_full$N <- nrow(d)
dat_full$N_id <- length(unique(d$ID))
dat_full$Choice <- as.numeric(as.factor(d$Correct))
# to modify our code for your purposes, insert your response variable
# here. Replace dmabp$AverageLatencyAttemptNewLocusMABplastic with
# the column in your data sheet that is the response variable
dat_full$Response <- dmabp$AverageLatencyAttemptNewLocusMABplastic

# This STAN model, in addition to estimating phi and lambda for each
# individual, also estimates means for each site. It again starts
# with attractions set to 0.1 and assumes that individuals only learn
# about the option they chose.

# In case you want to learn how to convert R code to STAN code, you
# can use the function stancode(). In this case, where we want to use
# the gamma poisson distribution, we can see the STAN code
# translation from the rethinking model mplat1 with stancode(mplat1)

# DEFINE the model in STAN. This model links phi and lambda from
# reversal learning to the MAB plastic latency to switch data per
# bird
reinforcement_model_id_mablatency_nonzeroattraction_gammapoisson <- "
data{
  int N;
  int N_id;
  int ID[N];
  int Choice[N];
  int Correct[N];
  int Response[N_id];
}

parameters{
  real logit_phi;
  real log_L;

  // Varying effects clustered on individual

```

```

matrix[2,N_id] z_ID;
vector<lower=0>[2] sigma_ID;           //SD of parameters among individuals
cholesky_factor_corr[2] Rho_ID;

// GLM
real alpha;
real b_phi;
real b_lambda;
real b_int;
real <lower=0> spread;
}

transformed parameters{
matrix[N_id,2] v_ID; // varying effects on individuals

v_ID = ( diag_pre_multiply( sigma_ID , Rho_ID ) * z_ID )';
}

model{
matrix[N_id,2] A; // attraction matrix

vector[N_id] phi_i;
vector[N_id] lambda_i;

vector[N_id] phi_i_s ;
vector[N_id] lambda_i_s ;
vector[N_id] binomial_lambda;

alpha ~ normal(5,0.5);
b_phi ~ normal(0,0.3);
b_lambda ~ normal(0,0.3);
b_int ~ normal(0,0.3);
spread ~ exponential(1);

logit_phi ~ normal(0,1);
log_L ~ normal(0,1);

// varying effects
to_vector(z_ID) ~ normal(0,1);
sigma_ID ~ exponential(1);
Rho_ID ~ lkj_corr_cholesky(4);

// initialize attraction scores, which are set to 0.1 for both choices (lt gray and dk gray)
for ( i in 1:N_id ) A[i,1:2] = rep_vector(0.1,2)';

// loop over Choices
for ( i in 1:N ) {
vector[2] pay;
vector[2] p;
real L;
real phi;

// first, what is log-prob of observed choice
}
}

```

```

L = exp(log_L + v_ID[ID[i],1]);
p = softmax(L*A[ID[i],1:2]');
Choice[i] ~ categorical( p );

// second, update attractions conditional on observed choice
phi = inv_logit(logit_phi + v_ID[ID[i],2]);
pay[1:2] = rep_vector(0,2);
pay[ Choice[i] ] = Correct[i];
A[ ID[i] , Choice[i] ] = ((1-phi)*(A[ ID[i] , Choice[i] ]) + phi*pay[Choice[i]] );
} // i

// Define bird specific values on the outcome scale and standardize
lambda_i = exp(log_L + v_ID[,1]);
phi_i = inv_logit(logit_phi + v_ID[,2]);

lambda_i_s = (lambda_i - mean(lambda_i)) / sd(lambda_i);
phi_i_s = (phi_i - mean(phi_i)) / sd(phi_i);

binomial_lambda = alpha + b_lambda * lambda_i_s + b_phi * phi_i_s + b_int * lambda_i_s .* phi_i_s;
binomial_lambda = exp(binomial_lambda);

Response ~ neg_binomial_2(binomial_lambda, spread);
}

"""

### Prepare to run the model using cmdstan NOTE: CmdStan will help
### the stan models run faster. Instructions on how to install this
### are at https://mc-stan.org/cmdstanr/articles/cmdstanr.html

# Save where your working directory is so we can reset it to this at
# the end of the session. You might have to copy and paste the
# following 2 sections directly into the Console because they
# sometimes don't otherwise run
currentlocation <- getwd()
cmdstanlocation <- cmdstan_path()
setwd(cmdstanlocation)

# access the output file created by the model running the
# reinforcement model
write(reinforcement_model_id_mablatency_nonzeroattraction_gammapoisson,
      file = "myowntrial.stan")
file <- file.path(cmdstan_path(), "myowntrial.stan")
mod <- cmdstan_model(file)
options(mc.cores = 4)

# RUN the model
fit <- mod$sample(data = dat_full, seed = 123, chains = 4, parallel_chains = 4,
                  refresh = 500)
# Extract relevant variables
outcome <- data.frame(fit$summary())
rownames(outcome) <- outcome$variable

```

```

# Show the 90% compatibility intervals for the association between
# latency to switch loci on the plastic multi-access box and lambda
# and phi, and the interaction between lambda and phi from the
# reinforcement learning model
drawsarray <- fit$draws()
drawsdataframe <- as_draws_df(drawsarray)
drawsdataframe <- data.frame(drawsdataframe)
HPDI(drawsdataframe$b_lambda)
HPDI(drawsdataframe$b_phi)
HPDI(drawsdataframe$b_int)
# all values cross zero so there is no correlation between mab
# latencies and phi or lambda

# Plot the distribution of the estimated associations to see whether
# they overlap zero (if so, then there is no effect)
library(bayesplot)
mcmc_hist(fit$draws("b_lambda"))
mcmc_hist(fit$draws("b_phi"))
mcmc_hist(fit$draws("b_int"))

# Calculate the lambda and phi values for each individual
lambda <- sapply(1:dat_full$N_id, function(x) exp(mean(drawsdataframe$log_L) +
  mean(drawsdataframe[, 36 + x])))
# 2.733134 4.955325 4.195128 3.346893 3.934143 4.651078 3.408593
# 2.709205 2.763549 3.197556 2.594222
phi <- sapply(1:dat_full$N_id, function(x) inv_logit(mean(drawsdataframe$logit_phi) +
  mean(drawsdataframe[, 47 + x])))
# 0.02692541 0.08285155 0.06224467 0.05683807 0.04781117 0.05612348
# 0.02987072 0.01878873 0.01372789 0.02764422 0.01833556

# Here, for the last reversal data, lambda and phi are correlated
# across individuals
plot(lambda ~ phi)

# Remove the stan command line file we created for this particular
# model from your computer
fn <- "myowntrial"
file.remove(fn)

# Reset your working directory to what it was before we ran the model
setwd(currentlocation)

### NOTE: if you aren't running cmdstan, then run the model with this
### code instead of the above 'fit' model
run_reinforcement_model_id_mablatency_nonzeroattraction_gammapoisson <- stan(model_code = reinforcement,
  data = dat_full, iter = 5000, cores = 4, chains = 4, control = list(adapt_delta = 0.9,
  max_treedepth = 12))

```

729 **Serial reversals improved switch latencies on both multi-access boxes**

730 Grackles that were faster to reverse a preference in their first and last reversals were also faster to attempt to
731 solve a new locus on the **plastic** multi-access box, and individuals in the manipulated condition had faster
732 switch times than those in the control condition. This indicates that, while these variables were already
733 positively correlated before conducting a manipulation, the serial reversal flexibility manipulation improved
734 multi-access box switching latencies. In contrast, there was no difference between control and manipulated
735 switching performance on the **wooden** multi-access box. Instead, serial reversal experience changed the
736 relationship between the number of trials to reverse and switch latencies from being negative in the first
737 reversal to having no relationship in the last reversal. This indicates that the flexibility manipulation had
738 some effect on changing the latency to switch to attempting different loci on the wooden multi-access box.
739 Because there was no correlation between the number of trials to pass the last reversal and the latency to
740 attempt a different locus on the wooden multi-access box, we added motor diversity (the number of motor
741 actions used on the wooden multi-access box) to the model as a measure of innovativeness to determine
742 whether switch latencies might measure both flexibility and innovativeness. This addition did not improve
743 the model fit and indicates that innovativeness is likely not a confound in switch latencies, which were
744 influenced by serial reversals.

745 **Serial reversals improved problem solving on both multi-access boxes**

746 Grackles in the manipulated condition solved on average 1.2 more loci on the **wooden** multi-access box
747 than those birds in the control condition. The relationship for the **plastic** multi-access box did show an
748 improvement, but not as we originally predicted. We predicted (P2) that there would be differences in
749 multi-access box performance between individuals in the control and manipulated conditions in the reversal
750 experiment, however this was not the case: there was no difference between the conditions. However, even
751 in the control group there were several individuals who solved their first and only reversal in very few trials.
752 These individuals might have had other previous experiences that shaped their flexibility, and therefore also
753 influenced their performance on the plastic multi-access box. We might have therefore not found differences
754 between the control and manipulated groups because the average of our small sample of individuals in the
755 control group did not perform noticeably differently from the manipulated group. This suggests that the
756 flexibility manipulation trained individuals who were not already fast to become faster at reversing, and, for
757 those individuals who were already fast at reversing when they began the experiment, that other previous
758 experience likely led to differences in their performance on the plastic multi-access box. This could indicate
759 that the important variable is the ability to be flexible, which individuals could already possess or could be
760 trained to improve on during the experimental manipulation. That there was no correlation between the
761 number of trials to reverse in the first reversal and the number of loci solved on either multi-access box
762 indicates that flexibility is not an inherent ability, but one that is shaped by experience as demonstrated
763 by the effect of the manipulation. If it was an inherent ability, the first reversals of the manipulated group
764 would likely have resulted in a correlation with problem solving. Instead, what appears to be important is
765 the current state of the bird as they attempt the multi-access box, which is captured by the final reversal
766 performance.

767 **Multi-access box differences, repeatability, and learning strategies**

768 **Performance differed between the two multi-access boxes.** The number of trials to reverse a preference
769 in the first reversal positively correlated with switch latencies on the plastic multi-access box, but
770 negatively on the wooden multi-access box, which calls into question what switching latencies actually mea-
771 sure. For the number of loci solved, there was a negative correlation with trials to pass the last reversal on the
772 plastic multi-access box (birds who reversed faster solved more loci), and a difference between manipulated
773 and control birds on the wooden multi-access box (manipulated birds solved more loci). The differences
774 between the two multi-access boxes could be due to a small sample size, which means that we were not
775 able to detect an association with all reversal learning measures (first reversal, last reversal, control versus
776 manipulated).

777 Examining only the manipulated grackles, there was **repeatability of flexibility performance within**
778 **a context (serial reversal learning with colored tubes)**, but not across contexts (correlation of

779 **reversal learning and solution switching on the multi-access boxes).** Individuals who were faster
780 at reversing a color preference in reversal one were also generally faster at reversing in subsequent reversals.
781 However, individuals who were consistently faster at reversing in each reversal were not also those who
782 were faster at switching latencies on either multi-access box. Therefore, individual-level flexibility did not
783 generalize to a new context, though the individual's reinforcement history and motivation levels could play a
784 role, and it is also possible that performance on the multi-access boxes additionally relies on other cognitive
785 abilities in which individuals may differ.

786 While one third of the grackles switched from an exploratory **strategy** (epsilon-decreasing) to an exploitative
787 strategy (epsilon-first) in their last reversal, there was no correlation between either strategy and reversal
788 number, indicating that the grackles did not use a particular strategy earlier or later in their serial reversals.
789 This could suggest that the grackles did not learn the overarching rule that once food is not present in the
790 preferred color's tube, they must switch to preferring the other color. Instead, they may learn each preference
791 change as if it was new.

792 Why did performance on a touchscreen vary so drastically from a traditional approach?

793 We assumed that reversal learning performance using **shape on the touchscreen** would directly compare to
794 and be interchangeable with reversal learning performance using color on tubes. However, as we were testing
795 the four grackles in the touchscreen experiment, it quickly became clear that the touchscreen experiment
796 may have been asking a different question compared with the traditional reversal learning approach using
797 physical objects. Unfortunately, we are unaware of what that question could be. We did not have the time
798 to explore what might have caused the differences between the two tests, but we speculate below. Because
799 we were unable to investigate why the results from the two reversal experiments differed from each other, we
800 are left with the conclusion that these two methods, the traditional physical object and the touchscreen, do
801 not measure the same construct in this species and with this reversal learning experiment. Therefore, after
802 testing four grackles in the reversal touchscreen experiment, we decided to discontinue it because we would
803 not be able to include these data in our analyses of reversal learning speeds and because the touchscreen
804 test took too long to conduct.

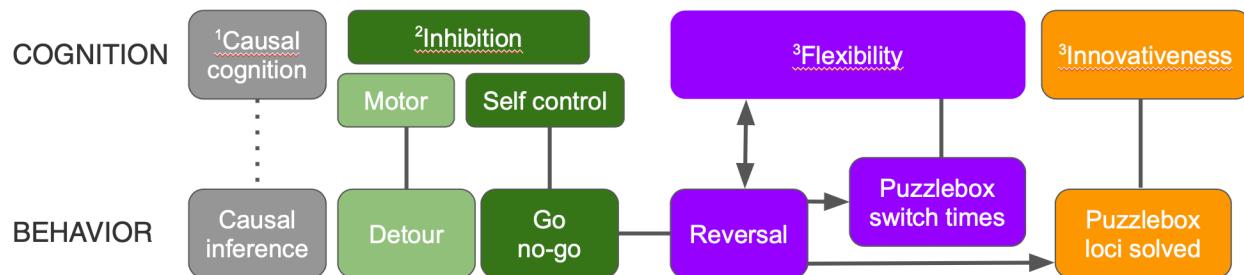
805 One possibility for the difference between the two experiments is that grackles may not have understood
806 how the touchscreen worked and therefore it was the apparatus that interfered with their performance. We
807 ruled out this potential explanation because the grackles successfully completed a go no-go inhibition task
808 using the same touchscreen apparatus, reaching the 85% correct criterion for discriminating between two
809 shapes in 60 to 290 trials (n=8; Logan, McCune, et al. (2021)). The go no-go task similarly used two
810 different white shapes (wavy lines or a heart) where one was associated with receiving food and the other
811 was associated with receiving no food and a longer inter-trial interval. Rather than the two stimuli being
812 presented on the screen at the same time (as in the reversal touchscreen experiment), they were presented
813 one at a time sequentially. Given this difference between the two touchscreen experiments, it is possible
814 that the grackles found touching the screen in the reversal experiment rewarding in and of itself because
815 something happened whenever they made a response. That is, if they touched the correct stimulus, they
816 received food; if they touched the incorrect stimulus, the screen went blank immediately. This is in contrast
817 with the go no-go experiment where the stimulus stayed on the screen for a set amount of time after an
818 incorrect choice. Another potential reason for the difference between performances on the two touchscreen
819 experiments was that making the incorrect choice in the reversal experiment was not costly enough. In the
820 reversal touchscreen experiment, they could get through many trials in a short amount of time, therefore
821 there was potentially not enough incentive to learn quickly, thus explaining the differences in learning speeds
822 between the two reversal experiments.

823 We are not the first group to attempt to transfer a traditional lab or field task to a touchscreen apparatus.
824 Drayton & Santos (2014) tested whether capuchins would prosocially deliver food to a partner using a
825 touchscreen based task. This prosocial behavior was documented using traditional laboratory measures in
826 capuchins in which subjects chose between being the sole recipient of a reward or receiving a reward along
827 with a partner who also received the reward (De Waal et al., 2008; Lakshminarayanan & Santos, 2008).
828 However, on the touchscreen version of this procedure, the monkeys failed to demonstrate a preference for
829 the prosocial response. In a similar vein to our reversal learning data, Drayton and Santos believe this to

be more an artifact of the touchscreen itself and not evidence against prosociality in capuchins (or ability to complete a reversal learning task in our case). Further testing on their task suggested the capuchins did not properly learn the reward contingencies for each response option. Other attempts to transfer tasks to a touchscreen have been more successful (e.g, A. P. Blaisdell & Cook, 2005; Kangas & Bergman, 2017; Sawa et al., 2005). Despite some of the challenges associated with touchscreen apparatuses and the possibility that traditional lab tasks will not always be transferable to a touchscreen, we maintain that touchscreens have the potential to be an incredibly useful tool for studying comparative cognition, indeed some researchers have already successfully done so (for reviews and methods, see Bussey et al., 2008; Cook et al., 2004; Kangas & Bergman, 2017; Logan, McCune, et al., 2021; Seitz et al., 2021; Wolf et al., 2014).

839 Conclusion

Considering the flexibility results we have so far obtained from the Arizona population of great-tailed grackles, we are starting to understand how cognition and behavior, using various tests, are related, either correlationally or causally (Figure 11). We now know that flexibility is correlated with self control, a measure of inhibition, in that the birds who are faster to reverse and faster to switch loci on the multi-access boxes are also the ones to pass go no-go criterion faster (Logan, McCune, et al., 2021). We do not have evidence that this species uses causal cognition, and their causal scores did not correlate with flexibility (reversal learning and plastic multi-access box) (A. Blaisdell et al., 2021). In the current investigation, we were able to make causal conclusions, rather than only correlational: we manipulated reversal learning, which caused changes in a different flexibility measure (multi-access box switch latencies) and in an innovativeness measure (multi-access box loci solved), as well as validating that this manipulation had an effect on the cognitive ability we think of as flexibility.



851

Figure 11. A directed acyclic graph (DAG) of the behavioral flexibility results from the Arizona population of great-tailed grackles (2018-2020). There was no relationship between causal cognition scores and performance on their last reversal or the wooden multi-access box switch times (first reversal and plastic multi-access box were not investigated) (1: A. Blaisdell et al., 2021). There was no relationship between detour performance and performance on go no-go, first or last reversal, or with wooden or plastic multi-access box switch times (2: Logan, McCune, et al., 2021). There was a positive and a negative correlation between go no-go and first and last reversal performance depending on whether Taquito was included, however the negative relationship in the last reversal was most supported: the faster to reverse were also the faster to pass criterion on go no-go (2: Logan, McCune, et al., 2021). Serial reversals improved switch latencies on both multi-access boxes and improved the number of loci solved on the plastic multi-access box (but no correlation on the wooden multi-access box), as well as validating that we were able to causally effect flexibility (3: current investigation).

That it is possible to manipulate flexibility using a paradigm such as reversal learning opens up many opportunities to better understand what flexibility is and whether and how it is causally related to other behaviors or forms of cognition. Understanding how flexibility causally relates to other traits will allow researchers to develop robust theory about what flexibility is and when to invoke it as a primary driver in a given context, such as a rapid geographic range expansion. Indeed, we are already in the process of testing the latter hypothesis by conducting cross-population research on great-tailed grackles to test whether a population on the range edge is more flexible (Logan CJ et al., 2020). That we were able to manipulate flexibility, which had causal effects on flexibility in a different context (multi-access box) as well

872 as a different cognitive ability (innovativeness), demonstrates that flexibility manipulations could be useful
873 in training individuals of other species in how to be more flexible. This could have important implications
874 for threatened and endangered taxa (such as informing the choice of individuals for captive breeding or
875 introduction programs where individuals or their offspring are released into novel areas), as well as for
876 habituating zoo animals or other managed populations to novelty. If such a flexibility manipulation was
877 successful, it could then change their behavior in this and other domains, giving them a better chance of
878 succeeding in human modified environments.

879 METHODS

880 Below is our preregistration that received in principle acceptance at PCI Ecology ([PDF version](#))

881 A. STATE OF THE DATA

882 This preregistration was written (2017) prior to collecting data. Pilot data on serial reversal learning (using
883 colored tubes) in one grackle was collected January through April 2018, which informed the revision of 1)
884 the **criterion to pass serial reversal learning**, 2) more accurate language for H1 P1 (each subsequent reversal
885 may not be faster than the previous, however their average reversal speed decreases), 3) the removal of
886 shape reversals from H3a and H3b (to reduce the amount of time each bird is tested), and 4) a new passing
887 criterion for touchscreen serial reversals in H3b. Part way through data collection on reversal learning (using
888 colored tubes) for the first two birds, the criterion for what counts as making a choice was revised (October
889 2018) and part way through data collection on the first four birds (October 2018; see below for details) the
890 number of trials that birds in the control group receive was revised to make the test battery feasible in the
891 time given.

892 This preregistration was submitted to PCI Ecology for peer review (July 2018), we received the first round
893 of peer reviews a few days before data collection began (Sep 2018), we revised and resubmitted after data
894 collection had started (Feb 2019) and it passed peer review (Mar 2019) before any of the planned analyses
895 had been conducted. See the [peer review history](#) at PCI Ecology.

896 B. PARTITIONING THE RESULTS

897 We may present the different hypotheses in separate papers (Nov 2020: all hypotheses are included in this
898 one post-study article).

899 D. METHODS

900 **Planned Sample** Great-tailed grackles will be caught in the wild in Tempe, Arizona, USA for individual
901 identification (colored leg bands in unique combinations). Some individuals (~32: ~16 in the control group
902 (they receive 1 reversal) and ~16 in the flexibility manipulation (they receive multiple reversals)) will be
903 brought temporarily into aviaries for testing, and then they will be released back to the wild.

904 **Sample size rationale** We will test as many birds as we can in the approximately three years at this field
905 site given that the birds only participate in tests in aviaries during the non-breeding season (approximately
906 September through March).

907 **Data collection stopping rule** We will stop testing birds once we have completed two full aviary sea-
908 sons (likely in March 2020) if the sample size is above the minimum suggested boundary based on model
909 simulations (see section “[Ability to detect actual effects](#)” below). If the minimum sample size is not met by
910 this point, we will continue testing birds at our next field site (which we move to in the summer of 2020)
911 until we meet the minimum sample size.

912 **Open materials** [Design files](#) for the plastic multi-access box: 3D printer files and laser cutter files

913 [Testing protocols](#) for all three experiments: colored tube reversal learning, plastic multi-access box, wooden
914 multi-access box, and touchscreen reversal learning

915 NOTE (Oct 2020): Touchscreen training data and a summary of the training process is detailed in Seitz et
916 al. (2021)

917 **Open data** The data are available at the Knowledge Network for Biocomplexity's data repository: https://knb.ecoinformatics.org/view/corina_logan.84.42.

919 **Randomization and counterbalancing** H1: Subjects will be randomly assigned to the manipulated or
920 control group. In the reversal learning trials, the rewarded option is pseudorandomized for side (and the
921 option on the left is always placed first). Pseudorandomization consisted of alternating location for the first
922 two trials of a session and then keeping the same color on the same side for at most two consecutive trials
923 thereafter. A list of all 88 unique trial sequences for a 10-trial session, following the pseudorandomization
924 rules, will be generated in advance for experimenters to use during testing (e.g., a randomized trial sequence
925 might look like: LRLRRLRRLR, where L and R refer to the location, left or right, of the rewarded tube).
926 Randomized trial sequences will be assigned randomly to any given 10-trial session using a random number
927 generator (random.org) to generate a number from 1-88.

928 **Blinding of conditions during analysis** No blinding is involved in this study.

929 **Dependent variables P1-P3**

930 Number of trials to reverse a preference. An individual is considered to have a preference if it chose the
931 rewarded option at least 17 out of the most recent 20 trials (with a minimum of 8 or 9 correct choices out
932 of 10 on the two most recent sets of 10 trials). We use a sliding window to look at the most recent 10 trials
933 for a bird, regardless of when the testing sessions occurred.

934 *P2 alternative 2: additional analysis: latency and motor diversity*

935 1) Number of trials to attempt a new locus on the multi-access boxes

936 2) Number of trials to solve (meet criterion) a new locus on the multi-access boxes

937 *P3b: additional analysis: individual consistency in flexibility across contexts + flexibility is correlated across
938 contexts*

939 Number of trials to solve a new locus on the multi-access boxes

940 *P4: learning strategies*

941 Proportion of correct choices in a non-overlapping sliding window of 4-trial bins across the total number of
942 trials required to reach the criterion of 17/20 correct choices (as in P1-P3).

943 **Independent variables**

944 *P1: reversal speed gets faster with serial reversals*

945 1) Reversal number

946 2) Batch (random effect because multiple batches included in the analysis). Note: batch is a test cohort,
947 consisting of 8 birds being tested simultaneously

948 3) ID (random effect because repeated measures on the same individuals)

949 *P2: serial reversals improve rule switching & problem solving*

950 1) Average latency to attempt to solve a new locus after solving a different locus

951 2) Average latency to solve a new locus after solving a different locus

952 3) Total number of loci solved

953 4) Experimental group (manipulated=multiple reversals with color stimuli; control=one reversal plus
 954 equalized experience making choices where both are the same color and both contain a reward)

955 5) Batch (random effect because multiple batches included in the analysis). Note: batch is a test cohort,
 956 consisting of 8 birds being tested simultaneously

957 Note April 2020: we realized that the average latency to solve a new locus after solving a different locus
 958 is confounded with the total number of loci solved because the measure of innovation is included in the
 959 definition. Therefore, we will remove this independent variable when conducting the analysis so that we
 960 are only examining pure measures of flexibility (average latency to attempt to solve) and innovation (total
 961 number of loci solved).

962 ***P2 alternative 2: additional analysis: latency and motor diversity***

- 963 1) Number of trials to reverse a preference in the last reversal that individual participated in
- 964 2) Motor diversity: the number of different motor actions used when attempting to solve the multi-access
 965 boxes
- 966 3) ID (random effect because repeated measures on the same individuals)

967 ***P3a: repeatable within individuals within a context***

- 968 1) Reversal number
- 969 2) ID (random effect because repeated measures on the same individuals)

970 ***P3a alternative 1: was the potential lack of repeatability on colored tube reversal learning due
 971 to motivation or hunger?***

- 972 1) Trial number
- 973 2) Latency from the beginning of the trial to when they make a choice
- 974 3) Minutes since maintenance diet was removed from the aviary
- 975 4) Cumulative number of rewards from previous trials on that day
- 976 5) ID (random effect because repeated measures on the same individuals)
- 977 6) Batch (random effect because repeated measures on the same individuals). Note: batch is a test cohort,
 978 consisting of 8 birds being tested simultaneously

979 ***P3b: repeatable across contexts***

- 980 1) Reversal number
- 981 2) Condition (colored tubes, plastic multi-access box, wooden multi-access box, touchscreen)
- 982 3) Latency to solve a new locus
- 983 4) Number of trials to reverse a preference (colored tubes)
- 984 5) Number of trials to reverse a preference (touchscreen)
- 985 6) ID (random effect because repeated measures on the same individuals)

986 ***P4: serial reversal learning strategy***

- 987 1) Trial number
- 988 2) ID (random effect because repeated measures on the same individuals)

989 **E. ANALYSIS PLAN**

990 We do not plan to **exclude** any data. When **missing data** occur, the existing data for that individual will be
 991 included in the analyses for the tests they completed. Analyses will be conducted in R [current version 4.0.3;
 992 R Core Team (2017)], using several R packages: Zhu (2021), Hlavac (2018), J. D. Hadfield (2010), Bartoń
 993 (2020), McElreath (2020), Stan Development Team (2020), Xie (2019), Ushey et al. (2020), Eddelbuettel &
 994 François (2011), Wickham (2016), knitr (Xie, 2013, 2017, 2018), Wickham et al. (2021), Gabry & Češnovar
 995 (2021), posterior (Bürkner et al., 2020), cowplot (Wilke, n.d.), bayesplot (Gabry et al., 2019), irr (Gamer
 996 et al., 2012), psych (Revelle, 2014, 2017), Lin (2020), DHARMA (Hartig, 2019), lme4 (Bates et al., 2012;
 997 Bates et al., 2015). When there is more than one experimenter within a test, experimenter will be added as
 998 a random effect to account for potential differences between experimenters in conducting the tests. If there
 999 are no differences between models including or excluding experimenter as a random effect, then we will use
 1000 the model without this random effect for simplicity.

1001 **Unregistered analysis: interobserver reliability of dependent variables** To determine whether
 1002 experimenters coded the dependent variables in a repeatable way, hypothesis-blind video coders were first
 1003 trained in video coding the dependent variable, and then they coded at least 20% of the videos in the reversal
 1004 (tubes) and multi-access box experiments. We randomly chose a subset of all of the birds who participated
 1005 in each experiment using random.org:

- 1006 • Reversal 6/20 grackles (30% with half from the control group): Chalupa, Avocada, Diablo, Fideo,
 1007 Tomatillo, Adobo
- 1008 • Multi-access box plastic 3/15 grackles (20%): Habanero, Queso, Chalupa
- 1009 • Multi-access box log 3/12 grackles (25%): Diablo, Adobo, Yuca

1010 Video coders then analyzed all videos from these birds. The experimenter's data was compared with the
 1011 video coder data using the intra-class correlation coefficient (ICC) to determine the degree of bias in the
 1012 regression slope (Hutcheon et al. (2010), using the irr package in R: Gamer et al. (2012)). Note that the
 1013 data in columns from coders 1 and 2 in the data sheets were aligned based on similar numbers between
 1014 coders to prevent disagreements near the top of the data sheet from misaligning all subsequent entries.

1015 **Interobserver reliability training** To pass **interobserver reliability (IOR) training**, video coders
 1016 needed an ICC score of 0.90 or greater to ensure the instructions were clear and that there was a high degree
 1017 of agreement across coders (see R code comments for details).

1018 **Alexis Breen** (compared with experimenter's live coding):

- 1019 • Multi-access box: correct choice unweighted Cohen's Kappa=0.90 (confidence boundaries=0.77-1.00,
 1020 n=33 data points)
- 1021 • Multi-access box: locus solved unweighted Cohen's Kappa=0.90 (confidence boundaries=0.76-1.00,
 1022 n=33 data points)

1023 Note: Breen was not a hypothesis-blind video coder. She contributed to extensive video coding across
 1024 the whole project, however, for interobserver reliability analyses, her data were always compared with a
 1025 hypothesis-blind coder's data.

1026 **Anja Becker** (compared with experimenter's live coding):

- 1027 • Reversal: correct choice ICC=1.00 (confidence boundaries=1.00-1.00, n=25 data points)

1028 **Tiana Lam** (compared with experimenter's live coding):

- 1029 • Multi-access box: correct choice ICC=0.90 (confidence boundaries=0.77-1.00, n=33 data points)
- 1030 • Multi-access box: locus solved unweighted Cohen's Kappa=0.95 (confidence boundaries=0.84-1.00,
 1031 n=33 data points)

1032 **Brynnna Hood** (compared with experimenter's live coding):

- 1033 • Multi-access log: correct choice unweighted Cohen's Kappa=1.00 (confidence boundaries=1.00-1.00,
 1034 n=29 data points)
- 1035 • Multi-access log: locus solved unweighted Cohen's Kappa=1.00 (confidence boundaries=1.00-1.00,
 1036 n=29 data points)

1037 **Interobserver reliability** Interobserver reliability scores (minimum 20% of the videos) were as follows:

1038 **Bryonna Hood** (compared with experimenter's live coding):

- 1039 • Multi-access log: correct choice unweighted Cohen's Kappa=0.91 (confidence boundaries=0.76-1.00,
 1040 n=39 data points)
- 1041 • Multi-access log: locus solved unweighted Cohen's Kappa=1.0 (confidence boundaries=1.0-1.00, n=39
 1042 data points)

1043 **Tiana Lam** (compared with experimenter's live coding):

- 1044 • Multi-access box: correct choice unweighted Cohen's Kappa=0.83 (confidence boundaries=0.73-0.92,
 1045 n=102 data points)
- 1046 • Multi-access box: locus solved unweighted Cohen's Kappa=0.90 (confidence boundaries=0.830-0.97,
 1047 n=102 data points)

1048 **Anja Becker** (compared with experimenter's live coding):

- 1049 • Reversal: correct choice ICC=0.99 (confidence boundaries=0.98-0.99, n=3280 data points)

1050 These scores indicate that the dependent variables are repeatable to a high or extremely high degree given
 1051 our instructions and training.

```
# Inter/intra-rater reliability using Cohen's kappa when the variable
# is categorical (scale=1+) or intra-class correlation coefficient
# when the variable is continuous (Mandrekar 2011 J Thoracic Oncology
# 6(1):6-7 https://doi.org/10.1097/JTO.0b013e318200f983)

# Intra-class correlation / reliability coefficient / the # degree of
# bias in the regression slope (Hutcheon et al. 2010. Random
# measurement error and regression dilution bias
# www.bmjjournals.org/content/340/bmj.c2289). 'The ratio of variation in
# error-free (true) X values to the variation in the observed
# error-prone (observed) values is known as the reliability
# coefficient, attenuation factor, or intra-class correlation. '

# Cohen's kappa = Good for nominal data (where distance doesn't mean
# anything; don't use the weighted Kappa bc it is like the ICC)
# https://www.rdocumentation.org/packages/psych/versions/1.9.12.31/topics/cohen.kappa

# ICC / Cohen's Kappa must be 0.90 or greater to be considered
# reliable and pass training ICCs for agreement between the 2 coders
# (live coder and video coder)

#### PASSING interobserver reliability TRAINING so they can become
#### second coders for experiments Note: this data counts as second
#### coder data if they have ICC or Kappa > 0.89

library(irr)  #ICC package
library(psych) #Cohen's kappa package
```

REVERSAL

```
# coder 1=experimenter live coding coder 2=Anja Becker

# IOR TRAINING: did ANJA BECKER pass interobserver reliability
# training? YES
l <- c(1, -1, 1, 1, 0, 1, 1, -1, -1, -1, 1, 1, -1, 1, 1, 1, 1, 1,
      1, 1, 1, 1)
# live coder data from CorrectChoice column for videos below
v <- c(1, -1, 1, 1, 0, 1, 1, -1, -1, -1, 1, 1, -1, 1, 1, 1, 1, 1,
      1, 1, 1, 1)
# video coder data for videos A064LR 2019-09-25 Color Reversal 0 S1
# T1, A064LR 2019-09-25 Color Reversal 0 S2 T2, A064LR 2019-09-25
# Color Reversal 0 S3 T8, A064LR 2019-09-26 Color Reversal 0 S4 T8,
# A064LR 2019-09-26 Color Reversal 0 S5 T8, A064LR 2019-09-26 Color
# Reversal 0 S6 T10
df <- data.frame(l, v)
cohen.kappa(df, w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL)
# Anja = unweighted kappa = 1 (1-1=lower and upper bounds, n=25 data
# points)

# IOR: 20% of videos
becker <- read.csv("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations")
  header = TRUE, sep = ",", stringsAsFactors = FALSE)
head(becker)
cohen.kappa(becker[, c("X1CorrectChoice", "X2CorrectChoice")], w = NULL,
            n.obs = NULL, alpha = 0.05, levels = NULL)
# unweighted kappa = 0.99; upper and lower CIs = 0.98 - 0.99, n =
# 3280
```

MULTIACCESS BOX PLASTIC

```
# coder 1=experimenter live coding coder 2=Tiana Lam coder 3=Alexis
# Breen

### IOR TRAINING: did Tiana Lam pass? YES Cohen's unweighted kappa =
### 0.90 and 0.95 all videos from bird 31

lamtrain <- read.csv("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations")
  header = TRUE, sep = ",", stringsAsFactors = FALSE)
head(lamtrain) #Check to make sure it looks right

# correct choice
lamtrain[, 3] #1CorrectChoice = live coder
lamtrain[, 4] #2CorrectChoice = Coder2 data from Tiana
cohen.kappa(lamtrain[, c(3, 4)], w = NULL, n.obs = NULL, alpha = 0.05,
            levels = NULL) #unweighted kappa = 0.90, confidence boundary = 0.77-1.00, n=33 data points

# locus solved
lamtrain[, 5] #1LocusSolved = live coder
lamtrain[, 6] #2LocusSolved = Coder2 data from Tiana
cohen.kappa(lamtrain[, c(5, 6)], w = NULL, n.obs = NULL, alpha = 0.05,
```

```

levels = NULL) #unweighted kappa = 0.95, confidence boundary = 0.84-1.00, n=33 data points

### IOR: interobserver reliability score from Tiana Lam on 20% of the
### videos
lam <- read.csv("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations/I
  header = TRUE, sep = ",", stringsAsFactors = FALSE)
head(lam) #Check to make sure it looks right

# correct choice
lam[, 3] #1CorrectChoice = live coder
lam[, 4] #2CorrectChoice = Coder2 data from Tiana
cohen.kappa(lam[, c(3, 4)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL) #unweighted kappa = 0.95

# locus solved
lam[, 5] #1LocusSolved = live coder
lam[, 6] #2LocusSolved = Coder2 data from Tiana
cohen.kappa(lam[, c(5, 6)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL) #unweighted kappa = 0.95

### IOR TRAINING: did Alexis Breen pass? YES Cohen's unweighted kappa
### = 0.90 and 0.90 all videos from bird 31

data <- read.csv("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations/I
  header = TRUE, sep = ",", stringsAsFactors = FALSE)
head(data) #Check to make sure it looks right

# correct choice
data[, 3] #1CorrectChoice = live coder
data[, 4] #2CorrectChoice = Coder2 data from Tiana
cohen.kappa(data[, c(3, 4)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL) #unweighted kappa = 0.90

# locus solved
data[, 5] #1LocusSolved = live coder
data[, 6] #2LocusSolved = Coder2 data from Tiana
cohen.kappa(data[, c(5, 6)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL) #unweighted kappa = 0.90

##### MULTIACCESS BOX LOG

# coder 1=experimenter live coding coder 2=Brynnna Hood

### IOR TRAINING: did Brynnna Hood pass? YES didn't need to calculate
### it because everything matched perfectly (all videos from birds 73
### and 87) - Brynnna's training data is in the data sheet below with
### 20% of the videos (all of her training data was used in the 20%
### IOR calculation) correct choice unweighted Cohen's Kappa=1.00
### (confidence boundaries=1.00-1.00, n=29 data points) locus solved
### unweighted Cohen's Kappa=1.00 (confidence boundaries=1.00-1.00,
### n=29 data points)

## IOR: Brynnna Hood interobserver reliability score for 20% of the

```

```

## videos = 0.91 & 1.00 20% of the videos = all videos from birds 64,
## 73, and 87

data <- read.csv("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations/
  header = TRUE, sep = ",", stringsAsFactors = FALSE)
head(data) #Check to make sure it looks right

# correct choice Note: c(3,4) is telling R to look at columns 2
# ('1CorrectChoice') and 3 ('2CorrectChoice') and compare them.
# Double check this:
data[, 3] #1CorrectChoice = live coder
data[, 4] #2CorrectChoice = Coder2 data from Brynna

cohen.kappa(data[, c(3, 4)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL)
# unweighted kappa = 0.91, confidence boundary = 0.76-1.00, n=39 data
# points

# locus solved
data[, 5] #1LocusSolved = live coder
data[, 6] #2LocusSolved = Coder2 data from Brynna

cohen.kappa(data[, c(5, 6)], w = NULL, n.obs = NULL, alpha = 0.05, levels = NULL)
# unweighted kappa = 1.00 confidence boundary = 1-1, n=39 data points

```

1052 **Ability to detect actual effects** To begin to understand what kinds of effect sizes we will be able to
 1053 detect given our sample size limitations and our interest in decreasing noise by attempting to measure it,
 1054 which increases the number of explanatory variables, we used G*Power (v.3.1, Faul et al., 2007, 2009) to
 1055 conduct power analyses based on confidence intervals. G*Power uses pre-set drop down menus and we chose
 1056 the options that were as close to our analysis methods as possible (listed in each analysis below). Note that
 1057 there were no explicit options for GLMs (though the chosen test in G*Power appears to align with GLMs) or
 1058 GLMMs or for the inclusion of the number of trials per bird (which are generally large in our investigation),
 1059 thus the power analyses are only an approximation of the kinds of effect sizes we can detect. We realize that
 1060 these power analyses are not fully aligned with our study design and that these kinds of analyses are not
 1061 appropriate for Bayesian statistics (e.g., our MCMCglmm below), however we are unaware of better options
 1062 at this time. Additionally, it is difficult to run power analyses because it is unclear what kinds of effect sizes
 1063 we should expect due to the lack of data on this species for these experiments.

1064 To address the power analysis issues, we will run simulations on our Arizona data set before conducting any
 1065 analyses in this preregistration. We will first run null models (i.e., dependent variable $\sim 1 +$ random effects),
 1066 which will allow us to determine what a weak versus a strong effect is for each model. Then we will run
 1067 simulations based on the null model to explore the boundaries of influences (e.g., sample size) on our ability
 1068 to detect effects of interest of varying strengths. If simulation results indicate that our Arizona sample size
 1069 is not larger than the lower boundary, we will continue these experiments at the next field site until we meet
 1070 the minimum suggested sample size.

1071 **SIMULATIONS APRIL 2020 (pre-data analysis):** following procedures in McElreath (2018), we first
 1072 constructed a **hypothesis-appropriate mathematical model** that encompasses the relationship between
 1073 the variables of interest for each analysis: 1) number of loci solved on the multi-access box \sim trials to reverse,
 1074 and 2) latency to attempt a new locus on the multi-access box \sim trials to reverse.

1075 **Simulation and model: number of loci solved on the multi-access box \sim trials to reverse**

1076 The model takes the form of:

1077 $\text{locisolved} \sim \text{Binomial}(4, p)$ [likelihood]

1078 $\text{logit}(p) \sim \alpha[\text{batch}] + \beta[\text{trials}]$ [model]

1079 locisolved is the number of loci solved on the multi-access box, 4 is the total number of loci on the multi-
 1080 access box, p is the probability of solving any one locus across the whole experiment, α is the intercept and
 1081 each batch gets its own, β is the expected amount of change in locisolved for every one unit change in trials,
 1082 and trials is the number of trials to reverse a color preference.

1083 Expected values for the number of loci solved on the multi-access box were set to either 2 or 0 (out of
 1084 4 loci maximum) because we were unsure of whether the grackles would be able to solve any loci on the
 1085 multi-access box because this experiment had never been done on this species before. Expected values for
 1086 reversal learning using colored tubes (mean, standard deviation, and range of number of trials to reverse a
 1087 color preference) were based on previously published data on great-tailed grackles (Logan, 2016). This data
 1088 indicates that the average number of trials to reverse a preference is 91 and the standard deviation is 21. In
 1089 our model, the variation in the actual data is reflected by both the population standard deviation and the
 1090 expected amount of change related to the explanatory variable. After running simulations, we identified the
 1091 following distributions and priors to be the most likely for our expected data:

1092 $\alpha \sim \text{Normal}(4, 10)$ [α prior]

1093 $\beta \sim \text{Normal}(0, 5)$ [β prior]

1094 We used normal distributions for α and β because they are (or are based on) sums with large means (see
 1095 Figure 10.6 in McElreath, 2018). For the β prior, we had no expectation about whether the relationship
 1096 would be positive or negative, therefore we centered it on 0 (the mean).

```

library(rethinking)
library(rstan)
library(formatR)

### SIMULATION
#SET PARAMETERS for population values = these are what we are varying!

#Setting beta
b <- 0.1
plot(x=21*c(-2:2)+91,y=4*inv_logit(0+b*c(-2:2))) #plot expected relationship between loci solved (y axis)

#Setting b prior: our prior expectation for b is that it is around 0, can be negative or positive, and ...
x <- seq(-2,2,length=100) #make a normal distribution
hx <- dnorm(x,mean=0,sd=0.4) #change sd until you get the width you want
plot(x,hx,xlim=c(-2,2),ylim=c(0,1)) #plot to see whether values now match our expectation for this prior
#Result2 = in the model (ulam) we want to set the b prior to be (0,0.4)

#Figuring out probability, p
batch1mean <- 2 #solves on average 2 loci
batch2mean <- 1.6 #solves on average 1.6 loci

batch1mean <- log((batch1mean/4)/(1-(batch1mean/4))) #convert to the logit scale: log(p/1-p) p=4/probab
batch2mean <- log((batch2mean/4)/(1-(batch2mean/4)))

#Figuring out alpha prior
probabilities<-inv_logit(rnorm(10000,mean=-2,sd=0.5))
mean(probabilities) #this is the mean number of loci solved
loci <- vector()
for(i in 1:10000) {loci[i]<-rbinom(1,size=4,prob=probabilities[i])}
hist(loci) #we didn't know whether they would be able to solve any loci bc this species had never been ...

probabilities<-inv_logit(rnorm(10000,mean=0,sd=0.3))

```

```

loci <- vector()
for(i in 1:10000) {loci[i]<-rbinom(1,size=4,prob=probabilities[i])}
mean(loci) #this is the mean number of loci solved
hist(loci) #Alternatively, we expect a bell curve with most of the individuals being average at solving

#Figuring out how much noise we expect (sd in alpha) = 0.4
hist(inv_logit(rnorm(10000,mean=0,sd=1))) #it is spread out along the x axis so the many individuals in
hist(inv_logit(rnorm(10000,mean=0,sd=0.4))) #this is much narrower, thus most of the individuals will m

#Result = in the simulation alpha sd should not be larger than 1 because at 1 it ranges from a probabil

#RUN SIMULATION WITH PARAMETERS (this is the simulated data that the model (below) will use to estimate
b <- 1 #beta
asd <- 0.3 #alpha sd for the population. We set this smaller than what we had it above bc we wanted to r
batch1mean <- 1.9 #alpha batch mean: solves on average 2 loci
batch2mean <- 2.1 #alpha batch mean: solves on average 1.6 loci
n <- 16

batch1mean <- log((batch1mean/4)/(1-(batch1mean/4))) #convert to the logit scale: log(p/1-p) p=4/probab
batch2mean <- log((batch2mean/4)/(1-(batch2mean/4)))

individuals<-matrix(nrow=16,ncol=8)
colnames(individuals)<-c("loci","trials","batch","probability","logit trials","logit base value","base p
for (i in 1:n/2) {
  trials<-rnorm(1,0,1)
  batch1 <- rnorm(1,batch1mean,asd) #n, mean, sd of probability of solving a locus. SD is the noise
  p <- batch1 + b*trials
  individuals[i,1]<-sum(rbinom(50,1,inv_logit(p)/12.5)) #50 trials (drawing 50 times (the highest number
  ifelse(individuals[i,1]>4,individuals[i,1]<-4,individuals[i,1]<-individuals[i,1])
  individuals[i,2]<-trials*21+91 #column: number trials to reverse (standardized) and then unstandardiz
  individuals[i,3]<-1 #column: batch=1
  individuals[i,4]<-inv_logit(p) #column: p (probability)
  individuals[i,5]<-trials #the logit of trials to reverse
  individuals[i,6]<-batch1 #logit base value of alpha (for the intercept for this ind)
  individuals[i,7]<-inv_logit(batch1) #base probability is the inverse logit of the previous column
  individuals[i,8]<-p #logit probability
}

for (i in (n/2+1):n) {
  trials<-rnorm(1,0,1)
  batch2 <- rnorm(1,batch2mean,asd) #n, mean, sd
  p <- batch2 + b*trials
  individuals[i,1]<-sum(rbinom(50,1,inv_logit(p)/12.5))
  ifelse(individuals[i,1]>4,individuals[i,1]<-4,individuals[i,1]<-individuals[i,1])
  individuals[i,2]<-trials*21+91
  individuals[i,3]<-2 #batch=2
  individuals[i,4]<-inv_logit(p)
  individuals[i,5]<-trials
  individuals[i,6]<-batch2
  individuals[i,7]<-inv_logit(batch2)
  individuals[i,8]<-p
}

```

```

#individuals #check the data
plot(individuals[,1]~individuals[,2]) #visualize the relationship
#plot(individuals[1:8,1]~individuals[1:8,2]) #batch1 goes full range of both variables
#plot(individuals[9:16,1]~individuals[9:16,2]) #batch2 goes full range of both variables

### RUN MODEL
#don't change alpha or beta parameters here because they are changed above
dat <- list(locisolved = individuals[,1],
            trials = standardize(individuals[,2]),
            batch = individuals[,3]
            )

m1 <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[batch] + b*trials , #batch=random effect, standardize trials so 0=mean
  a[batch] ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive, and
) , data=dat , chains=4 , log_lik=TRUE )

precis(m1,depth=2)
#mean(individuals[1:8,1])
#mean(individuals[9:16,1])

#check posterior for p to look at the distribution of probabilities that are probable
prior <- extract.prior(m,n=1e4)
p <- inv_logit(prior$a) #convert from logit to actual probability
dens(p,adj=0.1)
#result1: it was a normal curve with a peak at 3.5, let's see what happens if we flatten it saying that
#result2: this worked - the distribution is flat at 1.2

#check to see if including batch has an influence on the estimate of b by removing batch
mwobatch <- ulam( alist(
  locisolved ~ dbinom(4,p) ,
  logit(p) <- a + b*trials , #standardize trials so 0=mean
  a ~ dnorm(0,0.5) ,
  b ~ dnorm(0,2)
) , data=dat , chains=4 , log_lik=TRUE )

precis(mwobatch,depth=2)
mean(individuals[1:8,1])
mean(individuals[9:16,1])
#result = really similar to model m1

```

1097 **Simulation and model: latency to attempt a new locus on the multi-access box ~ trials to
1098 reverse**

1099 For the average latency to attempt a new locus on the multi-access box as it relates to trials to reverse (both
1100 are measures of flexibility), we simulated data and set the model as follows:

1101 latency ~ gamma-Poisson(λ_i , ϕ) [likelihood]
1102 $\log(\lambda_i) \sim \alpha[\text{batch}] + \beta\text{trials}$ [the model]

1103 latency is the average latency to attempt a new locus on the multi-access box, λ_i is the rate (probability of
 1104 attempting a locus in each second) per bird (and we take the log of it to make sure it is always positive; birds
 1105 with a higher rate have a smaller latency), ϕ is the dispersion of the rates across birds, α is the intercept
 1106 for the rate per batch, β is the expected amount of change in the rate of attempting to solve in any given
 1107 second for every one unit change in trials, and trials is the number of trials to reverse a color preference.

1108 Expected values for the latency to attempt a new locus on the multi-access box was set to between 1-2700
 1109 sec because the experiment ends for a bird if they do not obtain the food in 3 consecutive trials, and each
 1110 trial can last up to 15 min. Because we did not have prior data for this species on this test, we set the mean
 1111 to 300 sec, which is half way through a usual 10 min trial because it seems likely that if a bird is going to
 1112 attempt another locus, it will likely do so at the next opportunity, especially after being successful in the
 1113 previous trial. Expected values for reversal learning using colored tubes are the same as above. After running
 1114 simulations, we identified the following to be the most likely distributions and priors for our expected data:

1115 $\phi \sim 1/(\text{Exponential}(1))$ [ϕ prior]

1116 $\alpha \sim \text{Normal}(300, 50)$ [α prior]

1117 $\beta \sim \text{Normal}(0, 0.5)$ [β prior]

1118 We used a gamma-Poisson distribution for latency because it constrains the values to be positive and to
 1119 primarily occur sooner rather than later, which is what we expect from the grackles (based on data from
 1120 New Caledonian crows and kea in Auersperg et al., 2011). For ϕ , we used an exponential distribution because
 1121 it is standard for this parameter. We used normal distributions for α and β because they are (or are based
 1122 on) sums with large means (see Figure 10.6 in McElreath, 2018). For the β prior, we had no expectation
 1123 about whether the relationship would be positive or negative, therefore we centered it on 0 (the mean).

```
library(rethinking)
```

```
library(rstan)
```

```
library(formatR)
```

SIMULATIONS: GAMMA-POISSON

```
n <- 16 #number of individuals
```

```
b <- 1 #slope between latency and trials, want positive and negative values so mean=0
```

```
phi <- 150 #this gives us a distribution that we expect (long right tail)
```

```
asd <- 0.5 #alpha sd is our noise parameter. Decrease this to make the upper bound come to a reasonable
```

```
individuals <- matrix(nrow = 16, ncol = 3)
```

```
colnames(individuals) <- c("trials", "latency", "batch")
```

```
for (i in 1:n/2) {
```

```
  trials <- rnorm(1, 0, 1) #distribution for trials. These are standardized values. To convert back
  a1 <- rnorm(1, mean = 6.5, asd) #intercept for batch 1, mean=log of 450 sec, sd puts the range at
  lambda <- exp(a1 + b * trials) #the linear model for batch 1
  latency <- rgampois(1, lambda, phi) #this is the latency per individual
```

```
  individuals[i, 1] <- trials * 21 + 91
```

```
  individuals[i, 2] <- latency
```

```
  individuals[i, 3] <- 1
```

```
}
```

```
for (i in (n/2 + 1):n) {
```

```
  trials <- rnorm(1, 0, 1)
```

```
  a2 <- rnorm(1, mean = 5.5, sd = asd)
```

```
  lambda <- exp(a2 + b * trials)
```

```
  latency <- rgampois(1, lambda, phi)
```

```

    individuals[i, 1] <- trials * 21 + 91
    individuals[i, 2] <- latency
    individuals[i, 3] <- 2
}

### RUN THE MODEL Load packages
library("Rcpp")
library("rstan")
library(rethinking)
library(ggplot2)

dat <- list(trials = standardize(as.numeric(individuals[, 1])), latency = as.integer(individuals[, 2]), batch = as.integer(individuals[, 3]))

m2 <- ulam(alist(latency ~ dgampois(lambda, phi), log(lambda) <- a[batch] +
  b * trials, a[batch] ~ dnorm(1, 1), b ~ dnorm(0, 1), phi ~ dexp(1)),
  data = dat, log_lik = TRUE, messages = FALSE)

### To make the model work, need to set up a few things... (this took
### me a few days because at every stage there is an error message
### and it isn't clear what the problem is or what to do next)

### Update R install installr package updateR(TRUE) #didn't work bc
### it can't find my R folder on my computer updateR(fast = FALSE,
### browse_news, install_R, copy_packages, copy_Rprofile.site,
### keep_old_packages, update_packages, start_new_R, quit_R,
### print_R_versions = TRUE, GUI = TRUE, to_checkMD5sums = FALSE,
### keep_install_file = FALSE, download_dir =
### '/Users/corina/Library/R', silent = FALSE, setInternet2 = TRUE,
### cran_mirror = 'https://cran.rstudio.com/') #didn't work bc it
### can't find my R folder on my computer manually updated R and
### reinstalled packages

### Install rethinking install package devtools
### devtools::install_github('rmcelreath/rethinking', ref='Experimental')

### Install xcode (first download the app from the app store) In
### terminal, type: 'xcode-select --install'

### Get STAN working https://github.com/rmcelreath/rethinking Install
### C++ toolchain and configuration
### https://github.com/stan-dev/rstan/wiki/Installing-RStan-from-source-on-a-Mac
### install.packages('Rcpp', repos =
### 'https://rcppcore.github.io/drat') Then install rstan per
### instructions at the previous link

### Now we're ready to go!

```

- 1124 We translated the simulation output into effect sizes and examined what kind of effect size these
 1125 parameter values represent (Table M1). For each β , we calculated the effect size (Box 13.3 in Lajeunesse et
 1126 al., 2013: linear regression):
- 1127 $r = \beta (\text{SD}_x / \text{SD}_y) = \beta (1.5 / 21)$
- 1128 Where r is the Pearson product moment correlation and SD is the standard deviation. For the standard

1129 deviation of x (number of loci solved on the multiaccess box), we estimated a possible value of 1.5. For the
 1130 standard deviation of y (trials to reverse), we used 21 from the Santa Barbara grackle data (Logan, 2016).
 1131 We then calculated the effect sizes and R² values for each value of β .

1132 **Table M1.** The connection between β and effect sizes (SDx=standard deviation of x, which is the number
 1133 of loci solved; SDy=standard deviation of y, which is the number of trials to reverse; R²=R squared).

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",",
  stringsAsFactors = F)

library(reactable)
reactable(d, highlight = TRUE, bordered = FALSE, compact = TRUE, wrap = TRUE,
  resizable = TRUE, columns = list(V1 = colDef(name = "Beta"), V2 = colDef(name = "SDx"),
  V3 = colDef(name = "SDy"), V4 = colDef(name = "Effect size"), V5 = colDef(name = "R2")))

## PhantomJS not found. You can install it with webshot::install_phantomjs(). If it is installed, please
```

1134 We then used the simulations to run **models** on simulated data to estimate the measurement error associated
 1135 with varying sample size, β , and the range of multi-access box loci solved or latency to attempt a new locus
 1136 (Table M2). Before running the models, we decided that a model would detect an effect if 89% of the
 1137 posterior sample was on the same side of zero (following McElreath, 2018). We ran the simulation with
 1138 $\beta=3$ (latency) because this was a high value at which an appropriate range of values were observed in the
 1139 simulation testing phase, $\beta=0$ because this would be the scenario in which there is no relationship between
 1140 the response variable and the trials to reverse, and $\beta=-1$ to determine how small of a difference we can
 1141 detect and with what amount of associated noise (σ). Sigma (σ) is the standard deviation in the
 1142 trials to reverse if the trials to reverse is a normal distribution. In all simulations, the mean
 1143 in the trials to reverse was set to 91. Therefore, a (σ) of 14 is 15% noise (14/91). We found
 1144 that when (σ) is larger than 14, we cannot detect even the largest effect of trials to reverse
 1145 on loci solved or latency because there are some simulations where the estimated regression
 1146 coefficient crosses zero. When $\beta=0$ we want all of the regression coefficients to cross zero (10 out of 10
 1147 random repetitions) and when $\beta \neq 0$ we want none of the regression coefficients to cross zero (0 out of 10
 1148 random repetitions). We ran the models several times with various parameters to determine at what point
 1149 this was the case for each combination of parameters.
 1150

1151 **Table M2.** Simulation outputs from varying β , sample size (n), σ , and whether the actual range of multi-
 1152 access box [MAB] loci solved were 0-2 or 0-4 (we did not know how many loci the grackles would
 1153 be able to solve before we started collecting data so we ran two simulations. The grackles
 1154 ended up being able to solve all four loci on both multi-access boxes, therefore we must use
 1155 only those rows associated with “Range of MAB loci solved” = 0-4). This table is useful for
 1156 the analyses involving the number of loci solved on the multi-access box, but not the latency
 1157 to switch to attempting a new locus on the multi-access box, which uses a different (gamma
 1158 poisson) model.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",",
  stringsAsFactors = F)

library(reactable)
reactable(d, highlight = TRUE, bordered = FALSE, compact = TRUE, wrap = TRUE,
  resizable = TRUE, columns = list(V1 = colDef(name = "Beta"), V2 = colDef(name = "n"),
  V3 = colDef(name = "Sigma"), V4 = colDef(name = "Regression coefficient crosses zero"),
  V5 = colDef(name = "Regression coefficient"), V6 = colDef(name = "Range of MAB loci solved")))
```

1159 This shows that we would have the power to detect a medium effect (-0.357 in Table M1) with a sample
 1160 size of 15 if the noise (σ) is <15%. We would be unlikely to get a false negative because there were no false
 1161 negatives in the simulations (i.e., the posterior sample range did not cross zero). With this sample size, when
 1162 $\beta=0$, there are no false positives (i.e., the posterior sample range always included zero). However, we would
 1163 not be able to detect a weak effect unless the noise (σ) was much smaller.

1164 **Data checking** The data will be checked for overdispersion, underdispersion, zero-inflation, and heteroscedasticity with the DHARMA R package (Hartig, 2019) following methods by Hartig. Note: DHARMA
 1165 doesn't support MCMCglmm, therefore we will use the closest supported model: glmer from the R package
 1166 lme4 (Bates et al., 2015).

1168 **Determining the threshold: How many reversals are enough?** We initially (in 2017) set as the
 1169 passing criterion: During the data collection period, the number of trials required to reverse a preference will
 1170 be documented per bird, and reversals will continue until the first batch of birds tested reaches an asymptote
 1171 (i.e., there are negligible further decreases in the number of trials required to reverse a preference). The
 1172 number of reversals to reach the asymptote will be the number of reversals that subsequent birds experience.

1173 Due to delays in setting up the field site, we were only able to test two grackles in early 2018 (January
 1174 through April) and, due to randomization, only one (Fajita) was in the experimental condition that involved
 1175 undergoing the flexibility manipulation (Empanada was in the control condition). While Fajita's reversal
 1176 speeds generally improved with increasing serial reversals, she never reached an asymptote (which we defined
 1177 as passing three consecutive reversals in the same number of trials), even after 38 reversals. These 38 reversals
 1178 took 2.5 months, which is an impractical amount of time if birds are to participate in the rest of the test
 1179 battery after undergoing the reversal manipulation (we are permitted to keep them in aviaries for up to three
 1180 months per bird). Because our objective in this experiment is to manipulate an individual's flexibility, we
 1181 decided to revise our serial reversal passing criterion to something more species relevant based on Fajita's
 1182 serial reversal performance and the performance of seven grackles in Santa Barbara who underwent only one
 1183 reversal in 2014 and 2015 (Logan, 2016). **The revised serial reversal passing criterion is: passing two**
 1184 **sessions in a row at or under 50 trials.** 50 trials is fewer trials than any of the nine grackles required
 1185 to pass their first reversal (range 70-130), therefore it should reflect an improvement in flexibility.

1186 **Revising the choice criterion and the criterion to pass the control condition** **Choice criterion:**
 1187 At the beginning of the second bird's initial discrimination in the reversal learning colored tube experiment
 1188 (October 2018), we revised the criterion for what counts as a choice from A) the bird's head needs to pass
 1189 an invisible line on the table that ran perpendicular to the the tube opening to B) the bird needs to bend its
 1190 body or head down to look in the tube. Criterion A resulted in birds making more choices than the number
 1191 of learning opportunities they were exposed to (because they could not see whether there was food in the
 1192 tube unless they bent their head down to look in the tube) and appeared to result in slower learning. It is
 1193 important that one choice equals one learning opportunity, therefore we revised the choice criterion to the
 1194 latter. Anecdotally, this choice matters because the first three birds in the experiment (Tomatillo, Chalupa,
 1195 and Queso) learned faster than the pilot birds (Empanada and Fajita) in their initial discriminations and
 1196 first reversals. Thus, it was an important change to make at the beginning of the experiment.

1197 **Criterion to pass the control condition:** Before collecting experimental data, we set the number of
 1198 trials experienced by the birds in the control group as 1100 because this is how many trials it would have
 1199 taken the pilot bird in the manipulated group, Fajita, to pass serial reversals 2-17 according to our revised
 1200 serial reversal passing criterion. However, after 25 and 17 days (after Tomatillo and Queso's first reversals,
 1201 respectively) of testing the first two individuals in the control group it became apparent that 1100 trials
 1202 is impractical given the time constraints for how long we are permitted to keep each bird temporarily in
 1203 captivity and would prevent birds from completing the test battery before their release. Additionally, after
 1204 revising the choice criterion, it was going to be likely that birds in the manipulated group would require
 1205 fewer than 1100 trials to meet the serial reversal passing criterion. Therefore, reducing the number of trials
 1206 control birds experience would result in a better match of experience with birds in the manipulated group.
 1207 On 2 November 2018 we set the number of trials control birds experience after their first (and only) reversal
 1208 to the number of trials it requires the first bird in the manipulated group to pass (the first bird has not
 1209 passed yet, therefore we do not yet know what this number is). After more individuals in the manipulated
 1210 group pass, we will update this number to the average number of trials to pass. Note on 16 April 2020: this
 1211 is what we did for all birds in the control condition, except Mofongo who was a slow participator and would
 1212 not have finished his test battery by the time it got too hot to keep birds in the aviaries if we used the current
 1213 average number of trials (420). Instead, we matched him with the fastest bird in the manipulated group

1214 (Habanero=290 trials) to make it more likely that Mofongo could get through the rest of the test battery in
 1215 time.

1216 **P1: negative relationship between the number of trials to reverse a preference and the number of**
 1217 **reversals?** Analysis: A Generalized Linear Mixed Model [GLMM; MCMCglmm function, MCMCglmm
 1218 package; J. D. Hadfield (2010)] will be used with a Poisson distribution and log link using 13,000 iterations
 1219 with a thinning interval of 10, a burnin of 3,000, and minimal priors ($V=1$, $nu=0$) (J. Hadfield, 2014). We
 1220 will ensure the GLMM shows acceptable convergence [lag time autocorrelation values <0.01 ; J. D. Hadfield
 1221 (2010)], and adjust parameters if necessary. We will determine whether an independent variable had an effect
 1222 or not using the Estimate in the full model.

1223 We do not need a power analysis to estimate our ability to detect actual effects because, by definition, the
 1224 individuals that complete this experiment must get faster at reversing in order to be able to pass the stopping
 1225 criterion (two consecutive reversals in 50 trials or less). According to previous grackle data (from the pilot
 1226 and from Santa Barbara), the fastest grackle passed their first reversal in 70 trials, which means that passing
 1227 our serial reversal stopping criterion would require them to have improved their passing speed.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"))
  header = T, sep = ",",
  stringsAsFactors = F)
d <- d[!d$ID == "Fajita" & !d$ID == "Empanada", ] #remove Fajita because she was a pilot bird

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d[["TrialsToReverse"]])))
d <- subset(d, !(is.na(d[["ReverseNumber"]])))

# include only those birds in the reversal tubes experiment and only
# those in the manipulation condition bc only these will have more
# than one reversal (and thus something to correlate)
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
      ]

# factor variables
d$Batch <- as.factor(d$Batch)
d$ID <- as.factor(d$ID)

# DATA CHECKING
library(DHARMa)
library(lme4)
simulationOutput <- simulateResiduals(fittedModel = glmer(TrialsToReverse ~
  ReverseNumber + (1 | ID) + (1 | Batch), family = poisson, data = d),
  n = 250) #250 simulations, but if want higher precision change n>1000
plot(simulationOutput$scaledResiduals) #Expect a flat distribution of the overall residuals, and uniform
# Looks randomly scattered
testDispersion(simulationOutput) #if under- or over-dispersed, then p-value<0.05, but then check the distribution
# p=0.00, it is underdispersed according to the plot at
# https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html.
testZeroInflation(simulationOutput) #compare expected vs observed zeros, not zero-inflated if p<0.05
# p=1 so not zero inflated
testUniformity(simulationOutput) #check for heteroscedasticity ('a systematic dependency of the dispersion on the mean')
# p=0.06 so it is not heteroscedastic
plot(simulationOutput) #...there should be no pattern in the data points in the right panel
# There is a pattern in the right panel January 2021: My interpretation is that this was a manipulation, therefore, by definition
# the data is not randomly (normally) distributed. Therefore, we
```

```

# will move forward with the glmm as planned.

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0)), G = list(G1 = list(V = 1,
  nu = 0), G2 = list(V = 1, nu = 0)))
serial <- MCMCglmm(TrialsToReverse ~ ReverseNumber, random = ~ID + Batch,
  family = "poisson", data = d, verbose = F, prior = prior, nitt = 3e+05,
  thin = 500, burnin = 90000)
# reverse number significantly negatively correlates with trials to
# reverse, as expected due to the manipulation
summary(serial)
# Did fixed effects converge (<0.1)? Yes
autocorr(serial$Sol)
# Did random effects converge (<0.1)? Yes except for 2 values: 0.11
# and 0.12
autocorr(serial$VCV)

# AIC calculation
library(MuMIn)
options(na.action = "na.fail")
base <- dredge(MCMCglmm(TrialsToReverse ~ ReverseNumber, random = ~ID +
  Batch, family = "poisson", data = d, verbose = F, prior = prior, nitt = 3e+05,
  thin = 500, burnin = 90000))
library(knitr)
kable(base, caption = "")

```

1228 **P2: serial reversal improves rule switching and problem solving** Note on 14 May 2020: Please
 1229 see our Alternative Analyses section where we describe that we will conduct this analysis as in the new
 1230 models in the Ability to detect actual effects section, which will replace the analysis listed below.

1231 **Analysis:** Because the independent variables could influence each other, we will analyze them in a single
 1232 model. A Generalized Linear Mixed Model [GLMM; MCMCglmm function, MCMCglmm package; J. D.
 1233 Hadfield (2010)] will be used with a Poisson distribution and log link using 13,000 iterations with a thinning
 1234 interval of 10, a burnin of 3,000, and minimal priors ($V=1$, $\nu=0$) (J. Hadfield, 2014). We will ensure the
 1235 GLMM shows acceptable convergence [lag time autocorrelation values <0.01 ; J. D. Hadfield (2010)], and
 1236 adjust parameters if necessary. We will determine whether an independent variable had an effect or not
 1237 using the Estimate in the full model.

1238 To roughly estimate our ability to detect actual effects (because these power analyses are designed for
 1239 frequentist statistics, not Bayesian statistics), we ran a power analysis in G*Power with the following settings:
 1240 test family=F tests, statistical test=linear multiple regression: Fixed model (R^2 deviation from zero), type
 1241 of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the
 1242 effect size until the total sample size in the output matched our projected sample size (n=32). The number
 1243 of predictor variables was restricted to only the fixed effects because this test was not designed for mixed
 1244 models. The protocol of the power analysis is here:

1245 *Input:*

1246 Effect size $f^2 = 0.41$

1247 err prob = 0.05

1248 Power (1- err prob) = 0.7

1249 Number of predictors = 5

1250 *Output:*

1251 Noncentrality parameter = 13.1200000
 1252 Critical F = 2.5867901
 1253 Numerator df = 5
 1254 Denominator df = 26
 1255 Total sample size = 32
 1256 Actual power = 0.7103096

1257 This means that, with our sample size of 32, we have a 71% chance of detecting a large effect (approximated
 1258 at $f^2=0.35$ by Cohen, 1988).

1259 We will first determine whether the total loci solved, the latency to solve or attempt at new loci are correlated
 1260 across the two distinct multi-access boxes. If there is a positive correlation, then we will only use the variables
 1261 for the plastic multi-access box (for which we will likely have more data), as presented below. If there is no
 1262 correlation, we will incorporate the total loci solved, the latencies to solve and attempt at new loci for each
 1263 of the multi-access boxes as independent variables in our model.

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"))

##### This is the model code from the ability to detect actual effects section, copied here for clarity
#remove pilot birds and Taco because he was the only one in batch "Juvenile"
d2 <- d[!d$Bird=="Fajita" & !d$Bird=="Empanada",]

#ulam doesn't like that batch is not consecutive (there is no batch 2 in this sample, only 1, 3 and 4),
d2$Batch[d2$Batch==3]<-2
d2$Batch[d2$Batch==4]<-3
d2$Batch[d2$Batch=="3a"]<-4 #This is Taco bc he wasn't officially in a batch due to him being the first
d2$Batch<-as.integer(d2$Batch)

#load libraries
library(rethinking)
library(rstan)
library(formatR)

### MAB PLASTIC LOCI last reversal
#remove NAs from the variables that will be in the models. n=17
d3 <- subset(d2,!is.na(d2["Trialstoreverselast"])) & !(is.na(d2["TotalLoci_plastic"])))

dlist <- list(locisolved = d3$TotalLoci_plastic,
              trials = standardize(d3$Trialstoreverselast),
              batch = as.integer(d3$Batch)
            )

mloci <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[batch] + b*trials , #batch=random effect, standardize trials so 0=mean
  a[batch] ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive, and
) , data=dlist , chains=4 , log_lik=TRUE )

precis(mloci,depth=2)
# a=number of loci solved: was there a difference between batches? Yes, batch 1 solved more loci
```

```

#b=effect of trials to reverse last on the number of loci solved. Results show that there are no relati
#mean sd 5.5% 94.5% n_eff Rhat
#a[1] 0.61 0.39 0.01 1.22 3289 1
#a[2] 0.44 0.39 -0.19 1.06 2763 1
#a[3] -0.76 0.56 -1.65 0.11 3031 1
#a[4] -0.48 0.75 -1.70 0.65 3743 1
#b -0.28 0.26 -0.69 0.13 2905 1

### MAB LOG LOCI last reversal
#remove NAs from the variables that will be in the models. n=12
d4 <- subset(d2,!is.na(d2["Trialstoreverselast"])) & !is.na(d2["TotalLoci_wooden"]))

dlistLog <- list(locisolved = d4$TotalLoci_wooden,
                  trials = standardize(d4$Trialstoreverselast),
                  batch = as.integer(d4$Batch)
)

mlociw <- ulam( alist(
  locisolved ~ dbinom(4,p) , #4 loci, p=probability of solving a locus
  logit(p) <- a[batch] + b*trials , #batch=random effect, standardize trials so 0=mean
  a[batch] ~ dnorm(0,1) , #each batch gets its own intercept
  b ~ dnorm(0,0.4) #our prior expectation for b is that it is around 0, can be negative or positive, and
) , data=dlistLog , chains=4 , log_lik=TRUE )

precis(mlociw,depth=2)
#a=number of loci solved: was there a difference between batches? Yes, batches 2 and 3 (actually 3 and
#b=effect of trials to reverse last on the number of loci solved. There was no relationship between tri
#mean sd 5.5% 94.5% n_eff Rhat
#a[1] 1.09 0.75 -0.09 2.35 2820 1
#a[2] 0.83 0.37 0.26 1.44 2595 1
#a[3] 1.45 0.63 0.47 2.49 2432 1
#a[4] 1.08 0.76 -0.10 2.36 2573 1
#b 0.14 0.29 -0.32 0.62 2539 1

#plot
op <- par(mfrow=c(1,1), oma=c(0,0,0,0), mar=c(4.5,4.5,2,0.2), cex.lab=1.8, cex.axis=2)
plot(jitter(d3$Trialstoreverselast),jitter(d3$TotalLoci_plastic), ylab="Number of loci solved", xlab="T
points(jitter(d4$Trialstoreverselast),jitter(d4$TotalLoci_wooden), cex=4, pch=1, yaxt="n")
legend(x="topright", y=8, legend=c(pch2="Plastic", pch1="Wooden"), pch=c(2,1), box.lty=1, cex=2)
axis(side=2, at=c(1,2,3,4))
par(op)

### MAB PLASTIC SWITCH last reversal
#Load packages
library("Rcpp")
library(ggplot2)

#remove NAs from the variables that will be in the models. n=11
d5 <- subset(d2,!is.na(d2["Trialstoreverselast"])) & !is.na(d2["AvgLatencyAttemptNewLoci_plastic"]))

```

```

dlist5 <- list(latency = d5$AvgLatencyAttemptNewLoci_plastic,
               trials = standardize(d5$Trialstoreverselast),
               batch = as.integer(d5$Batch)
)

mswitchhp <- ulam(
  alist(
    latency ~ dgampois(lambda, phi),
    log(lambda) <- a[batch] + b*trials,
    a[batch] ~ dnorm(1,1),
    b ~ dnorm(0,1),
    phi ~ dexp(1)
  ), data=dlist5, log_lik=TRUE, messages=FALSE)

precis(mswitchhp, depth=2)
#phi=dispersion of gamma poisson, b=effect of trials to reverse on latency, a=were some batches faster
#b=no correlation between average switch latencies and number of trials in last reversal

#mean sd 5.5% 94.5% n_eff Rhat
#a[1] 4.74 0.45 3.97 5.39 208 1
#a[2] 3.64 0.42 2.99 4.32 278 1
#a[3] 4.63 0.58 3.69 5.53 216 1
#b 0.32 0.26 -0.06 0.77 438 1
#phi 0.78 0.43 0.27 1.60 200 1

### MAB LOG SWITCH last reversal
#remove NAs from the variables that will be in the models. n=11
d6 <- subset(d2,!is.na(d2["Trialstoreverselast"])) & !is.na(d2["AvgLatencyAttemptNewLoci_wooden"]))

dlist6 <- list(latency = d6$AvgLatencyAttemptNewLoci_wooden,
               trials = standardize(d6$Trialstoreverselast),
               batch = as.integer(d6$Batch)
)

mswitchw <- ulam(
  alist(
    latency ~ dgampois(lambda, phi),
    log(lambda) <- a[batch] + b*trials,
    a[batch] ~ dnorm(1,1),
    b ~ dnorm(0,1),
    phi ~ dexp(1)
  ), data=dlist6, log_lik=TRUE, messages=FALSE)

precis(mswitchw, depth=2)
#phi=dispersion of gamma poisson, b=effect of trials to reverse on latency, a=were some batches faster
#b=no correlation between average switch latencies and number of trials in last reversal

#mean sd 5.5% 94.5% n_eff Rhat
#a[1] 4.17 0.68 3.07 5.25 208 1
#a[2] 4.52 0.60 3.54 5.43 237 1
#a[3] 4.27 0.60 3.36 5.22 207 1
#a[4] 2.66 0.73 1.57 3.89 304 1

```

```

#b      -0.27 0.36 -0.81  0.36   304     1
#phi    0.20 0.12  0.06  0.45   162     1

#plot
op <- par(mfrow=c(1,1), oma=c(0,0,0,0), mar=c(4.5,4.5,2,0.2), cex.lab=1.8, cex.axis=2)
plot(jitter(d5$Trialstoreverselast),jitter(d5$AvgLatencyAttemptNewLoci_plastic), ylab="Average seconds"
points(jitter(d6$Trialstoreverselast),jitter(d6$AvgLatencyAttemptNewLoci_wooden), cex=4, pch=1, yaxt="n")
legend(x="topright", y=8, legend=c(pch2="Plastic", pch1="Wooden"), pch=c(2,1), box.lty=1, cex=2)
axis(side=2, at=c(100,200,300,400,500,600,700,800,900,1000,1100,1200,1300,1400,1500))
par(op)

##### BELOW was in the original preregistration #####
#Is performance on the two multi-access boxes correlated?
#cor(d$AvgLatencySolveNewLoci_plastic, d$AvgLatencySolveNewLoci_wooden) #we no longer run this analyses
cor.test(d$AvgLatencyAttemptNewLoci_plastic, d$AvgLatencyAttemptNewLoci_wooden, use="pairwise.complete.obs")
#plastic and wooden are not significantly correlated cor=0.74 (95% CI=-0.19-0.97), t=2.18, df=4, p=0.09
cor.test(d$TotalLoci_plastic, d$TotalLoci_wooden, use="pairwise.complete.obs", method="pearson")
#plastic and wooden are not significantly correlated cor=0.51 (95% CI=-0.09-0.84), t=1.86, df=10, p=0.07

# DATA CHECKING
library(DHARMA)
library(lme4)
simulationOut <- simulateResiduals(fittedModel = glmer(TrialsToReverse ~ Condition + AvgLatencySolveNewLoci + TotalLoci, data = d, family = "poisson", control = list(maxfun = 10000)))
simulationOut$scaledResiduals #Expect a flat distribution of the overall residuals, and uniformity in y-axis
testDispersion(simulationOut) #if under- or over-dispersed, then p-value<0.05, but then check the dispersion
testZeroInflation(simulationOut) #compare expected vs observed zeros, not zero-inflated if p<0.05
testUniformity(simulationOut) #check for heteroscedasticity ("a systematic dependency of the dispersion parameter on the mean")
plot(simulationOut) #...there should be no pattern in the data points in the right panel
plotResiduals(Condition, simulationOut$scaledResiduals) #plot the residuals against other predictors (including random effects)

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0)), G = list(G1 = list(V = 1, nu = 0), G2 = list(V = 1, nu = 0)))
imp <- MCMCglmm(TrialsToReverse ~ Condition + AvgLatencySolveNewLoci + TotalLoci, data = d, family = "poisson", random = ~Batch, nitt = 13000, thin = 10, burnin = 3000, prior = prior)
summary(imp)
# autocorr(imp$Sol) #Did fixed effects converge?
# autocorr(imp$VCV) #Did random effects converge?

```

1264 **P2 alternative 2: additional analysis: latency and motor diversity** A Generalized Linear Mixed
 1265 Model [GLMM; MCMCglmm function, MCMCglmm package; J. D. Hadfield (2010)] will be used with a
 1266 Poisson distribution and log link using 13,000 iterations with a thinning interval of 10, a burnin of 3,000, and
 1267 minimal priors ($V=1$, $\nu=0$) (J. Hadfield, 2014). We will ensure the GLMM shows acceptable convergence

1268 [lag time autocorrelation values <0.01; J. D. Hadfield (2010)], and adjust parameters if necessary. We will
 1269 determine whether an independent variable had an effect or not using the Estimate in the full model.

1270 To roughly estimate our ability to detect actual effects (because these power analyses are designed for
 1271 frequentist statistics, not Bayesian statistics), we ran a power analysis in G*Power with the following settings:
 1272 test family=F tests, statistical test=linear multiple regression: Fixed model (R^2 deviation from zero), type
 1273 of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the
 1274 effect size until the total sample size in the output matched our projected sample size (n=32). The number
 1275 of predictor variables was restricted to only the fixed effects because this test was not designed for mixed
 1276 models. The protocol of the power analysis is here:

1277 *Input:*

1278 Effect size $f^2 = 0.27$

1279 err prob = 0.05

1280 Power (1- err prob) = 0.7

1281 Number of predictors = 2

1282 *Output:*

1283 Noncentrality parameter = 8.6400000

1284 Critical F = 3.3276545

1285 Numerator df = 2

1286 Denominator df = 29

1287 Total sample size = 32

1288 Actual power = 0.7047420

1289 This means that, with our sample size of 32, we have a 70% chance of detecting a medium (approximated
 1290 at $f^2=0.15$ by Cohen, 1988) to large effect (approximated at $f^2=0.35$ by Cohen, 1988).

1291 We will perform separate models for each multi-access box (plastic and wooden).

1292 NOTE (Aug 2021): when attempting to run the below model, we realized the model has to be a GLM and
 1293 not a GLMM because there is only one data point per bird, so we changed this accordingly.

```
# Latency to attempt to solve a new locus
dp <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))
  header = F, sep = ",",
  stringsAsFactors = F)

dp <- data.frame(dp)
colnames(dp) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLocisSolvedMABplastic",
  "TotalLocisSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
dp <- subset(dp, !(is.na(dp["MotorActionsPlastic"])) & !(is.na(dp["TrialsLastReversal"])) &
  !(is.na(dp["AverageLatencyAttemptNewLocusMABplastic"])))

# n=11: 6 in manipulated group, 5 in control group
# length(dp$AverageLatencyAttemptNewLocusMABplastic)

# look at the data hist(dp$AverageLatencyAttemptNewLocusMABplastic)
```

```

# mean(dp$AverageLatencyAttemptNewLocusMABplastic) #208
# sd(dp$AverageLatencyAttemptNewLocusMABplastic) #226

# hist(dp$MotorActionsPlastic) mean(dp$MotorActionsPlastic) #14
# sd(dp$MotorActionsPlastic) #3

# mean(dp$TrialsLastReversal) #52 sd(dp$TrialsLastReversal) #22
# mean(dp$TrialsFirstReversal) #70 sd(dp$TrialsFirstReversal) #21

# PLASTIC MULTI-ACCESS BOX (P) DATA CHECKING
library(DHARMA)
library(lme4)
simulationOutp <- simulateResiduals(fittedModel = glmer(AverageLatencyAttemptNewLocusMABplastic ~ TrialsLastReversal + MotorActionsPlastic + (1 | Bird), family = poisson,
  data = dp), n = 250) #250 simulations, but if want higher precision change n>1000
plot(simulationOutp$scaledResiduals) #Expect a flat distribution of the overall residuals, and uniform
testDispersion(simulationOutp) #if under- or over-dispersed, then p-value<0.05, but then check the dis...
testZeroInflation(simulationOutp) #compare expected vs observed zeros, not zero-inflated if p<0.05. p=...
testUniformity(simulationOutp) #check for heteroscedasticity ('a systematic dependency of the dispersi...
plot(simulationOutp) #...there should be no pattern in the data points in the right panel. There is no

# GLM
motp <- glm(dp$AverageLatencyAttemptNewLocusMABplastic ~ dp$TrialsLastReversal +
  dp$MotorActionsPlastic)

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
dredgemp <- dredge(glm(dp$AverageLatencyAttemptNewLocusMABplastic ~ dp$TrialsLastReversal +
  dp$MotorActionsPlastic))
library(knitr)
kable(dredgemp, caption = "")
# Akaike weights are all >0.5, therefore the models are essentially
# the same

# GLMM - can't use this because only 1 data point per bird
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
  G = list(G1 = list(V = 1, nu = 0)))
div <- MCMCglmm(AverageLatencyAttemptNewLocusMABplastic ~ TrialsLastReversal +
  MotorActionsPlastic, random = ~Bird, family = "poisson", data = diversity,
  verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000)
summary(div)
# autocorr(div$Sol) #Did fixed effects converge? autocorr(div$VCV)
# #Did random effects converge?

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
base1 <- dredge(MCMCglmm(TrialsToSolveNewLociP ~ TrialsToReverseLast +
  NumberMotorActionsMultiP, random = ~ID, family = "poisson", data = diversity,

```

```

    verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000))
library(knitr)
kable(base1, caption = "")

# WOODEN MULTI-ACCESS BOX (W)
dw <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",", stringsAsFactors = F)

dw <- data.frame(dw)
colnames(dw) <- c("Bird", "Batch", "Sex", "Trials to learn", "TrialsFirstReversal",
  "TrialsLastReversal", "ReversalsToPass", "TotalLociSolvedMABplastic",
  "TotalLociSolvedMABwooden", "AverageLatencyAttemptNewLocusMABplastic",
  "AverageLatencyAttemptNewLocusMABwooden", "Trials to learn (touchscreen)",
  "Trials to first reversal (touchscreen)", "MotorActionsPlastic", "MotorActionsWooden")

# Remove NAs
dw <- subset(dw, !(is.na(dw["MotorActionsWooden"])) & !(is.na(dw["TrialsLastReversal"])) &
  !(is.na(dw["AverageLatencyAttemptNewLocusMABwooden"])))

# n=11: 5 in manipulated group, 6 in control group
# length(dw$AverageLatencyAttemptNewLocusMABwooden)

# look at the data hist(dw$AverageLatencyAttemptNewLocusMABwooden)
# mean(dw$AverageLatencyAttemptNewLocusMABwooden) #463
# sd(dw$AverageLatencyAttemptNewLocusMABwooden) #481

# hist(dw$MotorActionsWooden) mean(dw$MotorActionsWooden) #13
# sd(dw$MotorActionsWooden) #4

# mean(dw$TrialsLastReversal) #60 sd(dw$TrialsLastReversal) #38

# DATA CHECKING
library(DHARMA)
library(lme4)
simulationOutw <- simulateResiduals(fittedModel = glm(dw$AverageLatencyAttemptNewLocusMABwooden ~
  dw$TrialsLastReversal + dw$MotorActionsWooden), n = 250) #250 simulations, but if want higher prec
plot(simulationOutw$scaledResiduals) #Expect a flat distribution of the overall residuals, and uniform
testDispersion(simulationOutw) #if under- or over-dispersed, then p-value<0.05, but then check the dis
testZeroInflation(simulationOutw) #compare expected vs observed zeros, not zero-inflated if p<0.05. p=
testUniformity(simulationOutw) #check for heteroscedasticity ('a systematic dependency of the dispersi
plot(simulationOutw) #...there should be no pattern in the data points in the right panel. It says 'qu

# GLM
motw <- glm(dw$AverageLatencyAttemptNewLocusMABwooden ~ dw$TrialsLastReversal +
  dw$MotorActionsWooden)

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
dredgemw <- dredge(glm(dw$AverageLatencyAttemptNewLocusMABwooden ~ dw$TrialsLastReversal +
  dw$MotorActionsWooden))
library(knitr)
kable(dredgemw, caption = "")
# Akaike weights = 0.71 null and <0.15 for the rest, therefore the

```

```
# models with or without motor actions are essentially the same
```

```
# GLMM - does not work because only one data point per bird
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
            G = list(G1 = list(V = 1, nu = 0)))
div <- MCMCglmm(TrialsToSolveNewLociW ~ TrialsToReverseLast + NumberMotorActionsMultiW,
                 random = ~ID, family = "poisson", data = diversity, verbose = F, prior = prior,
                 nitt = 13000, thin = 10, burnin = 3000)
summary(div)
# autocorr(div$Sol) #Did fixed effects converge? autocorr(div$VCV)
# #Did random effects converge?

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
base1 <- dredge(MCMCglmm(TrialsToSolveNewLociW ~ TrialsToReverseLast +
                           NumberMotorActionsMultiW, random = ~ID, family = "poisson", data = diversity,
                           verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000))
library(knitr)
kable(base1, caption = "")

# Latency to solve a new locus
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
              header = F, sep = ",", stringsAsFactors = F)
diversity <- read.csv("/Users/corina/GTGR/data/data_reversemulti.csv",
                      header = T, sep = ",", stringsAsFactors = F)

# PLASTIC MULTI-ACCESS BOX (P) DATA CHECKING
library(DHARMA)
library(lme4)
simulationOutpu <- simulateResiduals(fittedModel = glmer(TrialsToAttemptNewLociP ~
                                                          TrialsToReverseLast + NumberMotorActionsMultiP + (1 | ID), family = poisson,
                                                          data = diversity), n = 250) #250 simulations, but if want higher precision change n>1000
simulationOutpu$scaledResiduals #Expect a flat distribution of the overall residuals, and uniformity in the distribution of the residuals
testDispersion(simulationOutpu) #if under- or over-dispersed, then p-value<0.05, but then check the dispersion of the residuals
testZeroInflation(simulationOutpu) #compare expected vs observed zeros, not zero-inflated if p<0.05
testUniformity(simulationOutpu) #check for heteroscedasticity ('a systematic dependency of the dispersion of the residuals on the mean')
plot(simulationOutpu) ##...there should be no pattern in the data points in the right panel
plotResiduals(NumberMotorActionsMultiP, simulationOutpu$scaledResiduals) #plot the residuals against other variables
plotResiduals(TrialsToReverseLast, simulationOutpu$scaledResiduals)

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
            G = list(G1 = list(V = 1, nu = 0)))
div <- MCMCglmm(TrialsToAttemptNewLociP ~ TrialsToReverseLast + NumberMotorActionsMultiP,
                 random = ~ID, family = "poisson", data = diversity, verbose = F, prior = prior,
                 nitt = 13000, thin = 10, burnin = 3000)
summary(div)
# autocorr(div$Sol) #Did fixed effects converge? autocorr(div$VCV)
# #Did random effects converge?
```

```

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
base1 <- dredge(MCMCglmm(TrialsToAttemptNewLociP ~ TrialsToReverseLast +
  NumberMotorActionsMultiP, random = ~ID, family = "poisson", data = diversity,
  verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000))
library(knitr)
kable(base1, caption = "")

# Latency to solve a new locus
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations"))
  header = F, sep = ",", stringsAsFactors = F)
diversity <- read.csv("/Users/corina/GTGR/data/data_reversemulti.csv",
  header = T, sep = ",", stringsAsFactors = F)

# WOODEN MULTI-ACCESS BOX (W) DATA CHECKING
library(DHARMA)
library(lme4)
simulationOutpu <- simulateResiduals(fittedModel = glmer(TrialsToAttemptNewLociW ~
  TrialsToReverseLast + NumberMotorActionsMultiW + (1 | ID), family = poisson,
  data = diversity), n = 250) #250 simulations, but if want higher precision change n>1000
simulationOutpu$scaledResiduals #Expect a flat distribution of the overall residuals, and uniformity in the spread of residuals
testDispersion(simulationOutpu) #if under- or over-dispersed, then p-value<0.05, but then check the dispersion
testZeroInflation(simulationOutpu) #compare expected vs observed zeros, not zero-inflated if p<0.05
testUniformity(simulationOutpu) #check for heteroscedasticity ('a systematic dependency of the dispersion on the mean')
plot(simulationOutpu) ##...there should be no pattern in the data points in the right panel
plotResiduals(NumberMotorActionsMultiW, simulationOutpu$scaledResiduals) #plot the residuals against one another
plotResiduals(TrialsToReverseLast, simulationOutpu$scaledResiduals)

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
  G = list(G1 = list(V = 1, nu = 0)))
div <- MCMCglmm(TrialsToAttemptNewLociW ~ TrialsToReverseLast + NumberMotorActionsMultiW,
  random = ~ID, family = "poisson", data = diversity, verbose = F, prior = prior,
  nitt = 13000, thin = 10, burnin = 3000)
summary(div)
# autocorr(div$Sol) #Did fixed effects converge? autocorr(div$VCV)
# #Did random effects converge?

# AIC calculation
library(MuMin)
options(na.action = "na.fail")
base1 <- dredge(MCMCglmm(TrialsToAttemptNewLociW ~ TrialsToReverseLast +
  NumberMotorActionsMultiW, random = ~ID, family = "poisson", data = diversity,
  verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000))
library(knitr)
kable(base1, caption = "")

```

1294 **P3a: repeatable within individuals within a context (reversal learning)** Analysis: Is reversal
 1295 learning (colored tubes) repeatable within individuals within a context (reversal learning)? We will obtain
 1296 repeatability estimates that account for the observed and latent scales, and then compare them with the
 1297 raw repeatability estimate from the null model. The repeatability estimate indicates how much of the total

1298 variance, after accounting for fixed and random effects, is explained by individual differences (ID). We will
 1299 run this GLMM using the MCMCglmm function in the MCMCglmm package (J. D. Hadfield, 2010) with a
 1300 Poisson distribution and log link using 13,000 iterations with a thinning interval of 10, a burnin of 3,000, and
 1301 minimal priors [V=1, nu=0; J. Hadfield (2014)]. We will ensure the GLMM shows acceptable convergence
 1302 [i.e., lag time autocorrelation values <0.01; J. D. Hadfield (2010)], and adjust parameters if necessary.

1303 NOTE (Aug 2021): our data checking process showed that the distribution of values of the data (number of
 1304 trials to reverse) in this model was not a good fit for the Poisson distribution because it was overdispersed
 1305 and heteroscedastic. However, when log-transformed the data approximate a normal distribution and pass
 1306 all of the data checks, therefore we used a Gaussian distribution for our model, which fits the log-transformed
 1307 data well.

1308 To roughly estimate our ability to detect actual effects (because these power analyses are designed for
 1309 frequentist statistics, not Bayesian statistics), we ran a power analysis in G*Power with the following settings:
 1310 test family=F tests, statistical test=linear multiple regression: Fixed model (R^2 deviation from zero), type
 1311 of power analysis=a priori, alpha error probability=0.05. The number of predictor variables was restricted
 1312 to only the fixed effects because this test was not designed for mixed models. We reduced the power to 0.70
 1313 and increased the effect size until the total sample size in the output matched our projected sample size
 1314 (n=32). The protocol of the power analysis is here:

1315 *Input:*

1316 Effect size $f^2 = 0.21$
 1317 err prob = 0.05
 1318 Power (1- err prob) = 0.7
 1319 Number of predictors = 1

1320 *Output:*

1321 Noncentrality parameter = 6.7200000
 1322 Critical F = 4.1708768
 1323 Numerator df = 1
 1324 Denominator df = 30
 1325 Total sample size = 32
 1326 Actual power = 0.7083763

1327 This means that, with our sample size of 32, we have a 71% chance of detecting a medium effect (approximated
 1328 at $f^2=0.15$ by Cohen, 1988).

```
d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = T, sep = ",",
  stringsAsFactors = F)

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d[["TrialsToReverse"]])))
d <- subset(d, !(is.na(d[["ReverseNumber"]])))

# include only those birds in the reversal tubes experiment
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
  ]

# factor variable
d$ID <- as.factor(d$ID)

# remove pilot birds
```

```

d <- d[!d$ID == "Fajita" & !d$ID == "Empanada", ]

# n=9 length(unique(d$ID))

# DATA CHECKING ADDED Aug 2021 - Although our dependent variable
# (number of trials to reverse) is a count variable, the distribution
# of values was not appropriate for a poisson regression. When
# checking the fit of our data to a Poisson model the data were
# overdispersed and heteroscedastic. However, when log-transformed
# the data approximate a normal distribution and pass all of the
# below data checks, indicating the Gaussian model fits our
# log-transformed data well.
library(DHARMa)
library(lme4)
simulationOutput <- simulateResiduals(fittedModel = glmer(log(TrialsToReverse) ~
  ReverseNumber + (1 | ID), family = gaussian, data = d), n = 250) #250 simulations, but if want higher
plot(simulationOutput$scaledResiduals) #Expect a flat distribution of the overall residuals, and uniform
testDispersion(simulationOutput) #if under- or over-dispersed, then p-value<0.05, but then check the dispersion
testZeroInflation(simulationOutput) #compare expected vs observed zeros, not zero-inflated if p>0.05.
testUniformity(simulationOutput) #check for heteroscedasticity ('a systematic dependency of the dispersion
plot(simulationOutput) #...there should be no pattern in the data points in the right panel. There does not appear to be any.

# GLMM
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0)), G = list(G1 = list(V = 1,
  nu = 0)))
serial <- MCMCglmm(log(TrialsToReverse) ~ ReverseNumber, random = ~ID,
  family = "gaussian", data = d, verbose = F, prior = prior, nitt = 50000,
  thin = 100, burnin = 500)
summary(serial)
autocorr(serial$Sol) #Did fixed effects converge (<0.1)? yes, except for 2
autocorr(serial$VCV) #Did random effects converge (<0.1)? yes, except for 4

# REPEATABILITY

# In MCMCglmm, the latent scale adjusted repeatability and its
# credible interval can simply be obtained by:
# serial$VCV[,ID]/(serial$VCV[,ID]+serial$VCV[,units]) - advice from
# Maxime Dahirel
repeata <- serial$VCV[, "ID"]/(serial$VCV[, "ID"] + serial$VCV[, "units"]) #latent scale adjusted repeatability
mean(repeata) #0.13
var(repeata) #0.02 variance
posterior.mode(repeata) #-0.0003
HPDinterval(repeata, 0.95) #5.77e-16 to 0.42, probability=0.95

# ADDED Aug 2021 Is 0.13 a statistically significant repeatability?
# Test whether it is significantly greater than expected at chance by
# permuting number of trials to reverse among individuals. NOTE:
# Because the flexibility manipulation requires the last two
# reversals to be less than or equal to 50 trials, and ReverseNumber
# is significant, indicating birds generally get faster over time, we
# must permute TrialsToReverse across birds within ReverseNumber.

```

```

results = rep(NA, 1000)
for (i in 1:1000) {
  tmp1 = data.frame(ID = d$ID[which(d$ReverseNumber == 1)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 1)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 1)], replace = F))
  tmp2 = data.frame(ID = d$ID[which(d$ReverseNumber == 2)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 2)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 2)], replace = F))
  tmp3 = data.frame(ID = d$ID[which(d$ReverseNumber == 3)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 3)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 3)], replace = F))
  tmp4 = data.frame(ID = d$ID[which(d$ReverseNumber == 4)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 4)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 4)], replace = F))
  tmp5 = data.frame(ID = d$ID[which(d$ReverseNumber == 5)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 5)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 5)], replace = F))
  tmp6 = data.frame(ID = d$ID[which(d$ReverseNumber == 6)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 6)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 6)], replace = F))
  tmp7 = data.frame(ID = d$ID[which(d$ReverseNumber == 7)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 7)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 7)], replace = F))
  tmp8 = data.frame(ID = d$ID[which(d$ReverseNumber == 8)], ReverseNumber = d$ReverseNumber[which(d$ReverseNumber == 8)], TrialsToReverse = sample(d$TrialsToReverse[which(d$ReverseNumber == 8)], replace = F))
  tmp = rbind(tmp1, tmp2, tmp3, tmp4, tmp5, tmp6, tmp7, tmp8)
  m <- MCMCglmm(log(TrialsToReverse) ~ ReverseNumber, random = ~ID, family = "gaussian",
    data = tmp, verbose = F, prior = prior, nitt = 50000, thin = 100,
    burnin = 500)
  rpt <- m$VCV[, "ID"]/(m$VCV[, "ID"] + m$VCV[, "units"]) #latent scale adjusted repeatability and i
  results[i] = mean(rpt)
}
hist(results)
abline(v = 0.13, col = "red")
sum(results > 0.13)/1000
# p = 0.001 - Our repeatability value of 0.13 is significantly
# greater than that expected if birds are performing randomly in each
# reversal

# WE DID NOT end up using the code below because the above gave us
# what we needed Repeatability on the data/observed scale (accounting
# for fixed effects) code from Supplementary Material S2 from
# Villemereuil et al. 2018 J Evol Biol
vf <- sapply(1:nrow(serial[["Sol"]]), function(i) {
  var(predict(serial, it = i))
}) #estimates for each iteration of the MCMC

repeataF <- (vf + serial$VCV[, "ID"])/(vf + serial$VCV[, "ID"] + serial$VCV[, "units"]) #latent scale adjusted + data scale
posterior.mode(repeataF) #0.998
HPDinterval(repeataF, 0.95) #0.992 to 0.9998, probability=0.952

```

```

# Now compare with the raw repeatability: null model. NOTE: we
# shouldn't run this one because the reversal was a manipulation so
# the reverse number must be included
serialraw <- MCMCglmm(TrialsToReverse ~ 1, random = ~ID, family = "poisson",
  data = d, verbose = F, prior = prior, nitt = 50000, thin = 100, burnin = 25000)
# summary(serialraw)

repeataraw <- serialraw$VCV[, "ID"]/(serialraw$VCV[, "ID"] + serialraw$VCV[, "units"])
#latent scale adjusted repeatability and its credible interval
posterior.mode(repeataraw) # -0.00002
HPDInterval(repeataraw, 0.95) #7.2e-16 to 0.18, probability=0.952
  
```

1329 **P3a alternative: was the potential lack of repeatability on colored tube reversal learning due**
 1330 **to motivation or hunger?** **Analysis:** Because the independent variables could influence each other or
 1331 measure the same variable, I will analyze them in a single model: Generalized Linear Mixed Model [GLMM;
 1332 MCMCglmm function, MCMCglmm package; J. D. Hadfield (2010)] with a binomial distribution (called
 1333 categorical in MCMCglmm) and logit link using 13,000 iterations with a thinning interval of 10, a burnin
 1334 of 3,000, and minimal priors ($V=1$, $nu=0$) (J. Hadfield, 2014). We will ensure the GLMM shows acceptable
 1335 convergence [lag time autocorrelation values <0.01 ; J. D. Hadfield (2010)], and adjust parameters if necessary.
 1336 The contribution of each independent variable will be evaluated using the Estimate in the full model. NOTE
 1337 (Apr 2021): This analysis is restricted to data from their first reversal because this is the only reversal data
 1338 that is comparable across the manipulated and control groups.

1339 To roughly estimate our ability to detect actual effects (because these power analyses are designed for
 1340 frequentist statistics, not Bayesian statistics), we ran a power analysis in G*Power with the following settings:
 1341 test family=F tests, statistical test=linear multiple regression: Fixed model (R^2 deviation from zero), type
 1342 of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the
 1343 effect size until the total sample size in the output matched our projected sample size ($n=32$). The number
 1344 of predictor variables was restricted to only the fixed effects because this test was not designed for mixed
 1345 models. The protocol of the power analysis is here:

1346 *Input:*

1347 Effect size $f^2 = 0.31$

1348 err prob = 0.05

1349 Power (1- err prob) = 0.7

1350 Number of predictors = 4

1351 *Output:*

1352 Noncentrality parameter = 11.4700000

1353 Critical F = 2.6684369

1354 Numerator df = 4

1355 Denominator df = 32

1356 Total sample size = 37

1357 Actual power = 0.7113216

1358 This means that, with our sample size of 32, we have a 71% chance of detecting a large effect (approximated
 1359 at $f^2=0.35$ by Cohen, 1988).

```

d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = T, sep = ",", stringsAsFactors = F)
  
```

```

d <- d[d$Reversal == 1, ]
# want only data from reversal 1 (their first reversal) because this
# is the only reversal data that is comparable across birds in the
# control and manipulated groups
head(d)

# DATA CHECKING
library(DHARMa)
library(lme4)
simulationOutput <- simulateResiduals(fittedModel = glmer(CorrectChoice ~
  Trial + LatencyToChoose + MinSinceFoodRemoved + NumberRewardsFromPrevTrials +
  (1 | ID) + (1 | Batch), family = binomial, data = d), n = 250) #250 simulations, but if want h
simulationOutput$scaledResiduals #Expect a flat distribution of the overall residuals, and uniformity
testDispersion(simulationOutput) #if under- or over-dispersed, then p-value<0.05, but then check the d
testZeroInflation(simulationOutput) #compare expected vs observed zeros, not zero-inflated if p<0.05
testUniformity(simulationOutput) #check for heteroscedasticity ('a systematic dependency of the disper
plot(simulationOutput) #...there should be no pattern in the data points in the right panel
plotResiduals(LatencyToChoose, simulationOutput$scaledResiduals) #plot the residuals against other pre

# GLMM - Is trial the main independent variable associated with
# learning performance (CorrectChoice) or are other variables
# associated with performance, including motivation and hunger?
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0),
  R3 = list(V = 1, nu = 0), R4 = list(V = 1, nu = 0)), G = list(G1 = list(V = 1,
  nu = 0), G2 = list(V = 1, nu = 0)))

rr1 <- MCMCglmm(CorrectChoice ~ Trial + LatencyToChoose + MinSinceFoodRemoved +
  NumberRewardsFromPrevTrials, random = ~ID + Batch, family = "categorical",
  data = d, verbose = F, prior = prior, nitt = 13000, thin = 10, burnin = 3000)
summary(rr1)
autocorr(rr1$Sol) #Did fixed effects converge?
autocorr(rr1$VCV) #Did random effects converge?

```

1360 **P3b: individual consistency across contexts** Analysis: Do those individuals that are faster to reverse
 1361 a color preference also have lower latencies to switch to new options on the multi-access box? Do those
 1362 individuals that are faster to reverse a color preference also have lower latencies to switch to new options
 1363 on the multi-access box? A Generalized Linear Mixed Model [GLMM; MCMCglmm function, MCMCglmm
 1364 package; (J. D. Hadfield, 2010) will be used with a Poisson distribution and log link using 13,000 iterations
 1365 with a thinning interval of 10, a burnin of 3,000, and minimal priors (V=1, nu=0) (J. Hadfield, 2014). We
 1366 will ensure the GLMM shows acceptable convergence [lag time autocorrelation values <0.01; J. D. Hadfield
 1367 (2010)], and adjust parameters if necessary. We will determine whether an independent variable had an effect
 1368 or not using the Estimate in the full model.

1369 To roughly estimate our ability to detect actual effects (because these power analyses are designed for
 1370 frequentist statistics, not Bayesian statistics), we ran a power analysis in G*Power with the following settings:
 1371 test family=F tests, statistical test=linear multiple regression: Fixed model (R^2 deviation from zero), type
 1372 of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the
 1373 effect size until the total sample size in the output matched our projected sample size (n=32). The number
 1374 of predictor variables was restricted to only the fixed effects because this test was not designed for mixed
 1375 models. The protocol of the power analysis is here:

1376 *Input:*

1377 Effect size $f^2 = 0.21$
 1378 err prob = 0.05
 1379 Power (1- err prob) = 0.7
 1380 Number of predictors = 1
 1381 *Output:*
 1382 Noncentrality parameter = 6.7200000
 1383 Critical F = 4.1708768
 1384 Numerator df = 1
 1385 Denominator df = 30
 1386 Total sample size = 32
 1387 Actual power = 0.7083763

1388 This means that, with our sample size of 32, we have a 71% chance of detecting a medium effect (approximated
 1389 at $f^2=0.15$ by Cohen, 1988).

```

d <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistrations.csv"),
  header = T, sep = ",",
  stringsAsFactors = F)

# remove NAs from the variables that will be in the model
d <- subset(d, !(is.na(d[["TrialsToReverse"]])))
d <- subset(d, !(is.na(d[["ReverseNumber"]])))

# include only those birds in the reversal tubes experiment
d <- d[d$TubesOrTouchscreen == "TUBES" & d$ExperimentalGroup == "Manipulation",
  ]

# factor variable
d$ID <- as.factor(d$ID)

# remove pilot birds (Fajita and Empanada) and Memela who did not
# pass the reversal experiment and therefore was not offered the MAB
# experiments
d <- d[!d$ID == "Fajita" & !d$ID == "Empanada" & !d$ID == "Memela", ]

# n=8 length(unique(d$ID))

# NOTE: removed 'touchscreen trials to reverse' from the models below
# because the touchscreen experiment did not end up working out.
# Removed 'condition' from the models below because this analysis
# only works on birds that have had serial reversals, which are only
# those in the manipulated group

# DATA CHECKING
library(DHARMA)
library(lme4)
simulationOutput <- simulateResiduals(fittedModel = glmer(LatencyMABplastic ~
  ReverseNumber + TrialsToReverse + (1 | ID), family = poisson, data = d),
  n = 250) #250 simulations, but if want higher precision change n>1000
plot(simulationOutput$scaledResiduals) #Expect a flat distribution of the overall residuals, and uniform
testDispersion(simulationOutput) #if under- or over-dispersed, then p-value<0.05, but then check the dispersion
  
```

```

testZeroInflation(simulationOutput) #compare expected vs observed zeros, not zero-inflated if p<0.05.
testUniformity(simulationOutput) #check for heteroscedasticity ('a systematic dependency of the dispersion of the data points around the mean')
plot(simulationOutput) #...there should be no pattern in the data points in the right panel. There are
# January 2021: My interpretation of the patterns is that this was a
# manipulation, therefore, by definition the data will not be
# randomly (normally) distributed. Therefore, we will move forward
# with the glmm as planned.

# GLMM color reversal tubes compared with multi-access box plastic
library(MCMCglmm)
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
            G = list(G1 = list(V = 1, nu = 0)))
rm <- MCMCglmm(LatencyMABplastic ~ ReverseNumber * TrialsToReverse, random = ~ID,
                family = "poisson", data = d, verbose = F, prior = prior, nitt = 130000,
                thin = 1000, burnin = 30000)
summary(rm)
# post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 2.08708
# -4.45451 11.67734 100 0.66 ReverseNumber 1.01476 -2.75484 5.49974
# 100 0.42 TrialsToReverse 0.01693 -0.09999 0.11593 100 0.58
# ReverseNumber:TrialsToReverse -0.01159 -0.07061 0.03283 100 0.42
# nothing significant so no consistent individual differences across
# contexts on MAB plastic and trials to reverse

# autocorr(rm$Sol) #Did fixed effects converge (<0.1)? yes
# autocorr(rm$VCV) #Did random effects converge (<0.1)? yes except
# for 3 values

# GLMM color reversal tubes compared with multi-access box wooden
prior = list(R = list(R1 = list(V = 1, nu = 0), R2 = list(V = 1, nu = 0)),
            G = list(G1 = list(V = 1, nu = 0)))
rmw <- MCMCglmm(LatencyMABwooden ~ ReverseNumber * TrialsToReverse, random = ~ID,
                  family = "poisson", data = d, verbose = F, prior = prior, nitt = 130000,
                  thin = 1000, burnin = 30000)
# summary(rmw) post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept)
# 3.622381 0.148743 7.810863 159.0 0.08 . ReverseNumber 0.211605
# -1.843271 2.126334 100.0 0.88 TrialsToReverse 0.032183 -0.019718
# 0.076067 147.9 0.14 ReverseNumber:TrialsToReverse -0.004685
# -0.037464 0.014299 100.0 0.62 nothing significant so no consistent
# individual differences across contexts on MAB wooden and trials to
# reverse

# autocorr(rmw$Sol) #Did fixed effects converge (<0.1)? yes except
# for 1 value autocorr(rmw$VCV) #Did random effects converge (<0.1)?
# yes

```

¹³⁹⁰ **P4: learning strategies (for birds in the manipulated group only)** Analysis: Learning strategies
¹³⁹¹ will be identified by matching them to the two known approximate strategies of the contextual, binary
¹³⁹² multi-armed bandit: epsilon-first and epsilon-decreasing (McInerney, 2010; as in Logan, 2016).

¹³⁹³ From Logan (2016) (emphasis added):

¹³⁹⁴ The following equations refer to the different phases involved in each strategy:

1395 Equation 1 (exploration phase):

$$\epsilon N$$

1396 Equation 2 (exploitation phase):

$$(1 - \epsilon)N$$

1397 N is the number of trials given, and epsilon,

$$\epsilon$$

1398 , represents the subject's uncertainty about the location of the reward, starting at complete
 1399 uncertainty ($\epsilon = 1$) at the beginning of the experiment and decreasing rapidly as individuals gain
 1400 experience with the task (exploration phase where the rewarded [option] is chosen below or at
 1401 chance levels) and switch to the exploitative phase (the rewarded [option] is chosen significantly
 1402 above chance levels). Because the [subjects] needed to learn the rules of the task, they necessarily
 1403 had an exploration phase. The **epsilon-first strategy** involves an exploration phase followed
 1404 by an entirely exploitative phase. The optimal strategy overall would be to explore one color in
 1405 the first trial and the other color in the second trial, and then switch to an exploitative strategy
 1406 (choose the rewarded [option] significantly above chance levels). In this case there would be
 1407 no pattern [in the learning curve] in the choices [during] the exploration phase because it would
 1408 consist of sampling each [option] only once. In the **epsilon-decreasing strategy**, subjects would
 1409 start by making some incorrect choices and then increase their choice of the rewarded [option]
 1410 gradually as their uncertainty decreases until they choose the rewarded [option] significantly
 1411 above chance levels. In this case, a linear pattern emerges [in the learning curve] during the
 1412 exploration phase.

1413 We will then quantitatively determine to what degree each bird used the exploration versus exploitation
 1414 strategy using methods in (Fedderspiel et al., 2017) by calculating the number of 20-trial blocks where birds
 1415 were choosing “randomly” (6-14 correct choices; called sampling blocks; akin to the exploration phase in our
 1416 preregistration) was divided by the total number of blocks to reach criterion per bird. This ratio was also
 1417 calculated for “acquisition” blocks where birds made primarily correct choices (15-20 correct choices; akin to
 1418 the exploitation phase in our preregistration). These ratios, calculated for each bird for their serial reversals,
 1419 quantitatively discern the exploration from the exploitation phases.

1420 NOTE (Aug 2021): the grackles were tested in 10-trial blocks and not 20-trial blocks as in Fedderspiel et al.
 1421 (2017), which would mean that if there were <20 trials in the last block of a reversal, they would be omitted
 1422 from the analysis. Therefore, we changed the block size to 10 trials and adjusted the sampling blocks to 2-9
 1423 correct choices, and the acquisition blocks to 9-10 correct choices using significance levels in the binomial
 1424 test as did Fedderspiel et al. (2017).

```
rr <- read.csv(url("https://raw.githubusercontent.com/corinalogan/grackles/master/Files/Preregistration"))
  header = T, sep = ",",
  stringsAsFactors = F)

# remove NAs from the variables that will be in the model
rr <- subset(rr, !(is.na(rr[["SamplingRatio"]])))
rr <- subset(rr, !(is.na(rr[["AcquisitionRatio"]])))

# GLMM is sampling ratio (exploration) higher earlier in serial
# reversals?
rr1 <- glmer(SamplingRatio ~ Reversal + (1 | ID), family = binomial, data = rr)
summary(rr1)
# There is no significant correlation between reversal number and
# sampling ratio

# GLMM is acquisition ratio (exploitation) higher earlier in serial
# reversals?
rr2 <- glmer(AcquisitionRatio ~ Reversal + (1 | ID), family = binomial,
```

```

  data = rr)
summary(rr2)
# There is no significant correlation between reversal number and
# acquisition ratio

```

1425 **Alternative Analyses** We anticipate that we will want to run additional/different analyses after reading
 1426 McElreath (2016). We will revise this preregistration to include these new analyses before conducting the
 1427 analyses above.

1428 **14 May 2020:** After reading McElreath (2018) and taking McElreath's stats course, we changed a couple
 1429 of things about the analysis plan in this preregistration (before we analyzed any of our data). These are the
 1430 changes we made:

- 1431 1) **Ability to detect actual effects:** We added two simulations and hypothesis-specific models for P2. One
 1432 examines the relationship between the number of loci solved on the multi-access box and the number
 1433 of trials to reverse a preference. The other examines the latency to attempt another locus on the
 1434 multi-access box and the number of trials to reverse a preference.
- 1435 2) **P2: serial reversal improves rule switching and problem solving:** In conducting point 1, we realized that
 1436 we had misinterpreted which variable should be the response variable in this analysis. We originally set
 1437 the number of trials to reverse as the response variable, however we should have instead set the number
 1438 of loci solved as the response variable and then planned to conduct a second model with the latency
 1439 to attempt a new locus as the response variable and number of trials as the explanatory variable. This
 1440 is because a) we manipulated the number of trials to reverse, therefore it must be the explanatory
 1441 variable; and b) they should be split into two models because of a and because these are two very
 1442 different relationships that should be considered in their own models. We also realized that Condition
 1443 (manipulated or control) does not need to be a variable in any of our models because the manipulated
 1444 birds have, by definition, faster reversal speeds. For these reasons, when we conduct the P2 analysis in
 1445 this preregistration, we will use the custom models we made in point 1 above rather than the planned
 1446 MCMCglmm model.

1447 F. ETHICS

1448 This research is carried out in accordance with permits from the:

- 1449 1) US Fish and Wildlife Service (scientific collecting permit number MB76700A-0,1,2)
- 1450 2) US Geological Survey Bird Banding Laboratory (federal bird banding permit number 23872)
- 1451 3) Arizona Game and Fish Department (scientific collecting license number SP594338 [2017], SP606267
 1452 [2018], and SP639866 [2019])
- 1453 4) Institutional Animal Care and Use Committee at Arizona State University (protocol number 17-1594R)
- 1454 5) University of Cambridge ethical review process (non-regulated use of animals in scientific procedures:
 1455 zoo4/17 [2017])

1456 G. AUTHOR CONTRIBUTIONS

1457 **Logan:** Hypothesis development, protocol development, data collection, data analysis and interpretation,
 1458 write up, revising/editing, materials/funding.

1459 **Blaisdell:** Prediction revision, assisted with programming the reversal learning touchscreen experiment,
 1460 protocol development, data interpretation, revising/editing.

1461 **Johnson-Ulrich:** Prediction revision, programming, data collection, data interpretation, revising/editing.

1462 **Lukas:** Hypothesis development, simulation development, data interpretation, revising/editing.

1463 **MacPherson:** Data collection, data interpretation, revising/editing.

1464 **Seitz:** Prediction revision, programmed the reversal learning touchscreen experiment, protocol development,
1465 data interpretation, revising/editing.

1466 **Sevchik:** Data collection, revising/editing.

1467 **McCune:** Added MAB log experiment, protocol development, data collection, data interpretation, revising/
1468 editing, materials.

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1473 I. CONFLICT OF INTEREST DISCLOSURE

1474 We, the authors, declare that we have no financial conflicts of interest with the content of this article. CJ
1475 Logan is a Recommender and on the Managing Board at PCI Ecology.

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1493 K. REFERENCES

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