Final version for publication in Journal of Comparative Psychology –

accepted version 15 October 2020

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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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50   Psychology Division at the University of Stirling, the Living Links committee at the Royal

51   Zoological Society of Scotland (RZSS), and complied with APA and ASAB ethical

52   guidelines ("Guidelines for the treatment of animals in behavioural research and teaching,"

53   2012). All authors confirm no conflicts of interest.

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79   **Abstract**

80   Large-scale studies of individual differences in animal innovation are rare firstly

81 because discovery behaviour itself is often rare, and secondly because of logistical difficulties

82 associated with obtaining observational data on a large number of innovative individuals

83 across multiple groups and locations. Here we take a different approach, using observer

84 ratings to study innovative behaviour in 127 brown capuchin monkeys (*Sapajus* [*Cebus*] *sp.*)

85 from 15 social groups and 7 facilities. Capuchins were reliably rated by 1 to 7 raters (mean

86 3.2 ± 1.6 raters/monkey) on a 7-point Likert scale for levels of innovative behaviour, task

87 motivation, sociality, and dominance. In a subsample, we demonstrate these ratings are valid:

88 rated innovation predicted performance on a learning task, rated motivation predicted

89 participation in the task, rated dominance predicted social rank based on win/loss aggressive

90 outcomes, and rated sociality predicted the time that monkeys spent in close proximity to

91 others. Across all 127 capuchins, individuals that were rated as being more innovated were

92 significantly younger, more social, and more motivated to engage in tasks. Sociality, task

93 motivation, and age all had independent effects on innovativeness, whereas sex, dominance

94 and group size were non-significant. Our findings are consistent with long-term behavioural

95 observations of innovation in wild white-faced capuchins. Observer ratings may therefore be

96 a valid tool for studies of animal innovation, and our findings highlight in particular several

97 possible scenarios through which innovative behaviour might be selected for among

98 capuchins.

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Introduction

Some species have a proclivity towards behavioural innovation, in which members of those species use new or modified behaviours to solve new or existing problems (Lee, 1991; Reader & Laland, 2003). Innovation has significant links with intelligence (Lee & Therriault, 2013; Ramsey, Bastian, & van Schaik, 2007), species differences in brain size (Lefebvre, 2013; Lefebvre, Reader, & Sol, 2004; Reader, 2003; Reader & Laland, 2002), the evolution of tool use and "culture" (Biro et al., 2003; Boesch, 1995; Lefebvre, 2013; Reader, Hager, & Laland, 2011; Tian, Deng, Zhang, & Salmador, 2018), and the breadth of a species' ecological niche (Ducatez, Clavel, & Lefebvre, 2015; Overington, Griffin, Sol, & Lefebvre, 2011). To date, however, the proximate and ultimate causes that shape innovative behaviour remain largely unknown.

A range of dispositional and situational factors can play a role in generating innovative behaviour (Amici, Widdig, Lehmann & Majolo, 2019; Brosnan & Hopper, 2014; Griffin & Guez, 2014; Lee, 1991; Lee & Moura, 2015; Moura & Lee, 2004; Ramsey et al., 2007; Reader & Laland, 2003). At its core, however, being "innovative" requires, at the very least, being able to *discover* (implicitly or explicitly) novel or modified behaviours (Ramsey et al., 2007; Reader & Laland, 2003). Unless an animal learns to repeat a discovery, the discovery will likely be lost from the repertoire of the individual, thereby reducing the likelihood of it being detected and hence studied as "an innovation" by researchers. For this reason, large-scale studies on individual differences in animal innovation are relatively few in number firstly because observations on innovative behaviour itself are rare, and secondly

125   because of logistical difficulties associated with observing new innovations across a large,

126   multi-site sample of individuals, including time, money, and using standardised methods

127   (Biro et al., 2003; Haslam et al., 2009).

128   Observer ratings may help overcome such limitations. Indeed, a growing number of

129   studies have shown that observer ratings are a reliable and valid tool for assessing a wide

130   variety of behaviours and cognitive traits in animals, including primates which are renowned

131   for their innovative behaviour (Freeman et al., 2013; Freeman & Gosling, 2010; Morton, Lee,

132   & Buchanan-Smith, 2013; Morton, Lee, Buchanan-Smith, et al., 2013; Morton et al., 2015;

133   Weiss, Adams, Widdig, & Gerald, 2011; Weiss, Inoue-Murayama, King, Adams, &

134   Matsuzawa, 2012). Ratings also enable researchers to obtain data on multiple variables across

135   a large sample of subjects within a reasonable timeframe, with the same definitions and

136   methods (e.g. 7-point Likert scales) used consistently across observers, locations, and

137   subjects to facilitate comparability.

138   In the current study, we obtained observer ratings on innovative behaviour within a

139   large, multi-site sample of captive brown capuchin monkeys (*Sapajus* [*Cebus*] *sp.*). To help

140   explain individual variation in innovative behaviour, we examined six variables (age, sex,

141   dominance, task motivation, group size, and sociality) often linked to innovation that may

142   reflect a myriad of reasons why individuals might be innovative, such as individual

143   differences in personality (Benson-Amram, Weldele, & Holekamp, 2013; Huebner & Fichtel,

144   2015; Weiss & King, 2015), physiology (Hopper et al., 2014), brain development/decline

145   (Liao & Scholes, 2017), behavioural ecological niche (Aplin & Morand-Ferron, 2017;

146   Giraldeau & Lefebvre, 1987; Liker & Bokony 2009), and experience (Henke-von der

147   Malsburg & Fichtel, 2018). While indeed many other factors may contribute to innovative

148   behaviour, we opted to limit the number of variables to avoid oversaturating our model.

149   As with any study of animal innovation where subjects cannot be monitored

150   continuously across their lifespan, it was not possible in the current study to observe and

151   verify "new" innovations in our capuchins. Thus, to begin to assess the validity of observer

152   ratings on capuchins' innovative behaviour, we tested, in a subsample of our capuchins,

153   whether the ratings could predict a relevant psychological construct *related* to innovative

154   behaviour, specifically monkeys' associative learning abilities. Being able to discriminate

155   novel actions (e.g. exploring foreign objects) and learn associations between those actions

156   can play an important role in the innovative process (Reader & Laland, 2003). If, for

157   example, an animal cannot discriminate between novel actions and learn new associations

158   from those actions, then the chances of making a new discovery (and hence making an

159   association and repeating the innovation in the future) will be very limited. Under

160   experimental conditions, animals that are more innovative are also better associative learners

161   (Overington, Cauchard, Cote, & Lefebvre, 2011; Griffin, Guez, Lermite, & Patience, 2013).

162   Thus, in the current study, we predicted that "highly innovative" monkeys would have better

163   associative learning abilities than "less innovative" individuals.

164   To further assess the validity of our observer ratings, we determined whether the same

165   factors that predicted innovative behaviour across our entire sample of capuchins were

166   consistent with findings from a 10-year observational study of innovations in wild white-

167   faced capuchins (*Cebus capucinus*) (Perry, Barrett, & Godoy, 2017). Specifically, we

168   predicted that, like white-faced capuchins, individual differences in our capuchins' age and

169   sociality (defined in terms of the amount of time individuals spent within proximity to others)

170   would be the single most important predictors of their innovative behaviour, whereas sex and

171   dominance (defined in terms of avoids, cowers, flees, and supplants) would show minimal,

172   non-significant effects.

173   **Methods**

Study sites and subjects

Subjects were 127 captive brown capuchins that were at least 1 year old, belonging to 15 social groups from 5 sites in the United States, 1 site in the UK, and 1 site in France (Table S1). Across all sites there were 60 males and 67 females. Age ranged from 1 to 40 years and the mean age was 11.0 years ($SD = 8.9$). To test the validity of item ratings, eighteen of these monkeys were observed at the Living Links to Human Evolution Research Centre, affiliated with the Royal Zoological Society of Scotland (RZSS), U.K. Further details of housing and husbandry are provided in the 'Supplementary Information' (SI).

Observer ratings

Ratings data come from a previous study (Morton, Lee, Buchanan-Smith, et al., 2013). Raters consisted of 25 researchers and 3 care staff who had known their subjects for at least one year. Definitions and scales for observer ratings on capuchins' innovative behaviour, sociality, dominance, and task motivation came from items from the Hominoid Personality Questionnaire (Morton, Lee, Buchanan-Smith, et al., 2013; Weiss et al., 2009). Each subject was rated by one to seven raters (3.2±1.6 raters per monkey) on each item based on the frequency of monkeys' behaviour on a 1 (absent) to 7 (very common) scale. Ratings were averaged across raters for each monkey. Measures of innovative behaviour came from the "innovation" item in the HPQ, which was defined such behaviour as "the subject engages in new or different behaviours that may involve the use of objects or materials or ways of interacting with others". We later asked some of these raters to provide a few examples of innovative behaviour in their monkeys. For instance, one rater reported that one of their monkeys was seen on several occasions using a stick to sweep chow from under the fence into his reach, something others in his group did not do (Leverett and Rossetti, personal communication). In another instance, a rater reported that one of their female monkeys would take a piece of wood, break pieces off of it, and then use it to scratch or comb her

199   back, which had not been seen by anyone else in that group (Leverett and Rossetti, personal

200   communication).

201   Measures of dominance came from the "dominance" item in the HPQ, which was

202   defined as "the subject is able to displace, threaten, or take food from other individuals; or the

203   subject may express high status by decisively intervening in social interactions". Measures of

204   sociality came from the "sociability" item in the HQP, which was defined as "the subject

205   seeks and enjoys the company of other individuals and engages in amicable, affable,

206   interactions with them". Measures of task motivation came from the "curiosity" item in the

207   HPQ, which was defined as "the subject has a desire to see or know about objects, devices, or

208   other individuals; this includes a desire to know about the affairs of other individuals that do

209   not directly concern the subject".

210   Of the sample, 121 capuchins were rated by two to seven raters (M = 3.35; SD =

211   1.57). Two intraclass correlations (Shrout & Fleiss, 1979) were used to determine interrater

212   reliabilities for subjects rated by at least two raters. The first, ICC(3,1), indicates the

213   reliability of individual ratings. The second, ICC(3,k), indicates the reliability of the mean of

214   k ratings. Collectively, there was high inter-observer agreement across each item per monkey:

215   dominance [ICC(3,1)=0.57, ICC(3,k)=0.82], innovation [ICC(3,1)=0.57, ICC(3,k)=0.82],

216   sociability [ICC(3,1)=0.57, ICC(3,k)=0.82], and curiosity [ICC(3,1)=0.57, ICC(3,k)=0.82]

217   (from Morton et al. 2013). Since there was no evidence that raters were unreliable, mean

218   ratings for each item for all 127 monkeys were included in our analyses.

219   Raters' reliabilities were as good or even better than human studies, as well as other

220   studies using ratings to examine animal behaviour (e.g. McCrae and Costa, 1987; Freeman

221   and Gosling, 2010; Gartner et al., 2014). Because our raters passed the ICC reliability

222   criteria, this also meant that no single rater was significantly biased towards over or under-

223   rating a given monkey (e.g. if they witness more behaviours compared to the other raters).

224   Indeed, raters were instructed not to discuss their ratings and to make their ratings based on

225   their *own* observations (not those mentioned by other people). Regarding the innovation

226   ratings specifically, the Likert scale helped to ensure that raters made their ratings on the

227   basis of behavioural frequency – not just one-off observations. Ratings data were normally

228   distributed, not skewed, indicating that ratings were not biased towards raters recalling

229   particular occasions of striking innovation in some monkeys but not others.

230   **Testing the validity of observer ratings**

231   Behavioural data (Table S3) were collected by an independent observer on the 18

232   capuchin monkeys at Living Links up to a year after those monkeys were rated on items.

233   These data were used to validate interpretations of behaviour derived from ratings:

234   **Innovative behaviour.** Data on the Living Links capuchins' performances on a

235   discrimination learning task were used to validate innovative behaviour ratings. While all 18

236   subjects were given the opportunity to voluntarily participate in the task, 15 of these monkeys

237   participated. Testing occurred between 15 February 2012 and 1 April 2012, at 12 trials per

238   session, four sessions per week. Monkeys were tested individually in cubicles to ensure all

239   animals had the opportunity to engage in testing. The goal of the task was for individuals to

240   learn the location of a hidden food reward by discriminating between two cups that were

241   different sizes (details in SI). Learning performance was calculated for each monkey by

242   dividing the total number of trials they completed correctly by the total number of trials they

243   underwent, multiplied by 100.

244   **Task motivation.** Motivated animals are, of course, likely to voluntarily participate in

245   tasks that require them to use their cognitive abilities (Skinner, 1938). Data on rates of

246   voluntary participation in the learning task (see 'Innovative behaviour' above) were available

247   for all 18 of the Living Links monkeys and therefore used to validate ratings on task

248   motivation. Participation was calculated by dividing the number of sessions the monkey

249   engaged in by the total number of session offered to them, multiplied by 100 (Morton, Lee, &

250   Buchanan-Smith, 2013).

251   **Sociality.** Data on monkeys' time spent in close proximity to other group members

252   were available on 18 of the Living Links capuchins, and therefore used to validate ratings on

253   sociality. Capuchins who spend more time in close proximity with other group members are

254   more sociable; they are more likely to engage in affiliative acts like grooming, food sharing,

255   and coalitionary support (Morton et al., 2015), which is very typical of wild and captive

256   capuchins (Ferreira et al., 2006; Fragaszy et al., 2004). Focal observations on all 18 monkeys'

257   spatial proximity to others were made between May and August, 2011, totalling 3 hours per

258   individual. Monkeys were sampled evenly between 9:00 and 17:30. Using point sampling

259   methods (Martin & Bateson, 2007), group members within two body lengths from the focal

260   were recorded at 1-min intervals for ten minutes per animal per day. On a given point sample,

261   if no monkey was within two body lengths, the focal was described as "solitary". Scores were

262   recorded at 1-min intervals and calculated within 10-minute sessions. Monkeys were

263   observed on rotation across all 19 individuals; meaning, most of the time a given monkey was

264   observed once a day, but on 20 occasions a monkey was observed more than once. On these

265   occasions, sampling was separated by at least 21 minutes (M= 220.7 minutes, SD= 160.2

266   minutes).

267   **Dominance.** To test whether dominance ratings reflect social rank of individuals,

268   social dominance was determined using data that were available on 18 of the Living Links

269   capuchins (Morton, Lee, Buchanan-Smith, et al., 2013; Morton et al., 2015) by calculating

270   David's Scores (DS) using data on win/loss outcomes during monkey's aggressive

271   interactions (Gammell, De Vries, Jennings, Carlin, & Hayden, 2003). All occurrences of

272   fighting within the group were recorded while performing focal sampling of individuals

273   outlined above (see '*Sociality*').

274   **Statistical analyses**

275   In the subsample of 18 monkeys used to validate ratings, we used Pearson correlations

276   to examine relationships between individual differences in item ratings, behaviours, and task

277   performance. Across the entire sample (N=127 monkeys), age was skewed but normalised

278   with a log (base=10) transformation. A linear mixed effects model was used to test for

279   independent effects of age, sex, dominance, task motivation, sociality, and group size on

280   innovative behaviour. This approach facilitates unbiased linear estimation of coefficients and

281   robust standard errors that are adjusted for the clustering of animals by including random

282   effects variance components for social group (intercept) and group size (slope). For this

283   model, we calculated the percent adjusted R^2 that a particular covariate contributes to the full

284   model, which we estimated using the leave-one-out method. As our group-id captured

285   information about location, and group size is a group-level variable, models were fit using

286   linear mixed models with random intercept for group and random slope for group size. While

287   bounded between 1 and 7, our dependent variable (innovative behaviour) and our key

288   independent variables (sociality, task motivation, and dominance) are not discrete. Rather,

289   because we measured them using a robust multi-rater design where values were averaged

290   across raters as discussed above, they are continuous variables within the bounds. To bolster

291   our argument that a linear model is appropriate for these analyses, we performed Shapiro-

292   Wilk tests for the normality of each of these variables (Royston, 1982), though only our

293   dependent variable need meet this assumption.

294   All Pearson correlations and log transformations were performed in SPSS 24 (IBM

295   Corp., Chicago, IL, USA). Multivariate analyses were performed in the latest development

296   release of R (R Core Team, 2019) using the "lmerTest" library for tests of linear mixed

297   models (Kuznetsova, Brockhoff, and Christensen, 2017).

298   **Results**

299   **Validity of observer ratings**

300   Scores on innovative behaviour were significantly and positively related to

301   performance on the discrimination learning task when all participants were included in the

302   analysis (r=0.598, P=0.019, N=15 monkeys) and when only those participants that

303   participated in >80% of sessions were included (r=0.787, P=0.02, N=8 monkeys). Ratings on

304   task motivation were significantly and positively related to participation in the novel task

305   (r=0.618, P=0.006, N=18 monkeys). Dominance ratings were significantly and positively

306   related to social rank (r=0.833, P<0.001, N=18 monkeys). Sociality ratings were significantly

307   and positively related to the amount of time individuals spent with other group members

308   (r=0.495, P=0.037, N=18 monkeys).

309   **Independent effects between innovative behaviour and sociality scores**

310   One monkey was rated by a single rater. Given that ratings for monkeys with more

311   than one rater were reliable, and that ratings were valid (see above), we included this

312   individual with the remaining 126 monkeys for the following analysis.

313   A linear mixed effects regression model revealed that across all 127 capuchins,

314   sociality, motivation to engage in tasks, and age all had independent and significant effects on

315   innovativeness, whereas sex, dominance, and a random effect of group size did not (Table 1).

316   Individual differences in innovative behaviour were significantly and positively related to

317   sociality and task motivation, but negatively related to age (Figure 1).

318   The small amount of variation explained by group size warranted retaining the

319   covariate in the model as a random effect. We also ran a linear mixed model with an

320   equivalent specification as our GEE. The variance component associated with "location" was

321   0.004 which is negligible. The resulting random effects ("Supplementary information")

322   differed only slightly in magnitude and thus any concern over a location or group bias is

323   unfounded. With the exception of Dominance, each test resulted in our failure to reject the

324   null that each variable was drawn from an underlying normal distribution. For Dominance,

325   the deviation from normality is explained by the fact that dominance in these groups was

326   highly distributed across individuals. Moreover, the shape of the histogram of this variable

327   (Figure S1 and S2) suggested that it was drawn from an underlying uniform distribution

328   which is supported by a Kolmogorov-Smirnov test (Conover, 1971) of uniformity

329   (statistic=0.149, p-value=0.117) (Table S4). Such deviations might be problematic for the

330   linear model as an outcome (dependent variable) but it is fine for an independent variable.

331   Finally, the scatterplots of the dependent variable against the independent variables showed

332   no observable heteroscedasticity that would indicate a violation of the underlying linearity of

333   the relationship per the assumptions of the Pearson-product moment correlation or the linear

334   model estimation.

Discussion

336   We used reliable observer ratings to study innovative behaviour in a large, multi-site

337   sample of 127 brown capuchins. In a subsample of these capuchins, we show that the ratings

338   predict real-world behavioural patterns that were independently recorded up to a year later:

339   scores on innovative behaviour were correlated with performance on an operant learning task,

340   task motivation scores were correlated with participation in the learning task, dominance

341   scores were correlated with social rank based on win/loss aggressive outcomes, and sociality

342   scores were correlated with the amount of time spent with other group members. Across all

343   127 monkeys, sociality had a significant and positive association with innovative behaviour,

344   independently of age, sex, dominance, motivation to engage in tasks, and group size. Our

345   findings for sociality, age, sex, and dominance reflect those reported in wild white-faced

346   capuchins (Perry et al., 2017), ruling out captivity and methodological limitations of ratings

347   as likely explanations for our results. Collectively, our findings support the notion that

348   observer ratings may be a valid tool for studies of animal innovation.

349   As previously discussed, researchers very rarely have the luxury of being able to

350   follow the same population continuously and across multiple generations to observe and

351   verify new innovations. Thus, psychometric tasks (e.g. giving animals a puzzle feeder) are

352   often used as an objective approach to experimentally induce animals to innovate and solve

353   the novel task (Huebner & Fichtel, 2015; Lee & Therriault, 2013). Such approaches,

354   however, come with their own limitations. For instance, it can be difficult to establish

355   whether innovators are *truly* innovative or just more motivated, less distracted, or have better

356   experience or opportunities to engage in testing than other individuals. For this reason,

357   psychometric tasks are not necessarily any more objective than observer ratings. Thus, much

358   like on-going discussions from the animal personality literature (e.g. Freeman et al., 2013),

359   future studies will likely benefit from using a combination of psychometric and ratings data

360   to further test convergent validity between methods to study innovation.

361   In a similar vein, the psychological mechanisms that drive innovative behaviour in

362   capuchins and other animals remain largely unknown (Ramsey et al., 2007). As demonstrated

363   in a subsample of our monkeys, ratings used in the current study may reflect at least the

364   associative learning processes related to capuchins' innovative behaviour (Overington,

365   Cauchard, et al., 2011; Ramsey et al., 2007; Reader, 2003). To better understand the

366   psychological underpinnings of innovation in capuchins, we encourage future studies to use a

367   much broader range of tasks varying in complexity and design, particularly those that

368   measure other types of learning, inhibitory control, and intelligence (Huebner & Fichtel,

369   2015; Lee & Therriault, 2013). Studies of birds (*Sturnus tristis*), for instance, have shown that

370   better innovators are better at solving discrimination tasks, but do not perform as well on

371   reversal tasks, suggesting that associative learning, not flexible learning, is more relevant to

372   innovation within these animals (Griffin et al., 2013).

373   Regarding our measure of sociality (i.e. time in close proximity to others), Morton et

374   al. (2016) found that individuals who spend less time in close proximity to the alpha also take

375   longer to approach food when the alpha is close by, which reflects wild capuchin studies (e.g.

376   Janson, 1990). In a different study, Morton et al. (2015) found that proximity loads onto the

377   same factorial component as coalitions, food sharing, and grooming; meaning, at least in

378   capuchins, all of these more "subtle forms" of sociality simply map onto the same thing:

379   affiliative behaviour. Nevertheless, future work might consider whether these and other

380   specific forms of sociality are better predictors of innovativeness, particularly time spent

381   grooming, sharing food, and watching others while feeding. Using social network analysis

382   can also provide a multi-dimensional approach to sociality for comparison.

383   Finally, captive animals are unlikely to face the same level of ecological pressure as

384   in the wild (e.g. no predation risk), and can have a tendency to be more innovative than wild

385   individuals of the same species (Benson-Amram et al., 2013). Nevertheless, our findings are

386   consistent with those found in wild capuchin monkeys. Future comparisons between captive

387   and wild brown capuchins using the same or similar methods can therefore provide

388   *complimentary* insight into the innovativeness of this species, for instance, in terms of

389   controlling for factors like inter-group competition and predator vigilance, which might

390   impact the amount of time wild (but not captive) capuchins can devote to being innovative.

391   **Disentangling possible scenarios for the evolution of capuchin innovation**

392   Cognitive traits, including those linked to innovative behaviour, may be advantageous

393   to animals' fitness (O'Shea, Serrano-Davies, & Quinn, 2017; Pasquier & Grunter, 2016;

394   Polo-Cavia & Gomez-Mestre, 2014; Raine & Chittka, 2008; Rutkowska & Adkins-Regan,

395   2009; Whitfield, Kohler, & Nicholson, 2014), particularly when facing unpredictable

396   conditions within the environment (Lee & Moura, 2015). Nevertheless, it is difficult to

397   predict whether or how such pressures might affect the evolution of traits, like innovation,

398   that are themselves plastic. If, for example, plasticity always produces an optimal phenotype,

399   then genetic variation may be restrained from natural selection, thereby limiting the evolution

400   of that trait (Foster, 2013). Understanding the evolution of innovation therefore requires

401   having knowledge about different fitness optima and selective pressures on innovative

402   behaviour across time and contexts. Our study has identified at least three potential sources of

403   selective pressure to consider in future studies of brown capuchin innovation, including

404   sociality, task motivation, and age.

405   Sociality has been linked to better fitness in capuchins within stable groups (Kalbitzer

406   et al., 2017), but longitudinal, multi-generational data are needed using a direct measure of

407   fitness (e.g. reproductive success) to determine whether highly innovative and social

408   individuals have an advantage. We suggest at least two testable scenarios for how sociality

409   might – under optimal conditions (Foster, 2013) – provide fitness-related benefits to brown

410   capuchins. Like most group-living primates, capuchins use strategies such as grooming,

411   coalitions, and food sharing to achieve greater social embeddedness within their group

412   (Ferreira et al., 2006; Fragaszy et al., 2004; Morton et al., 2015; Tiddi et al., 2012), and being

413   more social may reduce stress, improve infant survival, provide better access to food and

414   mating opportunities, and, in turn, lead to better fitness (Kalbitzer et al., 2017; Ostner &

415   Schulke, 2018; Silk, 2007; Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Thus, a positive

416   association between innovative behaviour and sociality may arise if, for example, being

417   innovative enables individuals to concurrently improve their social status within groups

418   because doing so can result in fitness-related benefits. On the other hand, since sociality is

419   linked to better fitness, individuals that are more social may simply have better opportunities

420   in terms of the time and energy they can devote to experiment and engage in learning

421   compared to less social individuals (Kummer & Goodall 1985). Such opportunities may not

422   necessarily be used to improve one's social status *per se* (e.g. foraging and self-directed

innovativeness). This latter scenario might arise if "being social" is a means through which

capuchins solve an otherwise ecological problem (e.g. resource acquisition and protection

from predators), and in turn, allow more opportunities for innovative behaviour to aid an

individual's fitness. Examining longitudinal associations between capuchins' innovative

behaviour, sociality, and direct measures of fitness will help tease apart these and other

possibilities.

Motivation is an intrinsic part of innovative behaviour (Lee & Moura, 2015), and task

motivation was positively associated with capuchins' innovative behaviour independently of

sociality, age, sex, dominance, and group size. While task motivation explained the most

variance in innovative scores, this does not mean that motivation solely explains capuchins'

behaviour, which has been suggested in studies of problem-solving abilities in other animals

(van Horik & Madden, 2016). Rather, task motivation in capuchins appears to play a *partial*

role in their performance, explaining 21.17% of the variance (Table 1). It is unclear whether

capuchins' motivation to engage in tasks is underpinned by personality, particularly traits like

curiosity and neophobia (Benson-Amram et al., 2013; Kidd & Hayden, 2015; Overington,

Cauchard, et al., 2011). Although our task motivation data were based on an item labelled

'curiosity', scores on this item may simply reflect food-related motivation to engage in

cognitive testing since, indeed, scores on this item were positively correlated with

participation on a task in which participants received food rewards. That being said,

capuchins are naturally curious and readily investigate novel situations (Fragaszy & Adams-

Curtis, 1991; Visalberghi & Guidi, 1998), which likely facilitates innovative behaviour as

well as performance on cognitive tasks in general (Alberti & Witryol, 1994; Gottlieb,

Oudeyer, Lopes, & Baranes, 2013). Thus, delineating possible interactions between task

motivation (a situational effect) and personality (a dispositional effect) is required to better

understand how innovative behaviour is generated within this species.

448   Age had a significant and independent effect on capuchins' innovativeness, whereby

449   older individuals were rated as being less innovative in general. Such findings may be

450   explained by the simple fact that younger, small-bodied capuchins may not possess the

451   necessary physical strength and detention that older capuchins have, thereby making

452   innovations more necessary for them (Reader & Laland, 2001; Kummer & Goodall, 1985).

453   On the other hand, older capuchins may be less innovative due to age-related decreases in

454   general playfulness and objective manipulation compared to younger individuals, which may

455   reduce their probability of making innovative "discoveries" (Visalberghi & Guidi, 1998).

456   Lastly, ageing may place constraints on the natural selection of innovative behaviour due to

457   age-related neurological decline (Massimiliano, 2015; Roskos-Ewoldsen, Black, & McCown,

458   2008; Zwoinska, Maklakov, Kawecki, & Hollis, 2017).

459   While sex differences in psychological traits, including those related to

460   innovativeness, have been reported in in various birds and mammals (Amici et al., 2019;

461   Boogert, Fawcett, & Lefebvre, 2011; Reader & Laland, 2001), we found no evidence of a

462   significant and independent effect of sex on innovation within brown capuchins. Again, these

463   findings are similar to those reported in white-faced capuchins whereby males and females

464   show minimal differences in innovation (Perry et al., 2017). It is unclear why species show

465   sex differences in innovation, but the strength of sexual selection on cognitive traits related to

466   innovative behaviour may play a crucial role (Boogert et al., 2011; Chen, et al., 2019). For

467   capuchins specifically, sexual selection appears to be an unlikely pathway through which

468   innovation is selected for within either genera, and perhaps sexual differences in the cognitive

469   abilities that underpin their innovations as well.

470   **Future directions for cross-species studies of innovation using observer ratings**

471   Observer ratings are a reliable and valid tool for studying the behaviour and cognition

472   of many other wild and captive animals besides primates, such as horses (*Equus ferus*)

473   (Lloyd, Martin, Bornett-Gauci, & Wilkinson, 2008), hyenas (*Crocuta crocuta*) (Gosling,

474   1998), cats (*Felis spp.*) (Gartner, Powell, & Weiss, 2014), deer (*Dama dama*) (Bergvall,

475   Schapers, Kjellander, & Weiss, 2011), and elephants (*Loxodonta africana* and *Elephas*

476   *maximus*) (Lee & Moss, 2012; Seltmann, Helle, Adams, Mar, & Lahdenpera, 2018). Future

477   studies might therefore benefit from using the same or similar methods as in the present study

478   to compare our findings to innovative behaviour in other animal species. In particular, we

479   suggest that comparative studies focus on species that differ in ecological niche (e.g. dietary

480   specialists), social structure (e.g. "fission-fusion" societies), social tolerance (e.g. egalitarian

481   or highly despotic species), brain size, cognitive ability, and cultural diversity (e.g. number

482   and types of cultural traditions). Doing so will improve our understanding of the validity of

483   observer ratings in studies of animal innovation, as well as facilitate discussions on factors

484   that might impact the evolution of innovation throughout the animal kingdom.

485   **Conclusions**

486   Large-scale observational studies of individual differences in animal innovation are

487   rare due to logistical difficulties. We took a different approach using a large dataset of

488   reliable ratings of innovative behaviour brown capuchin innovation. Ratings were valid

489   predictors of real-world behavioural outcomes within a subsample of capuchins, and factors

490   associated with innovative behaviour across our entire sample were consistent with

491   observations on wild capuchins. Observer ratings may therefore provide researchers with a

492   valid alternative approach to studying innovation in capuchins and, perhaps, other species as

493   well.

494   **References**

495   Alberti, E. T., & Witryol, S. L. (1994). The relationship between curiosity and cognitive-

496   ability in 3rd-grade and 5th-grade children. *Journal of Genetic Psychology, 155*, 129-

497   145.

498 Amici, F., Widdig, A., Lehmann, J., & Majolo, B. (2019). A meta-analysis of interindividual

499   differences in innovation. *Animal Behaviour*, 155, 257-268.

500 Aplin, L. M., & Morand-Ferron, J. (2017). Stable producer–scrounger dynamics in wild

501   birds: sociability and learning speed covary with scrounging behaviour. *Proceedings*

502   *of the Royal Society B: Biological Sciences, 284*, 20162872.

503 Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative

504   problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*.

505   *Animal Behaviour, 85*, 349-356.

506 Bergvall, U. A., Schapers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging

507   decisions in fallow deer, *Dama dama*. *Animal Behaviour, 81*, 101-112.

508 Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T.

509   (2003). Cultural innovation and transmission of tool use in wild chimpanzees:

510   evidence from field experiments. *Animal Cognition, 6*, 213-223.

511 Boesch, C. (1995). Innovation in wild chimpanzees (*Pan troglodytes*). *International Journal*

512   *of Primatology, 16*, 1-16.

513 Boogert, N. J., Fawcett, T. W., & Lefebvre, L. (2011). Mate choice for cognitive traits: a

514   review of the evidence in nonhuman vertebrates. *Behavioral Ecology*, 22, 447-459.

515 Brosnan, S. F., & Hopper, L. M. (2014). Psychological limits on animal innovation. *Animal*

516   *Behaviour*, 92, 325-332.

517 Chen, J. N., Zou, Y. Q., Sun, Y. H., & ten Cate, C. (2019). Problem-solving males become

518   more attractive to female budgerigars. *Science, 363*, 166-167.

519 Conover, W.J. (1971). Practical Nonparametric Statistics. New York: John Wiley & Sons.

520   Pp: 295–314.

521   Ducatez, S., Clavel, J., & Lefebvre, L. (2015). Ecological generalism and behavioural

522   innovation in birds: technical intelligence or the simple incorporation of new foods?

523   *Journal of Animal Ecology, 84*, 79-89.

524   Ferreira, R. G., Izar, P., & Lee, P. C. (2006). Exchange, affiliation, and protective

525   interventions in semifree-ranging brown capuchin monkeys (*Cebus apella*). *American

526   Journal of Primatology, 68*, 765-776.

527   Foster, S. A. (2013). Evolution of behavioural phenotypes: influrences of ancestry and

528   expression. *Animal Behaviour*, 85, 1061-1075.

529   Fragaszy, D. M., & Adams-Curtis, L. E. (1991). Generative aspects of manipulation in tufted

530   capuchin monkeys (Cebus apella). *Journal of Comparative Psychology*, 105(4), 387–

531   397. https://doi.org/10.1037/0735-7036.105.4.387

532   Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The

533   biology of the genus Cebus*. Cambridge: Cambridge University Press.

534   Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S.

535   D. (2013). Developing a comprehensive and comparative questionnaire for measuring

536   personality in chimpanzees using a simultaneous top-down/bottom-up design.

537   *American Journal of Primatology, 75*, 1042-1053.

538   Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and

539   evaluation of past research. *American Journal of Primatology, 72*, 653-671.

540   Gammell, M. P., De Vries, H., Jennings, D. J., Carlin, C. M., & Hayden, T. J. (2003). David's

541   score: a more appropriate dominance ranking method than Clutton-Brock et al.'s

542   index. *Animal Behaviour, 66*, 601-605.

543   Gartner, M. C., Powell, D. M., & Weiss, A. (2014). Personality Structure in the Domestic Cat

544   (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard

545   (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera*

546   *leo*): A Comparative Study. *Journal of Comparative Psychology, 128*, 414-426.

547   Giraldeau, L. A., & Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-

548   finding behavior in pigeons. *Animal Behaviour, 35*, 387-394.

549   Gosling, S. D. (1998). Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal*

550   *of Comparative Psychology, 112*, 107-118.

551   Gottlieb, J., Oudeyer, P. Y., Lopes, M., & Baranes, A. (2013). Information-seeking, curiosity,

552   and attention: computational and neural mechanisms. *Trends in Cognitive Sciences,*

553   *17*, 585-593.

554   Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common

555   mechanisms. *Behavioural Processes*, 109, 121-134.

556   Griffin, A. S., Guez, D., Lermite, F., & Patience, M. (2013). Tracking changing

557   environments: Innovators are fast, but not flexible learners. *PLoS ONE*, e84907.

558   Guidelines for the treatment of animals in behavioural research and teaching. (2012). *Animal*

559   *Behaviour, 83*, 301-309.

560   Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., . .

561   . Warren, R. (2009). Primate archaeology. *Nature, 460*, 339-344.

562   Henke-von der Malsburg, J., & Fichtel, C. (2018). Are generalists more innovative than

563   specialists? A comparison of innovative abilities in two wild sympatric mouse lemur

564   species. *Royal Society Open Science, 5*, 180480.

565   Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L.

566   (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-

567   solving success. *Animal Cognition, 17*, 835-847.

568   Huebner, F., & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted

569   lemurs (*Eulemur rufifrons*). *Animal Cognition, 18*, 777-787.

570   Janson, C.H. (1990). Social correlates of individual spatial choice in foraging groups of

571   brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 40, 910-921.

572   Kalbitzer, U., Bergstrom, M. L., Carnegie, S. D., Wikberg, E. C., Kawamura, S., Campos, F.

573   A., . . . Fedigan, L. M. (2017). Female sociality and sexual conflict shape offspring

574   survival in a Neotropical primate. *Proceedings of the National Academy of Sciences*

575   *of the United States of America, 114*, 1892-1897.

576   Kidd, C., & Hayden, B. Y. (2015). The psychology and neuroscience of curiosity. *Neuron,*

577   *88*, 449-460.

578   Kummer, H. & Goodall, J. (1985). Conditions of innovative behaviour in primates.

579   *Philosophical Transactions of the Royal Society: Biological Sciences*, 308, 1135.

580   Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmerTest Package: Tests in Linear

581   Mixed Effects Models." *Journal of Statistical Software*, **82**(13), 1–26.

582   doi: 10.18637/jss.v082.i13.

583   Lee, C. S., & Therriault, D. J. (2013). The cognitive underpinnings of creative thought: A

584   latent variable analysis exploring the roles of intelligence and working memory in

585   three creative thinking processes. *Intelligence, 41*(5), 306-320.

586   doi:10.1016/j.intell.2013.04.008

587   Lee, P. C. (1991). Adaptations to environmental change: an evolutionary perspective. In H.

588   O. Box (Ed.), *Primate responses to environmental change* (pp. 39-56). Dordrecht:

589   Springer.

590   Lee, P. C., & Moss, C. J. (2012). Wild female African elephants (*Loxodonta africana*) exhibit

591   personality traits of leadership and social integration. *Journal of Comparative*

592   *Psychology, 126*, 224-232.

593   Lee, P. C., & Moura, A. C. D. (2015). Necessity, unpredictability and opportunity: an

594   exploration of ecological and social drivers of behavioural innovation. In A. Kaufman

595   & J. Kaufman (Eds.), *Animal Creativity and Innovation* (pp. 317-329). London:

596   Elsevier.

597   Lefebvre, L. (2013). Brains, innovations, tools and cultural transmission in birds, non-human

598   primates, and fossil hominins. *Frontiers in Human Neuroscience, 7*, 245.

599   Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and

600   primates. *Brain Behavior and Evolution, 63*, 233-246.

601   Liao, J., & Scholes, S. (2017). Association of social support and cognitive aging modified by

602   sex and relationship type: A prospective investigation in the English longitudinal

603   study of ageing. *American Journal of Epidemiology, 186*, 787-795.

604   Liker, A., & Bokony, V. (2009). Larger groups are more successful in innovative problem

605   solving in house sparrows. *Proceedings of the National Academy of Sciences of the

606   United States of America, 106*, 7893-7898.

607   Lloyd, A. S., Martin, J. E., Bornett-Gauci, H. L. I., & Wilkinson, R. G. (2008). Horse

608   personality: Variation between breeds. *Applied Animal Behaviour Science, 112*, 369-

609   383.

610   Martin, P., & Bateson, P. P. G. (2007). *Measuring behaviour : an introductory guide* (3rd

611   ed.). Cambridge ; New York: Cambridge University Press.

612   Massimiliano, P. (2015). The effects of age on divergent thinking and creative objects

613   production: a cross-sectional study. *High Ability Studies, 26*, 93-104.

614   McCrae, R.R., Costa, P.T. (1987). Validation of the five-factor model of personality across

615   instruments and observers. *Journal of Personality and Social Psychology*, 52, 81-90.

616   Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection

617   bias seriously in animal cognition research: a case study in capuchin monkeys

618   (*Sapajus apella*). *Animal Cognition, 16*, 677-684.

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., . . . Weiss, A. (2013). Personality Structure in Brown Capuchin Monkeys (*Sapajus apella*): Comparisons With Chimpanzees (*Pan troglodytes*), Orangutans (*Pongo spp.*), and Rhesus Macaques (*Macaca mulatta*). *Journal of Comparative Psychology, 127*, 282-298.

Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour, 105*, 163-171.

Morton, F.B., Brosnan, S.F., Pretot, L., Buchanan-Smith, H.M., O'Sullivan, E., Stocker, M., D'Mello, D., Wilson, V.A.D. (2016). Using photographs to study animal social cognition and behaviour: Do capuchins' responses to photos reflect reality? *Behavioural Processes*, 124, 38-46.

Moura, A. C. D., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science, 306*, 1909-1909.

O'Shea, W., Serrano-Davies, E., & Quinn, J. L. (2017). Do personality and innovativeness influence competitive ability? An experimental test in the great tit. *Behavioral Ecology*, 28, 1435-1444.

Ostner, J., & Schulke, O. (2018). Linking sociality to fitness in primates: A call for mechanisms. *Advances in the Study of Behavior, 50*, 127-175.

Overington, S. E., Cauchard, L., Cote, K. A., & Lefebvre, L. (2011). Innovative foraging behaviour in birds: What characterizes an innovator? *Behavioural Processes, 87*, 274-285.

Overington, S. E., Griffin, A. S., Sol, D., & Lefebvre, L. (2011). Are innovative species ecological generalists? A test in North American birds. *Behavioral Ecology, 22*, 1286-1293.

644   Pasquier, G., & Gruter, C. (2016). Individual learning performance and exploratory activity

645   are linked to colony foraging success in a mass-recruiting ant. *Behavioral Ecology,*

646   *27*, 1702-1709.

647   Perry, S. E., Barrett, B. J., & Godoy, I. (2017). Older, sociable capuchins (*Cebus capucinus*)

648   invent more social behaviors, but younger monkeys innovate more in other contexts.

649   *Proceedings of the National Academy of Sciences of the United States of America,*

650   *114*, 7806-7813.

651   Polo-Cavia, N., & Gomez-Mestre, I. (2014). Learned recognition of introduced predators

652   determines survival of tadpole prey. *Functional Ecology, 28*, 432-439.

653   Raine, N. E., & Chittka, L. (2008). The correlation of learning speed and natural foraging

654   success in bumble-bees. *Proceedings of the Royal Society B: Biological Sciences,*

655   *275*, 803-808.

656   Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and

657   operationalized. *Behavioral and Brain Sciences, 30*, 393-407.

658   Reader, S. M. (2003). Innovation and social learning: individual variation and brain

659   evolution. *Animal Biology, 53*, 147-158.

660   Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and

661   cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological*

662   *Sciences, 366*, 1017-1027.

663   Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank

664   differences. *International Journal of Primatology, 22*, 787-805.

665   Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain

666   size in primates. *Proceedings of the National Academy of Sciences of the United*

667   *States of America, 99*, 4436-4441.

668 Reader, S. M., & Laland, K. N. (2003). *Animal innovation*. Oxford ; New York: Oxford

669   University Press.

670 Roskos-Ewoldsen, B., Black, S. R., & McCown, S. M. (2008). Age-related changes in

671   creative thinking. *Journal of Creative Behavior, 42*, 33-59.

672 Royston, P. (1982). Algorithm AS 181: The W test for Normality. Applied Statistics, 31,

673   176–180. doi: 10.2307/2347986.

674 Rutkowska, J., & Adkins-Regan, E. (2009). Learning enhances female control over

675   reproductive investment in the Japanese quail. *Proceedings of the Royal Society B:*

676   *Biological Sciences, 276*, 3327-3334.

677 Seltmann, M., Helle, S., Adams, M. J., Mar, K. U., & Lahdenpera, M. (2018). Evaluating the

678   personality structure of semi-captive Asian elephants living in their natural habitat.

679   *Royal Society Open Science, 5*.

680 Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: uses in assessing rater reliability.

681   *Psychological Bulletin*, 86, 420-428.

682 Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical*

683   *Transactions of the Royal Society B: Biological Sciences, 362*, 539-559.

684 Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance

685   infant survival. *Science, 302*, 1231-1234.

686 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . .

687   Cheney, D. L. (2009). The benefits of social capital: close social bonds among female

688   baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological*

689   *Sciences, 276*, 3099-3104.

690 Skinner, B. F. (1938). *The behavior of organisms*. New York: Appleton-Century-Crofts.

691 Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains.

692   *Biology Letters, 5*, 130-133.

693   Team, R. C. (2019). R: A language and environment for statistical computing (Version

694   Development version: "Unsuffered Consequences" compiled on 2019-08-05). Vienna,

695   Austria R Foundation for Statistical Computing. Retrieved from https://www.r-

696   project.org/

697   Tian, M., Deng, P., Zhang, Y. Y., & Salmador, M. P. (2018). How does culture influence

698   innovation? A systematic literature review. *Management Decision, 56*, 1088-1107.

699   Tiddi, B., Aureli, F., & Schino, G. (2012). Grooming up the hierarchy: The exchange of

700   grooming and rank-related benefits in a New World primate. *Plos One, 7*, e36641.

701   van Horik, J. O., & Madden, J. R. (2016). A problem with problem solving: motivational

702   traits, but not cognition, predict success on novel operant foraging tasks. *Animal

703   Behaviour, 114*, 189-198.

704   Visalberghi, E., & Guidi, C. (1998). Play behaviour in young tufted capuchin monkeys. *Folia

705   Primatologica, 69*, 419-422.

706   Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca

707   mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal

708   of Comparative Psychology, 125*, 72-83.

709   Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., . . . King, J.

710   E. (2009). Assessing chimpanzee personality and subjective well-being in Japan.

711   *American Journal of Primatology, 71*, 283-292.

712   Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012). All too

713   human? Chimpanzee and orang-utan personalities are not anthropomorphic

714   projections. *Animal Behaviour, 83*, 1355-1365.

715   Weiss, A., & King, J. E. (2015). Great ape origins of personality maturation and sex

716   differences: A study of orangutans and chimpanzees. *Journal of Personality and

717   Social Psychology, 108*, 648-664.

718   Whitfield, M., Kohler, A., & Nicolson, S. W. (2014). Sunbirds increase foraging success by

719   using color as a cue for nectar quality. *Behavioral Ecology, 25*, 328-334.

720   Zwoinska, M. K., Maklakov, A. A., Kawecki, T. J., & Hollis, B. (2017). Experimental

721   evolution of slowed cognitive aging in *Drosophila melanogaster*. *Evolution, 71*, 662-

722   670.

723

724   **Table 1**

725   *Independent effects of sociality, age, sex, dominance, and motivation to engage in tasks on*

726   *individual differences in capuchins' scores on innovative behaviour*

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

727   *Note.* Significant results ($P < 0.05$) in boldface. *N* in all cases = 127 monkeys. % R^2 is the

728   percent contribution to the full model adjusted R^2 of a particular covariate by the leave-one-

729   out method. Model fit statistics: Approximate Adjusted $R^2 = 0.351$, F-test: 13.07 on 5 and

730   120 d.f., *P* < 0.0001. Random effects variance components were of trivial size (Social Group

731   Intercept < 0.002 and Group Slope < 0.005).

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Figure 1

Independent associations between capuchins' innovative behaviour and individual

differences in sociality, task motivation, and age (in years) (N=127 capuchins)
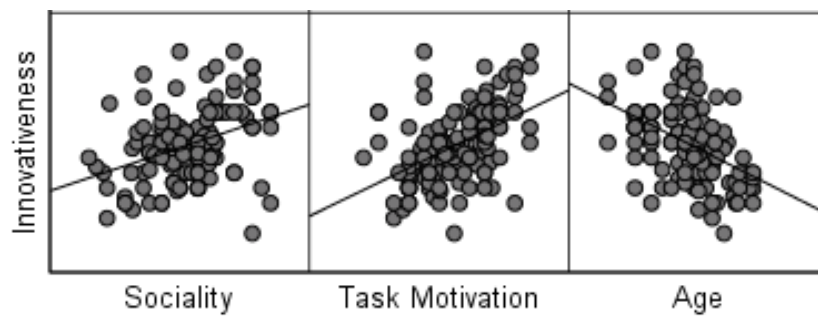
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Supplementary Online Materials

Information about monkey housing conditions:

The following information contains housing conditions of subject from each site

(further details in Morton et al. 2013):

Table S1

Age, sex, and number of study subjects at each research site

Location	N	Groups	Age (mean years ± SD)	Sex Ratio (M:F)
Bucknell University	13	1	8.77 ± 6.18	4:9
Primatology Centre, Strasbourg	18	1	13.67 ± 7.84	6:12
GSU	12	2	9.67 ± 5.65	7:5
Living Links, UK	19	2	10.32 ± 10.99	12:7
Living Links, USA	29	2	14.90 ± 11.06	11:18
National Institutes of Health	26	6	8.39 ± 7.33	16:10
Yale University	10	1	7.9 ± 5.28	4:6

Living Links, UK. Nineteen capuchins were from the 'Living Links to Human

Evolution' Research Centre at the Royal Zoological Society of Scotland, Edinburgh Zoo, UK

(MacDonald and Whiten, 2011). These individuals were from two breeding groups, and each

774   cohabited with a group of common squirrel monkeys. One of these individuals died prior to

775   collecting behavioural data used to validate item ratings. Groups were housed in identically

776   designed, mutually exclusive, 189 m^3 indoor enclosures with natural light and near-

777   permanent access to a 900 m^2 outdoor enclosure containing trees and other vegetation,

778   providing ample opportunity to engage in natural behaviours. At the time the ratings were

779   made, the first group contained 4 adult males, 3 adult females, no sub-adults, 1 juvenile, and

780   3 infants (following age-sex class definitions in Fragaszy et al. 2004). The second group

781   contained 4 adult males, 3 adult females, no sub-adults, 4 juveniles, and 1 infant. All group

782   members were captive born except an adult male from the first group, who was hand-reared,

783   and the original wild-caught alpha male of the second group; both of these individuals came

784   to LL as established members of their groups. All monkeys received commercial TrioMunch

785   pellets supplemented with fresh fruits/vegetables three times daily, and were given cooked

786   chicken and hard boiled eggs weekly. Water was available *ad libitum* at all times.

787   **Primatology Centre, University of Strasbourg.** Eighteen capuchins belonged to a

788   single group at the Primatology Centre of the University of Strasbourg, France, and consisted

789   of 6 adult males, 12 adult females, 4 juveniles, and 0 infants. All monkeys were captive born

790   except for the eldest female, which was hand-reared and most likely wild-born. The hand-

791   reared female has been a member of the group since 1987. Monkeys were provided

792   commercial monkey diet pellets and water *ad libitum*, and received fruit once a week.

793   Monkeys were never food-deprived. All subjects were housed in an indoor (99m^3) and

794   outdoor (45m^2) enclosure, consisting of multiple compartments.

795   **Language Research Center, Georgia State University.** Twelve capuchins belonged

796   to two groups at Georgia State University (GSU) in Atlanta, Georgia, USA. The first group

797   consisted of 2 adult males, 2 adult females, 2 juveniles, and 0 infants. The second group

798   consisted of 1 adult male, 2 sub-adult males, 2 adult females, 1 juvenile, and 0 infants. All

799 monkeys were captive born. For both groups, enclosures consisted of an indoor room (Group

800 1: 75.84m^3; Group 2: 54.42m^3) connected to a large outdoor enclosure (Group 1: 13.51m^2;

801 Group 2: 21.15m^2). Group members spent most of their time in the outdoor area throughout

802 the year, except when engaged in research, during bad weather, or overnight. Monkeys were

803 provided commercial monkey chow three times a day (morning, noon, evening), and fruits

804 and vegetables were given every evening. Water was available *ad libitum* at all times,

805 including during cognitive and behavioural testing. The enclosures were made of chain link

806 fencing and were equipped with swings, ropes, and other materials to create three-

807 dimensional living conditions to enrich the monkeys. The older study subjects had previously

808 been housed together in various combinations at Yerkes National Primate Research Center,

809 before being relocated to GSU 5 years ago, prior to the survey. S. F. B. worked with the

810 animals at both facilities.

811   **Bucknell Primate Lab, Bucknell University.** Fourteen of the capuchins belonged to

812 a single group at Bucknell University in Lewisburg, Pennsylvania, USA. They were housed

813 in one social group consisting of 2 adult males, 2 adult females, 5 sub-adult females, 5

814 juveniles, and 0 infants. All monkeys were captive born. The enclosure consisted of a series

815 of seven compartments (totalling 630m^3) made of caging wire, which were interconnected by

816 doorways or tunnels also made of caging wire. The compartments included various perches,

817 swings, and poles to ensure a most naturalistic environment for climbing and movement.

818 Monkeys were provided commercial monkey chow twice per day (morning, evening), fruits

819 and vegetables were given once per day (morning), and an afternoon snack consisting largely

820 of peanuts, raisins, and low-sugar cereal was given in the afternoon. Water was available *ad*

821 *libitum* at all times. The older subjects (N = 4) had previously been housed at Yerkes

822 National Primate Research Center before being relocated to Bucknell University 12 years

823 ago.

824   **Living Links, Yerkes National Primate Research Center, USA.** Twenty-six brown

825   capuchin monkeys housed in two separate social groups at Living Links, part of the Yerkes

826   National Primate Research Center. One group consisted of 15 monkeys housed in 25 m^2, and

827   the other of 11 monkeys in 31 m^2. Both groups had access to indoor and outdoor areas and

828   were visually, but not acoustically isolated from each other. The monkeys received Purina

829   monkey chow and water *ad libitum*, and trays containing fresh produce every evening.

830   Monkeys were never food or water deprived and all procedures were approved by the

831   Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the

832   study.

833   **Laboratory of Comparative Ethology, National Institutes of Health.** Twenty-six

834   capuchins came from two captive breeding group and several small bachelor groups at the

835   Laboratory of Comparative Ethology, NICHD. At the time of the study, one group comprised

836   5 adults (4 female and 1 male, aged 7-30 years) and 4 juveniles (2 female and 2 male, aged 1-

837   3 years). Three infants (1 female and 2 male, aged <6 months) were part of the group but

838   were not rated for the current study. The second breeding group comprised 4 adults (3 female

839   and 1 male, aged 5-12 years) and 4 juveniles (1 female and 3 male, aged 2-4 years). A further

840   nine animals were pair-housed in cages; two pairs and a group of 3 animals were subadult to

841   adult males (aged 4-9 years), and one pair was an adult female with a juvenile male (aged 25

842   and 1 year respectively). All monkeys were captive born, mother-reared, and housed in the

843   LCE primate facilities at the NIH Animal Center near Poolesville, MD. Breeding groups

844   were housed in one or two parts of three indoor runs (6.9 x 4.1 x 2.1m each), which were

845   connected via sliding doors. Runs were furnished with swings, ladders and various platforms.

846   Cage-housed monkeys were housed in quad cages (1.63 x 1.63 x .71 m per pair). All

847   monkeys were provided with a variety of plastic and metal manipulanda. Monkeys were not

848   food deprived for this study, and received daily nutritional supplements of seeds and fresh

849   fruit or nuts. Commercial monkey biscuits (Labdiet 5045) and water were available *ad*

850   *libitum*.

851   **Comparative Cognition Laboratory, Yale University.** Ten monkeys were at the

852   Comparative Cognition Laboratory at Yale University, New Haven, Connecticut, USA. This

853   group consisted of 4 adult males, 4 adult females, and 2 juvenile females. All monkeys were

854   captive born. The monkeys were housed in an indoor enclosure (32 m^3) consisting of multiple

855   compartments. Commercial monkey pellets were provided twice daily (morning, afternoon)

856   and supplemented with fruits, vegetables, nuts, and cereal daily. Water was available *ad*

857   *libitum*.

858

859   **Methods for the learning task at Living Links**

860   The Living Links monkeys can volunteer to participate in non-invasive cognitive and

861   learning experiments during morning and afternoon sessions four times a week (Monday,

862   Tuesday, Thursday, Friday). On each research day, each group undergoes a morning session

863   from 8:30 to 10:30, and an afternoon session from 11:00 to 13:00. Typically, due to

864   scheduling demands from other researchers, each group undergoes testing on a particular

865   experiment per day (either the morning or afternoon session). Since the establishment of LL

866   in 2008, subjects have been involved in a number of cognitive studies, with a wide array of

867   methodological designs; however, the tasks and methods of administration in the present

868   study had not been used before.

869   All monkeys (N=18, excluding infants) were given the opportunity to engage in a

870   learning task, but only 15 monkeys volunteered to participate in the task. Testing took place

871   in research cubicles, which were divided into two compartments (both 54.6cm x 66cm x 71.1

872   cm) and separated by a transparent plastic door that was halfway open. Subjects could freely

873   volunteer to participate in testing by walking into the research cubicles, which were

874   connected to monkeys' indoor/outdoor enclosures. Participating monkeys could freely walk

875   between the two compartments.

876   During each trial, two white-opaque cups were placed in front of the monkey, one cup

877   was on the left side of the sliding door and one cup was on the right side. The position of

878   each cup (left or right compartment) was randomly selected for each new trial. The two cups

879   differed in size, with one cup twice as tall as the other cup. For this task, the goal was for the

880   monkey to learn that by moving and sitting in the compartment facing the larger cup, they

881   would receive a food reward that was located inside the cup. If the monkey failed a trial, no

882   food was rewarded, and the trial was ended. Monkeys received a maximum of 12 trials per

883   session, with each trial separated by 5-7 seconds. Each monkey received 12 trials per session

884   per day until they met learning criteria (i.e. >80% correct across three consecutive sessions),

885   or for a maximum of 264 trials. For each correct trial, subjects received a food reward (e.g.

886   raisin or piece of papaya). During testing, movements made by the experimenter (F.B.M.)

887   were limited only to setting up each new trial. Temperature and lighting are controlled within

888   the indoor testing enclosures (V. Dufour, pers. com.). Eye gaze of the experimenter during

889   testing was directed at the floor; eye gaze and position of the experimenter behind the

890   apparatus remained the same for each trial to prevent subjects from making "associative

891   cues". All sessions were video recorded using a SONY 60X HD camcorder mounted 1.5m

892   away from the test subject (and directly behind the experimenter) on a tripod; videos were

893   later coded by the experimenter. A binomial test established that subjects would need to score

894   at least 80% of trials (i.e. $\geq$10/12 trials) correctly on a given session for it to be statistically

895   above chance (Morton et al. 2013). Individuals scoring $\geq$80% of trials correctly on three

896   consecutive sessions were considered to have learned the task, and their training subsequently

897   ended.

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905   **Table S2**

906   *Data used to perform analyses on 127 capuchins*

Monkey	Location	Social Group	Group size	Age (Years)	Log_Age	Sex	Dominance	Curiosity	Sociability	Innovation
1	6	1	22	15	1.18	M	6.67	5.33	4.67	3.67
2	6	1	22	12	1.08	F	3	4	4.6	3.8
3	3	7	11	14	1.15	F	5.86	4.38	5.29	3.29
4	5	12	9	7	0.85	F	5	4	4.5	3.5
5	6	1	22	13	1.11	M	6.2	5.6	3.2	3.8
6	6	1	22	22	1.34	F	2.33	3	4.33	2.67
7	7	15	10	14	1.15	M	1	2.5	2.5	1.5
8	4	10	15	12	1.08	F	3.33	5.33	4.67	4.33
9	4	10	15	6	0.78	F	4	4.67	4.67	3.33
10	4	10	15	8	0.9	M	3.67	5.67	4.67	3.33
11	4	10	15	25	1.4	F	3.67	4.67	4.33	2.67
12	6	1	22	38	1.58	F	1.2	3	2.4	3
13	3	7	11	5	0.7	M	2.43	5.57	6	5.71
14	3	7	11	2	0.3	M	3	5.17	6.33	4.83
15	1	2	14	16	1.2	M	3.5	5	3.5	5.5
16	1	2	14	10	1	F	1	3.5	3.5	3
17	3	14	12	40	1.6	M	6.67	3.67	5	2.48
18	3	14	12	10	1	M	2.4	2.8	3.2	1.78
19	2	9	6	21	1.32	M	5	4.75	5.25	4
20	7	15	10	12	1.08	M	7	4	4.5	3
21	3	14	12	5	0.7	M	3.5	5.5	5.5	4.98
22	2	8	6	13	1.11	M	7	5.25	4.25	3.25
23	2	8	6	14	1.15	F	1.2	3	2.2	3.2
24	5	12	9	19	1.28	M	6.67	4	5.33	4.33
25	4	10	15	6	0.78	F	4.33	3.67	4	4.33
26	4	10	15	8	0.9	F	3.33	4	3.33	4
27	2	9	6	14	1.15	M	7	5	4.25	3.5
28	7	15	10	2	0.3	M	4	6	4.5	4.5

29	7	15	10	1	0	F	2.5	6	6.5	6
30	7	15	10	9	0.95	F	1.5	3	5	2.5
31	7	15	10	4	0.6	F	2	3	4.5	2.5
32	5	5	3	9	0.95	M	6.67	4.33	3.67	3.67
33	5	4	2	6	0.78	M	6.33	5.33	3.33	4.33
34	5	12	9	3	0.48	M	2	5.5	5	4.5
35	5	12	9	2	0.3	M	1.5	5.5	4	4.5
36	4	11	11	36	1.56	M	3.5	3	4.5	2.5
37	3	14	12	2	0.3	M	2.75	5.75	6.75	2.5
38	5	12	9	10	1	F	1.67	2.67	4.67	3
39	5	12	9	31	1.49	F	3.5	3	5	3.5
40	5	12	9	3	0.48	M	4.5	6	4.5	4.5
41	5	12	9	13	1.11	F	5.5	4.5	5.5	3.5
42	5	4	2	5	0.7	M	1.33	5.33	3.67	4
43	7	15	10	13	1.11	F	6	4	6.5	4.5
44	5	5	3	7	0.85	M	3.67	4.33	4	3.67
45	3	7	11	11	1.04	F	3.86	5.23	5.29	5.14
46	3	7	11	6	0.78	M	2.14	5.95	2.57	5.29
47	6	1	22	19	1.28	F	3.4	3.4	5	3.8
48	6	1	22	24	1.38	F	4.6	3.8	3	2.2
49	6	1	22	12	1.08	F	4.2	5	5.4	3.6
50	3	14	12	11	1.04	F	3	4	4	4
51	4	11	11	10	1	F	6	4.83	4.83	3
52	4	11	11	9	0.95	F	3.5	5.5	5.5	5.5
53	5	3	2	5	0.7	M	3	4	5.5	4
54	2	9	6	3	0.48	F	4	5.67	4	5
55	2	8	6	7	0.85	M	1	7	5	4
56	5	13	8	5	0.7	F	4.25	5.5	5.25	4.75
57	2	9	6	14	1.15	F	6	4.5	4	4
58	5	13	8	12	1.08	F	5	4.2	5.2	4
59	5	13	8	3	0.48	M	6.5	4	4.5	4
60	5	6	2	1	0	M	1.5	4.5	4.5	4
61	2	8	6	6	0.78	M	3.5	6.25	5.25	6.25
62	5	13	8	5	0.7	F	2.67	5.33	5.33	5
63	4	11	11	12	1.08	M	5.5	5.5	6	3
64	5	6	2	26	1.41	F	2	3	4	2
65	5	13	8	2	0.3	M	1.5	5.5	5	4
66	4	11	11	28	1.45	F	4	5.5	6	3
67	4	11	11	7	0.85	M	3.5	5.5	5.5	6.5
68	5	13	8	12	1.08	F	2	3.67	3.67	3.67
69	4	10	15	40	1.6	F	3.33	4.67	3.67	2
70	3	7	11	4	0.6	M	2.33	3.60	3.67	3.1
71	5	13	8	11	1.04	M	6.67	4.33	4.33	4.67
72	4	10	15	14	1.15	M	6	4.33	5	3

73	3	7	11	40	1.6	M	3.57	3.52	5.14	2.83
74	7	15	10	8	0.9	F	6.5	5.5	6.5	4.5
75	3	14	12	3	0.48	M	2.6	5.4	6.2	5
76	1	2	14	16	1.2	M	7	6.5	7	2
77	7	15	10	2	0.3	F	5.5	6.5	6.5	6.5
78	5	5	3	7	0.85	M	1.33	4	4.33	4
79	4	11	11	10	1	F	4	5	2.5	2.5
80	2	8	6	9	0.95	F	6	5.5	5.18	4.23
81	4	11	11	27	1.43	F	4	4	4	2
82	1	2	14	16	1.2	F	1	1.5	2	3.5
83	4	11	11	7	0.85	M	3.5	3.5	6	7
84	4	11	11	2	0.3	M	2	2	7	5
85	1	2	14	8	0.9	F	1	4	5.5	4
86	7	15	10	14	1.15	M	2	2.5	3	2
87	4	11	11	12	1.08	F	4.5	5.5	3.5	2.5
88	2	8	6	3	0.48	M	2.67	5.67	5.67	5
89	1	2	14	9	0.95	F	5	7	6.5	6.5
90	1	2	14	3	0.48	F	4	7	4.5	7
91	1	2	14	1	0	M	2	6.5	6.5	5.5
92	6	1	22	11	1.04	F	1.33	3.67	4.33	3.33
93	4	11	11	24	1.38	M	4	3.5	6.5	5.5
94	5	12	9	2	0.3	F	1.5	6	5	3.5
95	6	1	22	10	1	F	3.8	4.6	5.2	4
96	3	14	12	3	0.48	F	1.6	4.6	5.4	4.16
97	3	7	11	6	0.78	F	3.67	3.77	5.33	2.82
98	6	1	22	10	1	F	2.4	4.2	4.6	3.6
99	6	1	22	10	1	M	4.8	6.6	4.4	5.8
100	3	7	11	10	1	M	6.29	4.04	4.43	2.4
101	6	1	22	10	1	M	3.2	4.2	3.8	3.6
102	6	1	22	8	0.9	M	5.2	6	5.2	5.2
103	6	1	22	11	1.04	F	5.8	5.6	4.2	4.2
104	1	2	14	3	0.48	F	2	3	3	2
105	6	1	22	8	0.9	M	4.2	6	5.8	5
106	4	10	15	15	1.18	F	2	2	5	4
107	3	14	12	9	0.95	F	3.33	4.83	5	3.65
108	4	10	15	7	0.85	F	5	3.67	4.33	2.67
109	1	2	14	5	0.7	F	4	3	5	2.5
110	6	1	22	8	0.9	F	2.67	5	4.67	4.33
111	5	3	2	9	0.95	M	6.67	5	4	4.67
112	1	2	14	19	1.28	F	6	4.5	6.5	1
113	1	2	14	2	0.3	M	3	7	7	4.5
114	4	10	15	9	0.95	M	4	3.5	5.35	3.5
115	1	2	14	6	0.78	F	6.5	6.5	5.5	5
116	5	13	8	3	0.48	M	2.5	5	4	3.5

117	4	10	15	40	1.6	F	5	3.67	5	3
118	3	14	12	8	0.9	F	2.5	4.67	5.33	5
119	3	14	12	7	0.85	M	1.83	3.67	3.17	3
120	6	1	22	5	0.7	F	1.5	4.5	4	5
121	2	9	6	3	0.48	M	2	6	6	5
122	4	11	11	2	0.3	M	2	2	7	5
123	4	11	11	14	1.15	F	4.5	3	3.5	4.5
124	4	11	11	28	1.45	F	4.5	4	4.5	2.5
125	4	11	11	7	0.85	F	3.5	3.5	4.5	4
126	4	11	11	7	0.85	M	3	3.5	6	6
127	2	9	6	9	0.95	F	1.75	6.5	3.5	6.25

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Table S3

Behavioural data for Living Links monkeys

|	Behavioural Codings				Item Ratings			
Monkey	Social Rank	% Participation	Learning Performance	% Time Close Proximity	Dominance	Curiosity	Innovation	Sociability
1	14.58	88.89	59.10	55.87	5.86	4.38	3.29	5.29
2	-12.67	100.00	77.40	21.11	2.43	5.57	5.71	6.00
3	-8.00	100.00	79.30	51.11	3.00	5.17	4.83	6.33
4	9.33	.00	--	44.68	6.67	3.67	2.48	5.00
5	4.00	55.56	54.17	32.97	2.40	2.80	1.78	3.20
6	-.33	72.22	59.00	35.56	3.50	5.50	4.98	5.50
7	-1.67	100.00	51.70	53.51	2.75	5.75	2.50	6.75
8	.67	100.00	67.20	30.56	3.86	5.23	5.14	5.29
9	-6.17	100.00	86.70	15.56	2.14	5.95	5.29	2.57
10	6.67	5.56	41.70	71.19	6.00	4.83	3.00	4.83
11	-5.17	27.78	71.10	26.52	2.33	3.60	3.10	3.67
12	-6.67	72.22	59.20	40.00	2.60	5.40	5.00	6.20
13	-2.00	100.00	81.70	23.33	1.60	4.60	4.16	5.40
14	3.80	22.22	67.63	50.00	3.67	3.77	2.82	5.33
15	18.46	.00	--	45.81	6.29	4.04	2.40	4.43
16	4.67	11.11	50.00	58.10	3.33	4.83	3.65	5.00
17	-4.67	100.00	77.10	51.67	2.50	4.67	5.00	5.33
18	-9.33	.00	--	3.89	1.83	3.67	3.00	3.17

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Figure S1

Histograms of the distribution of each ratings item
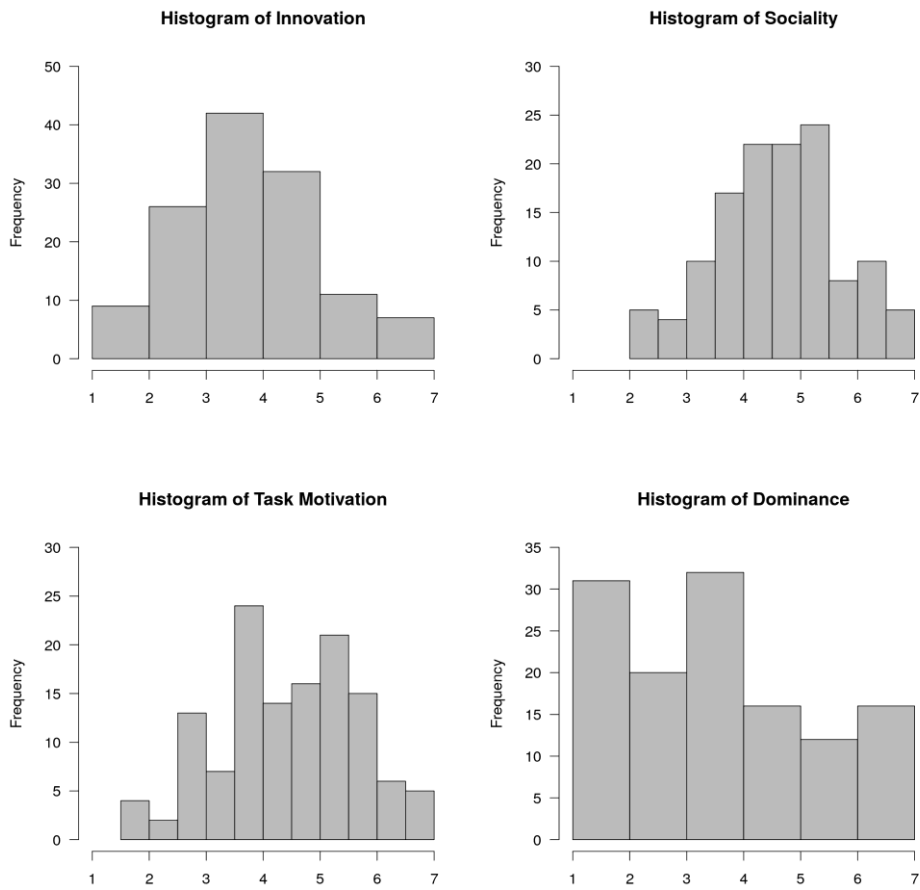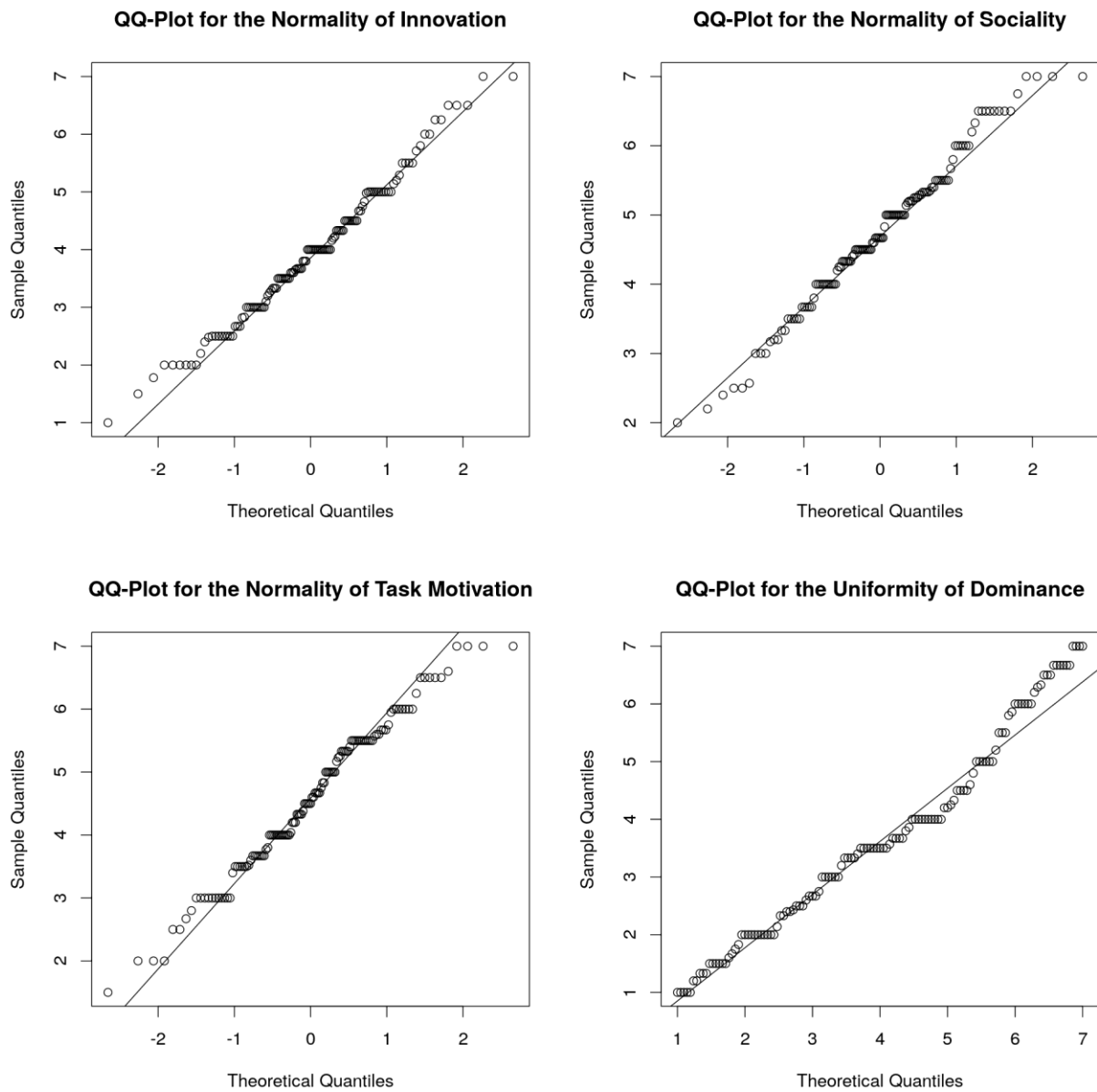

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960   **Figure S2**

961   *QQ-Plots for normality of innovation, sociality, task motivation and uniformity of dominance*

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969 **Table S4**

970 *Shapiro-Wilk test of normality*

Variable	Statistic	P-value
Innovation	0.987	0.27
Sociability	0.986	0.213
Task Motivation	0.983	0.121
Dominance	0.949	0.001

971

972

973 **Supplementary Analyses of Random Effects from Linear Mixed Models using Location**

974 **as Grouping Factor:**

975 Linear mixed model fit by REML ['lmerMod']

976 Formula: Innovation ~ Sociality + Group Size + log(Age, base = 10) + Sex + Dominance +
977 Curiosity + (1| Location))

978 Data: capu

979

980 REML criterion at convergence: 376.3

981

982 Scaled residuals:

983   Min   1Q   Median   3Q   Max

984 -2.83647 -0.65876 -0.07075   0.55400 3.01234

985

986   Random effects:

987   Groups   Name   Variance   Std.Dev.

988   Location (Intercept) 0.003887   0.06235

989   Residual   1.007382   1.00368

990   Number of obs: 127, groups: Location, 7

991

992   Linear mixed model fit by REML ['lmerMod']

993   Formula: Innovation ~ Sociality + log(Age, base = 10) + Sex + Dominance + Curiosity +
994   (Group.size | Location)

995   Data: capu

996

997   REML criterion at convergence: 369.8

998

999   Scaled residuals:

1000   Min   1Q   Median   3Q   Max

1001   -2.84633 -0.62431 -0.09026 0.54429 3.09354

1002

1003   Random effects:

1004   Groups   Name   Variance Std.Dev. Corr

1005   Location (Intercept) 0.000e+00 0.000e+00

1006   Group.size 1.346e-14 1.160e-07 NaN

1007   Residual   9.987e-01 9.994e-01

1008   Number of obs: 127, groups: Location, 7