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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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Abstract

Large-scale studies of individual differences in animal innovation are rare firstly because discovery behaviour itself is often rare, and secondly because of logistical difficulties associated with obtaining observational data on a large number of innovative individuals across multiple groups and locations. Here we take a different approach, using observer ratings to study innovative behaviour in 127 brown capuchin monkeys (*Sapajus [Cebus] sp.*) from 15 social groups and 7 facilities. Capuchins were reliably rated by 1 to 7 raters (mean 3.2 ± 1.6 raters/monkey) on a 7-point Likert scale for levels of innovative behaviour, task motivation, sociality, and dominance. In a subsample, we demonstrate these ratings are valid: rated innovation predicted performance on a learning task, rated motivation predicted participation in the task, rated dominance predicted social rank based on win/loss aggressive outcomes, and rated sociality predicted the time that monkeys spent in close proximity to others. Across all 127 capuchins, individuals that were rated as being more innovated were significantly younger, more social, and more motivated to engage in tasks. Sociality, task motivation, and age all had independent effects on innovativeness, whereas sex, dominance and group size were non-significant. Our findings are consistent with long-term behavioural observations of innovation in wild white-faced capuchins. Observer ratings may therefore be a valid tool for studies of animal innovation, and our findings highlight in particular several possible scenarios through which innovative behaviour might be selected for among capuchins.

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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 & Theriault, 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

because of logistical difficulties associated with observing new innovations across a large, multi-site sample of individuals, including time, money, and using standardised methods (Biro et al., 2003; Haslam et al., 2009).

Observer ratings may help overcome such limitations. Indeed, a growing number of studies have shown that observer ratings are a reliable and valid tool for assessing a wide variety of behaviours and cognitive traits in animals, including primates which are renowned for their innovative behaviour (Freeman et al., 2013; Freeman & Gosling, 2010; Morton, Lee, & Buchanan-Smith, 2013; Morton, Lee, Buchanan-Smith, et al., 2013; Morton et al., 2015; Weiss, Adams, Widdig, & Gerald, 2011; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012). Ratings also enable researchers to obtain data on multiple variables across a large sample of subjects within a reasonable timeframe, with the same definitions and methods (e.g. 7-point Likert scales) used consistently across observers, locations, and subjects to facilitate comparability.

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

As with any study of animal innovation where subjects cannot be monitored continuously across their lifespan, it was not possible in the current study to observe and verify “new” innovations in our capuchins. Thus, to begin to assess the validity of observer ratings on capuchins’ innovative behaviour, we tested, in a subsample of our capuchins, whether the ratings could predict a relevant psychological construct *related* to innovative behaviour, specifically monkeys’ associative learning abilities. Being able to discriminate novel actions (e.g. exploring foreign objects) and learn associations between those actions can play an important role in the innovative process (Reader & Laland, 2003). If, for example, an animal cannot discriminate between novel actions and learn new associations from those actions, then the chances of making a new discovery (and hence making an association and repeating the innovation in the future) will be very limited. Under experimental conditions, animals that are more innovative are also better associative learners (Overington, Cauchard, Cote, & Lefebvre, 2011; Griffin, Guez, Lermite, & Patience, 2013). Thus, in the current study, we predicted that “highly innovative” monkeys would have better associative learning abilities than “less innovative” individuals.

To further assess the validity of our observer ratings, we determined whether the same factors that predicted innovative behaviour across our entire sample of capuchins were consistent with findings from a 10-year observational study of innovations in wild white-faced capuchins (*Cebus capucinus*) (Perry, Barrett, & Godoy, 2017). Specifically, we predicted that, like white-faced capuchins, individual differences in our capuchins’ age and sociality (defined in terms of the amount of time individuals spent within proximity to others) would be the single most important predictors of their innovative behaviour, whereas sex and dominance (defined in terms of avoids, cowers, flees, and supplants) would show minimal, non-significant effects.

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

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

Measures of dominance came from the “dominance” item in the HPQ, which was defined as “the subject is able to displace, threaten, or take food from other individuals; or the subject may express high status by decisively intervening in social interactions”. Measures of sociality came from the “sociability” item in the HQP, which was defined as “the subject seeks and enjoys the company of other individuals and engages in amicable, affable, interactions with them”. Measures of task motivation came from the “curiosity” item in the HPQ, which was defined as “the subject has a desire to see or know about objects, devices, or other individuals; this includes a desire to know about the affairs of other individuals that do not directly concern the subject”.

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

Raters’ reliabilities were as good or even better than human studies, as well as other studies using ratings to examine animal behaviour (e.g. McCrae and Costa, 1987; Freeman and Gosling, 2010; Gartner et al., 2014). Because our raters passed the ICC reliability criteria, this also meant that no single rater was significantly biased towards over or under-rating a given monkey (e.g. if they witness more behaviours compared to the other raters).

Indeed, raters were instructed not to discuss their ratings and to make their ratings based on their *own* observations (not those mentioned by other people). Regarding the innovation ratings specifically, the Likert scale helped to ensure that raters made their ratings on the basis of behavioural frequency – not just one-off observations. Ratings data were normally distributed, not skewed, indicating that ratings were not biased towards raters recalling particular occasions of striking innovation in some monkeys but not others.

Testing the validity of observer ratings

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

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

Task motivation. Motivated animals are, of course, likely to voluntarily participate in tasks that require them to use their cognitive abilities (Skinner, 1938). Data on rates of voluntary participation in the learning task (see 'Innovative behaviour' above) were available for all 18 of the Living Links monkeys and therefore used to validate ratings on task motivation. Participation was calculated by dividing the number of sessions the monkey

engaged in by the total number of session offered to them, multiplied by 100 (Morton, Lee, & Buchanan-Smith, 2013).

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

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

Statistical analyses

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

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

Results

Validity of observer ratings

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

Independent effects between innovative behaviour and sociality scores

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

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

The small amount of variation explained by group size warranted retaining the covariate in the model as a random effect. We also ran a linear mixed model with an equivalent specification as our GEE. The variance component associated with "location" was 0.004 which is negligible. The resulting random effects ("Supplementary information") differed only slightly in magnitude and thus any concern over a location or group bias is unfounded. With the exception of Dominance, each test resulted in our failure to reject the

null that each variable was drawn from an underlying normal distribution. For Dominance, the deviation from normality is explained by the fact that dominance in these groups was highly distributed across individuals. Moreover, the shape of the histogram of this variable (Figure S1 and S2) suggested that it was drawn from an underlying uniform distribution which is supported by a Kolmogorov-Smirnov test (Conover, 1971) of uniformity (statistic=0.149, p-value=0.117) (Table S4). Such deviations might be problematic for the linear model as an outcome (dependent variable) but it is fine for an independent variable. Finally, the scatterplots of the dependent variable against the independent variables showed no observable heteroscedasticity that would indicate a violation of the underlying linearity of the relationship per the assumptions of the Pearson-product moment correlation or the linear model estimation.

Discussion

We used reliable observer ratings to study innovative behaviour in a large, multi-site sample of 127 brown capuchins. In a subsample of these capuchins, we show that the ratings predict real-world behavioural patterns that were independently recorded up to a year later: scores on innovative behaviour were correlated with performance on an operant learning task, task motivation scores were correlated with participation in the learning task, dominance scores were correlated with social rank based on win/loss aggressive outcomes, and sociality scores were correlated with the amount of time spent with other group members. Across all 127 monkeys, sociality had a significant and positive association with innovative behaviour, independently of age, sex, dominance, motivation to engage in tasks, and group size. Our findings for sociality, age, sex, and dominance reflect those reported in wild white-faced capuchins (Perry et al., 2017), ruling out captivity and methodological limitations of ratings as likely explanations for our results. Collectively, our findings support the notion that observer ratings may be a valid tool for studies of animal innovation.

As previously discussed, researchers very rarely have the luxury of being able to follow the same population continuously and across multiple generations to observe and verify new innovations. Thus, psychometric tasks (e.g. giving animals a puzzle feeder) are often used as an objective approach to experimentally induce animals to innovate and solve the novel task (Huebner & Fichtel, 2015; Lee & Therriault, 2013). Such approaches, however, come with their own limitations. For instance, it can be difficult to establish whether innovators are *truly* innovative or just more motivated, less distracted, or have better experience or opportunities to engage in testing than other individuals. For this reason, psychometric tasks are not necessarily any more objective than observer ratings. Thus, much like on-going discussions from the animal personality literature (e.g. Freeman et al., 2013), future studies will likely benefit from using a combination of psychometric and ratings data to further test convergent validity between methods to study innovation.

In a similar vein, the psychological mechanisms that drive innovative behaviour in capuchins and other animals remain largely unknown (Ramsey et al., 2007). As demonstrated in a subsample of our monkeys, ratings used in the current study may reflect at least the associative learning processes related to capuchins' innovative behaviour (Overington, Cauchard, et al., 2011; Ramsey et al., 2007; Reader, 2003). To better understand the psychological underpinnings of innovation in capuchins, we encourage future studies to use a much broader range of tasks varying in complexity and design, particularly those that measure other types of learning, inhibitory control, and intelligence (Huebner & Fichtel, 2015; Lee & Therriault, 2013). Studies of birds (*Sturnus tristis*), for instance, have shown that better innovators are better at solving discrimination tasks, but do not perform as well on reversal tasks, suggesting that associative learning, not flexible learning, is more relevant to innovation within these animals (Griffin et al., 2013).

Regarding our measure of sociality (i.e. time in close proximity to others), Morton et al. (2016) found that individuals who spend less time in close proximity to the alpha also take longer to approach food when the alpha is close by, which reflects wild capuchin studies (e.g. Janson, 1990). In a different study, Morton et al. (2015) found that proximity loads onto the same factorial component as coalitions, food sharing, and grooming; meaning, at least in capuchins, all of these more “subtle forms” of sociality simply map onto the same thing: affiliative behaviour. Nevertheless, future work might consider whether these and other specific forms of sociality are better predictors of innovativeness, particularly time spent grooming, sharing food, and watching others while feeding. Using social network analysis can also provide a multi-dimensional approach to sociality for comparison.

Finally, captive animals are unlikely to face the same level of ecological pressure as in the wild (e.g. no predation risk), and can have a tendency to be more innovative than wild individuals of the same species (Benson-Amram et al., 2013). Nevertheless, our findings are consistent with those found in wild capuchin monkeys. Future comparisons between captive and wild brown capuchins using the same or similar methods can therefore provide *complimentary* insight into the innovativeness of this species, for instance, in terms of controlling for factors like inter-group competition and predator vigilance, which might impact the amount of time wild (but not captive) capuchins can devote to being innovative.

Disentangling possible scenarios for the evolution of capuchin innovation

Cognitive traits, including those linked to innovative behaviour, may be advantageous to animals’ fitness (O’Shea, Serrano-Davies, & Quinn, 2017; Pasquier & Grunter, 2016; Polo-Cavia & Gomez-Mestre, 2014; Raine & Chittka, 2008; Rutkowska & Adkins-Regan, 2009; Whitfield, Kohler, & Nicholson, 2014), particularly when facing unpredictable conditions within the environment (Lee & Moura, 2015). Nevertheless, it is difficult to predict whether or how such pressures might affect the evolution of traits, like innovation,

that are themselves plastic. If, for example, plasticity always produces an optimal phenotype, then genetic variation may be restrained from natural selection, thereby limiting the evolution of that trait (Foster, 2013). Understanding the evolution of innovation therefore requires having knowledge about different fitness optima and selective pressures on innovative behaviour across time and contexts. Our study has identified at least three potential sources of selective pressure to consider in future studies of brown capuchin innovation, including sociality, task motivation, and age.

Sociality has been linked to better fitness in capuchins within stable groups (Kalbitzer et al., 2017), but longitudinal, multi-generational data are needed using a direct measure of fitness (e.g. reproductive success) to determine whether highly innovative and social individuals have an advantage. We suggest at least two testable scenarios for how sociality might – under optimal conditions (Foster, 2013) – provide fitness-related benefits to brown capuchins. Like most group-living primates, capuchins use strategies such as grooming, coalitions, and food sharing to achieve greater social embeddedness within their group (Ferreira et al., 2006; Frigaszy et al., 2004; Morton et al., 2015; Tiddi et al., 2012), and being more social may reduce stress, improve infant survival, provide better access to food and mating opportunities, and, in turn, lead to better fitness (Kalbitzer et al., 2017; Ostner & Schulke, 2018; Silk, 2007; Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Thus, a positive association between innovative behaviour and sociality may arise if, for example, being innovative enables individuals to concurrently improve their social status within groups because doing so can result in fitness-related benefits. On the other hand, since sociality is linked to better fitness, individuals that are more social may simply have better opportunities in terms of the time and energy they can devote to experiment and engage in learning compared to less social individuals (Kummer & Goodall 1985). Such opportunities may not 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.

Age had a significant and independent effect on capuchins' innovativeness, whereby older individuals were rated as being less innovative in general. Such findings may be explained by the simple fact that younger, small-bodied capuchins may not possess the necessary physical strength and dexterity that older capuchins have, thereby making innovations more necessary for them (Reader & Laland, 2001; Kummer & Goodall, 1985). On the other hand, older capuchins may be less innovative due to age-related decreases in general playfulness and objective manipulation compared to younger individuals, which may reduce their probability of making innovative "discoveries" (Visalberghi & Guidi, 1998). Lastly, ageing may place constraints on the natural selection of innovative behaviour due to age-related neurological decline (Massimiliano, 2015; Roskos-Ewoldsen, Black, & McCown, 2008; Zwoinska, Maklakov, Kawecki, & Hollis, 2017).

While sex differences in psychological traits, including those related to innovativeness, have been reported in various birds and mammals (Amici et al., 2019; Boogert, Fawcett, & Lefebvre, 2011; Reader & Laland, 2001), we found no evidence of a significant and independent effect of sex on innovation within brown capuchins. Again, these findings are similar to those reported in white-faced capuchins whereby males and females show minimal differences in innovation (Perry et al., 2017). It is unclear why species show sex differences in innovation, but the strength of sexual selection on cognitive traits related to innovative behaviour may play a crucial role (Boogert et al., 2011; Chen, et al., 2019). For capuchins specifically, sexual selection appears to be an unlikely pathway through which innovation is selected for within either genera, and perhaps sexual differences in the cognitive abilities that underpin their innovations as well.

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

Observer ratings are a reliable and valid tool for studying the behaviour and cognition of many other wild and captive animals besides primates, such as horses (*Equus ferus*)

(Lloyd, Martin, Bornett-Gauci, & Wilkinson, 2008), hyenas (*Crocuta crocuta*) (Gosling, 1998), cats (*Felis spp.*) (Gartner, Powell, & Weiss, 2014), deer (*Dama dama*) (Bergvall, Schapers, Kjellander, & Weiss, 2011), and elephants (*Loxodonta africana* and *Elephas maximus*) (Lee & Moss, 2012; Seltsmann, Helle, Adams, Mar, & Lahdenpera, 2018). Future studies might therefore benefit from using the same or similar methods as in the present study to compare our findings to innovative behaviour in other animal species. In particular, we suggest that comparative studies focus on species that differ in ecological niche (e.g. dietary specialists), social structure (e.g. “fission-fusion” societies), social tolerance (e.g. egalitarian or highly despotic species), brain size, cognitive ability, and cultural diversity (e.g. number and types of cultural traditions). Doing so will improve our understanding of the validity of observer ratings in studies of animal innovation, as well as facilitate discussions on factors that might impact the evolution of innovation throughout the animal kingdom.

Conclusions

Large-scale observational studies of individual differences in animal innovation are rare due to logistical difficulties. We took a different approach using a large dataset of reliable ratings of innovative behaviour brown capuchin innovation. Ratings were valid predictors of real-world behavioural outcomes within a subsample of capuchins, and factors associated with innovative behaviour across our entire sample were consistent with observations on wild capuchins. Observer ratings may therefore provide researchers with a valid alternative approach to studying innovation in capuchins and, perhaps, other species as well.

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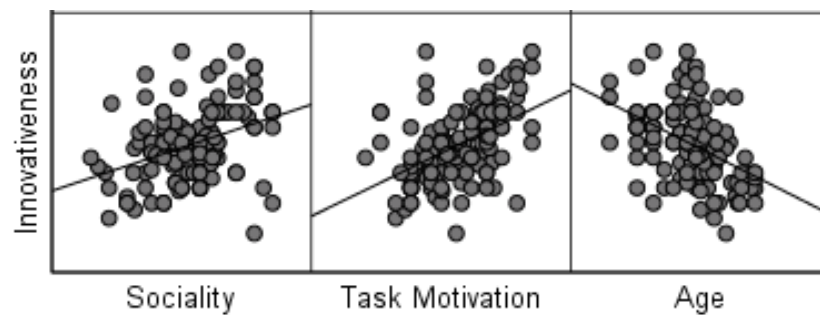
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Table 1

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

Note. Significant results ($P < 0.05$) in boldface. N in all cases = 127 monkeys. % R² is the percent contribution to the full model adjusted R² of a particular covariate by the leave-one-out method. Model fit statistics: Approximate Adjusted R² = 0.351, F-test: 13.07 on 5 and 120 d.f., $P < 0.0001$. Random effects variance components were of trivial size (Social Group Intercept < 0.002 and Group Slope < 0.005).



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

cohabited with a group of common squirrel monkeys. One of these individuals died prior to collecting behavioural data used to validate item ratings. Groups were housed in identically designed, mutually exclusive, 189 m³ indoor enclosures with natural light and near-permanent access to a 900 m² outdoor enclosure containing trees and other vegetation, providing ample opportunity to engage in natural behaviours. At the time the ratings were made, the first group contained 4 adult males, 3 adult females, no sub-adults, 1 juvenile, and 3 infants (following age-sex class definitions in Frigaszy et al. 2004). The second group contained 4 adult males, 3 adult females, no sub-adults, 4 juveniles, and 1 infant. All group members were captive born except an adult male from the first group, who was hand-reared, and the original wild-caught alpha male of the second group; both of these individuals came to LL as established members of their groups. All monkeys received commercial TrioMunch pellets supplemented with fresh fruits/vegetables three times daily, and were given cooked chicken and hard boiled eggs weekly. Water was available *ad libitum* at all times.

Primate Centre, University of Strasbourg. Eighteen capuchins belonged to a single group at the Primate Centre of the University of Strasbourg, France, and consisted of 6 adult males, 12 adult females, 4 juveniles, and 0 infants. All monkeys were captive born except for the eldest female, which was hand-reared and most likely wild-born. The hand-reared female has been a member of the group since 1987. Monkeys were provided commercial monkey diet pellets and water *ad libitum*, and received fruit once a week. Monkeys were never food-deprived. All subjects were housed in an indoor (99m³) and outdoor (45m²) enclosure, consisting of multiple compartments.

Language Research Center, Georgia State University. Twelve capuchins belonged to two groups at Georgia State University (GSU) in Atlanta, Georgia, USA. The first group consisted of 2 adult males, 2 adult females, 2 juveniles, and 0 infants. The second group consisted of 1 adult male, 2 sub-adult males, 2 adult females, 1 juvenile, and 0 infants. All

monkeys were captive born. For both groups, enclosures consisted of an indoor room (Group 1: 75.84m³; Group 2: 54.42m³) connected to a large outdoor enclosure (Group 1: 13.51m²; Group 2: 21.15m²). Group members spent most of their time in the outdoor area throughout the year, except when engaged in research, during bad weather, or overnight. Monkeys were provided commercial monkey chow three times a day (morning, noon, evening), and fruits and vegetables were given every evening. Water was available *ad libitum* at all times, including during cognitive and behavioural testing. The enclosures were made of chain link fencing and were equipped with swings, ropes, and other materials to create three-dimensional living conditions to enrich the monkeys. The older study subjects had previously been housed together in various combinations at Yerkes National Primate Research Center, before being relocated to GSU 5 years ago, prior to the survey. S. F. B. worked with the animals at both facilities.

Bucknell Primate Lab, Bucknell University. Fourteen of the capuchins belonged to a single group at Bucknell University in Lewisburg, Pennsylvania, USA. They were housed in one social group consisting of 2 adult males, 2 adult females, 5 sub-adult females, 5 juveniles, and 0 infants. All monkeys were captive born. The enclosure consisted of a series of seven compartments (totalling 630m³) made of caging wire, which were interconnected by doorways or tunnels also made of caging wire. The compartments included various perches, swings, and poles to ensure a most naturalistic environment for climbing and movement. Monkeys were provided commercial monkey chow twice per day (morning, evening), fruits and vegetables were given once per day (morning), and an afternoon snack consisting largely of peanuts, raisins, and low-sugar cereal was given in the afternoon. Water was available *ad libitum* at all times. The older subjects (N = 4) had previously been housed at Yerkes National Primate Research Center before being relocated to Bucknell University 12 years ago.

Living Links, Yerkes National Primate Research Center, USA. Twenty-six brown capuchin monkeys housed in two separate social groups at Living Links, part of the Yerkes National Primate Research Center. One group consisted of 15 monkeys housed in 25 m², and the other of 11 monkeys in 31 m². Both groups had access to indoor and outdoor areas and were visually, but not acoustically isolated from each other. The monkeys received Purina monkey chow and water *ad libitum*, and trays containing fresh produce every evening. Monkeys were never food or water deprived and all procedures were approved by the Institutional Animal Care and Use Committee (IACUC) prior to the commencement of the study.

Laboratory of Comparative Ethology, National Institutes of Health. Twenty-six capuchins came from two captive breeding group and several small bachelor groups at the Laboratory of Comparative Ethology, NICHD. At the time of the study, one group comprised 5 adults (4 female and 1 male, aged 7-30 years) and 4 juveniles (2 female and 2 male, aged 1-3 years). Three infants (1 female and 2 male, aged <6 months) were part of the group but were not rated for the current study. The second breeding group comprised 4 adults (3 female and 1 male, aged 5-12 years) and 4 juveniles (1 female and 3 male, aged 2-4 years). A further nine animals were pair-housed in cages; two pairs and a group of 3 animals were subadult to adult males (aged 4-9 years), and one pair was an adult female with a juvenile male (aged 25 and 1 year respectively). All monkeys were captive born, mother-reared, and housed in the LCE primate facilities at the NIH Animal Center near Poolesville, MD. Breeding groups were housed in one or two parts of three indoor runs (6.9 x 4.1 x 2.1m each), which were connected via sliding doors. Runs were furnished with swings, ladders and various platforms. Cage-housed monkeys were housed in quad cages (1.63 x 1.63 x .71 m per pair). All monkeys were provided with a variety of plastic and metal manipulanda. Monkeys were not 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 m³) 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

connected to monkeys' indoor/outdoor enclosures. Participating monkeys could freely walk between the two compartments.

During each trial, two white-opaque cups were placed in front of the monkey, one cup was on the left side of the sliding door and one cup was on the right side. The position of each cup (left or right compartment) was randomly selected for each new trial. The two cups differed in size, with one cup twice as tall as the other cup. For this task, the goal was for the monkey to learn that by moving and sitting in the compartment facing the larger cup, they would receive a food reward that was located inside the cup. If the monkey failed a trial, no food was rewarded, and the trial was ended. Monkeys received a maximum of 12 trials per session, with each trial separated by 5-7 seconds. Each monkey received 12 trials per session per day until they met learning criteria (i.e. $>80\%$ correct across three consecutive sessions), or for a maximum of 264 trials. For each correct trial, subjects received a food reward (e.g. raisin or piece of papaya). During testing, movements made by the experimenter (F.B.M.) were limited only to setting up each new trial. Temperature and lighting are controlled within the indoor testing enclosures (V. Dufour, pers. com.). Eye gaze of the experimenter during testing was directed at the floor; eye gaze and position of the experimenter behind the apparatus remained the same for each trial to prevent subjects from making "associative cues". All sessions were video recorded using a SONY 60X HD camcorder mounted 1.5m away from the test subject (and directly behind the experimenter) on a tripod; videos were later coded by the experimenter. A binomial test established that subjects would need to score at least 80% of trials (i.e. $\geq 10/12$ trials) correctly on a given session for it to be statistically above chance (Morton et al. 2013). Individuals scoring $\geq 80\%$ of trials correctly on three consecutive sessions were considered to have learned the task, and their training subsequently 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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932 **Table S3**933 *Behavioural data for Living Links monkeys*

Monkey	Behavioural Codings				Item Ratings			
	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

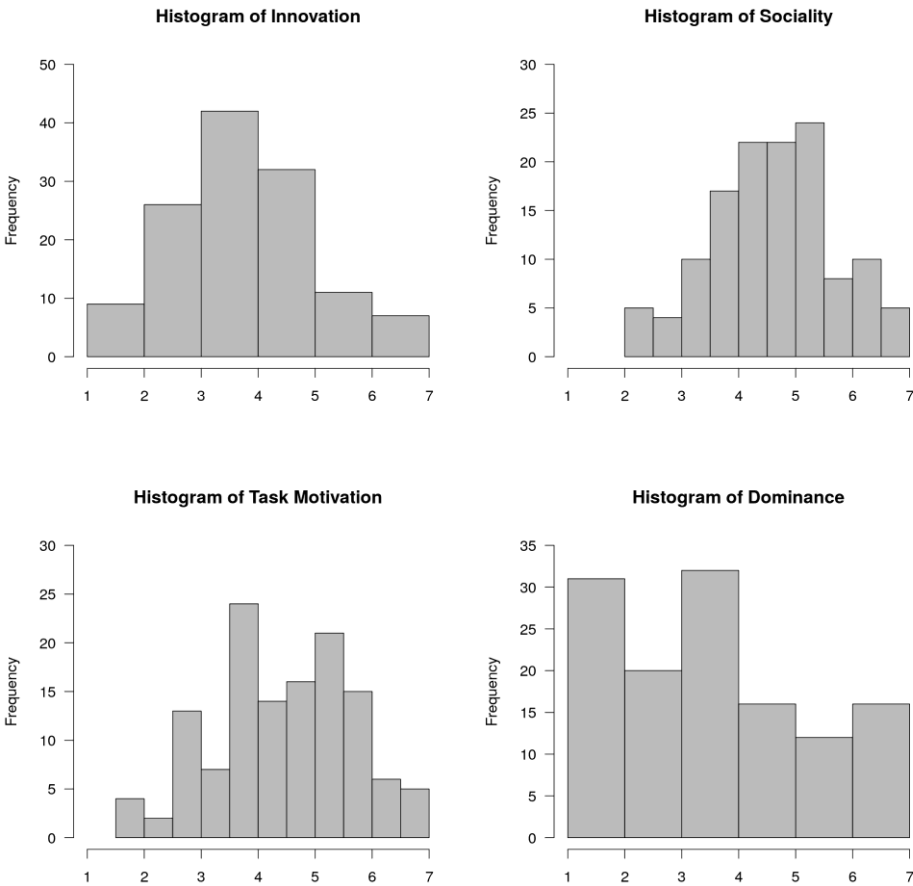


Figure S2
QQ-Plots for normality of innovation, sociality, task motivation and uniformity of dominance

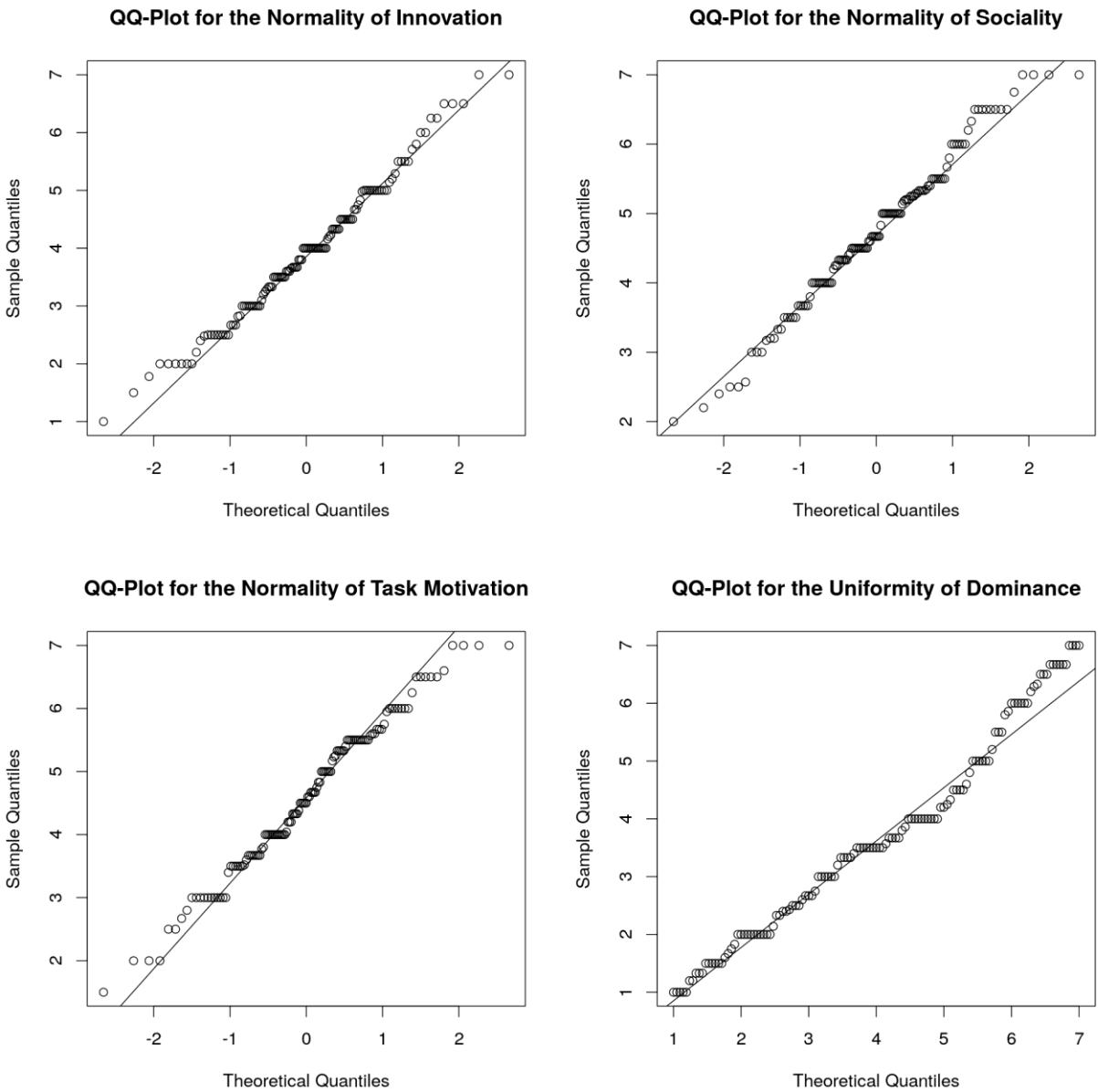


Table S4*Shapiro-Wilk test of normality*

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

Supplementary Analyses of Random Effects from Linear Mixed Models using Location**as Grouping Factor:**

Linear mixed model fit by REML ['lmerMod']

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

Data: capu

REML criterion at convergence: 376.3

Scaled residuals:

Min	1Q	Median	3Q	Max
-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