

# Studying Animal Innovation at the Individual Level: A Ratings-Based Assessment in Capuchin Monkeys (*Sapajus [Cebus] sp.*)

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Large-scale studies of individual differences in innovative behavior among nonhuman animals are rare because of logistical difficulties associated with obtaining observational data on a large number of innovative individuals across multiple locations. Here, we take a different approach, using observer ratings to study individual differences in innovative behavior 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  $3.2 \pm 1.6$  raters/monkey) on a 7-point Likert scale for levels of innovative behavior, 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 proximity to others. Across all 127 capuchins, individuals that were rated as being more innovative were significantly younger, more social, and more motivated to engage in tasks. Age, sociality, and task motivation all had independent effects on innovativeness, whereas sex, dominance, and group size were nonsignificant. Our findings are consistent with long-term behavioral observations of innovation in wild white-faced capuchins. Observer ratings may, therefore, be a valid tool for studies of animal innovation.

**Keywords:** observer ratings, validity, innovativeness, cognitive evolution, associative learning

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Some species have a proclivity for behavioral innovation, in which individuals of those species use new or modified behaviors to solve new or existing problems (Lee, 1991; Reader & Laland, 2003). Innovation has significant links with intelligence (Lee & Theriault, 2013; Ramsey et al., 2007), species differences in brain size (Lefebvre, 2013; Lefebvre et al., 2004; Reader, 2003; Reader & Laland, 2002), the evolution of tool use and culture (Biro et al., 2003; Boesch, 1995; Lefebvre, 2013; Reader et al., 2011; Tian et al., 2018), and the breadth of a species' ecological niche

(Ducatez et al., 2015; Overington, Griffin, et al., 2011). At the proximate level, a range of dispositional and situational factors likely play a role in generating innovative behavior (Amici et al., 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 behaviors (Ramsey et al., 2007; Reader & Laland, 2003). Unless an animal learns

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from its innovative action, and can repeat that action, the discovery will be lost from the repertoire of the individual.

Large-scale studies on individual differences in animal innovation are relatively few in number firstly because observations on innovative behavior itself are rare, and secondly because of logistical difficulties (e.g., time, money, and standardizing methods) associated with documenting innovations across a large, multisite sample of individuals (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 behaviors and cognitive traits in animals (Freeman et al., 2013; Freeman & Gosling, 2010; Morton et al., 2015; Morton, Lee, & Buchanan-Smith, 2013; Morton, Lee, Buchanan-Smith, et al., 2013; Weiss et al., 2011, 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 behavior within a large, multisite sample of captive brown capuchin monkeys (*Sapajus [Cebus] sp.*). To help explain individual variation in innovative behavior, we considered 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 et al., 2013; Henke-von der Malsburg & Fichtel, 2018; Huebner & Fichtel, 2015), physiology (Hopper et al., 2014), brain development and decline (Roskos-Ewoldsen et al., 2008), behavioral ecological niche (Aplin & Morand-Ferron, 2017; Giraldeau & Lefebvre, 1987; Liker & Bokony, 2009), and experience (Daveri & Parisi, 2015; Huebner & Fichtel, 2015). Although many other factors may contribute to innovative behavior, 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 life span, 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 behavior, we tested, in a subsample of our capuchins, whether the ratings could predict a relevant psychological construct related to innovative behavior, specifically monkeys’ associative learning abilities. Being willing and able to discriminate and learn associatively from one’s actions can play an important role in the innovative process (Reader & Laland, 2003). If, for example, an animal cannot discriminate between old versus new actions, and learn new associations from its actions, then the chances of making a new discovery (i.e., making an association and repeating the innovative behavior in the future) will be very limited. Under experimental conditions, animals that are more innovative are better at solving associative learning tasks (Griffin et al., 2013; Overington, Cauchard, et al., 2011). Thus, in the current study, we predicted that highly innovative monkeys would perform better on an associative learning task than less innovative individuals.

To further assess the validity of our observer ratings, we determined whether the same factors that predicted innovative behavior 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 et al., 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 important negative and positive predictors of their innovative behavior, respectively, whereas sex and dominance (defined in terms of avoids, cowers, flees, and supplants) would show minimal, nonsignificant effects.

## Method

### Ethics

This study was approved by the ethics committee of the Psychology Division at the University of Stirling, the Living Links committee at the Royal Zoological Society of Scotland, and complied with American Psychological Association and Association for the Study of Animal Behaviour ethical guidelines (*Guidelines for the Use of Animals*, 2012).

### Subjects

Subjects were 127 captive brown capuchins that were at least 1-year-old, belonging to 15 social groups from five sites in the United States, one site in the United Kingdom, and one site in France (Table S1 in online supplemental materials). 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, 18 of these monkeys were observed at the Living Links to Human Evolution Research Centre, affiliated with the Royal Zoological Society of Scotland, United Kingdom. Further details of housing and husbandry are provided in the “Supplementary Information” (SI) in online supplemental materials.

### Observer Ratings

Ratings were collected between 2010 and 2011 for a previous study (Morton, Lee, Buchanan-Smith, et al., 2013). Raters consisted of 25 researchers and three care staff who had known their subjects for at least 1 year. Definitions and scales for observer ratings on capuchins’ innovative behavior, 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 ( $3.2 \pm 1.6$  raters per monkey) on each item based on the frequency of monkeys’ behavior on a 1 (*absent*) to 7 (*very common*) scale. Ratings were averaged across raters for each monkey. Measures of innovative behavior came from the “innovation” item in the HPQ, which defined such behavior as “the subject engages in new or different behaviors 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 behavior in their monkeys. For instance, one rater reported that a monkey was observed using a stick on several occasions to reach chow from under the fence, which other monkeys in the group did not do (Leverett and Rossetti, personal communication). In another instance, a rater reported that one of their monkeys would take a piece of wood, break pieces off of it, and then use it to scratch or comb its back, which had not been seen in any other monkey in that group by any rater (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.”

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. Of the sample, 121 capuchins (out of the total 127 subjects) were rated by at least two raters ( $M = 3.35$ ;  $SD = 1.57$ ). Collectively, there was high interobserver agreement across each item per monkey: dominance [ICC(3, 1) = .57, ICC(3, k) = .82], innovation [ICC(3, 1) = .57, ICC(3, k) = .82], sociability [ICC(3, 1) = .57, ICC(3, k) = .82], and curiosity [ICC(3, 1) = .57, ICC(3, k) = .82] (Morton, Lee, Buchanan-Smith, et al., 2013).

Raters' reliabilities across all items were as good or even better than similar ratings reported in studies of humans and other animals (Freeman & Gosling, 2010; Gartner et al., 2014; McCrae & Costa, 1987). Because our raters passed the ICC reliability criteria, this also meant that no single rater was significantly biased toward over- or underrating a given monkey (e.g., if they witnessed more behaviors compared to the other raters). 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 behavioral frequency—not just one-off observations. Ratings data were normally distributed, not skewed, indicating that ratings were not biased toward raters recalling particular occasions of striking innovation in some monkeys but not others. Collectively, because there was no evidence that raters were unreliable, mean ratings for each item for all 127 monkeys were included in our analyses.

### Testing the Validity of Observer Ratings

Behavioral data (Table S3 in online supplemental materials) 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 behavior derived from ratings:

#### *Innovative Behavior*

Data on the Living Links capuchins' performances on a discrimination learning task were used to validate innovative behavior ratings. Although 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 S1 in online supplemental materials). 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*

Motivation is, of course, crucial for participating in tasks that require the use of cognitive abilities (Skinner, 1938). Data on rates of voluntary participation in the learning task (see “Innovative behavior” 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 sessions offered to them, multiplied by 100 (Morton, Lee, & Buchanan-Smith, 2013).

#### *Sociality*

Data on monkeys' time spent in 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 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; Fragaszy et al., 2004). Focal observations on all 18 monkeys' spatial proximity to others were made between May and August 2011, totaling 3 hr 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 10 min 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-min sessions. Monkeys were observed on rotation across all 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 min ( $M = 220.7$  min,  $SD = 160.2$  min).

#### *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 et al., 2015; Morton, Lee, Buchanan-Smith, et al., 2013) by calculating David's Scores (DS) using data on win/loss outcomes during monkey's aggressive interactions (Gammell et al., 2003). All occurrences of fighting within the group were recorded while performing focal sampling of individuals outlined above (see “Sociality”).

#### *Analyses*

In the subsample of 18 monkeys used to validate ratings, we used Pearson correlations to examine relationships between individual differences in item ratings, behaviors, and task performance. Across the entire sample ( $N = 127$  monkeys), age was skewed but normalized 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 behavior. 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” variable 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. Although bounded between 1 and 7, our dependent variable (innovative behavior) and our key independent variables (sociality, task motivation, and dominance) are not discrete. Rather, because we measured them using a robust multirater 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 26 (IBM Corp., Chicago, IL, United States). 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 et al., 2017).

## Results

### Validity of Observer Ratings

Ratings on innovative behavior were significantly and positively related to performance on the discrimination learning task when all participants were included in the analysis ( $r = .598, p = .019, N = 15$  monkeys) and when only individuals that participated in >80% of sessions were included ( $r = .787, p = .02, N = 8$  monkeys). Ratings on task motivation were significantly and positively related to participation in the novel task ( $r = .618, p = .006, N = 18$  monkeys). Dominance ratings were significantly and positively related to social rank ( $r = .833, p < .001, N = 18$  monkeys). Sociality ratings were significantly and positively related to the amount of time individuals spent with other group members ( $r = .495, p = .037, N = 18$  monkeys).

### Independent Effects Between Innovative Behavior and Sociality Scores

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 (see Table 1). Individual differences in innovative behavior were significantly and positively related to sociality and task motivation, but negatively related to age (see 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 generalized estimating equation. The variance component associated with “location” was .004, which is negligible. The resulting random effects (Table S1 in online supplemental materials)

**Table 1**

*Independent Effects of Sociality, Age, Sex, Dominance, and Task Motivation on Individual Differences in Capuchins’ Ratings on Innovative Behavior*

Effect	Estimate	Robust SE	Robust <i>t</i>	% $R^2$	Pr (>  <i>t</i>  )
<b>(Intercept)</b>	<b>2.17</b>	<b>.66</b>	<b>3.29</b>	—	<b>&lt;.01</b>
<b>Sociality</b>	<b>.22</b>	<b>.09</b>	<b>2.44</b>	<b>8.37</b>	<b>.02</b>
<b>log(Age, base = 10)</b>	<b>−.79</b>	<b>.31</b>	<b>−2.49</b>	<b>9.66</b>	<b>.01</b>
Sex	.05	.18	.27	.18	.79
Dominance	−.05	.06	−.90	1.42	.37
<b>Task motivation</b>	<b>.36</b>	<b>.09</b>	<b>4.09</b>	<b>21.17</b>	<b>&lt;.001</b>

*Note.* Significant results ( $p < .05$ ) are in boldface. *N* in all cases = 127 monkeys. %  $R^2$  is the percent contribution to the full model adjusted  $R^2$  of a particular covariate by the leave-one-out method. Model fit statistics: approximate adjusted  $R^2 = .351$ , *F*-test: 13.07 on 5 and 120 d.f.,  $p < .0001$ . Random effects variance components were of trivial size (Social Group Intercept < .002 and Group Size Slope < .005).

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 in online supplemental materials) suggested that it was drawn from an underlying uniform distribution, which is supported by a Kolmogorov–Smirnov test (Conover, 1971) of uniformity (statistic = .149,  $p$  value = .117; Table S4 in online supplemental materials). 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.

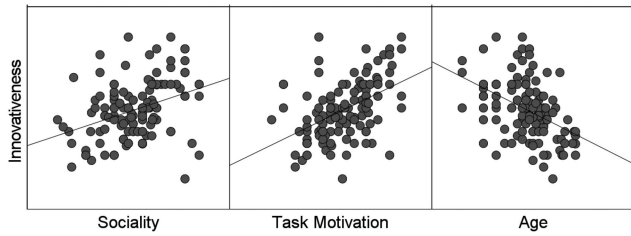
## Discussion

We used reliable observer ratings to study innovative behavior in a large, multisite sample of 127 brown capuchins. In a subsample of these capuchins, we found that the ratings predicted real-world behavioral patterns that were independently recorded up to a year later: Ratings on innovative behavior were correlated with performance on an associative learning task, task motivation scores were correlated with participation in the 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, the independent effects of age, sociality, sex, and dominance reflected 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 innovation.

As previously discussed, researchers very rarely have the luxury of being able to follow the same population continuously across

**Figure 1**

*Independent Associations Between Capuchins' Innovative Behavior and Individual Differences in Sociality, Task Motivation, and Age (in Years; N = 127 Capuchins)*



generations to observe and verify new innovations. Novel operant tasks (e.g., giving animals a puzzle feeder) are often used as an objective approach to experimentally induce animals to innovate (Benson-Amram et al., 2013; Henke-von der Malsburg & Fichtel, 2018; Huebner & Fichtel, 2015). Such approaches, however, come with their own limitations. For instance, it can be difficult to establish whether more frequent innovators are simply more motivated, less distracted, or have better experience or opportunities to engage in testing than other individuals. For this reason, operant tasks are not necessarily any more objective than observer ratings. Thus, much like ongoing discussions from the animal personality literature (Freeman et al., 2013), future studies will likely benefit from using a combination of operant tasks and ratings data to further test convergent validity between methods to study innovation.

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

Regarding our measure of sociality (i.e., time in proximity to others), Morton et al. (2015) found that proximity loads onto the same principal 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 behavior. 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 multidimensional 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, the same factors that predicted innovative behaviour in our captive capuchins were consistent with those found in wild capuchin monkeys (Perry et al., 2017). Future comparisons between captive and wild brown capuchins using the same or similar methods can therefore provide *complementary* 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 innovativeness in wild (but not captive) capuchins.

### Proximate Underpinnings of Capuchin Innovation

We suggest at least two testable scenarios for why sociality might be positively correlated with innovative behavior in brown capuchins. First, 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; Fragaszy 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 et al., 2003, 2009). Thus, a positive association between innovative behavior and sociality may arise if, for example, being innovative enables individuals to concurrently improve their social status within groups. Second, 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). Indeed, this latter scenario might arise if sociality is a means through which capuchins solve an otherwise ecological problem (e.g., resource acquisition and protection from predators), and, in turn, allow more time and/or opportunities for innovative behavior. Examining longitudinal associations between capuchins' innovative behavior and sociality will help tease apart these and other possibilities.

The positive association between our measure of task motivation and innovative behaviour could reflect food-related motivation (i.e., a situational effect), as capuchins' scores on task motivation were positively correlated with their willingness to participate in a task that involved food rewards. On the other hand, capuchins are naturally curious and readily investigate novel situations (Fragaszy & Adams-Curtis, 1991; Visalberghi & Guidi, 1998). Thus, their motivation to engage in innovative behavior could be underpinned by personality traits like curiosity, exploration, persistence, or neophobia (Benson-Amram et al., 2013; Daniels et al., 2019; Kidd & Hayden, 2015; Overington, Cauchard, et al., 2011). Behavioral and cognitive traits are useless to animals if they are not willing to perform them, and so further studies to delineate situational versus dispositional drivers of capuchin motivation are needed to understand how innovative behavior is generated within this species.

At least three possible scenarios could explain the negative association between capuchins' age and innovative behavior. First, younger, smaller-bodied capuchins may not possess the necessary

physical strength and dentition that older, larger-bodied capuchins have, which, in turn, could make innovations more necessary for them (Kummer & Goodall, 1985; Reader & Laland, 2001). Second, older capuchins may be less innovative due to age-related decreases in general playfulness and objective manipulation compared with younger individuals, which may reduce the probability of them making “discoveries” (Visalberghi & Guidi, 1998). Third, ageing may place constraints on innovative behavior due to age-related neurological decline (Massimiliano, 2015; Roskos-Ewoldsen et al., 2008; Zwoinska et al., 2017).

Although sex differences in psychological traits, including those related to innovativeness, have been reported in various birds and mammals (Amici et al., 2019; Boogert et al., 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 some species show sex differences in innovation, whereas others do not, and so further studies are needed.

### Implications for Other Species

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

### Conclusions

Due to the logistical difficulties of conducting large-scale observational studies of animal innovation, we took a different approach using a large dataset of reliable ratings to study the innovative behavior of brown capuchins. Ratings were valid predictors of real-world behavioral outcomes within a subsample of these capuchins, and factors associated with innovative behavior across our *whole* sample were consistent with observations on wild capuchins. Observer ratings may, therefore, provide researchers with a valid approach to studying innovation in capuchins and, perhaps, other species as well.

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