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The Relationship Between Variation in Social Complexity and Cognitive Performance in Brown Capuchins (Cebus [Sapajus] apella)

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THE RELATIONSHIP BETWEEN VARIATION IN SOCIAL COMPLEXITY AND
COGNITIVE PERFORMANCE IN BROWN CAPUCHINS *(CEBUS [SAPAJUS]*
APELLA)

by

Juliana F. Berhane

A Thesis

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Abstract

The cognitive demand on animals to learn, maintain, and remember the complexities of social relationships is higher for individuals who live more complex social lives. Previous research has suggested that both across and within species, as social complexity increases so does the ability to flexibly learn and manipulate information. Elucidating the relationship between social complexity and cognition is therefore essential to understanding how evolutionary pressures have shaped cognitive development. In this study, I determined if there was a relationship between social complexity and cognitive performance on two standard tests of learning, associative learning and reversal learning. Subjects were 16 members of a socially housed group of brown capuchin monkeys (*Cebus [Sapajus] apella*). Each subject completed up to five rounds of testing on a series of associative learning and reversal learning tasks. A general learning score was extracted from a principal component analysis on cognitive testing performance across the two tasks. Behavioral observations of affiliative and grooming interactions were used to characterize the complexity of each monkey's social life in the social network of the group. Generalized linear models revealed that learning performance was best explained by centrality in the grooming social network ($p = 0.076$), although this relationship was not significant. While results from these analyses were interpreted with caution as data collection is ongoing, results clearly do not show strong support for a positive relationship between learning performance and social complexity as predicted. Brown capuchins may gain a social benefit from cognitive abilities not tested or when the information learned has direct social implications. My findings

suggest that there may not be a clear link between cognition and social behavior, or that our methods were not appropriate for answering this question.

Introduction

For social animals, successful navigation of the social environment depends on their ability to attend to and respond to individuals around them. These animals maintain complex relationships based on past interactions that may require them to identify individuals they have relationships with, associate personal characteristics with those individuals, remember prior interactions, and infer information about group members they do not often interact with (Tomasello & Call, 1997). More complex social environments therefore pose increased cognitive demand to keep track of relationships with group members (Cheney & Seyfarth, 1990). Individuals that are better able to learn and remember information about their social group may have a selective advantage, manifested as increased social or reproductive success.

Primates that live in complex social groups need to be able to recognize familiar conspecifics, know the rank and kinship relations of third-party group members, and learn information about other's relationships through observation (Tomasello & Call, 1997). Indeed, capuchin monkeys (*Cebus [Sapajus] apella*) recognize familiar in-group and out-group members (Pokorny & de Waal, 2009; Talbot, Leverett, & Brosnan, 2016) and rhesus monkeys (*Macaca Mulatta*) recognize familiar conspecifics from faces and voices (Adachi & Hampton, 2011; Silwa, Duhamel, Pascalis, & Wirth, 2011). Baboons and macaques appear to know the rank and kinship relationships between group members. When played vocalizations from a fight between two individuals where the outcome is incongruent with the dominance hierarchy, baboons (*Papio hamadryas ursinus*) respond more strongly when the fight is between matrilines (lineage through the

mother) rather than within matrilines (Bergman, Beehner, Cheney, & Seyfarth, 2003). During confrontations, male bonnet macaques (*Macaca radiata*) use information of third-party rank relationships to recruit males that outrank both themselves and their opponent (Silk, 1999). Hamadryas baboons (*Papio hamadryas*) are more likely to affiliate with a conspecific that is kin of a combatant after a fight (Judge & Mullen, 2005). Rhesus monkeys look longer to images of individuals that they have a close affiliative relationship with than individuals with whom they have an agonistic relationship (Silwa et al., 2011). Because it cannot come from personal experience, third-party information comes from inferences based on "eavesdropping" (Wey, Blumstein, Shen, & Jordán, 2008). By eavesdropping, animals can observe the behavior of conspecifics to infer characteristics, such as dominance and kinship, of non-affiliates to avoid costly situations such as a fight. Gelada (*Theropithecus gelada*) bachelor males attend to male-male fights, perhaps in an attempt to assess the competitive ability of resident males (le Roux & Bergman, 2012). Overall, these studies indicate that primates can identify, learn, and track relationships between other members of the group, all of which require cognitive skills in learning and remembering information.

The cognitive demand on animals to learn, maintain, and remember the complexities of relationships in their group is likely higher for species living in groups with more complex social structures. This may have resulted in the evolution of faster and more flexible learning mechanisms in these species. For example, the highly social pinyon jay (*Gymnorhinus cyanocephalus*) learns dyadic relationships faster and more accurately than the less social scrub jay (*Aphelocoma californica*). Additionally, the

pinyon jay is better at flexibly inferring relationships between these learned pairs (Bond,

Kamil, & Balda, 2003). Another study on prosimians found similar results, with highly

social ring-tailed lemurs (*Lemur catta*) outperforming the less social mongoose lemur

(*Eulemur mongoz*) on an inference task (MacLean, Merritt, & Brannon, 2008). In both of

these examples, the social species lived in more complex social environments than the

less social species. These studies suggest that, as social complexity in a species increases,

so may the ability to flexibly learn and manipulate information.

Studies of the evolution of cognitive abilities often focus on broad species level

differences in cognitive performance in order to understand how evolutionary pressures

have shaped cognition. However, cognitive skills mostly exist on a spectrum, with

differences in cognitive skill between individuals even within a species (Thornton &

Lukas, 2012). Like the cognitive differences between species, these individual

differences may be of interest in understanding the evolution and development of

cognition. Individual animals that live simpler social lives with fewer strong relationships

may be under less pressure to develop and tune their cognitive abilities than animals with

more social relationships. Alternatively, animals who have better memory or learn faster

may be more capable of maintaining more social relationships, resulting in those

individuals having more complex social relationships. Regardless of the direction of this

relationship, individuals who live more complex social lives may perform better on

cognitive tasks compared to their less social counterparts. Indeed, individual cowbirds

(*Molothrus ater*) that live in groups with changing membership show more complex song

repertoires than cowbirds from simpler, static groups (White, Gersick, & Snyder-

Mackler, 2012). Individual wild Australian magpies (*Cracticus tibicen dorsalis*) living in larger groups performed better on a battery of cognitive tasks including associative learning, reversal learning, spatial memory, and inhibitory control than magpies living in smaller groups (Ashton, Ridley, Edwards, & Thornton, 2018). Pheasants (*Phasianus colchicus*) housed in groups of five performed with higher accuracy on two spatial discrimination tasks than pheasants housed in small groups of three (Langley, van Horik, Whiteside, & Madden, 2018). This suggests that there may be a link between cognitive ability and sociality even at the individual level.

As evidenced by the studies presented above, the number of social relationships an animal has is often used as a proxy for the complexity of their social life. These direct connections in the group are important, as close affiliates often turn to one another for coalitionary support in conflict and share resources (Bonnie & de Waal, 2006; Eppley, Suchak, Crick, & de Waal, 2013; Seyfarth & Cheney, 1984). However, the simple number of direct social relationships an individual has does not take into account indirect relationships, which can exponentially increase the number of individuals in an animal's social circle. For example, it is not just important for an animal to know its relationship with its close affiliates, but also to know the relationship between those close affiliates and their affiliates, as these relationships play an important role in the animal's day-to-day social environment (Brent, 2015). Social network analysis reveals how each member of a group is connected to other members of the group. A key advantage to social network measures over traditional dyadic interaction measures is that it takes into account not only dyadic relationships, but also indirect relationships (Wey et al., 2008), providing

a more accurate picture of the complexity of the social life of an individual (Brent, 2015).

Information centrality measures an individual's connectedness in the social network

(dyadic; Figure 1a) as well as the connectedness of the other animals with whom they are

connected (indirect; Figure 1b). Specifically, it measures how often an individual lies on

a path (or series of connections) between other members of the group (Stephenson &

Zelen, 1989). The paths or connections found in social networks can be used to predict

the spread of information across social groups. Birds that were central to their group's

network were more likely to discover novel food patches compared to less connected

individuals (Aplin, Farine, Morand-Ferron, & Sheldon, 2012). Social network position

and information centrality in adolescence has long-lasting effects into adulthood. Juvenile

long-tailed manakins (*Chiroxiphia linearis*) with high infocentrality are more likely to

become adults with high social rank and status in a lek system, providing these males

with more breeding opportunities with passing females (McDonald, 2007). Due to the

increased complexity of their social interactions, individuals with higher information

centrality may be under increased cognitive demand to acquire social information and

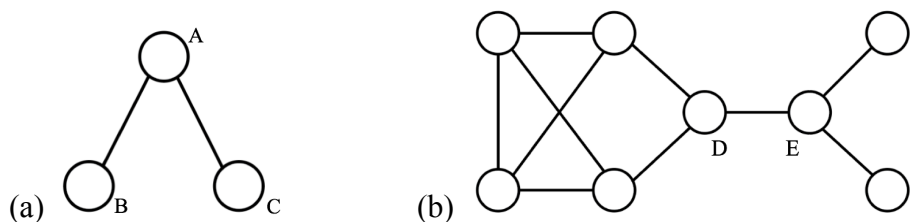flexibly learn, remember, and use that information.

Figure 1. Hypothetical social networks. (a) A simple social network for a group of three

individuals. Each individual is represented by a node (circle) with edges (lines) showing

the relationships between individuals. Individual A is more central to the network and has

more direct connections (2) than individuals B (1) and C (1). (b) A more complex

hypothetical social network for a group of 8 individuals. Individuals D and E have the

same number of direct connections (3) but D has more indirect connections (D = 6, E =

2). D would therefore have higher information centrality than E.

Present Study

In this study, I determined if variation in social network centrality correlated with

variation in cognitive performance at the individual level in 16 socially housed brown

capuchin monkeys (*Cebus [Sapajus] apella*). Capuchin monkeys are a highly social

species with complex social interactions, stable linear dominance hierarchies, and long

term social relationships (Fragaszy, Visalberghi, & Fedigan, 2004). Additionally,

capuchins are able to remember events over long delays (D'amato & Buckiewicz, 1980),

select appropriate tools for different functions (Judge & Bruno, 2012), learn patterns and

orders of items (D'amato & Salmon, 1984), recognize familiar individuals (Talbot et al.,

2016), exercise self control (Judge & Essler, 2013), preferentially observe successful

individuals for social learning (Ottoni, de Resende, & Izar, 2005), cooperate with a

partner to achieve a shared goal (Mendres & de Waal, 2000), and learn a concept in

same/different tasks (Wright, Rivera, Katz, & Bachevalier, 2003). This species is therefore capable of employing a wide range of cognitive abilities during daily social challenges.

The complexity of each group member's social life was characterized using a social network derived from affiliative social interactions. The social network of the group was created from long-term behavioral observations on both grooming and general affiliative interactions, and individual measures of information centrality extracted. Grooming occurs when an animal combs through the hair or picks at the skin of another animal. This can be done for hygienic purposes or as an affiliative behavior, and is important for maintaining and strengthening social bonds (Dunbar, 1991; Henzi & Barrett, 1999). Like grooming, proximity (being near one another) and social contact occur more between close affiliates and can help maintain social bonds (Smuts, 1985). Although an animal must be in proximity to another animal in order to groom them, the social network derived from proximity is independent of the network derived from grooming and may therefore measure different aspects of social relationships (Brent et al., 2013). In captive settings, it is difficult to interpret proximity measures due to restricted space. How frequently an animal is in physical contact with another group member provides an alternative measure of affiliation for captive groups. Physical contact in the group can occur during a wide range of affiliative behavior such as resting, grooming, social play, and eating. In this study, contact was therefore used to measure general affiliation.

Each subject monkey was tested on two well studied, basic cognitive tasks; object discrimination and reversal learning. These tasks test basic learning and flexibility, cognitive abilities that are at the heart of almost all real world social interactions (Shettleworth, 1998; Thorndike, 1998). Object discrimination tasks present a subject with two or more stimuli where a subset of stimuli is associated with a reinforcer. Reversal learning tasks then change the food reward associations for stimuli so that the stimuli that was not previously reinforced now results in a food reward when selected. In the present study, both tasks were presented as a two-choice task where two stimuli were presented at once and one was associated with a food reward.

Most previous studies of individual differences are conducted in the field and test animals one time on a specific task, due to practical limitations on subject access (Ashton et al., 2018; Pritchard, Hurly, Tello-Ramos, & Healy, 2016). However if an animal is only tested once and happens to be distracted and perform poorly, their performance does not accurately reflect their ability (Thornton & Lukas, 2012). Unusual performance can be difficult to catch with single instances of cognitive testing, but when tests are conducted multiple times the average performance across all testing periods can provide a more representative and robust measure of an animal's ability (Boogert, Madden, Morand-Ferron, & Thornton, 2018). One solution to this problem is to conduct transfer tests where an animal is tested on the same paradigm multiple times but with a new set of stimuli each time. There is evidence showing the importance of transfer tests in repeatability, with inconsistent results found on individual instances of testing when subjects are tested on the same tasks multiple times (Anderson et al., 2017; Boogert et al.,

2018). To address this concern, each capuchin in this study was tested on the learning and reversal learning tasks five times, with each presentation of the task using a different set of stimuli. This provided a robust measure of each individual's performance on these tasks. Consistent and repeatable performance on a cognitive task is important for determining a relationship between cognition and behavior (Griffin, Guilette, & Healy, 2015). Each monkey's average performance on these cognitive tasks was compared to their location in the social network of the group. If monkeys that are more central in the social network perform better on the learning tasks, it would suggest a relationship between real world social skills and cognitive abilities at the individual level.

Methods

Subjects and Housing

Subjects were 16 members of a socially housed group of 18 brown capuchins (*Cebus [Sapajus] apella*) housed at Bucknell University's Animal Behavior Lab. The group contained three adult males, nine adult females, three juvenile males, and three juvenile females. The enclosure the subjects were housed in consisted of three separate rooms, two of which contained adjacent smaller compartments. Each section of the home enclosure could be temporarily closed off, allowing subjects to be separated for cognitive testing.

In the present study, each monkey was tested in their home enclosure which consisted of three rooms. Because the front-most room can be separated from the other two using an opaque sliding door, subjects were tested in this room in order to minimize

rank related audience effects (Bunnell, Gore, & Perkins, 1980; Drea & Wallen, 1999). Subjects did not have visual access to group members during testing but did maintain auditory contact through the doors. Food and water were available ad libitum.

Some subjects had extensive experience with cognitive testing while others had no previous cognitive testing experience (Table 1). Cognitive testing experience in the last five years was coded for each subject and included in statistical analyses. Experience was coded as "High" (included in 5+ previous studies involving cognitive testing), "Moderate" (included in 3-4 previous studies), "Low" (included in 1-2 previous studies) or "None" (included in no previous studies).

Behavioral Data

Data collection. Behavioral data on the group has been collected since March 2015. One 15 minute focal observation was conducted on each of the 16 subjects approximately once per week. The initiator and recipient of all behaviors were recorded for grooming, aggressive (bite, chase, rough behavior, threat), and submissive (bare teeth, crouch, avoid) behavior (see Appendix for ethogram with behaviors of interest for this study). All aggressive and submissive behavior were recorded as counts (how many times they happened), while grooming behavior was recorded as duration (for how long did it happen). General affiliative behavior was recorded as whether animals were in contact using scan sampling every one minute during the focal observations. This measure therefore captured affiliative behaviors including play, resting in contact, grooming, and touching. Data were collected using the Animal Observer app for iPad (Caillaud, 2017).

Dominance rank analysis. Dominance rank was calculated for each of the subjects using Elo ratings (EloRating package for R). Elo ratings use the outcome of aggressive and submissive interactions to determine the rank of each animal in the group (Neumann & Kulik, 2014). Each animal starts with a baseline score of 1000 that changes in response to dominance interactions based on how consistent the interaction is with the current rank order. If an interaction is consistent with the existing hierarchy, then scores change less compared to an interaction that goes against the current hierarchy. Elo ratings used in analyses were extracted on the first day of cognitive testing for each subject to capture their status in the group at the time they were tested.

Social network analysis. Behavioral data collected from focal and scan observations were used to create two separate un-directed, weighted social networks based on affiliative behavior; one based on grooming interactions and one based on general affiliative behavior. For each possible pair in the group, the rate of these interactions was calculated. Rates of grooming interactions were calculated as the hourly rate of grooming between that pair ([Total seconds of A grooming B + Total seconds of B grooming A]/[Total hours of A focal observations + Total hours of B focal observations]). These interactions and the resulting models were non-directional, such that the rates of general affiliation and grooming for A-B were the same as those of B-A. Rate of general affiliation for each pair was calculated as the proportion of total scans during which the animals in a pair were in contact (e.g., Number of A's scans in which it was in contact with B + Number of B's scans in which it was in contact with A/ [Total number of A scans + Total number of B scans]).

Information centrality was extracted for each subject from the grooming and general affiliation networks on their first day of testing to capture their location in the network of the group at the time of testing. These measures reflected how directly connected an individual was to other members of the group *and* how connected these secondary individuals were to others (Stephenson & Zelen, 1989). Social network analyses were conducted using the ERGM package for R (Handcock et al., 2018; R Core Development Team, 2008).

Cognitive Testing

Apparatus and basic procedure. The testing apparatus was mounted 1.14 m from the floor to allow subjects to sit on a perch as they tested. Subjects interacted with an 28.6 cm x 28.6 cm wooden board containing nine choice locations arranged in three rows of three through 2.54 cm by 5.08 cm caging. Each choice location was made of PVC pipe 4.1 cm in diameter and 4.8 cm long so that the ends of the PVC protruded from the front and back of the apparatus. Each choice location contained a slit at the top and bottom of the PVC end facing the subject's side so that a 3.8 cm x 5.1 cm paper stimulus could be slid in to cover the opening. The PVC end facing the experimenter was used to place a food reward behind a paper stimulus out of sight of the subject. The apparatus could slide forward and back onto four metal rods that were attached to the subject's caging such that it could be brought within reach for the subject to make a choice (Figure 2a), and removed from reach during the inter-trial interval (Figure 2b). A cardboard occluder was placed in front of the apparatus during the inter-trial interval so that the subject did not see the placement of the stimuli or the baiting of the food reward (Figure

2c). If the subject attempted to move or look around the occluder by climbing the caging, the experimenter stopped setting up the apparatus and used vocal commands and hand gestures until the subject sat behind the occluder. The food reward was either a piece of cashew or dried mango, specific to each subject, determined by previous food preference testing.
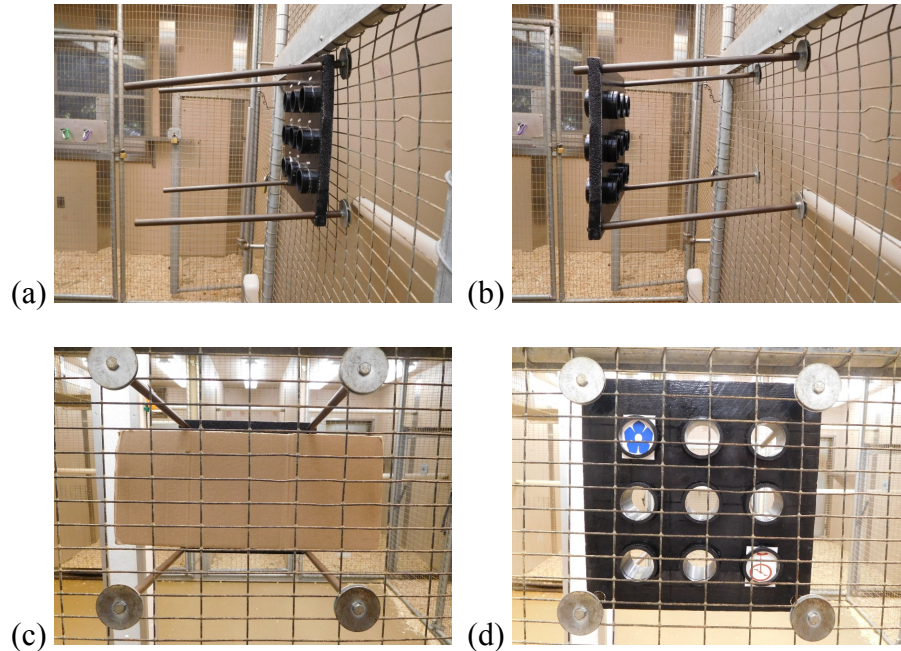
Figure 2. Experimental apparatus. Apparatus within reach (a) as it was presented during a trial, and out of reach (b) as it was presented during the inter-trial interval. The subject's view of the apparatus during the inter-trial interval with the occluder present (c) and during a trial (d).

Once the stimuli and food reward were in place, the apparatus was slid towards the subject. The subject made a choice by removing their chosen stimulus. The subject could only make one choice. If the subject made the correct choice it was given time to retrieve the food reward. If it made an incorrect choice, the subject did not receive a food

reward and the apparatus was quickly slid away from the subject so that it could not reach for the other choice location where the food was hidden.

Training. All subjects underwent an initial training phase to ensure that they knew how to interact with the apparatus. Subjects were presented with a single location covered with a white stimulus behind which a preferred food was hidden. Subjects were trained to remove the stimulus in order to retrieve the food reward until they reached criterion (removing the stimulus 8 out of 10 trials). A trial was scored as incorrect if the subject took longer than 10 s to remove the stimulus while actively trying, or if they ignored the apparatus for one min.

Associative learning. Subjects were presented with a two-item object discrimination in which one stimulus was reinforced (S+) and one stimulus was not reinforced (S-). Correct selection of the S+ resulted in a high value food reward, selection of the S- resulted in no food reward. Stimuli were solid color images of a blue dolphin, green giraffe, orange letter M, grey letter R, black leaf, blue flower, green bowling pin, orange unicycle, grey disco ball, and black teapot (Figure 3). Stimulus pairings and S+/S-assignments were counterbalanced across subjects.
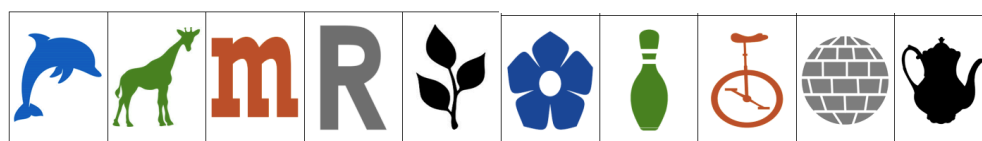

Figure 3. The ten stimuli used in learning tasks.

On each trial, two of the nine locations were covered, one by the S+ and one by the S- (Figure 2d). The choice locations were semi-randomly assigned so no location was used more than twice in a session. Each subject was presented with one nine-trial session

per day until they correctly selected the S+ over the S- on 8 out of 10 trials on a sliding scale. This means that trials across sessions were considered consecutive and a subject could pass by correctly selecting the S+ frequently towards the end of a previous session and at the beginning of the current session. If a subject reached criterion in the middle of a session, the experimenter continued the session until all nine trials were complete. The number of errors made before reaching this criterion were measured for each subject as a measure of learning rate.

Reversal learning. Once a subject reached criterion on the associative learning task, they began the reversal learning task using the same two choice stimuli the next day. The procedure was the same as the associative learning task except that the S- image became the S+ and the S+ became the S-. As in associative learning, the subject tested on this single discrimination for one nine-trial session per day until they chose the S+ over the S- 8 out of 10 times on a sliding scale. The number of errors made before reaching this criterion was measured for each subject as a measure of reversal learning rate.

Design. The goal of conducting the associative and reversal learning tasks was to determine how successful each subject was on learning tasks generally. We therefore tested each subject on the two learning tasks five times to increase reliability of the performance scores. The first iteration of the associative learning task was followed by the reversal learning task with the same two images. Once the subject reached criterion on the reversal learning task, they were presented with a new pair of images on which they repeated the associative learning-reversal learning sequence. Subjects were tested on consecutive days unless a female in the group was cycling. If the subject being tested was

the female cycling or a male potential mate of that female, they were not tested until the cycling ended. Subjects were tested in one 5 min session approximately six days per week.

Statistical Analysis

Extraction of a general learning score. To determine whether performance between the two tasks showed consistency, average errors to criterion for each subject were subjected to a principal component analysis (PCA) using the FactoMineR package for R (Husson, Josse, Le, & Mazet, 2018). If behavioral flexibility was influenced by a general ability to learn, then a subject who showed few errors to criterion on the associative learning task would also show few errors to criterion on the reversal learning task. PCA reduces the number of variables in a large data set into a smaller set of measures that explains the variation present in the original data, functionally creating a new variable that explains the shared variance (Jolliffe, 1986). Consequently, the PCA on performance on the associative and reversal learning tasks should result in a single factor representing an individual's general learning performance. Additional components may be explained by additional factors influencing learning such as habit formation.

The output of interest in a PCA are the eigenvalues, communalities (h^2), and loadings for each component. Eigenvalues indicated how much variance in the data was explained by each component, with larger eigenvalues indicating that the component explains more of the variance. The standard is to extract components that have eigenvalues above 1 (Budaev, 2010). The communality of each variable is the proportion of variance due to common factors, or how much each component correlates with the

original variables (MacCallum, Widaman, Zhang, & Hong, 1999). How much a variable loads onto a principal component is a representation of how correlated the variable is to the new measure. When multiple variables all load onto a component highly, it is suggested that this component explains some underlying cause or mechanism in the tasks. For small sample sizes such as that in this study, the loading onto a component should be higher than 0.70 (Budaev, 2010). PCA analyses used the psych package in R (Revelle, 2019).

If a single component explained the variability on the associative learning and reversal learning tasks, a single score for each individual on that component could be extracted. This score represented a general learning score, capturing the commonality in performance across the learning tasks. This score was therefore used in all subsequent analyses as a measure of learning performance.

Relationship between behavioral and cognitive measures of success. Generalized linear models (GLM) were used to determine which variables of interest related to the general learning score from the PCA. Variables of interest included centrality in the social grooming network (grooming information centrality), centrality in the affiliation network (affiliation information centrality), dominance rank (Elo score), age, sex, and cognitive testing experience. The first model included all variables of interest. The best fit model for explaining the variation in learning score was determined by Akaike Information Criteria (AIC) using the MASS package in R (Ripley et al., 2019). AIC is an evaluation criterion for model selection that assigns a number to each model that can be compared to select the best approximating model, with lower AIC scores

attributed to models that are both a better fit and simpler (Symonds & Moussalli, 2011).

Variables were dropped from the model in a step-wise fashion until continuing to drop

variables resulted in an increase in AIC, indicating a worse model. The generalized linear

model then revealed if the remaining variables significantly predicted learning using the

stats package in R (R Core Development Team, 2008). If the analyses revealed that

monkeys who are more central to the social network perform better on the learning tasks,

it suggested a relationship between real-world social skills and cognitive abilities.

Results and Discussion

Behavioral Data

Social networks were created from affiliative (Figure 4a) and grooming behavior

(Figure 4b). Information centrality scores from the grooming and affiliation networks

were extracted on the first day of testing for each of the 16 subjects. Grooming and

affiliation information centrality scores were not correlated (Table1), and therefore

represented distinct measures of sociality, $r(14) = 0.45$, $p = 0.080$.
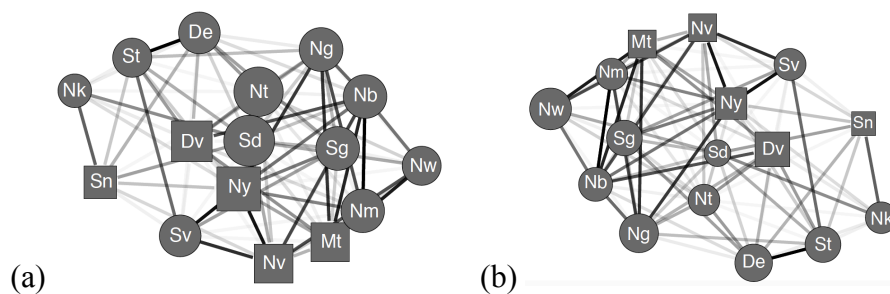

(a)   (b)

Figure 4. Social networks from behavioral observations. Visual representations of the (a)

affiliation and (b) grooming social networks extracted from the first day of testing

(8/17/18).

Table 1

Demographic, behavioral, and learning performance scores used for the regression analysis

Name	Age	Sex	1st Date of Testing	Elo Rating	Testing Experience	Grooming Information Centrality	Affiliation Information Centrality	Learning Score (3RC)
Nobel	9.75	Female	8/17/18	1459	Moderate	4.81	5.89	0.76
Stanley	3.7	Male	8/17/18	927	Low	3.82	4.93	-1.05
Deangela	17	Female	8/17/18	893	High	5.32	5.62	-0.07
Nemo	5.3	Female	10/7/18	1045	Moderate	5.20	6.10	-0.79
Savvy	5.5	Female	10/12/18	982	None	5.81	6.42	0.03
Sagan	10	Female	11/9/18	624	High	6.21	6.73	0.82
Schroeder	12	Female	11/13/18	329	High	4.95	7.21	-1.17
Newton	15	Female	11/30/18	1055	High	5.88	4.71	0.26
Niko	16	Female	12/7/18	292	High	4.88	3.95	-0.04
Stella	8	Female	11/14/18	467	High	5.65	5.36	1.20
Nye	8.25	Male	12/28/18	1227	High	5.44	5.90	-0.11
Nova	4.5	Male	1/19/19	329	High	6.50	5.68	-0.96
Davinci	23	Male	1/3/19	1218	Moderate	6.22	6.47	1.77
Natalie	23	Female	1/9/19	1466	Low	5.94	6.99	1.06
Monet	23	Male	1/19/19	1800	Moderate	5.35	6.18	-1.71
Nigel	6.25	Female	1/19/19	1125	High	6.50	6.49	NA

Note. The more negative the learning score the fewer errors the subject made on the cognitive tasks relative to other subjects' performance, and the more positive the learning score the more errors the subject made. A score of zero would indicate average performance within the group. NA indicates that Nigel did not have a learning score extracted.

Cognitive Data

The full set of cognitive testing will include five rounds of testing on the two

tasks by 16 subjects. Currently, 12 subjects have completed all five rounds of testing.

Fifteen subjects have completed at least three rounds of testing. Because data collection is

not complete, three separate analyses of cognitive performance across different numbers

of rounds of testing were conducted to determine which set of data should be used in the

generalized linear model: (1) all five rounds of testing (n = 12), (2) three rounds of testing

(n = 15), and (3) the first round of testing (n = 16).

Five rounds completed (5RC). For each subject (n = 12) that completed the

experiment (completing both of the cognitive tasks five times), performance on all rounds

of testing was within two standard deviations of their average performance across the five

rounds (Table 2). Because there were no outliers, average performance across the rounds

for each task was used in subsequent analyses. The two learning tasks loaded onto one

component (0.90) with an eigenvalue above 1 and high communalities (0.81). This

indicated that for each subject, their performance on the associative learning task and the

reversal learning task were best explained by a single underlying cognitive mechanism

representing general learning performance.

Three rounds completed (3RC). For the 15 subjects that completed each

cognitive task three times, performance on the three rounds of testing were within two

Table 2

Cognitive performance data

Name	Associative Learning			Reversal Learning		
	Round 1	Mean, SD (1-3)	Mean, SD (1-5)	Round 1	Mean, SD (1-3)	Mean, SD (1-5)
Nobel	16	20.67 ± 6.43	19.00 ± 6.40	29	43.33 ± 18.34	44.60 ± 13.09
Stanley	36	16.33 ± 17.62	13.20 ± 13.55	26	21.00 ± 15.13	27.40 ± 16.61
Deangela	30	28.67 ± 11.06	24.00 ± 10.20	21	22.00 ± 1.73	34.00 ± 16.72
Nemo	10	7.33 ± 4.62	6.40 ± 3.58	58	35.00 ± 19.92	29.00 ± 16.37
Savvy	29	17.67 ± 11.50	17.40 ± 8.62	55	35.67 ± 23.16	33.20 ± 17.02
Sagan	19	21.67 ± 9.29	19.40 ± 7.40	49	43.00 ± 25.53	47.80 ± 20.24
Schroeder	1	7.00 ± 6.00	8.60 ± 8.53	5	29.67 ± 23.18	27.20 ± 17.78
Newton	15	27.33 ± 21.36	19.00 ± 18.96	45	28.33 ± 22.30	32.20 ± 18.67
Niko	4	18.00 ± 14.52	15.80 ± 11.39	33	34.33 ± 24.03	37.20 ± 17.61
Stella	15	19.33 ± 19.86	19.00 ± 14.05	63	51.33 ± 19.35	47.40 ± 14.71
Nye	11	18.00 ± 6.24	16.60 ± 10.69	25	33.33 ± 7.23	30.00 ± 7.42
Nova	3	5.33 ± 2.08	5.20 ± 1.64	12	34.67 ± 19.73	27.60 ± 17.04
Davinci	46	30.33 ± 16.01	NA	1	47.67 ± 45.54	NA
Natalie	12	22.00 ± 8.72	NA	29	46.33 ± 30.89	NA
Monet	1	4.00 ± 5.20	NA	14	25.00 ± 20.81	NA
Nigel	12	NA	NA	45	NA	NA

Note. This shows total errors to criterion for the first round of testing and the mean and standard deviation for performance on the first three rounds and all five rounds of testing. NA indicates that subjects have not yet completed all of the rounds needed to calculate that score.

standard deviations of their average (Table 2). Because there were no outliers, average performance across the rounds for each task were used in subsequent analyses. The two learning tasks loaded onto a single component (0.80) with an eigenvalue above 1 and high communalities (0.64). As was the case for the data from the full five rounds of testing, this indicated that for each subject, their performance on the associative learning task and the reversal learning task were best explained by a single underlying cognitive mechanism.

One round completed (1RC). The principal component analysis showed that a two component solution best explained the variance in the data from the first round of testing for all 16 subjects. Eigenvalues for both components were around 1 (Table 3). This indicated that performance on the associative learning and reversal learning tasks were not related to one another, and that this performance was best explained by two separate sets of variance.

Comparison. For the 5RC and 3RC analyses, performance on the two tasks loaded onto a single principal component, suggesting that performance on these two tasks are underlied by the same cognitive mechanism. In contrast, the 1RC analysis revealed a two component solution, suggesting no relationship between performance on the associative and reversal learning tasks. This suggested that the more rounds of testing subjects completed, the better their performance scores on the two tasks were explained by a single learning score (Table 3). As the 5RC and 3RC analyses used average performance scores rather than individual values, they provided more reliable measures

Table 3

Component pattern and communality estimates from PCA

Analysis	Tasks	I	II	h^2
Rounds Completed = 5 (5RC) n = 12	Associative Learning	0.90	-0.44	**0.81**
	Reversal Learning	0.90	0.44	**0.81**
	Eigenvalues	**1.61**	0.39	
	% Variance	**81%**	19%	
Rounds Completed = 3 (3RC) n = 15	Associative Learning	0.80	0.60	**0.64**
	Reversal Learning	0.80	-0.60	**0.64**
	Eigenvalues	**1.28**	0.72	
	% Variance	**64%**	36%	
Rounds Completed = 1 (1RC) n = 16	Associative Learning	-0.72	0.69	**0.52**
	Reversal Learning	0.72	0.69	**0.52**
	Eigenvalues	**1.04**	**0.96**	
	% Variance	**52%**	**48%**	

Note. Bolded values indicate the factors that were interpreted.

of cognitive performance (Budaev, 2010). This suggested that repeated testing may

provide a better measure of an individual's overall learning skill than do individual

testing sessions.

Although average performance by 5RC subjects presented the best case for

extracting a single factor from the two tasks, 12 subjects was too small a sample size to

conduct the planned generalized linear model relating cognitive performance to

behavioral measures. While the 1RC analysis included all 16 subjects, PCA results

suggested that this single testing session resulted in high levels of variability that do not

capture general learning ability. In contrast, PCA on the 3RC showed eigenvalues,

communalities, and loadings comparable to those that completed all five rounds (Figure 5). Therefore, data from the 3RC subjects was used in the subsequent generalized linear model to determine if there was a relationship between learning performance and social factors. A single general learning score for each of these 15 subjects was extracted from the single component underlying associative and reversal learning performance revealed by the PCA (Table 1).
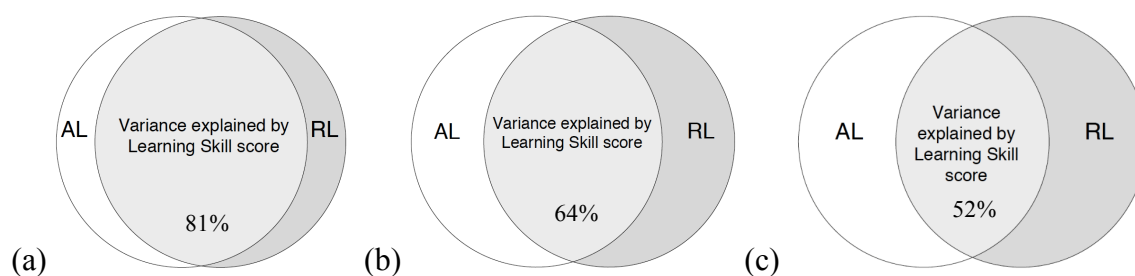

(a)   (b)   (c)

Figure 5. PCA Venn diagrams. Venn diagrams for the PCA analyses for subjects that completed five rounds (a), three rounds (b), and 1 round (c) of testing. Venn diagrams show the amount of overlapping variance in performance on the associative learning (AL) and reversal learning (RL) tasks that was explained by a single component.

Relationship Between Behavioral and Cognitive Measures of Success

The analysis on the relationship between behavioral and cognitive data was conducted on the data extracted from the 3RC analysis containing 15 subjects. The general learning score that was extracted for each subject from the PCA was used as the measure of learning performance for this analysis. These scores range from -1.71 to 1.77 (Table 1), with lower scores indicating faster learning and higher scores indicating slower learning. Regression analyses determined the relationship between this general learning score and social success (grooming information centrality and affiliation information

centrality) and demographic variables of interest (Elo score, sex, age, and cognitive testing experience; Figure 6). Model selection based on AIC revealed a best-fit model that included only grooming information centrality. However, the best-fit GLM between grooming information centrality and generalized learning scored did not reveal a significant relationship ($p = 0.076$). If anything, this preliminary analysis suggests a trend that the less central a subject is to the grooming network, the higher their learning score (Figure 6a).
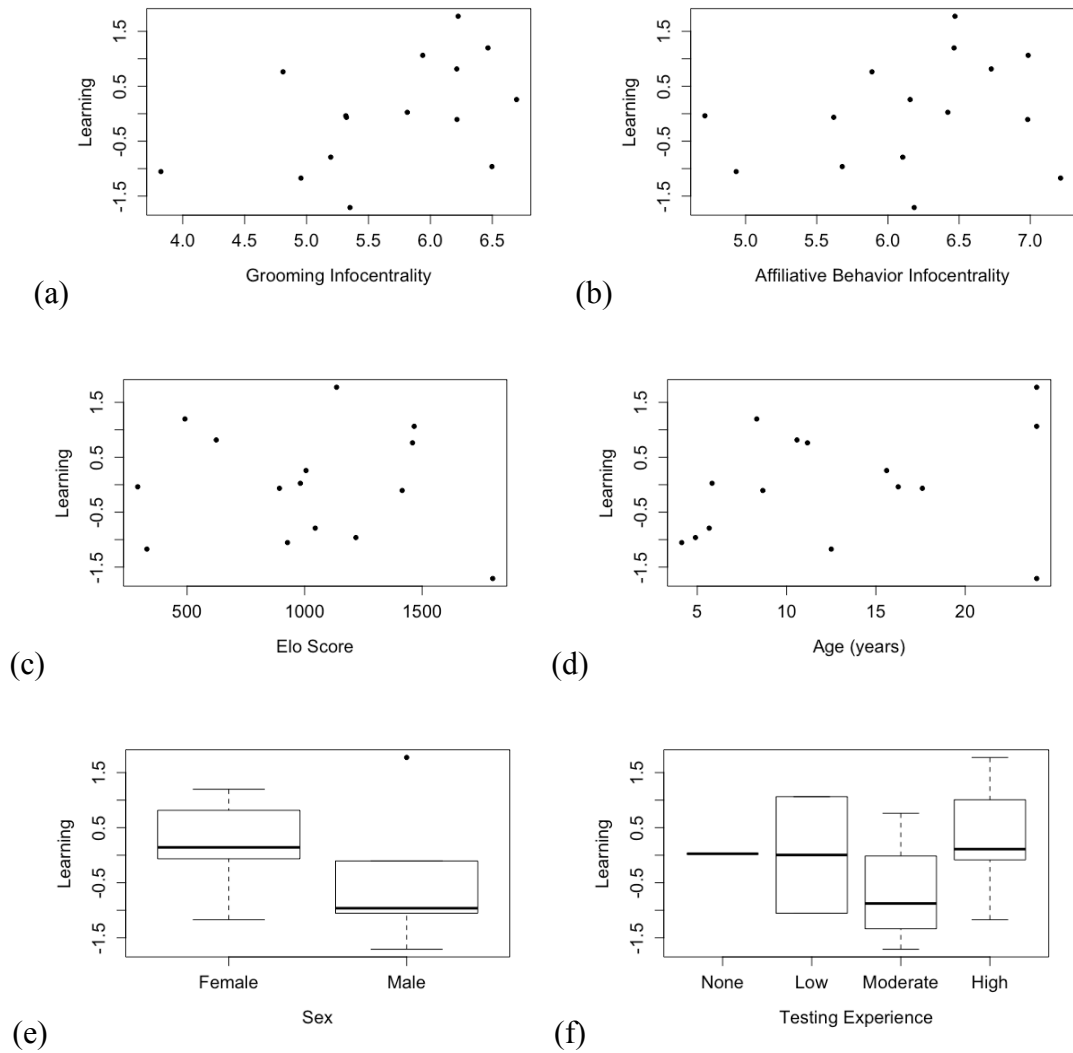
Figure 6. Learning score and predictor variables. This is for visualization purposes only. The full regression model was not bivariate. Learning plotted against predictor variables: grooming information centrality (a), affiliation information centrality (b), Elo score (c), age (d), sex (e), and cognitive testing experience (f). The more negative the learning score the fewer errors the subject made on the cognitive tasks relative to other subjects, and the more positive the learning score the more errors the subject made. A score of zero would indicate average performance relative to the group.

General Discussion

My results reveal the importance of repeated testing on characterizing individual

learning performance. PCA on performance on the associative and reversal learning tasks

showed different results based on how many times the subjects completed the two tasks.

The first round of testing showed high individual variability, and PCA revealed that the

variability on the associative learning task was not related to the variability on the

reversal learning task. In contrast, PCA on 3RC and 5RC revealed a single component

that explained variability across the two tasks, indicating a general learning ability.

Multiple rounds of testing may therefore be necessary to overcome natural variability in

performance and extract something like a measure of learning skill. Performance on any

single round of testing, but on the first round of testing specifically, may be confounded

by any number of variables including the novelty of the task, individual motivational

state at the time of testing, or distractions (Boogert et al., 2018; Cauchoix et al., 2018).

Repeated testing of a task over time (temporal repeatability) may therefore be essential to

providing a robust measure of individual ability.

Our preliminary data revealed no significant relationship between an individual's

learning performance and any of our predictor variables. We predicted that monkeys who

were more central to the social group would perform better on learning tasks, as theory

and previous research suggest a positive relationship between social complexity and

cognitive skill (Ashton et al., 2018; Bond et al., 2003; MacLean et al., 2008). However, if

anything, the relationship between centrality in the grooming network and learning

performance in the present study was trending towards less central individuals

performing more successfully on the two cognitive tasks. Although we can not draw strong conclusions based on these preliminary results, it was very clear that our original hypothesis, that monkeys that are more central to the social network of the group would also perform better on cognitive tasks, was not supported.

Previous research found a significant positive relationship between cognitive performance and indices of social complexity in Australian magpies, with individuals that live more complex social lives performing better on a battery of cognitive tasks (Ashton et al., 2018). In contrast, our findings suggested that there may not be a universal link between cognition and social behavior across species, or that our methods were not appropriate for answering this question. It was possible that in brown capuchins there was no social benefit in being a proficient learner. Alternatively, evolutionary pressures in this species may have favored other cognitive abilities not tested in the present study, such as memory or inference. A recent study in ring-tailed lemurs suggested that learning may be related to social network centrality when that learning occurs in a social context. Lemurs with high affiliative information centrality were more likely to learn how to solve a novel foraging task, and individuals that learned how to solve the task showed an increase in information centrality after the experiment (Kulahci, Ghazanfar, & Rubenstein, 2018). In contrast to the present study in which monkeys were tested independently and separated from the group, the lemurs were tested in a group setting with all group members having access to the foraging device at the same time. Network centrality may therefore be more relevant in social learning and information transmission rather than independent learning as measured in the current study.

The present study also did not find a significant relationship between dominance rank and learning performance. Previous literature in starlings (*Sturnus vulgaris*) suggests that rank had a positive relationship with learning, finding that high ranked individuals learned a novel foraging technique faster than low ranked group mates outside of the group (Boogert, Reader, & Laland, 2006). Another study on rhesus monkeys (*Macaca mulatta*) found that low ranked monkeys learned associations as well as their high ranked conspecifics and only exhibited this knowledge when tested alone (Drea & Wallen, 1999). Importantly, this highlighted that learning performance could be influenced by the presence of conspecifics, particularly for low ranking animals. The absence of a rank effect in the present study may be due to the social isolation used in testing, which allowed low ranked individuals to freely express their knowledge. Alternatively, there may be species differences in the effect of rank on learning, such that in brown capuchins rank may not be significantly related to learning performance.

Although our findings do not support prior findings that a strong relationship between cognitive performance and social behavior exists, our measure of social complexity was not extensively used in the field, and has rarely been studied for this question. Kulahci, Ghazanfar, and Rubenstein (2018) utilized social network analysis and found that information centrality positively related to learning a new skill; however, social network measures were separated based on whether the affiliative interactions were initiated or received by the subject. Our study differed by including instances where the subjects were the actor or the recipient of a behavior in the same network measure, providing a measure that focused less on individual activity, and more on each subject's

relationships in the group. Generalized linear models determined that none of our predictor variables significantly explained our composite learning score extracted from PCA. Perhaps for a socially housed group of capuchins, the selective advantage from learning information quickly or more accurately is weak and does not play an important role in their daily social lives. Another possible explanation for the discrepancy between our result and the few published studies that have found a significant positive relationship between cognition and sociality (Ashton et al., 2018; Bond et al., 2003; MacLean et al., 2008) may be that this field is particularly subject to publication bias, with the majority of non-significant findings being file drawered, making the relationship seem stronger than it actually is. Overall, our preliminary results suggest that the variation in cognitive performance found in associative and reversal learning were not explained by the social and demographic factors measured in this study and additional work is needed to elucidate the potential relationship between cognition and sociality.

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Appendix: Capuchin Behavioral Observation Ethogram

Behavior	Code	Definition	Duration Data?
		Behavioral Data	
		Behavior with Two Individuals	
		Dominance	
Bite	bit	An unrestrained clenching of the skin/limb of a recipient with teeth	
Chase	chs	Pursuit past the location the recipient maintained at the start of the interaction by running	
Rough behavior	rbr	Agnostic interactions involving grabbing, kicking, pushing, slapping, and pulling hair	
Scream	scrm	Loud high pitched vocalization occurring in a defensive or retreating context (>1 second)	
Threat	thr	Agnostic interactions involving lunging towards the recipient, typically with an open-mouth, laid-back ears, and raised-eyebrows	
Steal	stl	Taking or attempting to take food held by the recipient. May include food being held by the recipient or food in the recipient's mouth.	
Avoid	avd	Moving more than one step away from another animal at their approach to within one half meter	
Bare teeth display	brt	A facial expression characterized by open lips and teeth touching or slightly apart as well as high eyebrows, typically accompanies a retreat (if accompanied by scream or avoid, only write brt)	
Crouch	crh	A crouched posture with a facial expression characterized by lips apart along with vocalizations quieter than a scream. Only two of these three signs are needed for a crouch.	
		Affiliative	
Groom	grm	Separating hair with fingers and picking through fur or skin of another animal with the fingers or tongue, sometimes putting loose particles in mouth (3 second onset, 3 second offset)	YES
		Scan Data	
Contact	N/A	Any physical touching at the time of the scan	