

1 Thinking outside the box: Problem solving in free-living lizards

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10 Running title: Problem solving outside the box

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12 Keywords: behavioural flexibility, motor self-regulation; problem solving; natural conditions;
13 reptile; Anolis

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17 **ABSTRACT**

18 Despite evidence that organisms are more likely to exhibit their full range of cognitive abilities
19 under conditions found in nature, studies evaluating cognitive abilities under such conditions
20 remain rare, particularly in vertebrate species. Here we conducted an experiment to evaluate
21 problem solving and motor-self regulation in free-ranging arboreal lizards, *Anolis sagrei*, under
22 natural conditions. We presented lizards with a novel detour problem which challenged
23 individuals to circumvent a transparent barrier in order to obtain a food reward. Individuals
24 varied in their ability to solve the detour problem. Furthermore, those that solved the problem
25 were able to improve their performance across trials by inhibiting the natural response of
26 attempting to strike the reward through the transparent barrier, providing evidence of motor self-
27 regulation. Solving the problem required individuals to modify their typical foraging behavior, as
28 approaching the prey directly was an unsuccessful strategy. Our findings provide evidence of
29 motor self-regulation in a visually-oriented, sit-and-wait predator, further demonstrating that
30 cognitive abilities of reptiles have been underappreciated, and strongly suggesting a
31 reconsideration of factors favouring the evolution of motor self-regulation.

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40 1. INTRODUCTION

41 Research evaluating the cognitive abilities of animals has flourished over the last decade,
42 providing new insights into the potential mechanisms and evolutionary processes mediating
43 inter- and intra-specific variation in cognition [1, 2]. A recurrent prediction of these studies is
44 that the demands of a species' ecology have shaped the evolution of cognitive traits, particularly
45 behavioral flexibility and problem solving [1, 3-5 and references therein]. Therefore, in order to
46 observe a species' full range of cognitive abilities there has been a call to test animals under
47 conditions where they have access to the full repertoire of stimuli available in nature [6]. Two
48 approaches have been taken to answer this call. First, and more commonly, experiments are
49 conducted under semi-natural conditions with captive individuals, providing an opportunity for
50 the individuals to potentially experience a larger range of ecologically relevant conditions than
51 those experienced under laboratory conditions [e.g., 7-9]. Second, and relatively rarer, are studies
52 conducted with free-living organisms under natural conditions [e.g., 2, 10-12]. The latter
53 approach provides an opportunity to measure cognition under the conditions in which selection
54 has shaped the evolution of these traits and under which the ability to solve novel tasks is likely
55 to be a better predictor of behavioral flexibility and innovation [1, 2, 13].

56 Regardless of the approach used, a major goal of studies evaluating problem solving
57 abilities is the use of cognitive tasks indicative of the mechanisms contributing to general
58 cognition and for which variation between individuals in performance can be indicative of
59 ecologically relevant variation [1, 4, 14, 15]. When these studies evaluate the possibility of
60 solving novel problems, a recurrent concern is the potential transfer of previous experience to
61 what might be considered by the experimenter as novel [16-19]. Furthermore, due to a lack of

62 comprehensive knowledge of the behavior of many species, tasks that might be considered
63 unfamiliar could actually be regular components of a species' behavioral repertoire [4, 10, 15].

64 Transparent surfaces are extremely rare in nature and the capacity of organisms to
65 interact with those surfaces can provide insight into their cognitive abilities [e.g., 20-23]. In
66 particular, detour-reaching tasks have been developed in which a reward is placed behind a
67 transparent surface with the objective of evaluating motor self-regulation, a process in which an
68 individual inhibits the impulsive behavior of trying to reach the reward through a transparent
69 surface (i.e., the prepotent response) and instead successfully reaches the reward by detouring
70 around the barrier [e.g., 14, 21]. Motor self-regulation is a requirement for the evolution of self-
71 control and potentially underpins problem solving abilities [reviewed in 24]. For example, in
72 corvids performance in a detour-reaching task is associated with absolute and relative brain size
73 [14], which are positively correlated with general cognition [3]. Detour reaching tasks have been
74 mostly used with birds and mammals [reviewed in 23, but see 24, 25] and implemented under
75 laboratory conditions. Furthermore, all species tested consume a significant portion of non-
76 moving prey items in their diet, because the general expectation is that motor self-regulation
77 should be selected against in species that eat moving prey [1].

78 Compared to endothermic species, the cognitive abilities of reptiles have largely been
79 overlooked [15]. This is surprising when considering their evolutionary history, species richness,
80 and diverse natural history, which is likely to provide valuable insights into the evolution of
81 heavily studied avian and mammalian cognition [1]. In fact, recent studies have demonstrated
82 that cognitive abilities of reptiles are more complex than recognized historically [15, 26-28 and
83 references therein], raising questions about previous hypotheses addressing the evolution of
84 cognitive traits developed from studies on endothermic animals. For example, it has been

85 demonstrated that having a complex social structure or exploiting a diversity of food resources,
86 two of the main predictors of behavioral flexibility in endothermic species, are not predictors of
87 behavioral flexibility in the arboreal lizard *Anolis evermanni* [27]. In a similar vein, the ability to
88 learn by observing the behavior of conspecifics has been shown in the skink *Eulamprus quoyii*, a
89 mostly solitary lizard, suggesting that the potential for social learning is not limited to highly
90 social species [26, see also 28, 29]. Nevertheless, our ability to study reptile cognition has been
91 hampered by the difficulty of creating laboratory conditions under which reptiles might be
92 expected to behave naturally [15, 30]. Thus, our current understanding is based primarily on a
93 relatively small sample of the vast diversity of species of reptiles.

94 In this study, we evaluate if free-ranging individuals of *Anolis sagrei* can solve a novel
95 detour problem under natural conditions. The problem challenged individuals to circumvent a
96 transparent barrier in order to obtain a food reward, providing an opportunity to evaluate motor
97 self-regulation, as described above. Furthermore, by working with free-ranging individuals we
98 avoid the possibility of previous experience with transparent surfaces, thus presenting a novel
99 problem to the individuals. As a novel problem, the expectation is that motor-self regulation will
100 be exhibited in an incremental fashion, as individuals gain experience by interacting with the
101 transparent surface [22]. Therefore, we predicted that individuals of *A. sagrei* would solve the
102 detour reaching problem and in doing so would decrease the number of attempts to secure the
103 reward though the transparent surface as they gain experience with the novel problem.

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105 **2. MATERIALS and METHODS**

106 **Study system**

107 We carried out this study from June 19 through July 21, 2016 in Marsh Harbour on the island of
108 Great Abaco, Bahamas. *Anolis sagrei* ($n_{\text{male}}=10$, $n_{\text{female}}=13$) were sampled in a forest fragment of
109 approximately 7,500 m² located within the premises of The Abaco Beach Marina, which holds a
110 high density of lizards.

111 *Anolis sagrei* is a small-to-medium sized, sexually dimorphic (females to 39.5 mm; males
112 to 51.9 mm), arboreal, territorial lizard that inhabits open and semi-shaded forest [31].
113 Individuals are most commonly observed within 1.5m of the ground on the trunks of trees. From
114 these perches, males and females signal to conspecifics in the surrounding habitat and forage for
115 potential prey items, primarily insects [32]. *Anolis sagrei* is a sit-wait forager, and while foraging
116 individuals typically assume a survey posture – head-down position with the front limbs
117 extended and head elevated – while scanning the ground for the movement of potential prey [32,
118 33]. If a prey item is detected, individuals will sprint to the ground and capture the prey at the
119 end of the run, which commonly occurs as one sequence of events [34].

120 Lizards were located by walking slowly through the forest. Once a lizard was found, it
121 was captured by hand using a noose and its snout-vent-length ($\pm 0.1\text{mm}$) and weight ($\pm 0.1\text{g}$)
122 were measured and recorded (Table S1). It was then marked by attaching two temporary queen
123 bee tags (Bee Works, Ontario, Canada) with a small amount of cyanoacrylate adhesive to each
124 shoulder, providing each individual with a unique color and number combination. Lizards were
125 released at their site of capture, which was marked with flagging tape. We conducted
126 experiments from 0800 to 1800 hours, excluding periods of rain. The first trial for each lizard
127 occurred at least 24 hours after it was marked.

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129 **Testing apparatus**

130 A photo of the testing apparatus is presented in Figure 1a. The apparatus consisted of an acrylic
131 half-cylinder (11.5 L x 8 W x 4 H cm) divided into three segments: a removable transparent
132 center (5 cm) and two equally sized terminal segments (3 cm) that were attached to a green
133 painted wood platform (11.5 L x 10.5 W x 2 H cm). Both ends of the half-cylinder were open
134 and provided access to a live fly maggot used as a reward. The maggot was restrained at the
135 center of the half-cylinder by tethering it to a small piece of dental floss (ca. 1.5 cm) with
136 cyanoacrylate adhesive and then securing the other end between two strong magnets at the center
137 of the platform. The movements of the maggot are very salient to anoles [35], usually eliciting a
138 foraging response. Lizards were able to easily detach the maggot from the dental floss.

139 The terminal pieces of the half-cylinder were covered by one of two black-white patterns:
140 vertical lines or checkered (Fig 1b). Those patterns provided cues for the lizards to associate a
141 given pattern with access to the reward. However, it should be noted that the development of an
142 association was not a requirement to solve the detour task. Nevertheless, providing this
143 additional cue allows for the evaluation of this possibility, which has been shown before in other
144 species of lizards including anoles [27].

145

146 **Testing**

147 Lizards were located by walking slowly through the forest. Once a marked lizard was found we
148 walked slowly towards the lizard's perch and placed the apparatus perpendicular to the lizard's
149 line of sight within a meter of the base of its perch. The orientation of the patterns was randomly
150 determined for each trial relative to the lizard's line of sight; thus, from the lizard's perspective a
151 given pattern and the spatial position of an entrance were not correlated.

152 Prior to presenting the lizards with the complete half-cylinder, lizards were habituated to
153 the painted wood platform and the pattern sections of the half-cylinder by presenting the
154 apparatus with the reward, but without the central section (Fig. 1a). This allowed lizards to
155 access the reward unimpeded and controlled for the possibility that lack of participation in the
156 experiment was due to neophobia. A total of 23 lizards completed the habituation stage of the
157 experiment after grabbing the reward in seven consecutive trials, exhibiting behavior typical of
158 anoles while foraging. Individuals directly approached the reward, usually as part of a sprint that
159 concluded with the lizard striking the reward, all happening as a single event (Video S1).

160 After the lizards completed habituation, the central section of the half-cylinder was
161 replaced (Fig.1b), presenting the lizards with the novel detour problem of accessing the reward
162 through a transparent barrier (Fig. 2, Video S1). This problem is similar to that described by
163 Maclean et al. [21], because to access the reward, lizards must inhibit their natural response of
164 striking directly at potential prey [14, 20, 24]. Individuals completed the detour problem when
165 they accessed the reward in 7 of their previous 8 trials, which represents a binomial probability
166 of 0.03125 and is commonly used in similar learning experiments [i.e., 25].

167 A trial lasted a maximum of 15 min, beginning when the apparatus was placed in front of
168 a lizard, and ending when the lizard took the reward or the 15 min period elapsed. Using a
169 stopwatch and a notebook, we recorded all behaviors exhibited by the lizard, including the side
170 by which the lizard entered the apparatus and the number of errors (i.e., the number of times a
171 lizard placed its snout against the outside of the transparent barrier) made during each trial. To
172 reach the reward, lizards had to place most of their body inside the apparatus. Trials in which
173 individuals did not approach the apparatus within one body length are not included in the
174 analysis. We evaluated the strategies employed by individuals in solving the detour problem by

175 determining which cues were correlated with an individual's access to the reward. Individuals
176 demonstrated preference for access using spatial (i.e., side) cues, pattern cues, or neither. We
177 evaluated this by calculating a bias index as performed in Szabo et al. [2019]. The magnitude of
178 the bias index indicates the strength of the bias towards one cue, either spatial (left or right) or
179 pattern (checked or striped). A preference was indicated when the bias index for one cue was
180 greater than the other, and no preference was indicated when indices for each cue were equal.
181 Because we were working with free-living lizards and individuals can move outside the forest
182 fragment while the study was going on, we only counted lizards as having participated in the
183 detour problem if they attempted at least seven trials.

184

185 **Statistics**

186 All statistical test are two-tailed and were performed using R statistical software [36] with the
187 package nlme [37]. A linear mixed effects model was used to test for learning as individuals
188 progressed through the testing paradigm. In particular, the model evaluated if the number of
189 errors (see above), decreased with experience. Because each individual completed a different
190 number of trials to reach criterion, we scaled trial number for each individual between 0 and 1 by
191 dividing each trial number by the number of the last trial for each individual. Only successful
192 trials in which individuals accessed the reward were included in this analysis. We used a linear
193 mixed effects model with the number of errors as the response variable and scaled trial number
194 as the predictor with individual as a random effect. The graph was generated using the package
195 ggplot2 [38].

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198 **Ethical Note**

199 This research adhered to the guidelines of the Institutional Animal Care and Use Committee at
200 University of Missouri, Columbia protocol (#8244). Also, we followed the Recommendations for
201 the Care of Amphibians and Reptiles [39] in the treatment of all animals used in this study. This
202 is a field study, and as part of this study animals were only individually marked and immediately
203 released. The Bahamas Ministry of Agriculture and the Bahamas Environment, Science, and
204 Technology Commission of the Ministry of the Environment provided permission to conduct this
205 research.

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207 **3. RESULTS**

208 Twenty-three lizards completed habituation (Table 1). Of those, 17 lizards participated in the
209 detour problem, and 9 of those lizards solved the problem. Body size and mass did not differ
210 between the lizards that solved the detour problem and those that failed (Wilcoxon signed-rank
211 test, $P=0.49$ and $P=0.44$ respectively). Nine lizards solved the detour problem and did so by
212 using three strategies. Five lizards solved the problem by entering more often through a given
213 side (i.e., left or right entrance with respect to their line of sight). One lizard entered the half-
214 cylinder more often under a given pattern (i.e., striped or checkered) irrespective of its
215 orientation with respect to the lizard's perch site. Three lizards showed neither preference (Table
216 S2).

217 Lizards improved their performance by reducing the number of errors committed during
218 their approach to the reward, rather than through greater persistence (Fig. 2). The latter would
219 have resulted in an increase in errors rather than a decrease. A significant negative fixed effect of
220 scaled trial number on the number of errors was detected with individual as a random effect (Fig.

221 2, $n=74$, estimate \pm standard error = -5.98 ± 2.91 , $p = 0.04$), indicating that individuals decreased
222 the number of errors made during trials as they progressed through the detour problem and
223 reached criterion.

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226 4. DISCUSSION

227 Our findings demonstrate the feasibility of experimentally evaluating the cognitive abilities of
228 free-ranging lizards in nature and of the ability of *Anolis sagrei* to exhibit motor self-regulation
229 in response to interactions with a transparent surface, which contributed to their performance on
230 the detour task. The ability of *A. sagrei* to solve the detour problem provides further evidence
231 that the cognitive abilities of lizards and more specifically *Anolis*, can provide significant
232 insights into potential factors shaping the evolution of cognitive traits [15, 27]. The solution to
233 the problem required major changes to the highly stereotyped foraging behavior of *A. sagrei*
234 [31], which consists of scanning the habitat for moving prey and approaching them directly
235 before striking. In our experiment, a direct approach was ineffective because the transparent
236 section of the half-cylinder served as a physical barrier between the reward and the lizard.
237 Therefore, individuals needed to move along an indirect path, during which the prey was
238 temporarily not visible (i.e., out of the line of sight), to gain access to the reward, potentially
239 resulting in a temporal mismatch between reaching the reward and decision-making. Lizards
240 moved either towards an entrance before turning to enter the half-cylinder, that is, approached
241 the apparatus at an angle away from the prey, or moved toward the prey and detoured away from
242 it after reaching the apparatus in order to reach an open end.

243 Behavioral flexibility has received significant attention as a trait that contributes to
244 species' invasive abilities, particularly in birds [13, 40], although there are conflicting ideas
245 regarding the degree of flexibility needed for successful invasion [reviewed in 41]. *Anolis sagrei*
246 is the most invasive anole species [42], and our findings open the possibility for further work to
247 evaluate the potential contribution of behavioral flexibility to its invasive ability. Future work,
248 comparing the cognitive abilities of multiple species of anoles, including those with different
249 degrees of invasiveness, should shed light on this hypothesis [41]. Also, both *A. sagrei* and *A.*
250 *evermanni* are members of the Caribbean anole radiation which is characterized by the
251 independent evolution of ecological forms and convergence in morphological and behavioral
252 traits across those forms [31]. Behavioral flexibility has been proposed as a contributor to the
253 radiation of clades by facilitating the exploration of novel environments [27, 43, 44].

254 Lizards used three strategies to access the reward. The most common strategy was for a
255 lizard to preferentially enter the apparatus through the same side (i.e., right or left with respect to
256 the individual's line of sight), regardless of the pattern of the entrance, suggesting the use of
257 spatial cues to locate an accessible entrance (Table S2). A less common strategy was a
258 preference for entering the half-cylinder through an entrance covered in one pattern, regardless
259 of the side, suggesting the development of an association between access to the reward and one
260 of the distinct patterns at each entrance. Both strategies might be expected of a territorial species,
261 such as *A. sagrei*, where spatial memory and the ability to associate particular cues or landmarks
262 with ecologically important information can contribute to an individual's fitness [27, 45].
263 Alternatively, the prevalence of the spatial strategy may indicate the use of egocentric cues to
264 solve the problem [46], as the spatial cues are defined in reference to the individual's
265 perspective. The use of different strategies underscores the experimental advantages of

266 conducting cognitive experiments under natural conditions, in which unique factors of the
267 species' ecology are more likely to be exhibited and to contribute to problem-solving ability.

268 On average, the number of errors committed by individuals of *A. sagrei* that solved the
269 detour problem decreased significantly across trials (Fig. 2). This finding indicates that
270 individuals are not only learning how to reach the reward, but also to avoid using a natural
271 behavior (i.e., striking through the transparent barrier) that is ineffective at securing the reward.
272 Furthermore, as has been shown in corvid species [14], although individuals of *A. sagrei* had no
273 previous experience with transparent surfaces, relatively few presentations were needed to
274 control their motor response and improve their ability to cope with a transparent surface (Table
275 1). It should be noted that a reduction in the number of errors (i.e., motor self-regulation) is even
276 more surprising when considering that individuals performed the tasks while facing all the
277 potential distractions of a natural environment, including competition for food. The latter should
278 select for quick, impulsive behavior, which is commonly exhibited when multiple individuals are
279 chasing the same moving prey. However, individuals were able to modify the required behavior
280 to solve the task. Nonetheless, as shown in (Fig. 2), individuals varied in their ability to inhibit
281 striking at the reward through the transparent barrier (i.e., individual differences in the magnitude
282 of the decrease in errors). This suggests that the paradigm used in this study can reveal
283 differential performance of individuals across multiple cognitive modules.

284 The ability of individuals to inhibit the natural response of attempting to access a food
285 reward through a transparent barrier has been measured across a diversity of endothermic
286 species, and the findings suggest that in primates dietary breadth predicts cognitive performance
287 [14, 21]. However, compared to primates, the dietary breadth of *A. sagrei* is relatively narrow,
288 suggesting that other aspects of species ecology are also likely to contribute to the ability of

289 species to inhibit natural responses. Furthermore, our findings also challenge the prediction that
290 species like *A. sagrei*, for which success of prey capture is determined by their ability to surprise
291 moving prey, should exhibit low capacity for motor self-regulation [1]. This finding provides
292 further evidence of the potential insights that can be gained by studying lizard cognition.

293 Two factors that are commonly suggested to contribute to individual differences in
294 performance on cognitive tasks are body size and neophobia [1, 41]. The body size of *A. sagrei*
295 was not significantly different between those individuals that solved the detour problem and
296 those that failed. Furthermore, all of the individuals that participated in the detour problem had
297 completed the habituation period by grabbing the maggot from the same apparatus in seven
298 consecutive trials. Therefore, it seems unlikely that differences in body size or neophobia
299 account for our results.

300 Elucidating the shared ecological demands that have favored the evolution of cognitive
301 traits across species is a long-standing goal of cognitive ecology. Our findings that *A. sagrei*
302 exhibits motor self-regulation provide further evidence that the cognitive abilities of *Anolis*
303 lizards, and more generally reptiles, have been underappreciated, as this ability is commonly
304 suggested as a proxy for complex cognitive processes [14]. Furthermore, as discussed above, the
305 dietary breath, foraging behavior, and social structure of *A. sagrei* are not those previously
306 associated with the evolution of motor self-control, suggesting that other aspects of species
307 ecology might also contribute to this behavior. One possibility is that motor self-control is
308 necessary for the evolution of other cognitive traits, such as behavioral flexibility. Under this
309 scenario, selection favoring the ability to modify pre-existing behaviors would also favor the
310 evolution of motor self-control. Expanding our understanding of lizard cognition, particularly
311 under natural conditions, is needed to develop a cohesive framework to understand the factors

312 shaping the evolution of cognitive traits across vertebrate species. More generally the apparatus
313 used in this study can also be used to evaluate associate and reversal learning in free living
314 lizards, by limiting the access to the reward to a given pattern and/or changing the reward
315 contingency. Thus, providing an opportunity to evaluate performance of individuals across
316 different cognitive modules.

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318

319 **ACKNOWLEDGEMENTS**

320 We thank J. Jones and W. McHargue for assistance in the field; the members of the Chipajo lab,
321 D. Steinberg, R. Cocroft, and G. Burghardt for helpful comments that greatly improved this
322 manuscript; the National Science Foundation (DEB-0949357 and IOS-1051793); and the
323 Bahamas Ministry of Agriculture and the Bahamas Environment, Science, and Technology
324 Commission of the Ministry of the Environment for permission to conduct this research. We
325 followed the Recommendations for the Care of Amphibians and Reptiles [39] in the treatment of
326 all animals used in this study.

327

328 **ETHICS STATEMENT**

329 Research approved by University of Missouri Animal Care Committee (ACUC 8244).

330

331 **FUNDING STATEMENT**

332 This work was partially funded by the National Science Foundation (DEB-0949357 and IOS-
333 1051793 to M.L.).

334

335 **DATA ACCESSIBILITY**

336 The data will be uploaded as electronic supplementary material.

337

338 **COMPETING INTERESTS**

339 We have no competing interests.

340

341 **AUTHOR'S CONTRIBUTIONS**

342 LS carried out the experiment, participated in data analysis, participated in the design of the
343 study and helped drafted the manuscript; ML conceived of the study, helped with the data
344 analysis and drafted the manuscript. All authors gave final approval for publication.

345

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465 Table 1. Number of individuals of *Anolis sagrei* that participated in each of the stages and the
466 mean number of trials required to complete each stage. Individuals that failed attempted at least
467 seven trials but did not reach criterion.

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488 Table 1

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Stage	Failed	Solved	Mean trials to solve	Range trials to solve
Habituation	-	23	7	7
Detour	8	9	11	7-19

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493 Figure 1. Photos of the detour problem used in this study; (A) apparatus without the central
494 section of the half-cylinder, (B) apparatus with the central transparent section of the half cylinder
495 (right).

496

497 Figure 2: The relationship between scaled trial number and the number of errors made by
498 individuals of *Anolis sagrei* that solved the detour problem. Trial number was scaled for each
499 individual between 0 and 1 by dividing each trial number by the number of the last trial for each
500 individual. Values are the number of errors made by one individual during one trial in solving
501 the detour problem. A significant negative fixed effect of scaled trial number on the number of
502 errors was detected with individual as a random effect ($n=74$, estimate \pm standard error = $-5.98 \pm$
503 2.91 , $p = 0.04$).

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518 Figure 1

519 (A)

(B)



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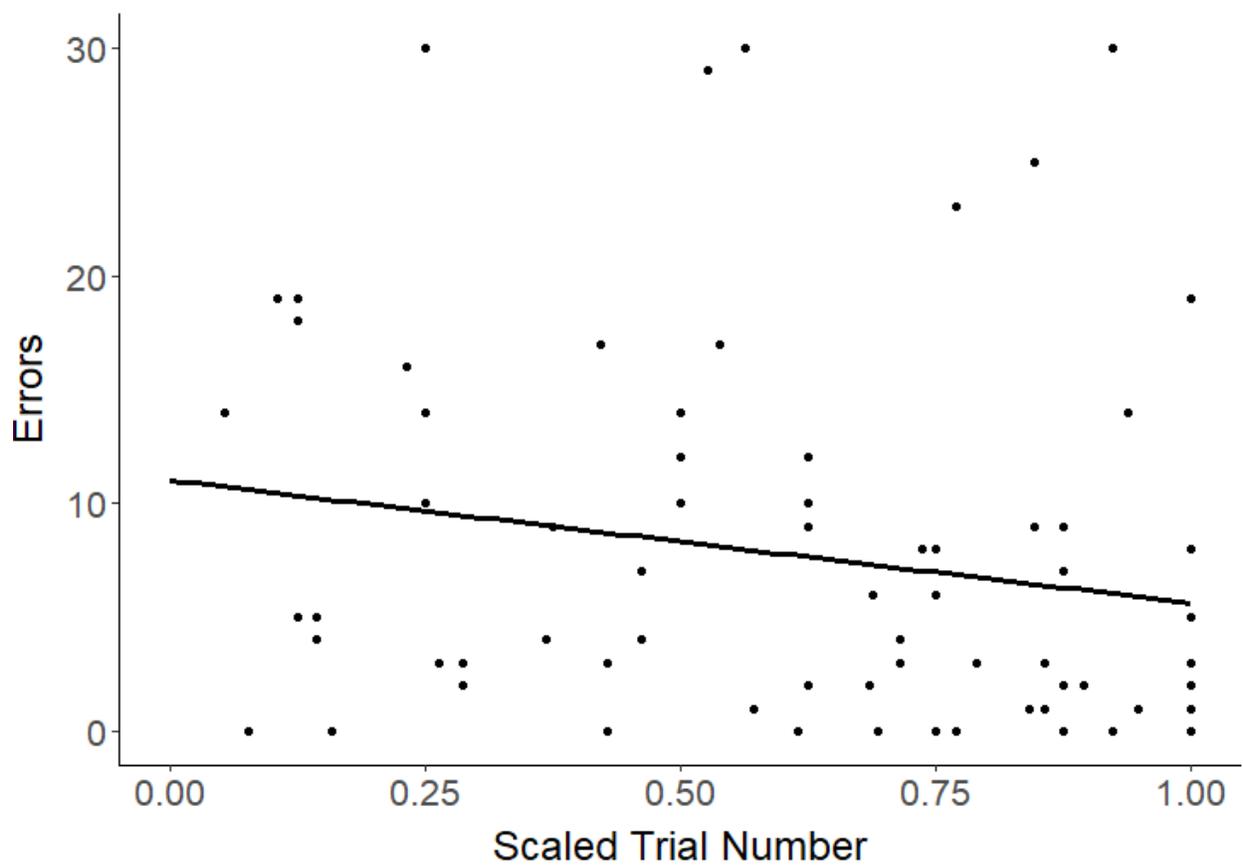
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533 Figure 2



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