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**Studying animal innovation at the individual level: A ratings-based assessment in capuchin monkeys (*Sapajus [Cebus] sp.*)**

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**Author Note**

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1 **Abstract**

2 Large-scale studies of individual differences in innovative behaviour among  
3 nonhuman animals are rare because of logistical difficulties associated with obtaining  
4 observational data on a large number of innovative individuals across multiple locations.  
5 Here we take a different approach, using observer ratings to study individual differences in  
6 innovative behaviour in 127 brown capuchin monkeys (*Sapajus [Cebus] sp.*) from 15 social  
7 groups and 7 facilities. Capuchins were reliably rated by 1 to 7 raters (mean  $3.2 \pm 1.6$   
8 raters/monkey) on a 7-point Likert scale for levels of innovative behaviour, task motivation,  
9 sociality, and dominance. In a subsample, we demonstrate these ratings are valid: rated  
10 innovation predicted performance on a learning task, rated motivation predicted participation  
11 in the task, rated dominance predicted social rank based on win/loss aggressive outcomes,  
12 and rated sociality predicted the time that monkeys spent in close proximity to others. Across  
13 all 127 capuchins, individuals that were rated as being more innovative were significantly  
14 younger, more social, and more motivated to engage in tasks. Age, sociality, and task  
15 motivation all had independent effects on innovativeness, whereas sex, dominance, and group  
16 size were non-significant. Our findings are consistent with long-term behavioural  
17 observations of innovation in wild white-faced capuchins. Observer ratings may therefore be  
18 a valid tool for studies of animal innovation.

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## 26 **Introduction**

27       Some species have a proclivity for behavioural innovation, in which individuals of  
28 those species use new or modified behaviours to solve new or existing problems (Lee, 1991;  
29 Reader & Laland, 2003). Innovation has significant links with intelligence (Lee & Therriault,  
30 2013; Ramsey et al., 2007), species differences in brain size (Lefebvre, 2013; Lefebvre et al.,  
31 2004; Reader, 2003; Reader & Laland, 2002), the evolution of tool use and culture (Biro et  
32 al., 2003; Boesch, 1995; Lefebvre, 2013; Reader et al., 2011; Tian et al., 2018), and the  
33 breadth of a species' ecological niche (Ducatez et al., 2015; Overington, Griffin, et al., 2011).  
34 At the proximate level, a range of dispositional and situational factors likely play a role in  
35 generating innovative behaviour (Amici et al., 2019; Brosnan & Hopper, 2014; Griffin &  
36 Guez, 2014; Lee, 1991; Lee & Moura, 2015; Moura & Lee, 2004; Ramsey et al., 2007;  
37 Reader & Laland, 2003). At its core, being “innovative” requires, at the very least, being able  
38 to *discover* (implicitly or explicitly) novel or modified behaviours (Ramsey et al., 2007;  
39 Reader & Laland, 2003). Unless an animal learns from its innovative action, and can repeat  
40 that action, the discovery will be lost from the repertoire of the individual.

41       Large-scale studies on individual differences in animal innovation are relatively few  
42 in number firstly because observations on innovative behaviour itself are rare, and secondly  
43 because of logistical difficulties (e.g. time, money, and standardising methods) associated  
44 with documenting innovations across a large, multi-site sample of individuals (Biro et al.,  
45 2003; Haslam et al., 2009). Observer ratings may help overcome such limitations. Indeed, a  
46 growing number of studies have shown that observer ratings are a reliable and valid tool for  
47 assessing a wide variety of behaviours and cognitive traits in animals (Freeman et al., 2013;  
48 Freeman & Gosling, 2010; Morton, Lee, & Buchanan-Smith, 2013; Morton, Lee, Buchanan-  
49 Smith, et al., 2013; Morton et al., 2015; Weiss et al., 2011; Weiss et al., 2012). Ratings also  
50 enable researchers to obtain data on multiple variables across a large sample of subjects

51 within a reasonable timeframe, with the same definitions and methods (e.g. 7-point Likert  
52 scales) used consistently across observers, locations, and subjects to facilitate comparability.

53 In the current study, we obtained observer ratings on innovative behaviour within a  
54 large, multi-site sample of captive brown capuchin monkeys (*Sapajus [Cebus] sp.*). To help  
55 explain individual variation in innovative behaviour, we considered six variables (age, sex,  
56 dominance, task motivation, group size, and sociality) often linked to innovation that may  
57 reflect a myriad of reasons why individuals might be innovative, such as individual  
58 differences in personality (Benson-Amram et al., 2013; Henke-von der Malsburg & Fichtel,  
59 2018; Huebner & Fichtel, 2015), physiology (Hopper et al., 2014), brain development and  
60 decline (Roskos-Ewoldsen et al., 2008), behavioural ecological niche (Aplin & Morand-  
61 Ferron, 2017; Giraldeau & Lefebvre, 1987; Liker & Bokony, 2009), and experience (Daveri  
62 & Parisi, 2015; Huebner & Fichtel, 2015). While many other factors may contribute to  
63 innovative behaviour, we opted to limit the number of variables to avoid oversaturating our  
64 model.

65 As with any study of animal innovation where subjects cannot be monitored  
66 continuously across their lifespan, it was not possible in the current study to observe and  
67 verify “new” innovations in our capuchins. Thus, to begin to assess the validity of observer  
68 ratings on capuchins’ innovative behaviour, we tested, in a subsample of our capuchins,  
69 whether the ratings could predict a relevant psychological construct *related* to innovative  
70 behaviour, specifically monkeys’ associative learning abilities. Being willing and able to  
71 discriminate and learn associatively from one’s actions can play an important role in the  
72 innovative process (Reader & Laland, 2003). If, for example, an animal cannot discriminate  
73 between old versus new actions, and learn new associations from its actions, then the chances  
74 of making a new discovery (i.e., making an association and repeating the innovative  
75 behaviour in the future) will be very limited. Under experimental conditions, animals that are

76 more innovative are better at solving associative learning tasks (Griffin et al., 2013;  
77 Overington, Cauchard, et al., 2011). Thus, in the current study, we predicted that highly  
78 innovative monkeys would perform better on an associative learning task than less innovative  
79 individuals.

80 To further assess the validity of our observer ratings, we determined whether the same  
81 factors that predicted innovative behaviour across our entire sample of capuchins were  
82 consistent with findings from a 10-year observational study of innovations in wild white-  
83 faced capuchins (*Cebus capucinus*) (Perry et al., 2017). Specifically, we predicted that, like  
84 white-faced capuchins, individual differences in our capuchins' age and sociality (defined in  
85 terms of the amount of time individuals spent within proximity to others) would be important  
86 negative and positive predictors of their innovative behaviour, respectively, whereas sex and  
87 dominance (defined in terms of avoids, cowers, flees, and supplants) would show minimal,  
88 non-significant effects.

## 89 **Method**

### 90 **Ethics**

91 This study was approved by the ethics committee of the Psychology Division at the  
92 University of Stirling, the Living Links committee at the Royal Zoological Society of  
93 Scotland (RZSS), and complied with APA and ASAB ethical guidelines ("Guidelines for the  
94 treatment of animals in behavioural research and teaching," 2012).

### 95 **Subjects**

96 Subjects were 127 captive brown capuchins that were at least 1 year old, belonging to  
97 15 social groups from 5 sites in the United States, 1 site in the UK, and 1 site in France  
98 (Table S1). Across all sites there were 60 males and 67 females. Age ranged from 1 to 40  
99 years and the mean age was 11.0 years ( $SD = 8.9$ ). To test the validity of item ratings,  
100 eighteen of these monkeys were observed at the Living Links to Human Evolution Research

101 Centre, affiliated with the Royal Zoological Society of Scotland (RZSS), U.K. Further details  
102 of housing and husbandry are provided in the ‘Supplementary Information’ (SI).

### 103 **Observer ratings**

104 Ratings were collected between 2010 and 2011 for a previous study (Morton, Lee,  
105 Buchanan-Smith, et al., 2013). Raters consisted of 25 researchers and 3 care staff who had  
106 known their subjects for at least one year. Definitions and scales for observer ratings on  
107 capuchins’ innovative behaviour, sociality, dominance, and task motivation came from items  
108 from the Hominoid Personality Questionnaire (Morton, Lee, Buchanan-Smith, et al., 2013;  
109 Weiss et al., 2009). Each subject was rated by one to seven raters ( $3.2 \pm 1.6$  raters per monkey)  
110 on each item based on the frequency of monkeys’ behaviour on a 1 (absent) to 7 (very  
111 common) scale. Ratings were averaged across raters for each monkey. Measures of  
112 innovative behaviour came from the “innovation” item in the HPQ, which defined such  
113 behaviour as “the subject engages in new or different behaviours that may involve the use of  
114 objects or materials or ways of interacting with others”. We later asked some of these raters  
115 to provide a few examples of innovative behaviour in their monkeys. For instance, one rater  
116 reported that a monkey was observed using a stick on several occasions to reach chow from  
117 under the fence, which other monkeys in the group did not do (Leverett and Rossetti,  
118 personal communication). In another instance, a rater reported that one of their monkeys  
119 would take a piece of wood, break pieces off of it, and then use it to scratch or comb its back,  
120 which had not been seen in any other monkey in that group by any rater (Leverett and  
121 Rossetti, personal communication).

122 Measures of dominance came from the “dominance” item in the HPQ, which was  
123 defined as “the subject is able to displace, threaten, or take food from other individuals; or the  
124 subject may express high status by decisively intervening in social interactions”. Measures of  
125 sociality came from the “sociability” item in the HQP, which was defined as “the subject

126 seeks and enjoys the company of other individuals and engages in amicable, affable,  
127 interactions with them”. Measures of task motivation came from the “curiosity” item in the  
128 HPQ, which was defined as “the subject has a desire to see or know about objects, devices, or  
129 other individuals; this includes a desire to know about the affairs of other individuals that do  
130 not directly concern the subject”.

131 Two intraclass correlations (Shrout & Fleiss, 1979) were used to determine interrater  
132 reliabilities for subjects rated by at least two raters. The first, ICC(3,1), indicates the  
133 reliability of individual ratings. The second, ICC(3,k), indicates the reliability of the mean of  
134 k ratings. Of the sample, 121 capuchins (out of the total 127 subjects) were rated by at least  
135 two raters ( $M = 3.35$ ;  $SD = 1.57$ ). Collectively, there was high inter-observer agreement  
136 across each item per monkey: dominance [ICC(3,1)=0.57, ICC(3,k)=0.82], innovation  
137 [ICC(3,1)=0.57, ICC(3,k)=0.82], sociability [ICC(3,1)=0.57, ICC(3,k)=0.82], and curiosity  
138 [ICC(3,1)=0.57, ICC(3,k)=0.82] (Morton, Lee, Buchanan-Smith, et al., 2013). Since there  
139 was no evidence that raters were unreliable, mean ratings for each item for all 127 monkeys  
140 were included in our analyses.

141 Raters’ reliabilities were as good or even better than similar ratings reported in studies  
142 of humans and other animals (Freeman & Gosling, 2010; Gartner et al., 2014; McCrae &  
143 Costa, 1987). Because our raters passed the ICC reliability criteria, this also meant that no  
144 single rater was significantly biased towards over- or under-rating a given monkey (e.g. if  
145 they witness more behaviours compared to the other raters). Indeed, raters were instructed not  
146 to discuss their ratings and to make their ratings based on their *own* observations (not those  
147 mentioned by other people). Regarding the innovation ratings specifically, the Likert scale  
148 helped to ensure that raters made their ratings on the basis of behavioural frequency – not just  
149 one-off observations. Ratings data were normally distributed, not skewed, indicating that



150 ratings were not biased towards raters recalling particular occasions of striking innovation in  
151 some monkeys but not others.

### 152 **Testing the validity of observer ratings**

153 Behavioural data (Table S3) were collected by an independent observer on the 18  
154 capuchin monkeys at Living Links up to a year after those monkeys were rated on items.  
155 These data were used to validate interpretations of behaviour derived from ratings:

#### 156 *Innovative behaviour*

157 Data on the Living Links capuchins' performances on a discrimination learning task  
158 were used to validate innovative behaviour ratings. While all 18 subjects were given the  
159 opportunity to voluntarily participate in the task, 15 of these monkeys participated. Testing  
160 occurred between 15 February 2012 and 1 April 2012, at 12 trials per session, four sessions  
161 per week. Monkeys were tested individually in cubicles to ensure all animals had the  
162 opportunity to engage in testing. The goal of the task was for individuals to learn the location  
163 of a hidden food reward by discriminating between two cups that were different sizes (details  
164 in SI). Learning performance was calculated for each monkey by dividing the total number of  
165 trials they completed correctly by the total number of trials they underwent, multiplied by  
166 100.

#### 167 *Task motivation*

168 Motivated animals are, of course, likely to voluntarily participate in tasks that require  
169 them to use their cognitive abilities (Skinner, 1938). Data on rates of voluntary participation  
170 in the learning task (see 'Innovative behaviour' above) were available for all 18 of the Living  
171 Links monkeys and therefore used to validate ratings on task motivation. Participation was  
172 calculated by dividing the number of sessions the monkey engaged in by the total number of  
173 session offered to them, multiplied by 100 (Morton, Lee, & Buchanan-Smith, 2013).

#### 174 *Sociality*

175 Data on monkeys' time spent in close proximity to other group members were  
176 available on 18 of the Living Links capuchins, and therefore used to validate ratings on  
177 sociality. Capuchins who spend more time in close proximity with other group members are  
178 more sociable; they are more likely to engage in affiliative acts like grooming, food sharing,  
179 and coalitionary support (Morton et al., 2015), which is very typical of wild and captive  
180 capuchins (Ferreira et al., 2006; Fragaszy et al., 2004). Focal observations on all 18 monkeys'  
181 spatial proximity to others were made between May and August, 2011, totalling 3 hours per  
182 individual. Monkeys were sampled evenly between 9:00 and 17:30. Using point sampling  
183 methods (Martin & Bateson, 2007), group members within two body lengths from the focal  
184 were recorded at 1-min intervals for ten minutes per animal per day. On a given point sample,  
185 if no monkey was within two body lengths, the focal was described as "solitary". Scores were  
186 recorded at 1-min intervals and calculated within 10-minute sessions. Monkeys were  
187 observed on rotation across all 19 individuals; meaning, most of the time a given monkey was  
188 observed once a day, but on 20 occasions a monkey was observed more than once. On these  
189 occasions, sampling was separated by at least 21 minutes (M= 220.7 minutes, SD= 160.2  
190 minutes).

### 191 *Dominance*

192 To test whether dominance ratings reflect social rank of individuals, social dominance  
193 was determined using data that were available on 18 of the Living Links capuchins (Morton,  
194 Lee, Buchanan-Smith, et al., 2013; Morton et al., 2015) by calculating David's Scores (DS)  
195 using data on win/loss outcomes during monkey's aggressive interactions (Gammell et al.,  
196 2003). All occurrences of fighting within the group were recorded while performing focal  
197 sampling of individuals outlined above (see '*Sociality*').

### 198 **Analyses**

199 In the subsample of 18 monkeys used to validate ratings, we used Pearson correlations  
200 to examine relationships between individual differences in item ratings, behaviours, and task  
201 performance. Across the entire sample (N=127 monkeys), age was skewed but normalised  
202 with a log (base=10) transformation. A linear mixed effects model was used to test for  
203 independent effects of age, sex, dominance, task motivation, sociality, and group size on  
204 innovative behaviour. This approach facilitates unbiased linear estimation of coefficients and  
205 robust standard errors that are adjusted for the clustering of animals by including random  
206 effects variance components for social group (intercept) and group size (slope). For this  
207 model, we calculated the percent adjusted  $R^2$  that a particular covariate contributes to the full  
208 model, which we estimated using the leave-one-out method. As our ‘group’ variable captured  
209 information about location, and group size is a group-level variable, models were fit using  
210 linear mixed models with random intercept for group and random slope for group size. While  
211 bounded between 1 and 7, our dependent variable (innovative behaviour) and our key  
212 independent variables (sociality, task motivation, and dominance) are not discrete. Rather,  
213 because we measured them using a robust multi-rater design where values were averaged  
214 across raters as discussed above, they are continuous variables within the bounds. To bolster  
215 our argument that a linear model is appropriate for these analyses, we performed Shapiro-  
216 Wilk tests for the normality of each of these variables (Royston, 1982), though only our  
217 dependent variable need meet this assumption.

218 All Pearson correlations and log transformations were performed in SPSS 24 (IBM  
219 Corp., Chicago, IL, USA). Multivariate analyses were performed in the latest development  
220 release of R (R Core Team, 2019) using the “lmerTest” library for tests of linear mixed  
221 models (Kuznetsova et al., 2017).

## 222 Results

### 223 Validity of observer ratings

224 Ratings on innovative behaviour were significantly and positively related to  
 225 performance on the discrimination learning task when all participants were included in the  
 226 analysis ( $r=0.598$ ,  $P=0.019$ ,  $N=15$  monkeys) and when only those participants that  
 227 participated in  $>80\%$  of sessions were included ( $r=0.787$ ,  $P=0.02$ ,  $N=8$  monkeys). Ratings on  
 228 task motivation were significantly and positively related to participation in the novel task  
 229 ( $r=0.618$ ,  $P=0.006$ ,  $N=18$  monkeys). Dominance ratings were significantly and positively  
 230 related to social rank ( $r=0.833$ ,  $P<0.001$ ,  $N=18$  monkeys). Sociality ratings were significantly  
 231 and positively related to the amount of time individuals spent with other group members  
 232 ( $r=0.495$ ,  $P=0.037$ ,  $N=18$  monkeys).

### 233 **Independent effects between innovative behaviour and sociality scores**

234 One monkey was rated by a single rater. Given that ratings for monkeys with more  
 235 than one rater were reliable, and that ratings were valid (see above), we included this  
 236 individual with the remaining 126 monkeys for the following analysis.

237 A linear mixed effects regression model revealed that across all 127 capuchins,  
 238 sociality, motivation to engage in tasks, and age all had independent and significant effects on  
 239 innovativeness, whereas sex, dominance, and a random effect of group size did not (Table 1).  
 240 Individual differences in innovative behaviour were significantly and positively related to  
 241 sociality and task motivation, but negatively related to age (Figure 1).

### 242 **Table 1**

243 *Independent effects of sociality, age, sex, dominance, and task motivation on individual*  
 244 *differences in capuchins' ratings on innovative behaviour*

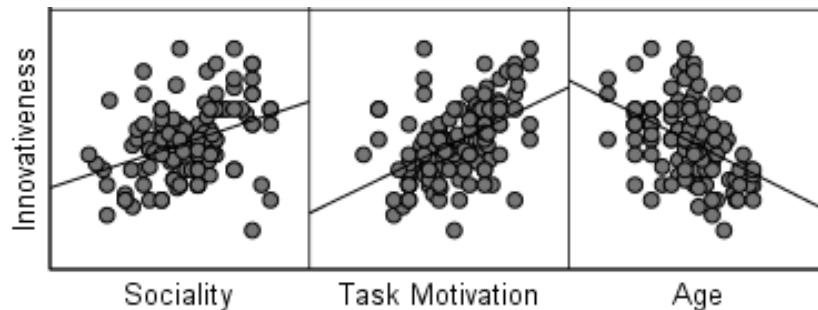
	Estimate	Robust S.E.	Robust t	%R <sup>2</sup>	Pr(> t )
<b>(Intercept)</b>	<b>2.17</b>	<b>0.66</b>	<b>3.29</b>	---	<b>&lt;0.01</b>
<b>Sociality</b>	<b>0.22</b>	<b>0.09</b>	<b>2.44</b>	<b>8.37</b>	<b>0.02</b>
<b>log(Age, base = 10)</b>	<b>-0.79</b>	<b>0.31</b>	<b>-2.49</b>	<b>9.66</b>	<b>0.01</b>
Sex	0.05	0.18	0.27	0.18	0.79
Dominance	-0.05	0.06	-0.90	1.42	0.37
<b>Task Motivation</b>	<b>0.36</b>	<b>0.09</b>	<b>4.09</b>	<b>21.17</b>	<b>&lt;0.001</b>

246

247 *Note.* Significant results ( $P < 0.05$ ) in boldface.  $N$  in all cases = 127 monkeys. %  $R^2$  is the percent contribution  
 248 to the full model adjusted  $R^2$  of a particular covariate by the leave-one-out method. Model fit statistics:  
 249 Approximate Adjusted  $R^2 = 0.351$ , F-test: 13.07 on 5 and 120 d.f.,  $P < 0.0001$ . Random effects variance  
 250 components were of trivial size (Social Group Intercept  $< 0.002$  and Group Size Slope  $< 0.005$ ).  
 251

252 **Figure 1**

253 *Independent associations between capuchins' innovative behaviour and individual*  
 254 *differences in sociality, task motivation, and age (in years) ( $N=127$  capuchins)*  
 255



256

257 The small amount of variation explained by group size warranted retaining the  
 258 covariate in the model as a random effect. We also ran a linear mixed model with an  
 259 equivalent specification as our generalised estimating equation. The variance component  
 260 associated with "location" was 0.004 which is negligible. The resulting random effects  
 261 ("Supplementary information") differed only slightly in magnitude and thus any concern over  
 262 a location or group bias is unfounded. With the exception of Dominance, each test resulted in  
 263 our failure to reject the null that each variable was drawn from an underlying normal  
 264 distribution. For Dominance, the deviation from normality is explained by the fact that  
 265 dominance in these groups was highly distributed across individuals. Moreover, the shape of  
 266 the histogram of this variable (Figure S1 and S2) suggested that it was drawn from an  
 267 underlying uniform distribution which is supported by a Kolmogorov-Smirnov test (Conover,  
 268 1971) of uniformity (statistic=0.149, p-value=0.117) (Table S4). Such deviations might be  
 269 problematic for the linear model as an outcome (dependent variable) but it is fine for an  
 270 independent variable. Finally, the scatterplots of the dependent variable against the  
 271 independent variables showed no observable heteroscedasticity that would indicate a

272 violation of the underlying linearity of the relationship per the assumptions of the Pearson-  
273 product moment correlation or the linear model estimation.

#### 274 **Discussion**

275 We used reliable observer ratings to study innovative behaviour in a large, multi-site  
276 sample of 127 brown capuchins. In a subsample of these capuchins, we found that the ratings  
277 predicted real-world behavioural patterns that were independently recorded up to a year later:  
278 ratings on innovative behaviour were correlated with performance on an associative learning  
279 task, task motivation scores were correlated with participation in the task, dominance scores  
280 were correlated with social rank based on win/loss aggressive outcomes, and sociality scores  
281 were correlated with the amount of time spent with other group members. Across all 127  
282 monkeys, the independent effects of age, sociality, sex, and dominance reflected those  
283 reported in wild white-faced capuchins (Perry et al., 2017), ruling out captivity and  
284 methodological limitations of ratings as likely explanations for our results. Collectively, our  
285 findings support the notion that observer ratings may be a valid tool for studies of innovation.

286 As previously discussed, researchers very rarely have the luxury of being able to  
287 follow the same population continuously across generations to observe and verify new  
288 innovations. Thus, novel psychometric tasks (e.g. giving animals a novel puzzle feeder) are  
289 often used as an objective approach to experimentally induce animals to innovate (Benson-  
290 Amram et al., 2013; Henke-von der Malsburg & Fichtel, 2018; Huebner & Fichtel, 2015).  
291 Such approaches, however, come with their own limitations. For instance, it can be difficult  
292 to establish whether more frequent innovators are simply more motivated, less distracted, or  
293 have better experience or opportunities to engage in testing than other individuals. For this  
294 reason, psychometric tasks are not necessarily any more objective than observer ratings.  
295 Thus, much like on-going discussions from the animal personality literature (Freeman et al.,

296 2013), future studies will likely benefit from using a combination of psychometric and ratings  
297 data to further test convergent validity between methods to study innovation.

298 In a similar vein, the psychological mechanisms that drive innovative behaviour in  
299 capuchins and other animals remain largely unknown (Ramsey et al., 2007). Studies of the  
300 common myna (*Sturnus tristis*) have shown that more frequent innovators are better at  
301 solving discrimination learning tasks, but do not perform as well on reversal learning tasks,  
302 suggesting that the associative learning underpinnings of the discrimination task were more  
303 relevant to innovation within this species than flexible learning (Griffin et al., 2013). As  
304 demonstrated in a subsample of our monkeys, ratings may reflect at least the associative  
305 learning processes related to capuchins' innovative behaviour (Griffin et al., 2013;  
306 Overington, Cauchard, et al., 2011; Ramsey et al., 2007; Reader, 2003). To better understand  
307 the psychological underpinnings of innovation in capuchins, we encourage studies to use a  
308 broader range of tasks varying in complexity and design, particularly those measuring other  
309 types of learning, inhibitory control, and intelligence (Huebner & Fichtel, 2015; Lee &  
310 Therriault, 2013).

311 Regarding our measure of sociality (i.e. time in close proximity to others), Morton et  
312 al. (2015) found that proximity loads onto the same factorial component as coalitions, food  
313 sharing, and grooming; meaning, at least in capuchins, all of these more "subtle forms" of  
314 sociality simply map onto the same thing: affiliative behaviour. Nevertheless, future work  
315 might consider whether these and other specific forms of sociality are better predictors of  
316 innovativeness, particularly time spent grooming, sharing food, and watching others while  
317 feeding. Using social network analysis can also provide a multi-dimensional approach to  
318 sociality for comparison.

319 Finally, captive animals are unlikely to face the same level of ecological pressure as  
320 in the wild (e.g. no predation risk), and can have a tendency to be more innovative than wild

321 individuals of the same species (Benson-Amram et al., 2013). Nevertheless, as previously  
322 discussed, our findings are consistent with those found in wild capuchin monkeys (Perry et  
323 al., 2017). Future comparisons between captive and wild brown capuchins using the same or  
324 similar methods can therefore provide *complimentary* insight into the innovativeness of this  
325 species, for instance, in terms of controlling for factors like inter-group competition and  
326 predator vigilance, which might impact the amount of time wild (but not captive) capuchins  
327 can devote to being innovative.

### 328 **Proximate underpinnings of capuchin innovation**

329         We suggest at least two testable scenarios for why sociality might be positively  
330 correlated with innovative behaviour in brown capuchins. First, like most group-living  
331 primates, capuchins use strategies such as grooming, coalitions, and food sharing to achieve  
332 greater social embeddedness within their group (Ferreira et al., 2006; Fragaszy et al., 2004;  
333 Morton et al., 2015; Tididi et al., 2012), and being more social may reduce stress, improve  
334 infant survival, provide better access to food and mating opportunities, and, in turn, lead to  
335 better fitness (Kalbitzer et al., 2017; Ostner & Schulke, 2018; Silk, 2007; Silk et al., 2003;  
336 Silk et al., 2009). Thus, a positive association between innovative behaviour and sociality  
337 may arise if, for example, being innovative enables individuals to concurrently improve their  
338 social status within groups. Second, individuals that are more social may simply have better  
339 opportunities in terms of the time and energy they can devote to experiment and engage in  
340 learning compared to less social individuals (Kummer & Goodall, 1985). Such opportunities  
341 may not necessarily be used to improve one's social status *per se* (e.g. foraging and self-  
342 directed innovativeness). This latter scenario might arise if sociality is a means through which  
343 capuchins solve an otherwise ecological problem (e.g. resource acquisition and protection  
344 from predators), and in turn, allow more time and/or opportunities for innovative behaviour.



345 Examining longitudinal associations between capuchins' innovative behaviour and sociality  
346 will help tease apart these and other possibilities.

347         While motivation may be the sole factor underlying individual differences in  
348 innovation in some species (van Horik & Madden, 2016), it only had a partial effect in our  
349 capuchins. Nevertheless, behavioural and cognitive traits are useless without animals being  
350 motivated enough to perform them, and so delineating possible interactions between task  
351 motivation (a situational effect) and personality (a dispositional effect) is required to better  
352 understand how innovative behaviour might be generated within these animals. Our findings  
353 may reflect food-related motivation (i.e. a situational effect) since capuchins' scores on task  
354 motivation were positively correlated with their willingness to participate in a task that  
355 involved food rewards. On the other hand, capuchins are naturally curious and readily  
356 investigate novel situations (Fragaszy & Adams-Curtis, 1991; Visalberghi & Guidi, 1998).  
357 Thus, their motivation to engage in innovative behaviour could be underpinned by  
358 personality traits like curiosity, exploration, persistence, or neophobia (Benson-Amram et al.,  
359 2013; Daniels et al., 2019; Kidd & Hayden, 2015; Overington, Cauchard, et al., 2011).

360         At least three possible scenarios could explain the negative association between  
361 capuchins' age and innovative behaviour. First, younger, smaller-bodied capuchins may not  
362 possess the necessary physical strength and dentition that older, larger-bodied capuchins  
363 have, which in turn could make innovations more necessary for them (Kummer & Goodall,  
364 1985; Reader & Laland, 2001). Second, older capuchins may be less innovative due to age-  
365 related decreases in general playfulness and objective manipulation compared to younger  
366 individuals, which may reduce their probability of making innovative "discoveries"  
367 (Visalberghi & Guidi, 1998). Third, ageing may place constraints on innovative behaviour  
368 due to age-related neurological decline (Massimiliano, 2015; Roskos-Ewoldsen et al., 2008;  
369 Zwoinska et al., 2017).

370 While sex differences in psychological traits, including those related to  
371 innovativeness, have been reported in various birds and mammals (Amici et al., 2019;  
372 Boogert et al., 2011; Reader & Laland, 2001), we found no evidence of a significant and  
373 independent effect of sex on innovation within brown capuchins. Again, these findings are  
374 similar to those reported in white-faced capuchins whereby males and females show minimal  
375 differences in innovation (Perry et al., 2017). It is unclear why some species show sex  
376 differences in innovation while others do not, and so further studies are needed.

### 377 **Implications for other species**

378 Cross-species comparisons using the same or similar methods will help with  
379 modelling (in relative terms) how different factors shape innovation throughout the animal  
380 kingdom. Beyond capuchins, observer ratings have been used to study the behaviour of many  
381 other animals, such as other primates (Freeman & Gosling, 2010), horses (*Equus ferus*)  
382 (Lloyd et al., 2008), hyenas (*Crocuta crocuta*) (Gosling, 1998), cats (*Felis spp.*) (Gartner et  
383 al., 2014), deer (*Dama dama*) (Bergvall et al., 2011), and elephants (*Loxodonta africana* and  
384 *Elephas maximus*) (Lee & Moss, 2012; Selmann et al., 2018). Researchers may therefore  
385 benefit from testing the validity of ratings to study innovative behaviour in these and other  
386 species. Such studies should consider using different items for innovation across specific  
387 domains (e.g. foraging, social, play, and others), and – for group-living species – specify  
388 within the definitions of those items that “new behaviours” should be new to the entire group,  
389 not just the individual.

### 390 **Conclusions**

391 Due to the logistical difficulties of conducting large-scale observational studies of  
392 animal innovation, we took a different approach using a large dataset of reliable ratings to  
393 study the innovative behaviour of brown capuchins. Ratings were valid predictors of real-  
394 world behavioural outcomes within a subsample of these capuchins, and factors associated

395 with innovative behaviour across our *whole* sample were consistent with observations on wild  
396 capuchins. Observer ratings may therefore provide researchers with a valid approach to  
397 studying innovation in capuchins and, perhaps, other species as well.

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