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Instituto de Psicologia

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**MARCELO FERNÁNDEZ-BOLAÑOS**

**The individual and the social structure in  
*Sapajus xanthosternos***

**O indivíduo e a estrutura social de *Sapajus  
xanthosternos***

**São Paulo**

**2018**

MARCELO FERNÁNDEZ-BOLAÑOS

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**O indivíduo e a estrutura social de *Sapajus xanthosternos***

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Área de Concentração: Psicologia  
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Orientadora: Prof<sup>a</sup>. Dra. Patrícia Izar

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*A Lino, por darme esperanza en el futuro de la humanidad*

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São Paulo, December 3, 2018

## RESUMO GERAL

Fernández-Bolaños, M. (2018). *O indivíduo e a estrutura social de Sapajus xanthosternos*. Tese de doutorado. Instituto de Psicologia, Universidade de São Paulo, SP, Brasil.

A Análise de Redes Sociais (Social Network Analysis, SNA) é uma ferramenta que vem se demonstrando muito útil para o estudo da estrutura social dos primatas, apresentando métricas que permitem quantificar vários aspectos das sociedades. Para compreender o padrão de associações de um grupo devemos atentar às diferenças individuais que existem entre os sujeitos, que promovem ou evitam o estabelecimento de relações sociais. Dentre essas diferenças individuais, tradicionalmente se estudam o sexo, a idade e a dominância, mas, ultimamente, tem sido destacada a importância da personalidade dos indivíduos, uma variável que pode ter um papel fundamental na construção da estrutura social, mas cujo estudo ainda apresenta um desafio metodológico, sobretudo com animais de vida livre. Alguns estudos demonstram como alguns indivíduos chave podem ter uma relevância especial dentro da estrutura social do grupo. O objetivo do presente estudo é investigar a importância de características individuais, incluindo a personalidade, assim como o papel de indivíduos chave, sobre a estrutura social de um grupo de *Sapajus xanthosternos* na reserva ReBio Una no estado de Bahia.

**Palavras chave:** análise de redes sociais, indivíduos chave, macaco-prego, temperamento, personalidade, MuxViz, traços

## GENERAL ABSTRACT

Fernández-Bolaños, M. (2018). *The individual and the social structure in Sapajus xanthosternos*. PhD thesis, Institute of Psychology, University of São Paulo, SP, Brazil.

Social Network Analysis (SNA) is a tool that has proved very useful for the study of the social structure of primates, presenting metrics that allow quantification of various aspects of societies. In order to understand the pattern of associations of a group we must pay attention to the individual differences that exist between-subjects, that promote or avoid the establishment of social relations. Among these individual differences, sex, age and dominance have traditionally been studied, but recently the importance of individuals' personality has been highlighted, a variable that may play a fundamental role in the construction of social structure, but whose study still presents a methodological challenge, especially with free-living animals. Some studies show how some key (keystone) individuals may have special relevance within the social structure of the group. The objective of the present study is to investigate the importance of individual characteristics, including personality, as well as the role of keystone individuals, on the social structure of a *Sapajus xanthosternos*' group in Una Biological Reserve in the state of Bahia, Brazil.

**Keywords:** social network analysis, keystone individuals, capuchin monkeys, temperament, personality, MuxViz, traits

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## Presentation

This thesis is the result of a long way that began in the final years of my undergraduate studies in Psychology, with a growing interest in Comparative Psychology, Ethology, Animal Behavior, and, finally, in Primatology. After an internship in Madrid, at the end of my undergraduate studies, with captive capuchin monkeys, an increased curiosity about these amazing animals was born inside of me. From there, it's been a long road that took me surprisingly to Brazil.

This thesis is divided in five chapters, being three main chapters, and, also, a general introduction and a final conclusion. The main chapters are formatted as original research articles, being Chapter Two already submitted to *The Journal of Comparative Psychology*. The other two main chapters will be submitted to international journals after the important feedback obtained from the examination board.

In Chapter One, we quickly reviewed the literature and main topics of animal personality research, individual variables and social network analysis, in order to help the reader to get contact with the main concepts of this area of study, and for a better understanding of previously research. In Chapter Two, we evaluated the personality traits of a wild group of capuchin monkeys, comparing our results with the personality structure that other researchers obtained in captive *Sapajus* spp. In Chapter Three we consider other variables affecting the behavioral variability of these animals. Chapter Four, besides developing the social networks of a wild group of capuchin monkeys, it also includes a novel methodology, multiplex network analysis, that helps in the understanding of different networks as a whole. Finally, Chapter Five discusses the relevance of all our findings.

I believe we have found relevant results here, but this is only the beginning of a major field of research.

# CHAPTER ONE

## General introduction

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Marcelo Fernández Bolaños

## INTRODUCTION

### Social Network Analysis and Social Structure in Primates

In his seminal work, Robert Hinde (1976) established the basis for the study of non-human animals social structures, which he defined as an emergent property of the relationships that individuals establish when they interact repeatedly over time. Hence, social relationships are inferred from the kind, quality, and pattern of social interactions. Social network analysis (SNA, onwards) is a practical tool that allows us to quantify this paradigm. Eighteenth-century graph theory (Euler, 1741) is on the basis of this technique, however, in the last decades it has experienced a revolutionary development linked to the advancement of computer technology (Brent, Lehmann, & Ramos-Fernández, 2011).

In its simpler version, a social network is a set of elements (nodes) and connections (edges) between them (Wasserman & Faust, 1994). With SNA we can evaluate with quantitative measures as well as graphically represent the social structure of a group. The node metrics allow us to estimate, for example, how central a subject is on the structure (Krause, James, & Croft, 2010; Krause, Lusseau, & James, 2009). Other metrics can evaluate general characteristics of the social network, such as *modularity*, which estimates if the group is evenly connected, or subdivided into modules or communities, in which members are tightly connected between them, but weakly connected with the rest (Newman, 2006). In addition, with SNA we can assess how individuals are organized according to characteristics such as sex, age, dominance, and personality. A community-building mechanism is *homophilia*, the preferential association

between individuals that are similar in some characteristic (Lusseau & Newman, 2004).

In the social structure there are particular individuals with great importance within the social network, either because they have a large number of contacts or because they occupy a position that interconnects the others (Krause et al., 2010). These are called *key* (Krause et al., 2010) or *keystone* (Sih & Watters, 2005) individuals. Examples of these *key* individuals are “brokers”, who connect communities (e.g., *Tursiops* ssp.: Lusseau & Newman, 2004), or “policers”, whose withdrawal from the group causes an imbalance in the social structure, possibly because of their conflict-mediating function (*Macaca nemestrina*: Flack, Girvan, de Waal, & Krakauer, 2006). Studies are required to investigate the individual characteristics associated with *key* individuals, and the study of personality is a field as promising as little explored.

The social structure defined by Hinde (1976) refers to the emergence structure of several networks. However, most SNA studies of animal societies analyze separately every network, ignoring crucial interdependencies of behaviors (Silk, Finn, Porter, & Pinter-Wollman, 2018). The multiplex networks can revert this caveat, analyzing the holistic properties of several networks (congregated in different layers), but their use in the study of animal societies is still incipient (Finn, Silk, Porter, & Pinter-Wollman, 2018).

### **Individual Variables Affecting the Social Structure of Primates**

Individual characteristics or attributes (referred as “individual variables” onward) may be intrinsic or relative (to other individuals). In this study, we will

analyze three intrinsic characteristics: sex, age, and personality; and one relative feature: dominance.

### **Sex**

In many primate species, the dispersal pattern predicts how same-sex relationships are established, usually weak between individuals of the dispersal sex, and strong in the philopatric sex (with a greater degree of kinship) (Lehmann & Boesch, 2009). Female philopatry is common in Old World monkeys, especially in cercopithecoids (Di Fiore & Rendall, 1994), but in most genera of neotropical primates, both sexes disperse or there is male philopatry, with the exception of *Cebidae* (Fedigan & Jack, 2009). In accordance, strong relationships established between females and dominant males have been described for capuchin monkeys (*Sapajus nigritus*: Tokuda, 2012). For females capuchin monkeys, a strong bond with the dominant male may bring benefits in the defense against predators, infanticide males, and in the access to aggregated resources (Izar, Stone, Carnegie, & Nakai, 2009).

### **Age**

Primates associate with respect to age of individuals. In the very beginning of life, mother-infant are tightly associated until weaning, which is variable period across species (Ross, 2003). In general, parental investment is lower in males than in females, except for monogamous species (Wright, 1990). However, some studies suggest the importance of paternal care even in multimale-multifemale species (*Papio cynocephalus*: Buchan, Alberts, Silk, & Altmann, 2003).

The position that an individual occupies during juvenility within the social network can be determinant for its future. For instance, in birds of the *Pipridae* family (*Chiroxiphia linearis*) there is no relation between reproductive success in adulthood and their SNA metrics values, but juvenility metrics were related to reproductive success five years later (McDonald, 2007). Similarly, in complex societies such as those of primates, the relationships that young individuals establish could be decisive in later life. For example, male spider monkeys (*Ateles geoffroyi*) prefer maintaining relationships with females at the beginning of the juvenility, but later they prefer to associate with adult males, lasting these relationships the rest of their lives (Ramos-Fernández, Boyer, Aureli, & Vick, 2009). This study also reveals the importance of immature primates within the social structure, suggesting a connective role of youngsters between male and female communities.

### ***Dominance***

Dominance relationships also affect the social structure of primates (Izar, Ferreira, & Sato, 2006). The dominance hierarchy is commonly established from win-lose results in contests, however, the importance of the dominants may depend on their role within the social network (Sih, Hanser, & McHugh 2009). In general, the literature reveals that dominants have greater centrality within the group, participating in more interactions and with more individuals (Ramos-Fernández et al., 2009; Tiddi, Aureli, Polizzi, Di Sorrentino, Janson, & Schino, 2011).

In primates, the dominance rank can be mediated by particular individual variables, which could be morphological features, such as body size (French & Smith, 2005), but also behavioral features, related to some personality traits (*Cercopithecus aethiops sabaeus*, Socially competent: McGuire, Raleigh and Pollack, 1994; *Semnopithecus entellus*, Confidence and Dominance: Konečná et al., 2008; *Macaca sylvanus*, Confidence: Konečná, Weiss, Lhota, & Wallner, 2012). The role of personality in primate hierarchy is still little known, highlighting the need for deepening studies.

Another important question is whether dominants tend to associate between them or prefer to associate with subordinate individuals. If relationships with dominant individuals brings advantages, we can expect that dominant ones interrelate between them, keeping the subordinates apart, as in female capuchin-monkeys, whose preferential social partner is the dominant male (Izar et al., 2009).

### ***Personality***

Personality can be described as intra-individual consistency and between-individuals differences in behavior (Sih & Bell, 2008). There are two main ways for evaluating personality: trait rating, and behavioral coding. In trait rating, experienced observers interpret the behavior of the animals and provide assessments of personality traits, using questionnaires (Vazire, Gosling, Dickey, & Schapiro, 2007). This methodology is commonly adopted by Comparative Psychology, continuing with the profuse line of investigation of human personality questionnaires. Among these works we can highlight studies that adapted the

famous Big Five to non-human primates (Paul T. Jr. Costa & McCrae, 1992): Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (OCEAN). Within this line, the Hominoid Personality Questionnaire (HPQ: Weiss et al., 2009) has been applied on a wide range of species (*Pan troglodytes*: King & Figueredo, 1997; *Semnopithecus entellus*: Konečná et al., 2008; *Macaca sylvanus*: Konečná, Weiss, Lhota, & Wallner, 2012; *Sapajus apella*: Morton et al., 2013; *Macaca mulatta*: Weiss, Adams, Widdig, & Gerald, 2011; *Pongo pygmaeus* and *Pongo abelii*: Weiss, King, & Perkins, 2006).

In behavioral coding, the observers register the animal behavior under experimental or naturalistic conditions (Vazire et al., 2007). This method is mostly used in Behavioral Ecology, where five traits of animal personality with “evolutionary significance”, have been proposed : shyness/boldness, that refers to the reaction to situations of risk; exploration/avoidance, which considers the reaction to new situations; general level of activity; aggressiveness with conspecifics; and, sociability (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Studies should be developed exploring similitudes and differences between trait rating and behavioral coding, looking for an integrative methodology.

Finally, personality is influenced by individual variables such as age (Stamps & Groothuis, 2010), sex (*Homo sapiens*: McCrae & Terracciano, 2005; *Pan troglodytes*: Weiss, King, & Hopkins, 2007), or dominance rank (*Semnopithecus entellus*: Konečná et al., 2008; *Macaca sylvanus*: Konečná et al., 2012; *Cercopithecus aethiops sabaeus*: McGuire, Raleigh, & Pollack, 1994). A complete description of personality should address how these individual variables interplays in the expression of personality.

The social structure in which an individual is inserted must influence his personality but, in turn, personality also may influence the pattern and quantity of relationships that an individual maintains (Krause et al., 2010). In humans, the relationship between personality and SNA metrics has been proven: algorithms used over Facebook predicted personality traits more accurately than human judgments (Youyou, Kosinski, & Stillwell, 2015). In non-human primates, there is some evidence of *homophilic* relationships based on personality traits (*Pan troglodytes*: Massen & Koski, 2014; *Sapajus* spp.: Morton, Weiss, Buchanan-Smith, & Lee, 2015). These findings motivate analyzing the role of personality in patterns of association in primate groups, the relation with other individual features (e.g. sex or dominance), and investigating the personality profile of *keystone* individuals.

### **Prior study with *Sapajus xanthosternos***

In the present study we are continuing the previous work developed by Dr. Priscila Suscke since 2003 in her MSc (Priscila Suscke, 2009) and PhD (Priscila Suscke, 2014) with the same wild group of *Sapajus xanthosternos*. Suscke analyzed the social structure with SNA over three social networks: proximity, grooming and agonistic behaviors (Priscila Suscke, 2014), using the latter for assessing the dominance rank of every individual. We can highlight two motivating results relevant for our research. First, Suscke found homophilic and heterophilic patterns in different networks according to sex: agonistic interactions were more common between males, grooming was more common between females and spatial proximity was more frequent between male-female dyads. Secondly, Suscke found sexual differences in males and females' dominance.

Alpha males participated in many interactions, receiving a lot of grooming, and occupying central positions in the spatial proximity network. There was a smaller influence of female dominance on SNA metrics, since the most dominant female did not have much relevance neither in the spatial proximity network, nor in grooming network. These results indicate the use of the multiplex approach, assessing the effect of these homophilic and heterophilic patterns, and the role of dominant individuals in the entire social structure.

## **OBJETIVES AND JUSTIFICATION**

Our first objective was analyzing the personality of individuals from a wild group of *S. xanthosternos*, using trait rating and behavioral coding, comparing results obtained with both methods, promoting an integrative approach to the study of personality (Chapter Two). The personality structure of *S. xanthosternos* was compared with other species of *Sapajus* and *Cebus* looking for the core elements of capuchin monkeys' personality. Personality studies with new world monkeys are infrequent, and studies conducted with wild populations are also scarce (Freeman & Gosling, 2010), in fact, this is the first study describing the personality of a wild group of the genus *Sapajus*. In addition, this is the first personality description of *S. xanthosternos*, a critically endangered species (Kierulff, Mendes, & Rylands, 2015; IUCN), and knowledge of personality is fundamental to effective conservation planning (Powell & Gartner, 2011, Malange, Izar, & Japyassú, 2016).

Our second objective was evaluating the impact of sex, age, and dominance over personality, completing a comprehensive description of *S. xanthosternos* personality (Chapter Three). Results were compared to findings with human and non-human primates looking for patterns commonly shared. We also emphasize the implications of controlling for these variables in personality studies. Finally, we analyzed whether dominant individuals were characterized by particular personality traits.

Our third, and last, objective was describing the social structure of *S. xanthosternos*, with special emphasis to analyzing the effect of individual variables (sex, age, dominance, and personality) and keystone individuals. We used a multiplex network approach, which allows analyzing the whole network, closer to the original concept of “social structure” as defined by Hinde (1976). This approach is rare in primatology; as far as we know, only two studies have been conducted with primates (Barrett, Peter Henzi, & Lusseau, 2012; Smith-Aguilar, Aureli, Busia, Schaffner, & Ramos-Fernández, 2018). Results were compared with findings on other capuchin monkeys, with special attention to Suscke’s (2014) prior work. By analyzing the differences of network of the same group in different moments, we could understand how the social structure of *S. xanthosternos* changes across time. The study of sociality through SNA may improve the wild life conservation (T. Wey, Blumstein, Shen, & Jordán, 2008), in that way the present work could contribute valuable information for management of this species.

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## CHAPTER TWO

# **Evaluating the Personality of Wild Capuchin Monkeys (*Sapajus xanthosternos*) using Trait Rating and Behavioral Coding**

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Patricia Izar

(Original article submitted to *The Journal of Comparative Psychology*)

## **Evaluating the Personality of Wild Capuchin Monkeys (*Sapajus xanthosternos*) using Trait Rating and Behavioral Coding**

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**Short running title:** Evaluating the Personality of Wild *Sapajus*

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## **ABSTRACT**

Non-human primates' personality is a growing area of knowledge, building strong bridges between human and animal research. Studying personality in wild populations of non-human primates enables a better understanding of the ecological significance of personality traits. Here, we analyzed the personality of wild capuchin monkeys (*Sapajus xanthosternos*) using two widespread methods: trait rating and behavioral coding. Trait rating was developed in two ways, obtaining a principal component analysis (PCA) structure with *S. xanthosternos* ratings on the Hominoid Personality Questionnaire (HPQ), and using a PCA structure developed previously with captive *Sapajus* spp. by Morton et al. (2013) with HPQ. By comparing these structures, we determined three personality traits: Openness-Neuroticism, Assertiveness, and Attentiveness-Sociability, which are herein described. Sixteen typical behaviors were coded and subject to a PCA,

also resulting in three components. Comparison of trait rating and behavioral coding components revealed that they were relatively analogous. The best description of personality arose, however, using trait rating components and observing the correlation between these traits and the 16 behaviors. The three observed personality traits of *S. xanthosternos* are significant when interpreted in the light of environmental pressures and the social structure in wild conditions. Our results are consistent with those of Morton et al. (2013), and we conclude that their personality structure could be used for evaluating free living populations of the genus *Sapajus*. Finally, by comparing our results with those of other studies on capuchin personality we propose the traits: Openness, Neuroticism, Assertiveness, and Sociability as the core elements of *Sapajus* personality.

*Keywords:* animal temperament, primates, free ranging, traits, New World monkeys

## **INTRODUCTION**

Personality can be defined as those characteristics of individuals that account for consistent patterns of feeling, thinking and behaving (Pervin & John, 1999). The study of animal personality has the potential to build strong bridges between human and animal research (Gosling, 2001). Non-human primates, due to their recent common ancestry with humans, can play a central role in this construction. Indeed, the study of non-human primate personality has increased exponentially in the last decades, but few studies have specifically investigated new world monkeys (Freeman & Gosling, 2010). Among the new world monkeys, capuchin monkeys are of special interest as they are phylogenetically separated

by 43.5 MYA from humans and chimpanzees (Perelman et al., 2011), and yet converge in terms of several traits, including high levels of encephalization (Stephan et al., 1986, 1988), the use of tools (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004), and social complexity (Izar et al., 2012). Capuchin monkeys are classified in two genera, *Cebus* and *Sapajus*. The personality of wild *Cebus* is described by Manson and Perry (*C. capucinus*: 2013), but there are no previous studies specifically observing wild *Sapajus*. This is an important caveat to be aware of, since the study of wild populations is especially relevant for understanding how ecology shapes personality, but most research has been carried out under captive conditions (Freeman & Gosling, 2010).

From a methodological perspective, two main approaches can be distinguished for evaluating animal personality: behavioral coding, in which observers register the behavior under experimental or natural conditions; and trait rating, in which observers interpret the behavior of the animal and provide ratings on personality traits (Vazire et al., 2007). Behavioral coding has mostly been used by behavioral ecologists, regarding fitness consequences related to differences in personality. From this perspective, Réale, Reader, Sol, McDougall, & Dingemanse, (2007) defined five personality traits that are relevant for adaptation across a wide range of animal species: shyness-boldness, which refers to the reaction to situations of risk; exploration, referring to the reaction to novel situations; aggressiveness to conspecifics; sociability; and general level of activity. There is one detailed previous study using behavioral coding to study the personality of captive capuchin monkeys (Uher, 2013). This study was also carried out under captive conditions; therefore, while aiming for an ecologically

relevant description of personality, this study might not reflect the natural ecological context of capuchin monkeys.

Trait rating is based on the application of personality questionnaires originally developed for human research (Buirski, Kellerman, Plutchik, Weininger, & Buirski, 1973; Stevenson-Hinde & Zunz, 1978), and some methodological differences between human and primate questionnaires should be underpinned. First, human personality questionnaires are validated across many different populations (e.g., McCrae & Terracciano, 2005), but this is not the case for non-human primates. Second, the most commonly used non-human primate questionnaires were originally constructed with a sample of captive individuals (Capitani, 1999; King & Figueredo, 1997; Stevenson-Hinde & Zunz, 1978); whereas most popular human questionnaires were developed with people in their natural settings (NEO-PI-R, Costa & McCrae, 1992b; EPQ-R: Eysenck & Eysenck, 1994). Third, human studies are based on the inferential statistics *modus operandi*, in which some parameters are calculated from a large representative sample (assumed to be similar to the entire population), and these parameters allow evaluating one or a small number of individuals, that do not necessarily pertain to the original sample (Figure 1a). In non-human primate personality studies, however, the parameters are usually obtained from a small sample of individuals, and then the same individuals are evaluated with these parameters (Figure 1b). Using the last method, we can obtain an adequate description of the sample, but it is risky to extrapolate conclusions to the population (i.e. the studied species). One exception is the research of captive

capuchin monkey (*Sapajus* spp.<sup>1</sup>) personality conducted by Morton et al. (2013). The authors evaluated 127 captive individuals using the Hominoid Personality Questionnaire (HPQ: Weiss et al., 2009) and described five traits: Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness. We consider that this personality structure for *Sapajus* should be validated for wild individuals if we are interested in understanding the relationship between personality and ecology.

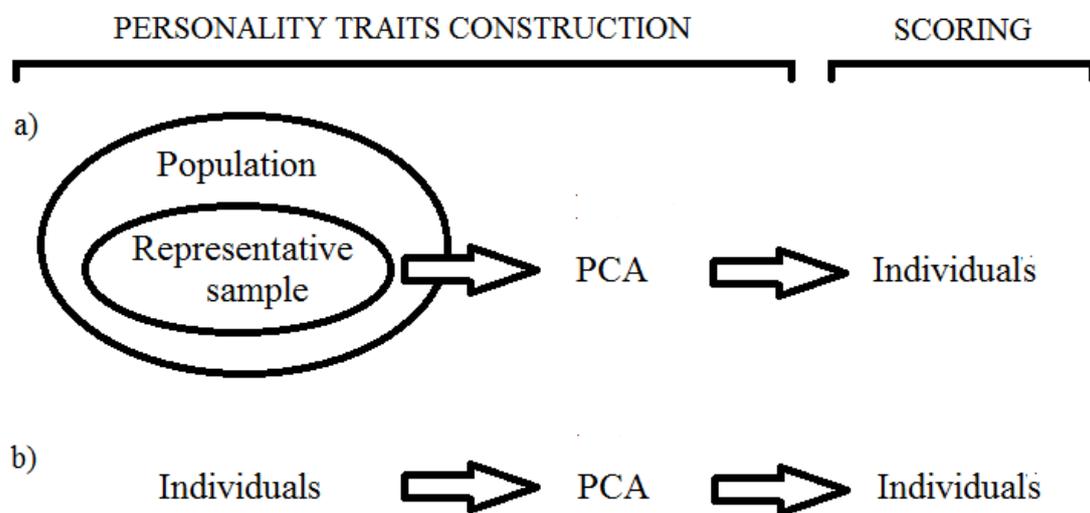


Figure 1. Scheme of questionnaire method based on inferential statistic (a) and method often used in primate personality studies (b).

<sup>1</sup> In the original text they used *Sapajus apella*, this term is used for captive individuals even from unknown origin or captive born hybrids. In this text we will use *Sapajus spp.* to refer to individuals from Morton et al. (2013).

Our aims in this study were twofold. First we aimed at evaluating the personality of wild individuals of *Sapajus xanthosternos* using trait rating assessed with the HPQ questionnaire (Weiss et al., 2009). To do this, we scored our studied individuals according to two structures of personality and then interpreted the findings of both structures. First, inspired by inferential statistics (Figure 1a), we used the structure for captive *Sapajus* spp. from Morton et al. (2013). Second, following a principal components analysis (PCA) to determine the personality structure of *S. xanthosternos*, we scored our studied individuals using this structure (as in Figure 1b). Other studies have used the personality structure of phylogenetically distant species to score their studied subjects (*Macaca sylvanus* vs *Macaca mulatta* and *Semnopithecus entellus*: Konečná, Weiss, Lhota, & Wallner, 2012; *Sapajus* spp. VS *Pan troglodytes*, *Pongo* spp., and *Macaca mulatta*: Morton et al., 2013). In the present study, we used phylogenetically close species, aiming to validate this method and encourage its application in future studies of different species of *Sapajus* in natural settings. Due to the phylogenetic proximity, we expected to find similar general trends in the personality structures of wild *S. xanthosternos* (XS) and of captive *Sapajus* spp. (SS). The differences between wild and captive living, however, may influence the expression of personality, so we also expected to find some fine-grained differences between XS and SS.

Our second objective was to evaluate the personality of wild *S. xanthosternos* using behavioral coding, and developing a PCA with 16 behaviors registered in their natural daily activities in order to compare the resulting structure with that of the trait rating analysis. We expected to find similar

structures from both methods, indicating the core elements of the personality of *S. xanthosternos*. The present study is the first to describe the personality of a wild group of the genus *Sapajus*, and, more particularly, the first personality description of *S. xanthosternos*. This is of special importance, as *S. xanthosternos* is a critically endangered species (Kierulff, Mendes, & Rylands, 2015; IUCN), and knowledge of personality is fundamental to effective conservation planning (Powell & Gartner, 2011, Malange, Izar, & Japyassú, 2016).

## **METHOD**

### **Study Site and Subjects**

This study was conducted at Una Biological Reserve, Bahia State, Brazil, a fully protected conservation area of ca. 18500 ha. The region is covered with lowland Atlantic Forest (Amorim et al., 2008), in a mosaic of mature forest, secondary forest, and patches of agriculture fields called “cabruca”, i.e., an agroforest where cocoa trees (*Theobroma cacao*) and jack fruit occupy the understory forest (Raboy, Christman, & Dietz, 2004).

The group of *S. xanthosternos* called Principe has been studied since 2005 when members were habituated and fitted with radio telemetry collars to monitor their behavior (Kierulff, Canale, & Suscke, 2005). Suscke (2009, 2014) conducted further studies on this group, and showed that the group has uniquely high levels of predator pressure (Suscke et al., 2017), and a tight female-bonded (Wrangham, 1980) with relaxed dominance hierarchy. In the present study, we

analyzed data from April 2015 to March 2016 in three weeks out of every month (121 days in total). During this period two researchers (ID & MFB) and one field assistant (RSO) accompanied the group from dawn to dusk, collecting behavioral data relevant for various research projects using focal sampling videos of juveniles; 5 minutes scans sampling every 20 minutes, and recording all occurrence events (Altmann, 1974).

During the study period, the group comprised  $26 \pm 2$  individuals, but present data were focused on the 26 (eight adult females, four adult males, five subadult males, two female juveniles, three male juveniles, and four infants born at the beginning of 2015, one female and three males). All 26 individuals were present during the entire period, with the exception of one subadult that emigrated in September 2015.

## **Ratings**

We used the HPQ of Weiss et al. (2009), which has previously been used with captive *Sapajus* spp. (Morton et al., 2013). The questionnaire was translated into Portuguese by ID and MFB. The HPQ contains 54 descriptive adjectives with a 1 to 7 Likert scale in which 1 indicates a display of either total absence or negligible amounts of the trait and 7 indicates a display of extremely high levels

of the trait<sup>2</sup>. The questionnaire was answered at the end of the study period by three raters (RSO, ID, and MFB), all of them with almost one year of experience with the studied group of primates and trained to recognize each individual. Five individuals (four infants and one subadult) were not evaluated by one rater (MFB), as he considered that he did not having enough knowledge to make accurate judgments, but the rest of individuals were completely evaluated by all three raters (i.e. without missing values).

### **Interrater Reliabilities of Items**

We calculated two intraclass correlations (ICC, Shrout & Fleiss, 1979) which determined the reliability of the questionnaire items between raters. The first, ICC(3,1), indicates the reliability of single raters, the second, ICC(3,k), indicates the reliability of the mean between raters. We calculated ICC for each item, and also, the general questionnaire ICC (with all items together). We recalculated the general questionnaire ICC removing one rater at a time, to asses if reliability improved without one of the raters. Reliabilities were calculated in the R statistical package, version 3.4.0 (R Development Core Team, 2017) using the ICC function of the package *psych* (Revelle, 2011).

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<sup>2</sup>English original version available in [http://extras.springer.com/2011/978-1-4614-0175-9/weiss\\_monkey\\_personality.pdf](http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf)

## Data Reduction

In order to select the number of components of XS we conducted a scree plot and a parallel analysis (Horn, 1965) using the *paran* R function (Dinno, 2008). We used the modification suggested by Glorfeld (1995) i.e., retaining components of the 95th percentile. We then calculated the mean between raters for every item and every individual and conducted a PCA using the principal function of R package *psych* (Revelle, 2011), with Varimax and Promax rotation.

To compare components, we calculated the congruence coefficient of the targeted orthogonal Procrustes rotation (Guadagnoli & Velicer, 1988) using the R function *Procrustes* of R package *smacof* (Leeuw & Mair, 2009). Internal consistencies of the components were calculated using the Cronbach's alpha with the R function *cronbach*, package *multilevel* (Bliese, 2016a,b)

## Comparison with Captive *Sapajus* spp. and Interpretation of Components

To compare the results between XS (this study) and SS (Morton et al., 2013), we transformed the components of XS and SS to unit-weighted scores (Gorsuch, 1974), changing loadings higher than or equal to  $|0.4|$  into 1 or  $-1$  depending on the direction, following the process described by Weiss et al. (2009). We then scored our studied individuals using the unit-weighted components of both structures and evaluated similarity between these components with a Pearson correlation, employing the R function *rcorr*, in the package *Hmisc* (Harrell, 2018). We also compared the component loadings of both PCA structures, as well as the components scored by our 26 individuals,

using targeted orthogonal Procrustes rotation. We interpreted our components by comparing XS and SS and evaluated if SS was validated for studying free living populations of *Sapajus* species.

## **Behavioral Coding**

During the study period MFB collected behavioral data at 5 minutes scans sampling every 20 minutes, and all occurrences events (Altmann, 1974). We analyzed 16 behaviors for evaluating the personality of *S. xanthosternos*. We selected these behaviors based on four of the five traits described by Réale et al. (2007) (shyness-boldness, aggressiveness to conspecifics, sociability, and general level of activity). We assigned *a priori* one of these traits for every behavior (Table 1). The absolute amount of behaviors was transformed into daily rates, or monthly rates, depending of the frequency of the behavior (see Table 1, indicated with asterisks). The rates were adjusted to the time each individual was observed, calculated by the number of scans that the individual was registered in the period (day or month). We calculated the rank order of these rates and standardized from 0 (minimum) to 1 (maximum). Finally, for each individual we estimated the total mean across periods. For the most frequent behaviors we first estimated the monthly mean of daily standardized rank orders, and then the mean of monthly means. For the infrequent behaviors we directly calculated the mean of monthly standardized rank orders. With these transformations, we converted the unequal absolute amount of different behaviors into a similar comparable scale, controlled by inter-individual differences in observation time. The influence of punctual variations in observed behaviors that could be due to seasonal

variation or stochastic causes, rather than true personality differences, was also reduced by these transformations.

With the standardized rank ordered behaviors we conducted a PCA as we did for the HPQ items, selecting the number of components with a scree plot and a parallel analysis (Horn, 1965). Then, with the obtained behavioral coding structure (BS), we transformed loadings into unit weights and scored the individuals with them.

Table 1.

*Behaviors Coded for Evaluating the Personality of Wild S. xanthosternos.*

Behavior	Definition	Method
Vigilance (SB)	Staying alert, watching environment, looking for danger	Scans*
Researcher react (SB)	Threaten a researcher	AO**
Height<5 (SB)	Scan at a canopy height lesser than 5 m.	Scans*
Height>20 (SB)	Scan at a canopy height higher than 20 m.	Scans*
Height difference (SB)	At every scan, absolute difference between individual and mean group height	Scans*
Aggression emission (AG)	Emitting a threat, chasing or beating to a conspecific	Scans+AO*
Aggression receiving (AG)	Receiving a threat, chasing or beating from a conspecific	Scans+AO*
Aggression participation (AG)	Emitting or receiving a threat, chasing or beating to a conspecific	Scans+AO*
Grooming emission (SC)	Picking through or manipulate the fur of another monkey with hands and/or mouth (Rose, 2000)	Scans+AO*
Grooming receiving (SC)	Receiving grooming	Scans+AO*
Grooming participation (SC)	Emitting or receiving grooming	Scans+AO*
Grooming reciprocity (SC)	Emitting grooming just before receiving grooming from a conspecific, or vice versa	AO**
Play (SC)	Engaging in sequences of spontaneous, apparently non-goal-oriented behaviors (Rose, 2000)	Scans+AO*
Scans accompanied (SC)	Total scans minus scans with nobody observed at 15 m.	Scans*
Activity (AC)	High expenditure activities (moving+ foraging +playing)	Scans
Inactivity (AC)	Resting, sleeping, or doing nothing physically active	Scans

*Note.* Abbreviations indicate the Réale et al. (2007) trait assigned for each behavior: (SB) shyness-boldness; (AG) aggressiveness; (SC) sociability; and, (AC) general level of activity. All occurrence method (AO). \*Indicates that the monthly mean of daily rank orders were calculated; \*\*indicates that monthly rank orders were calculated directly.

## **Comparison between HPQ Trait Rating (XS) and Behavioral Coding (BS)**

We ran a Pearson correlation between the individual scores for XS and BS to compare the results of both methods. We also ran a Pearson correlation between the XS component scores and the 16 standardized rank order behaviors to investigate the source of similarities and differences between both methods. We considered  $p \leq 0.05$  significantly correlated, and  $p \leq 0.005$  strongly significantly correlated.

## **RESULTS**

### **Interrater Reliabilities of Items**

The general questionnaire reliabilities (with all items together) between raters were ICC(3,1) 0.52 and ICC(3,K) 0.77. We then recalculated the index removing one rater at a time: without RSO it was ICC(3,1) 0.46 and ICC(3,K) 0.63, without ID it was ICC(3,1) 0.40 and ICC(3,K) 0.57, and without MFB it was ICC(3,1) 0.64 and ICC(3,K) 0.78. As the effect of removing MFB increased ICC(3,1) substantially, and as MFB did not evaluate five individuals, we decided to continue without using his ratings. Other studies have used two raters to assess the personality of primates (e.g., Konečná et al., 2012).

Interrater reliabilities of items are shown in Table 2, the mean of ICC(3,1) was 0.37 (SD = 0.25) and for ICC(3,k) it was 0.49 (SD = 0.31). We excluded items with an ICC less than 0 (following Konečná et al., 2012), these were: distractible, quitting, disorganized, intelligent, and erratic. Following the removal of these

items, interrater reliabilities were ICC(3,1) mean 0.42 (SD = 0.20) and ICC(3,k) mean 0.56 (SD = 0.22).

Table 2.

*Interrater Reliability of HPQ Items. Estimates Based on 26 S. xanthosternos, each Assessed by Two Raters.*

	ICC(3,1)	ICC(3,k)
Playful	0.83	0.91
Dominant	0.81	0.89
Aggressive	0.78	0.88
Stingy/Greedy	0.75	0.86
Submissive	0.73	0.85
Thoughtless	0.66	0.83
Dependent/Follower	0.66	0.80
Solitary	0.64	0.78
Timid	0.61	0.76
Lazy	0.61	0.76
Protective	0.58	0.73
Decisive	0.57	0.72
Depressed	0.55	0.71
Fearful	0.54	0.70
Sociable	0.53	0.69
Imitative	0.53	0.69
Sympathetic	0.52	0.69
Individualistic	0.49	0.65
Cool	0.48	0.65
Inquisitive	0.47	0.64
Vulnerable	0.46	0.63
Stable	0.45	0.62
Active	0.45	0.62
Autistic	0.44	0.61
Cautious	0.43	0.60
Manipulative	0.43	0.60
Independent	0.41	0.59
Gentle	0.40	0.57
Defiant	0.40	0.58
Excitable	0.38	0.55
Jealous	0.37	0.54
Helpful	0.35	0.52
Innovative	0.33	0.49
Curious	0.32	0.48

<b>Unemotional</b>	0.31	0.47
<b>Unperceptive</b>	0.30	0.46
<b>Anxious</b>	0.27	0.43
<b>Sensitive</b>	0.25	0.40
<b>Bullying</b>	0.24	0.39
<b>Affectionate</b>	0.22	0.36
<b>Reckless</b>	0.21	0.35
<b>Friendly</b>	0.19	0.31
<b>Clumsy</b>	0.16	0.28
<b>Inventive</b>	0.15	0.26
<b>Irritable</b>	0.14	0.24
<b>Persistent</b>	0.13	0.23
<b>Impulsive</b>	0.11	0.20
<b>Conventional</b>	0.04	0.07
<b>Predictable</b>	-0.01	0.01
<b>Distractible</b>	-0.02	-0.04
<b>Quitting</b>	-0.08	-0.18
<b>Disorganized</b>	-0.10	-0.21
<b>Intelligent</b>	-0.15	-0.35
<b>Erratic</b>	-0.18	-0.44

*Note.* ICC(3,1) reliability of individual ratings; ICC(3,k) reliability of mean ratings

## Data Reduction

The results of both Horn's parallel analysis and the scree plot (Figure S1) suggested that three components should be retained, with adjusted eigenvalues (8.8, 7.18, and 1.71) all of them larger than 1. We conducted a PCA with the three components using the mean between the two selected raters, which explained 60% of cumulative variance. We additionally explored two other possibilities, 1) removing the third component, and 2) adding a fourth component.

1) For the first possibility, we examined the third component (with the lowest eigenvalue). It had six items with loadings equal to or larger than |0.6|, which was larger than the minimum of four items recommended by Guadagnoli and Velicer

(1988). After this, we developed another PCA with two components, and the explained cumulative variance was reduced to 50%. These results suggested maintaining the third component.

2) For the second possibility, we conducted another PCA with four components, which explained 68% of cumulative variance. Therefore, to test if this gain in explained variance justified maintaining the fourth component, we ran the following analyses.

We calculated the interfactor correlation derived from the Promax rotation PCA. With the three-component solution, all correlations were low, indicating a great orthogonality between components. Conversely, with the four-component solution there was a correlation between the first and the fourth component (Table S1).

Finally, we evaluated the stability of components using a procedure described by Konečná et al. (2012), in which we compared the PCA structure using the mean between raters, with the PCA structure using all of the individual evaluations of the two raters. If components of both PCAs were replicated (that is, similar components arising with high congruence between them), it would indicate that the structure was stable. The comparison was made using targeted orthogonal Procrustes rotation. We performed this analysis with both the three- and four-component solutions, observing which better replicated the components. This allowed us to decide how many components should be retained. To interpret the results, we used the MacCallum's criteria (MacCallum, Widaman, Zhang, & Hong, 1999) for judging congruence between components (0.98-1.00 = excellent; 0.92–0.98 = good; 0.82-0.92 = borderline; 0.68-0.82 =

poor; and below 0.68 = terrible). Note that this is a strict criteria compared with others (e.g., 0.85-0.94 meaning fair similarity, Lorenzo-Seva & ten Berge, 2006; 0.80 or higher meaning identical congruence, Horn, Wanberg, & Appel, 1973), but MacCallum et al.'s criteria has the advantage of being more accurate than a simple borderline number.

The results suggested using the three-component solution (Table 3). First, in the three-component solution it was straightforward to establish how components were paired (1-2, 2-3, and 3-1, Table 3), because, for every component, one congruence coefficient stood out above the others. In contrast, for the four-component solution it was not clear how components were paired, as some components showed a similar congruence coefficient with more than one component. Second, in the three-component solution the paired components had large congruence coefficients  $\geq 0.82$  (meaning "good", according to MacCallum), and one "excellent" congruence (0.99). Conversely, the four-component solution showed inferior congruence coefficients, lower than 0.82, with the exception of the one found between 2 and 3 (0.97) (see Table 3). In light of these results we decided to use the three-component solution, which showed stable components that replicated properly.

Table 3.

*Congruence Coefficients After Targeted Orthogonal Procrustes Rotation Between HPQ PCA Components Constructed with the Mean Between Raters and then with all Ratings.*

	<b>RC1</b>	<b>RC2</b>	<b>RC3</b>		<b>RC1</b>	<b>RC2</b>	<b>RC3</b>	<b>RC4</b>
RC1	0.79*	0.85**	0.62	RC1	0.78*	0.74*	0.59	0.73*
RC2	0.65	0.63	0.99****	RC2	0.68*	0.61	0.97***	0.60

RC3	0.82**	0.69*	0.62	RC3	0.78*	0.75*	0.62	0.65
				RC4	0.62	0.77*	0.60	0.80*

Note. To the left is the three-component solution and to the right the four-component solution. Asterisks indicate the strength of congruence coefficients following MacCallum et al. (1999): \*poor, \*\*borderline, \*\*\*good, \*\*\*\*excellent.

Once we had concluded that the three-component solution was the best fit for XS, we verified that the Varimax and Promax rotation results were identical, with a congruence of 0.99 after orthogonal Procrustes rotation, so we use Varimax results in the next analysis (loadings can be observed in Table 4). We calculated the reliability of components and also the internal consistencies (Cronbach's alpha), all being equal or close to 0.8 (Table 5).

Table 4.

*Varimax-Rotated Components Loadings of XS.*

Adjective	RC1	RC2	RC3
Curious	0.86	0	0.13
Cool	-0.83	-0.03	0.22
Stable	-0.79	-0.09	0.25
Playful	0.79	-0.14	-0.29
Predictable	-0.76	0.15	0.02
Impulsive	0.75	0.13	0.04
Reckless	0.75	-0.13	-0.3
Inquisitive	0.71	-0.23	0.25
Imitative	0.69	-0.54	-0.17
Solitary	-0.67	-0.36	-0.5
Sensitive	-0.66	0.37	0.4
Cautious	-0.66	0.41	0.21
Thoughtless	0.65	-0.48	-0.12
Depressed	-0.63	-0.39	-0.39
Unemotional	-0.63	0.17	-0.32

<b>Inventive</b>	0.63	-0.01	0.03
<b>Jealous</b>	0.62	0.28	-0.04
<b>Conventional</b>	-0.59	-0.12	0.15
<b>Excitable</b>	0.57	0.03	0.13
<b>Stingy/Greedy</b>	0.57	0.47	-0.1
<b>Individualistic</b>	-0.52	0.33	-0.4
<b>Active</b>	0.47	0.3	0.03
<b>Innovative</b>	0.44	0	-0.08
<b>Clumsy</b>	0.39	-0.27	-0.1
<b>Lazy</b>	-0.39	-0.13	0.02
<b>Dominant</b>	-0.01	0.9	0.02
<b>Vulnerable</b>	0.03	-0.88	-0.2
<b>Aggressive</b>	0.11	0.88	-0.23
<b>Submissive</b>	-0.08	-0.87	-0.12
<b>Persistent</b>	-0.1	0.82	0.14
<b>Fearful</b>	-0.03	-0.81	-0.14
<b>Dependent/Follower</b>	0.17	-0.81	-0.32
<b>Decisive</b>	-0.5	0.76	0.13
<b>Defiant</b>	-0.13	0.71	-0.31
<b>Manipulative</b>	0.41	0.68	0.12
<b>Independent</b>	-0.56	0.61	0.07
<b>Timid</b>	-0.53	-0.59	-0.32
<b>Bullying</b>	0.49	0.59	-0.43
<b>Gentle</b>	-0.1	-0.55	0.44
<b>Protective</b>	-0.42	0.54	0.51
<b>Anxious</b>	-0.24	-0.43	-0.43
<b>Sympathetic</b>	-0.2	0.45	0.74
<b>Sociable</b>	0.24	0.36	0.71
<b>Friendly</b>	0.27	-0.33	0.7
<b>Helpful</b>	-0.28	0.46	0.64
<b>Affectionate</b>	-0.13	0.06	0.64
<b>Unperceptive</b>	0.2	0.02	-0.62
<b>Irritable</b>	0.34	0.42	-0.45
<b>Autistic**</b>	0.24	-0.03	-0.18
<b>Quitting*</b>			
<b>Disorganized*</b>			

Distractible*			
Erratic*			
Intelligent*			

Note. Loadings larger than or equal to  $|0.39|$  were highlighted in bold face. \* indicates removal due to  $ICC < 0$ ; \*\* indicates that the item was not used for scoring individuals due to a maximal loading was  $< |0.39|$ .

Table 5.

*Reliability and Internal Consistencies of XS*

Comp	ICC(3,1)	ICC(3,k)	alpha
RC1	0.66	0.80	0.80
RC2	0.63	0.77	0.80
RC3	0.65	0.78	0.78

### Comparison between XS and SS and Interpretation of Components

While transforming the components of personality into unit weights, one item (autism) was discarded as its maximum load was  $|0.24|$ , after that, our final questionnaire included 48 items. We maintained two items (clumsy and lazy) with maximum loadings  $|0.39|$ , close to the  $|0.4|$  threshold. One item (anxious) was maintained in two components since it loaded exactly the same in both.

In the XS the rotated components RC1, RC2, and RC3 were not correlated, indicating great orthogonality. In contrast, in the SS the components, Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness showed many significant correlations between them (Table 6).

Table 6.

*Pearson Correlation Between Scores of S. xanthosternos Individuals Using SS and XS.*

Asst	1							
Open	0.34	1						
Neura	-0.02	0.73**	1					
Socb	0.41*	0.33	0.17	1				
Attna	0.17	-0.46*	-0.49*	0.47*	1			
RC1	0.20	0.92**	0.90**	0.41*	-0.46*	1		
RC2	0.94**	0.10	-0.32	0.36	0.40*	-0.11	1	
RC3	0.20	-0.19	-0.33	0.75**	0.79**	-0.16	0.33	1
	Asst	Open	Neura	Socb	Attna	RC1	RC2	RC3

Note. SS components are Assertiveness (Asst), Openness (Open), Neuroticism (Neura), Sociability (Socb), and Attentiveness (Attna). XS components are RC1, RC2, and RC3. \* indicates  $p \leq 0.05$ , and \*\* indicates  $p \leq 0.005$ .

RC1 was strongly correlated with Openness and with Neuroticism (Table 6), suggesting that these personality traits should be combined, so we named RC1 as Openness-Neuroticism. This trait was also slightly correlated with Sociability and Attentiveness (the last in the opposite direction) (Table 6). Exploring in detail particular adjectives (Table 7), we found that, similar to SS Openness, RC1 loaded positively on items describing exploratory behaviors (e.g., inquisitive and curious), items accounting for creativity and originality (e.g., inventive and innovative), and items related to high-energy expenditure (e.g., active and playful). Conversely, RC1 did not load on items reflecting a tendency to persevere, such as persisting. RC1 also presented many parallels with SS Neuroticism, with items describing impulsive and volatile disposition (e.g.,

excitable and impulsive), and negatively loaded with components describing a calmer disposition (e.g., cool, stable, predictable, and unemotional).

The second component (RC2) was strongly correlated with Assertiveness (Table 6), and so was labeled as such. To a lesser extent, this component was correlated with Attentiveness (Table 6). Analogous to SS Assertiveness, it loaded on items related to aggressive tendencies (e.g., aggressive, dominant, or negatively with vulnerable), and also loaded negatively with items related to anxiety (e.g., fearful) (Table 7).

The third component (RC3) was strongly correlated with Sociability and with Attentiveness (Table 6), and so was defined as Attentiveness-Sociability. As with SS Sociability, RC3 also loaded on items indicative of overall social embeddedness and positive social interactions (e.g., sociable, friendly, and affectionate), and also loaded negatively on items describing negative affect (e.g., anxious) (Table 7). Despite the correlation with SS Attentiveness, RC3 only had two items in common with SS Attentiveness, helpful and unperceptive, and helpful was also clearly linked with Sociability.

Table 7.

*Comparison Between Unit-Weighted Components of XS and SS.*

Adjective	XS	SS		XS	SS	XS	SS	
	RC1	Open	Neura	RC2	Asst	RC3	Attna	Socb
Curious	1	1						
Cool	-1		-1					
Stable	-1		-1					
Playful	1	1						
Predictable	-1		-1					

Impulsive	1		1		
Reckless	1			1	
Inquisitive	1	1			
Imitative	1	1			
Solitary	-1				-1
Sensitive	-1				
Cautious	-1			-1	
Thoughtless	1				-1
Depressed	-1				-1
Unemotional	-1		-1		
Inventive	1	1			
Jealous	1			1	
Conventional	-1	-1			
Excitable	1		1		
Stingy/Greedy	1			1	
Individualistic	-1				
Active	1	1			
Innovative	1	1			
Clumsy	1				-1
Lazy	-1	-1			
Dominant				1	1
Vulnerable				-1	-1
Aggressive				1	1
Submissive				-1	-1
Persistent		1		1	
Fearful				-1	-1
Dependent/Follower				-1	-1
Decisive			-1	1	
Defiant		1		1	

Manipulative		1	1		
Independent		1	1		
Timid		-1	-1		
Bullying		1	1		
Gentle		-1	-1		
Protective		1			
Anxious		-1		-1	-1
Sympathetic	-1			1	
Sociable				1	1
Friendly				1	1
Helpful				1	1
Affectionate				1	1
Unperceptive				-1	-1
Irritable			1	-1	
Autistic**					-1
Quitting*	-1				
Disorganized*				-1	
Distractible*				-1	
Erratic*				-1	
Intelligent*					

Note. SS unit weighed components were obtained from Table 6 of Morton et al. (2013). Dark grey indicates positive unit weights and light grey indicates negative unit weights. \* indicates removal due to ICC < 0. \*\* indicates that the item was not used for scoring individuals due to a maximal loading < |0.39|.

In our final analysis, we compared XS and SS using targeted orthogonal Procrustes rotation in two ways. First, by directly comparing the PCA structures, and second by comparing the structures scored by our 26 individuals. Both comparisons reassembled the results obtained using a Pearson correlation (Table S2).

Finally, using the program Primer 6 (Clarke & Gorly, 2006), we created a PCA graphic with the 26 individual scorings in SS configured in three dimensions (Figure 2). As we expected, the graphic described clearly the XS results, with the trivial difference that the number of the first and second components appeared interchanged in the output (clarified in parentheses) (Figure 2). In the graphic, we can see how Openness and Neuroticism were aligned practically parallel to the RC1 axis; Assertiveness was alone parallel to the RC2 axis, and Sociability and Attentiveness were quite aligned to the RC3 axis.

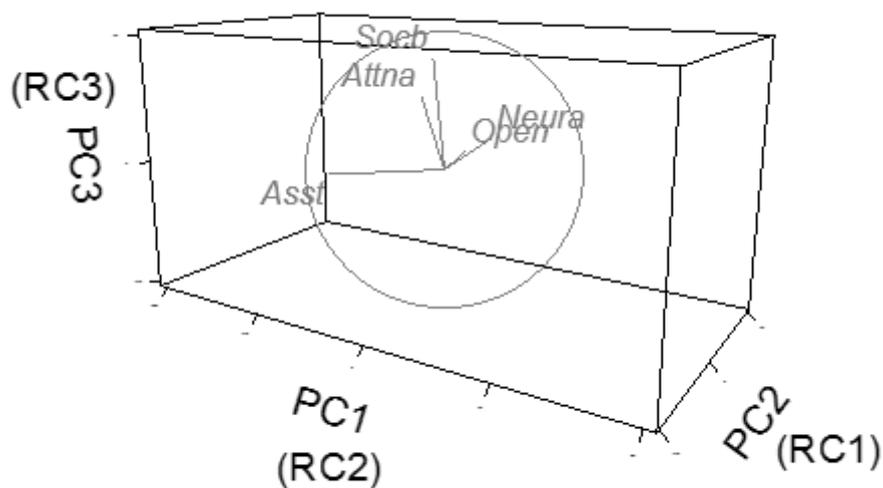


Figure 2. Three-dimensional representation of SS components scored by *S. xanthosternos*. The XS component is indicated in parentheses.

## Behavioral Coding

Before performing a PCA with the 16 standardized rank order behaviors we conducted a Horn's parallel analysis and scree plot (Figure S2). The results of this analysis suggested that we retain three components with adjusted eigenvalues 2.8, 2.7, and 1.14, all of them higher than 1, although the latter was very close to this limit.

We then performed a PCA with the three components, which explained 71% of cumulative variance. When performed with two components this value fell to 57%, so we decided to maintain the third component. Interfactor correlations derived from Promax rotation were low, indicating a great orthogonality between the components (Table S3). Varimax and Promax rotation results were identical, with a congruence of 1 after orthogonal Procrustes rotation, so, we used the Varimax results in the next analysis (loadings are shown in Table 8). Finally, we constructed the behavioral coding structure (BS) by transforming the loading into unit weights. No item was discarded as all behaviors had a maximum load higher than  $|0.4|$  (Table 8).

Table 8.

*Varimax-Rotated Components Loadings and Unit Weights of the Behavioral Coding Structure (BS).*

	RC1BS	RC2BS	RC3BS	RC1BS	RC2BS	RC3BS
Vigilance (SB)	0.01	<b>0.84</b>	0.27		1	
Researcher react (SB)	-0.17	0.04	<b>0.81</b>			1
Height <5 (SB)	<b>-0.65</b>	<b>0.51</b>	0.24	-1		
Height >20 (SB)	<b>0.66</b>	0.19	-0.27	1		

Height difference (SB)	0.11	<b>0.78</b>	<b>-0.49</b>		1		
Aggression emission (AG)	<b>0.43</b>	<b>0.72</b>	0.23		1		
Aggression receiving (AG)	-0.4	<b>0.61</b>	-0.37		1		
Aggression particip. (AG)	0.01	<b>0.9</b>	-0.11		1		
Grooming emission (SC)	<b>0.85</b>	0.17	0.19	1			
Grooming receiving (SC)	<b>0.66</b>	-0.4	-0.11	1			
Grooming particip. (SC)	<b>0.94</b>	-0.06	0.15	1			
Grooming recipro. (SC)	<b>0.83</b>	0.11	0.1	1			
Play (SC)	<b>-0.81</b>	-0.29	0.23	-1			
Scans accompanied (SC)	0.05	<b>-0.65</b>	<b>0.53</b>		-1		
Activity (AC)	-0.1	-0.02	<b>-0.82</b>			-1	
Inactivity (AC)	0.36	<b>0.49</b>	0.07			1	

Note. Bold font indicates a loading  $\geq |0.40|$ ; dark grey indicates a positive unit weight; light grey indicates a negative unit weight.

The first component (RC1BS) reflected a prosocial tendency, as it grouped all of the grooming behaviors, however, “play” had a negative weight in this component. This component also indicated a tendency to stay in the higher part of the canopy, with a positive weight in “height higher than 20 m”, and a negative weight in “height lower than 5 m”.

The second component (RC2BS) showed an aggressive tendency, grouping all aggressive behaviors. It also grouped “vigilance”, “height difference”, and, negatively, “scans accompanied”, these behaviors could be associated with an active predatory defense; remaining alert to possible dangers and staying in the more vulnerable canopy strata far from the group security. Finally, “inactivity” also loaded positively in this component.

The third (RC3BS) component only grouped two behaviors: “negative reaction to researchers”, which could be interpreted as curiosity as well as fear and lack of calmer disposition; and “activity”, loaded negatively.

### **Comparison between HPQ Trait Rating (XS) and Behavioral Coding (BS)**

The component RC1BS shared characteristics with the three XS traits. First, the largest correlation of RC1BS was with Attentiveness-sociability ( $r = 0.67^{**}$ , Figure 3c), being all grooming behaviors correlated positively with both components, and also “play”, but negatively (Table 9, 4<sup>th</sup> and 5<sup>th</sup> columns). Second, RC1BS also correlated positively with Assertiveness ( $r = 0.58^{**}$ , Figure 3b), being correlated in both components with the behaviors: “height higher than 20 m”, all grooming behaviors (with the exception of “grooming receiving”), and, negatively, “play” (Table 9, 3<sup>rd</sup>, and 6<sup>th</sup> columns). These results suggested a prosocial facet of Assertiveness throughout grooming behaviors. Finally, RC1BS correlated negatively with Openness-Neuroticism ( $r = -0.55^{**}$ , Figure 3a). The behaviors: “height lower than 5 m.” and “play” correlated positively, and “height higher than 20 m.” correlated negatively with Openness-Neuroticism. All these behaviors were also correlated with RC1BS but in opposite directions than in Openness-Neuroticism (Table 9, 2<sup>nd</sup>, and 5<sup>th</sup> columns). These results indicated that individuals scoring high in Openness-Neuroticism tended to occupy a lower part of the canopy and were involved in playing, contrary to the individuals that scored high in RC1BS.

The component RC2BS only correlated significantly with Assertiveness ( $r = 0.59^{**}$ , Figure 3e); and “vigilance”, “height difference”, “inactivity” and all aggressive behaviors (with the exception of “aggression receiving”) correlated positively with both components (Table 9, 3<sup>rd</sup> and 6<sup>th</sup> columns). These results suggested an aggressive and anti-predator tendency for the individuals characterized under Assertiveness, similar to those in RC2BS.

Finally, RC3BS only correlated significantly with Openness-Neuroticism ( $r = 0.54^{**}$ , Figure 3g). Some behaviors correlated with both components, namely, “negative reaction to researchers” and “scans accompanied” positively, and “height difference” and “activity” negatively (Table 9 2<sup>nd</sup> and 7<sup>th</sup> columns), indicating high levels of fear as well as a tendency to be highly active, common in both components. On the other hand, some behaviors correlated with Openness-Neuroticism but not with RC3BS, namely, “height lower than 5 m” positively and “height higher than 20 m.” negatively (reflecting a tendency to use the lowest canopy strata), and also, “play” was positively correlated.

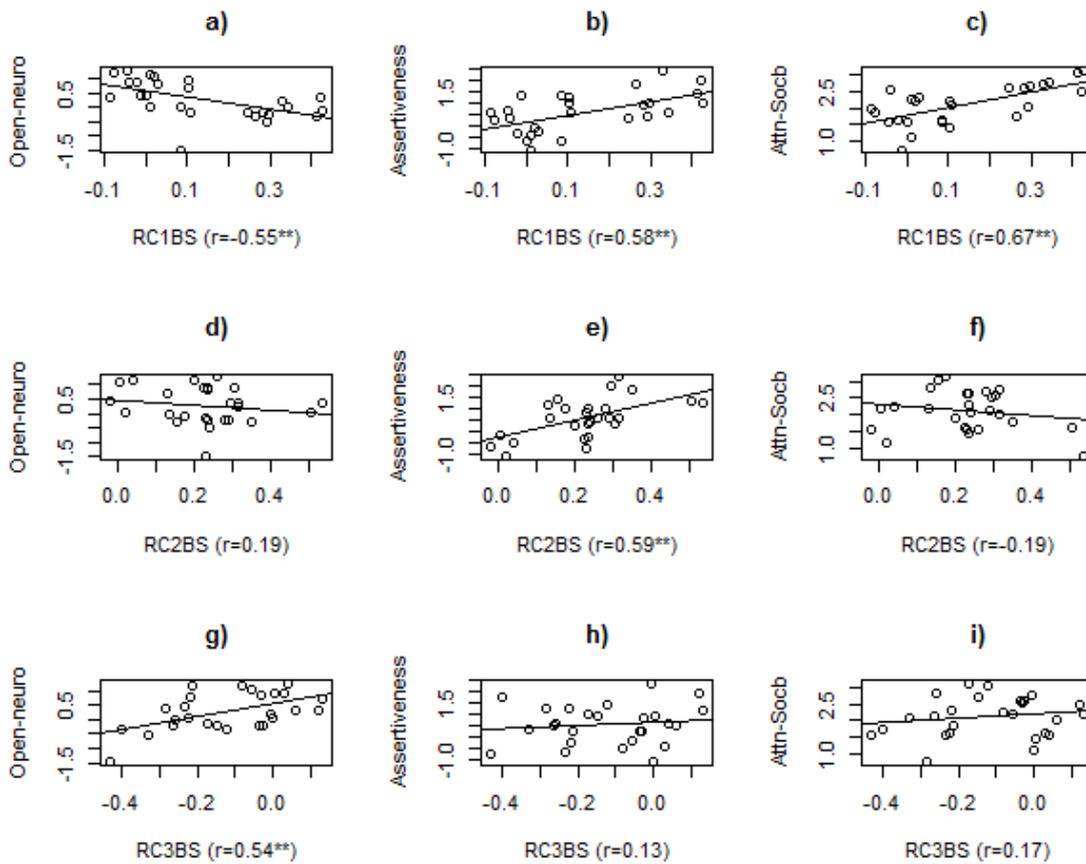


Figure 3. Relationships between the three XS traits and the three BS components. \*\* indicates  $p \leq 0.005$  with Pearson correlation.

Table 9.

Pearson Correlation Between the 16 Behaviors and the Three XS Traits and Three BS Components.

Behaviors	Open-neura.	Asst.	Attn-Socb	RC1BS	RC2BS	RC3BS
Vigilance (SB)	0.11	0.64**	-0.06	0	0.76**	0.21
Researcher react (SB)	0.41*	0.01	0.06	-0.19	-0.14	0.86**
Height<5 (SB)	0.54**	0.02	-0.3	-0.66**	0.41*	0.25
Height>20 (SB)	-0.55**	0.5**	0.33	0.62**	0.26	-0.28

Height difference (SB)	-0.42*	0.48*	-0.03	0.15	0.86**	-0.39*
Aggression emission (AG)	-0.1	0.71**	0.13	0.38	0.68**	0.16
Aggression receiving (AG)	0.08	0.09	-0.45*	-0.34	0.69**	-0.29
Aggression particip (AG)	-0.02	0.55**	-0.2	0.02	0.93**	-0.08
Grooming emission (SC)	-0.38	0.69**	0.66**	0.87**	0.14	0.14
Grooming receiving (SC)	-0.14	0.18	0.54**	0.65**	-0.29	-0.16
Grooming particip (SC)	-0.33	0.6**	0.73**	0.94**	-0.05	0.09
Grooming recipro (SC)	-0.37	0.61**	0.61**	0.83**	0.1	0.05
Play (SC)	0.7**	-0.52**	-0.45*	-0.83**	-0.34	0.2
Scans accompanied (SC)	0.44*	-0.27	0.18	0.02	-0.73**	0.45*
Activity (AC)	-0.5**	-0.21	-0.24	-0.05	0.18	-0.84**
Inactivity (AC)	-0.35	0.46*	-0.21	0.3	0.44*	0.12

Note. \* indicates  $p \leq 0.05$ ; \*\* indicates  $p \leq 0.005$ . Dark grey indicates a positive significant correlation; light grey indicates a negative significant correlation.

## DISCUSSION

Our first objective was to evaluate the personality of the individuals of a wild group of *S. xanthosternos* using trait rating. We used the HPQ (Weiss et al., 2009), and with the obtained ratings conducted a PCA with satisfactory performance in terms of: adequate ICC measures, good internal consistency of components and stability, and components showing little orthogonality. We scored our individuals with the PCA structure (XS), and also with the structure developed by Morton et al. (2013) with 127 captive *Sapajus* spp. (SS). By comparing the results of both structures, we could describe three components: 1) Openness-Neuroticism, which could be briefly defined as tendencies to explore, be creative, and engage in energetic behaviors, but with impulsiveness,

volatility, and lacking a calmer disposition; 2) Assertiveness, defined as having aggressive tendencies and a lack of anxiety or fear; and 3) Attentiveness-Sociability, defined as having prosocial tendencies.

As part of our first objective, we validated SS for evaluating the personality of wild individuals of the genus *Sapajus*. We conclude that SS was sufficiently comprehensive to explain the personality of a wild population of one species of *Sapajus*. Only three personality traits were observed in XS, in contrast to the five traits observed in SS, however we found high levels of congruence between the three XS and the five SS traits. Assertiveness was similar in both structures. Openness-Neuroticism appeared to be combined as one component in XS, but this merged component loaded in almost the same items as Openness and Neuroticism loaded in SS. Attentiveness-sociability showed correspondence with items loaded in SS's Sociability. Finally, Attentiveness-Sociability was strongly correlated with SS's Attentiveness, however, looking at the items commonly shared between these traits, we can conclude that the contribution of Attentiveness in Attentiveness-Sociability was negligible. This result does not necessarily mean that Attentiveness is not present in our study group or in other *Sapajus* species, rather, it could be an effect of the differences between captive and free-living individuals. When observing primate behavior in their natural habitat, Attentiveness seems to not be a meaningful characteristic, since individuals are usually either involved in a goal-oriented task (moving, foraging, grooming, etc.) or they are inactive (resting or sleeping). Conversely, features such "keep focus" or "be attentive" are easier to discriminate in captivity, where there are less stimuli and goal-oriented tasks, and also, the close-up observation

allows raters to appreciate these subtler attributes. Based on the results of our study, we suggest that further evaluations of other *Sapajus* species follow our methods, in particular developing a PCA and comparing the results with SS.

Our second objective was to evaluate the personality of *S. xanthosternos* using behavioral coding and to compare the results with those obtained from trait rating. Studies that have used these two methods for evaluating personality have always used behavioral coding to validate trait rating (Vazire et al., 2007). In the present study, however, we developed each approach independently and compared the results without submitting one to the other. In general, results from trait rating and behavioral coding were relatively analogous and complementary. Trait rating, however, allowed the observation of some aspects of personality that would be unnoticeable with behavioral coding alone. In fact, our comprehension of *S. xanthosternos* personality based on trait rating was enriched when observing the relationship between trait rating components and particular behaviors. Conversely, behavioral coding components were less clear and sometimes meaningless if not interpreted based on the correlated trait rating components

As with trait rating (XS), we also obtained three components employing behavioral coding (BS), which we considered relatively analogous as these components could be *grosso modo* paired as follows: Openness-Neuroticism with RC3BS, Attentiveness-sociability with RC1BS, and Assertiveness with RC2BS (Figure S3).

RC3BS did not consistently define any personality trait, as it only grouped two disconnected behaviors: “negative reaction to researchers” and, negatively,

“activity” (Figure S3). Conversely, Openness-Neuroticism was a well-defined trait and observing the behaviors with which it correlated, enhanced our definitions. Openness-Neuroticism reflects better the Neuroticism facet than the Openness one, as it correlated with behaviors related to a fear response. This includes the negative reaction to researchers, the tendency to be spatially close to other group members and in similar height strata, but also, avoiding the higher part of the canopy, a position more vulnerable to aerial predators, an important predation risk for this population (Suscke et al., 2016) (Figure S3). Openness was only represented by playing, a “volatile and energetic behavior”, which was positively correlated with Openness-Neuroticism, but this facet is imperceptible in RC3BS, as this behavior did not correlate with it (Figure S3).

RC1BS grouped all grooming behaviors, play (loaded negatively), and behaviors indicating the use of lower strata. Again, together these behaviors do not allow a comprehensive definition of a personality trait. Whereas, Attentiveness-Sociability (trait rating components correlated to RC1BS) was a consistent trait describing the pro-social aspects of *S. xanthosternos* personality. In addition, by considering the particular behaviors with which it correlated, it is apparent that grooming interactions are the backbone of this trait, but not “play”, nor “scans accompanied”.

RC2BS was the behavioral coding component that allowed the most coherent description of a personality trait, grouping the aggressive behaviors and behaviors indicating a fearless anti-predatory defense. This description was similar to Assertiveness but, considering the particular correlated behaviors, we could include a prosocial tendency throughout the grooming behaviors, a facet

that is not present in RC2BS. This suggests that the most social individuals participate in both affiliative and agonistic behaviors. Manson and Perry, (2013) found similar results related to the *C. capucinus*' Extraversion trait: "individuals high on this dimension are attractive as social interaction partners in addition to being formidable competitors" (Manson & Perry, 2013, p. 306). This was interpreted by the authors to be important for formation and maintenance of alliances and in status competitions.

In view of our results, we highly advise the use of trait rating combined with behavioral coding in studies of primate personality, but especially when analyzing free-living individuals. On the one hand, through the observation of the daily life of a wild group it is difficult to achieve a significant number of events indicative of some personality traits for each individual (e.g., Neuroticism, Extroversion, or Shyness). These aspects of personality are more likely to be captured by the rater's impressions during a trait rating assessment. On the other hand, some questionnaire items refer to abstract concepts which are difficult to define (e.g. thoughtless orsympathetic) which have controversial ecological validity. Including observations of daily behaviors increases the ecological validity of a study. In this regard, the behavioral ecology traits developed to explain the adaptive functions of personality (Réale et al., 2007), did not fit with our *S. xantosternos* personality description (Figure S3). By comparing our results with the traits described by Réale et al. (2007), Sociability was similar with the first component and Aggressiveness with the second, but the similarities of Shyness-boldness and General level of activity with any component were less clear. This should prevent us from taking an *ad hoc* posture in the study of personality, one trait can be

highly adaptive *a priori* (e.g., general level of activity) but this does not necessarily ensure its existence. The same is true for the behaviors selected for evaluating one trait, e.g., we expected that “scans accompanied” would be indicative of pro-sociality, but the results suggest that it is more important for group security.

Our study generally supported the five traits described by Morton et al. (2013), even if two of them, Openness and Neuroticism, appeared to be combined into one component and the presence of Attentiveness was uncertain. Five traits were also found in another study that investigated the closely related species *Cebus capucinus* in free ranging conditions (Manson & Perry 2013). That study did not use the same questionnaire as Morton et al. (2013), and yet, four of the five traits described were very similar: Neuroticism, Openness, Agreeableness (close to Sociability), and Extroversion (close to Assertiveness). Given the striking parallels between Morton and collaborators (2013), Manson and Perry (2013), and our results, we conclude that these four traits, Neuroticism, Openness, Sociability, and Assertiveness, are the core elements of a capuchin monkey’s personality. We recognize, however, that there is still much research needed to categorically determine the core personality traits common to all capuchin monkey species. In human personality studies it took many years and many discussions (e.g., Eysenck, 1992; Costa & McCrae, 1992a) to arrive at a common paradigm, so we should be cautious with our conclusions. Our results, however, are further supported by the work of Uher et al. (Uher, Addessi, & Visalberghi, 2013). The authors used a contrastingly different methodological paradigm and described “20 non-lexical emic personality constructs” for captive *Sapajus* that could relate to these four personality traits. Constructs such as creativenessinventiveness or curiousness fit into Openness; arousability,

impulsiveness, or anxiousness fit into Neuroticism; aggressiveness, competitiveness, or dominance into Assertiveness; and, social orientation to conspecifics or gregariousness, fit into Sociability.

Finally, our results suggest that comprehensive studies of primate (or animal) personality should include the use of trait rating alongside behavioral coding for personality assessment, and, if possible, a comparison against a personality structure determined from a large reference sample. We also suggest HPQ (Weiss et al., 2009) as the trait rating method to allow for broad interspecific comparisons.

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## Supplementary Material- Chapter Two

Table S1.

*Correlations Between XS Promax-Rotated Components, with 3 components (a) and 4 components (b).*

a)	RC1	RC2	RC3	b)	RC1	RC2	RC3	RC4
RC1	1.00	-0.01	-0.08	RC1	1.00	0.25	-0.04	-0.43*
RC2	-0.01	1.00	0.14	RC2	0.25	1.00	0.12	0.12
RC3	-0.08	0.14	1.00	RC3	-0.04	0.12	1.00	0.07
				RC4	-0.43*	0.12	0.07	1.00

Note. \* indicates  $p \leq 0.05$ .

Table S2.

*Congruence Coefficients After Targeted Orthogonal Procrustes Rotation Between SS and XS.*

Congruence between structures

	Asst	Open	Neura	Socb	Attna
RC1	0.66	0.76*	0.76*	0.65	0.65
RC2	0.84**	0.63	0.65	0.67	0.62
RC3	0.64	0.6	0.70*	0.78*	0.70*

Congruence between structures scored by our individuals

	Asst	Open	Neura	Socb	Attna
RC1	0.67	0.93***	0.92***	0.76*	0.70*
RC2	0.95***	0.64	0.70*	0.69*	0.67
RC3	0.69*	0.65	0.68*	0.79*	0.84**

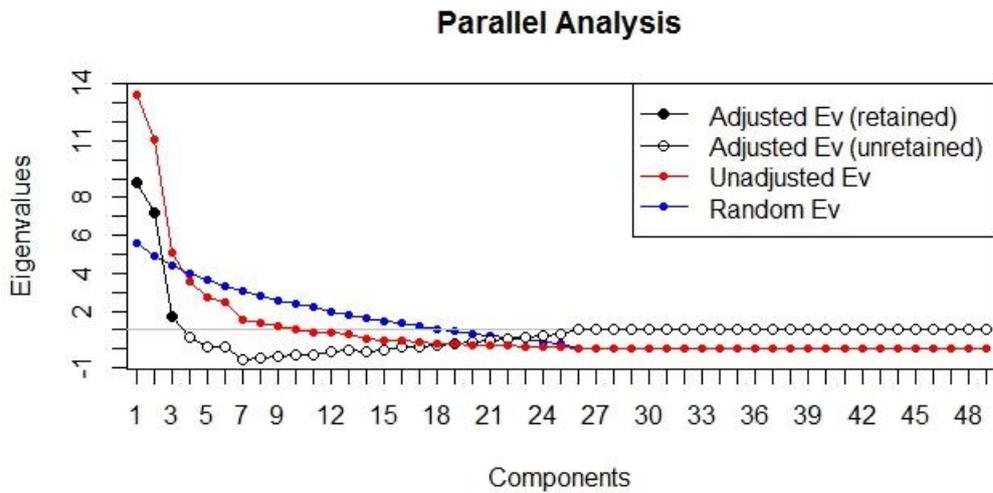
Note. Strength of congruence coefficients is indicated following MacCallum et al. (1999) as

such: \*poor, \*\*borderline, \*\*\*good, \*\*\*\*excellent.

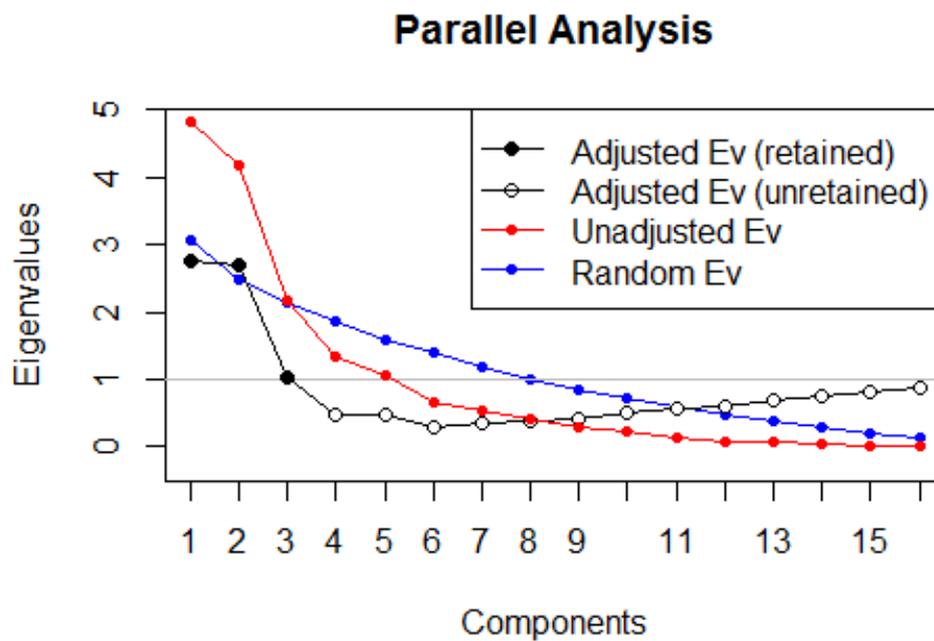
Table S3.

*Correlations Between Promax-Rotated Components of Behaviors PCA (BS)*

	RC1beh	RC2beh	RC3beh
RC1beh	1	0.02	-0.05
RC2beh	0.02	1	-0.10
RC3beh	-0.05	-0.10	1



*Figure S1.* Parallel analysis scree plot with the 49 first components eigenvalues (from 54 HPQ questions, after removing five items) taken from unadjusted, adjusted, and random components



*Figure S2.* Parallel analysis scree plot with the 16 first components eigenvalues (from 16 behaviors) taken from unadjusted, adjusted, and random components.

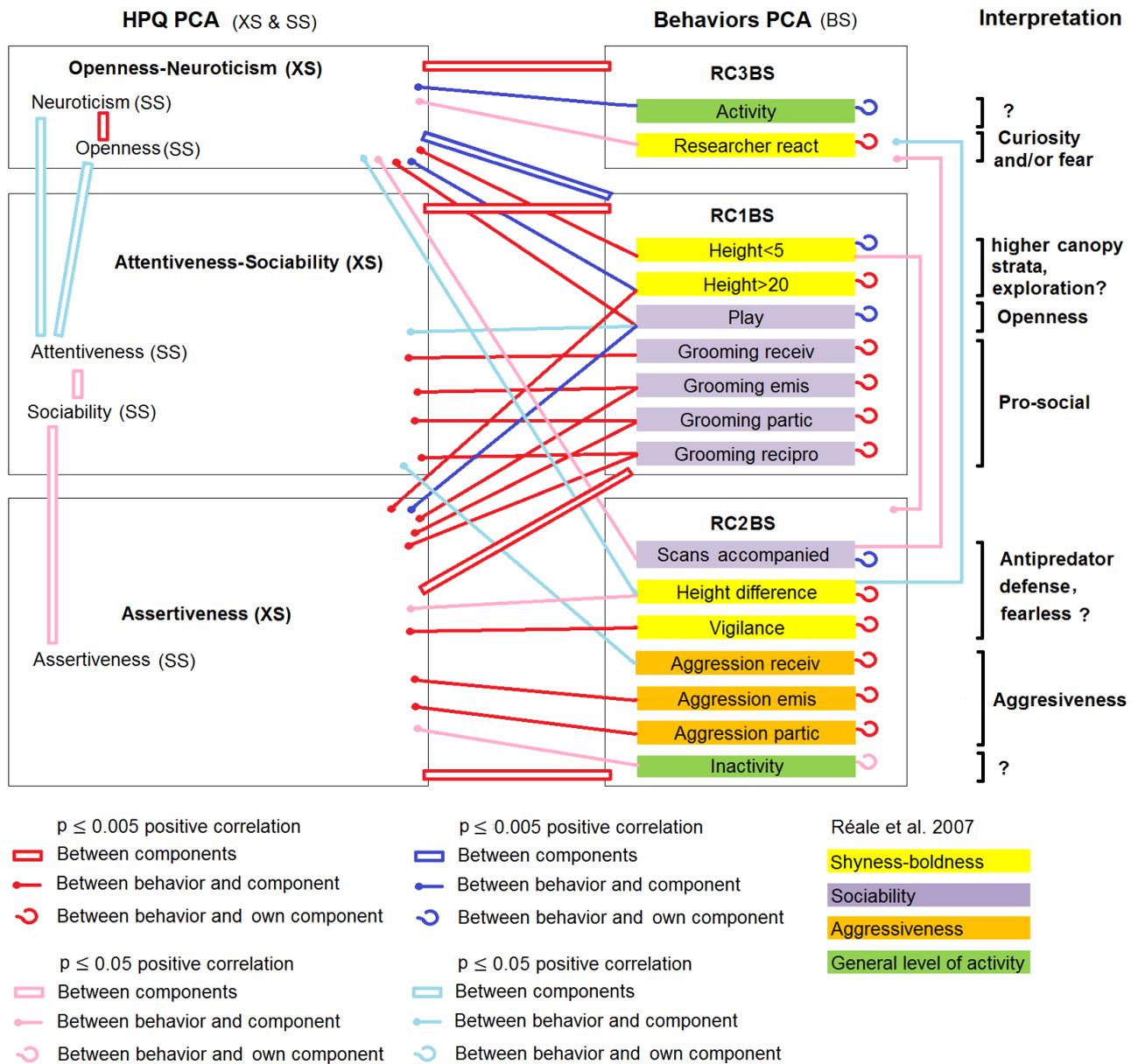


Figure S3. Scheme for wild *S. xanthosternos* personality traits based on our results.

XS and SS components are on the left, connections indicate the correlations between these components (see Table 6). BS components are shown in the center, connections indicating the correlations between behaviors and BS components (see Table 9); and the correlation between the BS components and the XS (see Figure 3).

## CHAPTER THREE

### **Age is the main influence on personality and behavioral similarities of capuchin monkeys (*Sapajus xanthosternos*)**

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Marcelo Fernández-Bolaños, Irene Delval, Patrícia Izar

(Paper presented, in part, in the XVII IPS Congress in 2018 Nairobi. It will be soon submitted to an international journal)

## **Age is the main influence on personality and behavioral similarities of capuchin monkeys (*Sapajus xanthosternos*)**

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**Short running title:** Age Influences Behavior and Personality of Wild *Sapajus*

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This research complied with protocols approved by the Animal Research Ethics Committee of the Institute of Psychology of the University of São Paulo (CEUA/IPUSP), Brazilian legal requirements (SISBIO permit 47501-5), and the

principles for the American Society of Primatologists for the ethical treatment of primates

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## **ABSTRACT**

Personality refers to the underlying tendencies that make individuals differ in the expression of their behaviors, being consistent within individuals over time and across situations. However, other variables such as sex, age, and dominance rank may also affect the behavioral repertoire and the expression of personality, what have relevant implications on personality studies. Here, we examine how these variables affect personality and behavioral similarities of 26 wild yellow-breasted capuchin monkeys (*S. xanthosternos*), living in Una Biological Reserve, Bahia, Brazil. Sex differences on personality traits were almost absent, probably because in this population males and females share dominant positions and are allies in agonistic contests. There was a small effect of dominance rank on Assertiveness, but this effect vanished after considering individuals which were dominants over an extended period, which suggests changes in personality after the acquisition of dominant positions. Age had the most striking effects on personality and behavioral similarities of this species. Openness-Neuroticism declined with age, Assertiveness increased throughout life, and Attentiveness-Sociability increased progressively until adulthood, after a slight drop in

adolescence. These patterns were similar to other primate species, including humans. We conclude that resemblances on developmental processes presented in the three personality traits suggest, not only a common personality structure for human and non-human primates, but also a common ontogenetic path.

*Keywords:* Primates, temperament, development, ontogeny, dominance rank, sex differences

## INTRODUCTION

As the study of personality is growing in primatology (Freeman & Gosling, 2010), several new questions arise. Animal personality refers to the underlying behavioral tendencies that are different across individuals and consistent within individuals over time, which affect behavior expressed in different contexts (Stamps & Groothuis, 2010). In that way, the personality categorizes individuals by similarities in behavioral output, however, variables other than personality such as sex, age, and dominance status may also affect the behavioral repertoire of individuals and thus the expression of personality.

Sex can cause consistent different behavioral responses, as well as differences in personality expression driven by sexual selection (Schuett, Tregenza, & Dall, 2010), and bias in dispersal (e.g. *Macaca mulata*, *Macaca fascicularis*, *Macaca nemestrina*: Sussman, Ha, Bentson, & Crockett, 2013). In fact, consistent sexual differences in some personality traits have been described in humans, being females more agreeable and neurotic than males (McCrae &

Terracciano, 2005) and in non-human primates, in which females are more agreeable and conscientious than males, which in turn, are more dominant and extraverted (*Pan troglodytes*: Weiss, King, & Hopkins, 2007).

Age can also affect behavior: primates show significant developmental changes in the behavioral repertoire (Kappeler & Pereira, 2003) and in personality traits. In humans, Neuroticism, Extraversion, and Openness decrease, while Agreeableness and Conscientiousness increase in adulthood (Roberts, Walton, & Viechtbauer, 2006; Srivastava, John, Gosling, & Potter, 2003), and in non-human primates, Extraversion and Openness decrease, while Agreeableness and Conscientiousness increase in adulthood (*Pan troglodytes*: Weiss et al. 2007; *Pan troglodytes*: King, Weiss, & Sisco, 2008).

Dominance is expected to affect the behavioral repertoire of primates, leading to differences between dominant and subordinate individuals. Also, personality might mediate the acquisition of dominance rank (*Cercopithecus aethiops sabaesus*, Socially competent: McGuire, Raleigh and Pollack, 1994; *Semnopithecus entellus*, Confidence and Dominance: Konečná et al., 2008; *Macaca sylvanus*, Confidence: Konečná, Weiss, Lhota, & Wallner, 2012), so that some authors propose Dominance as a primate personality trait (King & Figueredo, 1997).

In capuchin monkeys, evidence about the effects of sex, age and dominance on the personality is inconclusive. In captive *Sapajus* spp. males are more “aggressive” than females (Uher, Addessi, & Visalberghi, 2013); whereas in wild *Cebus capucinus* males are more “extraverted”, “open”, “neurotic” and “eccentric” than females, which, in turn, are more “agreeable” (Manson & Perry,

2013). In captive *Sapajus* spp. there is no effect of age on personality (Uher et al. 2013), while in wild *C. capucinus* “openness” and “agreeableness” decline with age, but “eccentricity” increases during adulthood (Manson & Perry 2013). In captivity, dominance is considered an aspect of capuchin monkeys’ personality linked to the trait Assertiveness (Morton et al., 2013; Uher et al., 2013), alpha males have an assertive personality, associated to special facial features (Lefevre et al. 2014). In wild *C. capucinus*, “extraverted” males attain the alpha status sooner (Perry, Godoy, Lammers, & Lin, 2017), suggesting that this trait facilitated acquiring the highest dominance rank.

In a previous study (Fernández-Bolaños et al., 2018, submitted), we analyzed the personality of wild yellow-breasted capuchin monkeys (*Sapajus xanthosternos*), describing three traits: 1) Openness-Neuroticism, defined as fear and curiosity tendencies, and engaging in behaviors with impulsive, volatile and lack of calmer disposition, as playing, 2) Assertiveness, defined as aggressive tendencies and lack of anxiety or fear, linked to anti-predatory defense behaviors, but also with certain prosocial tendencies, reflected in grooming behaviors, and, 3) Attentiveness-Sociability, defined as high prosocial tendencies, reflected in huge frequencies of grooming behaviors (see methods). In the present study we analyze whether sex, age, and dominance rank affect personality, and which of these variables affect the behavioral patterns of a wild group of *S. xanthosternos*. Our study adds ecological validity to primate personality studies, since most have been carried out in captive conditions (Freeman & Gosling, 2010). We were able to observe behavioral responses under natural ecological pressures, such as predatory threat, which is especially high in this population (Suscke et al., 2017).

We expected to find sex differences in personality of the studied group. Openness may be an adaptive trait for the migrant sex since it favors exploring new foods and establishing alliances for getting comigrants (Manson & Perry, 2013). In addition, fearfulness and reactivity, qualities usually related to Neuroticism, can be adaptive for a population submitted to high predatory pressure (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Since males actively defend the group against predators in this population (Suscke et al., 2017), we expected that males would be higher than females in Openness-Neuroticism. We did not expect to find remarkable sex differences in Assertiveness, a trait related to dominance, as *S. xanthosternos* has a relaxed hierarchy with males and females occupying the highest positions (Suscke, 2009, 2014).

We expected to find age differences in personality traits, as seen in other primate species (Weiss et al 2007; King et al *Pan troglodytes*; Manson and Perry 2013) and in humans (Roberts et al., 2006, Srivastava et al., 2003). We expected the youngsters to be high in Openness-Neuroticism, as this trait has an important fear component, what should be adaptive for the vulnerable juveniles, and low in Assertiveness, since this trait is more important in the adult dominance hierarchy.

In addition, we investigated whether dominance rank could be related to any personality trait in *S. xanthosternos* (Morton et al., 2013; Uher et al., 2013). We expected that dominant individuals would be higher in Assertiveness, as it involves adequate features for winning fights and for establishing alliances (Morton et al, 2013, Lefevre et al, 2014).

Finally, we analyzed which of the individual variables sex, age, dominance or personality traits have the greatest influence on the behavioral similarity of *S. xanthosternos* individuals. This analysis is relevant for personality studies, as they categorize individuals by behavioral similarities, but the aforementioned individual variables could be more determinant in the behavioral output.

## **METHODS**

### **Study site and subjects**

This study was conducted at Una Biological Reserve, (Bahia State, Brazil), a fully protected conservation area of ca. 18500 ha. The region is covered with lowland Atlantic Forest (Amorim, Thomas, Carvalho & Jardim, 2008), in a mosaic of mature forest, secondary forest, and patches of agriculture fields called “cabruca” (i.e., an agroforest where cocoa trees—*Theobroma cacao*— and jack fruit occupy the understory forest; see Raboy, Christman, & Dietz, 2004).

The group of *S. xanthosternos*, called Principe, has been studied since 2005 when it was habituated and accompanied systematically with the help of radio telemetry technology (Kierulff, Canale, & Suscke, 2005). In the present study we analyzed the period from April 2015 to March 2016; totalizing 121 days distributed in three weeks every month. During the time of this study the group had  $26 \pm 2$  individuals, but present data were focused on 26 (8 adult females, 4 adult males, 5 subadult males, 2 female juveniles, 3 male juveniles and four infants born at the beginning of 2015, 1 female and 3 males). All 26 individuals

were present during the entire study period, with the exception of one subadult that emigrated in September 2015.

## **Behaviors**

During the study period two researchers (ID & MFB) and one field assistant (RSO) accompanied the group on a 3 to 5 days weekly basis, from dawn to dusk (12:30 hours per day in media), and MFB collected behavioral data at 5' scans sampling every 20', and all occurrences events (Altmann, 1974). We analyzed 16 behaviors (table 1). Absolute amount of behaviors were transformed into daily rates, or monthly rates, depending of the frequency of behavior (see table 1, indicated with asterisks). The rates were adjusted for the time each individual was observed, calculated as the sum of scans in which that individual was observed. We calculated the rank order of these rates, and standardized from 0 (minimum) to 1 (maximum). Finally, for each individual we estimated the total mean across periods: for the most frequent behaviors we first estimated the monthly mean of daily standardized rank orders, and then the mean of monthly means; for the infrequent behaviors we directly calculated the mean of monthly standardized rank orders. With these transformations, we converted the unequal absolute amount of different behaviors into a similar comparable scale, controlling for interindividual differences in sampling.

Table 1.

*Behaviors analyzed on wild S. xanthosternos and recording method.*

<b>Behavior</b>	<b>Definition</b>	<b>Method</b>
<i>Vigilance</i>	Staying alert watching environment looking for any menace	Scans*
<i>Researcher react</i>	Threat a researcher	AO**
<i>Height&lt;5</i>	Scan at a canopy height lesser than 5 m.	Scans*
<i>Height&gt;20</i>	Scan at a canopy height higher than 20 m.	Scans*
<i>Height difference</i>	At every scans absolute difference between individual and mean group height	Scans*
<i>Aggression emission</i>	Emitting a threat, chase or beat to a conspecific	Scans+AO*
<i>Aggression receiving</i>	Receiving a threat, chase or beat from a conspecific	Scans+AO*
<i>Aggression participation</i>	Emitting or receiving a threat, chase or beat to a conspecific	Scans+AO*
<i>Grooming emission</i>	Emitting grooming, picking through or manipulate the fur of another monkey with hands and/or mouth (Rose, 2000)	Scans+AO*
<i>Grooming receiving</i>	Receiving grooming	Scans+AO*
<i>Grooming participation</i>	Emitting or receiving grooming	Scans+AO*
<i>Grooming reciprocity</i>	Emitting grooming just before receiving grooming of a conspecific, or vice versa	AO**
<i>Play</i>	Engaging in sequences of spontaneous, apparently non-goal oriented behaviors (Rose, 2000)	Scans+AO*
<i>Scans companied</i>	Total scans- scans with nobody observed at 15 m.	Scans*
<i>Activity</i>	High expenditure activities(moving +moving and foraging +playing)	Scans
<i>Inactivity</i>	Resting, sleeping or keeping without do anything	Scans

*Note.* \* indicated that, for this behavior, monthly mean of daily rank orders were calculated;

\*\*indicated that, for this behavior, monthly rank orders were calculated. AO – all occurrences

## **Sex and age**

For our analyses, we considered four age categories (4cat), based on Verderane (2010) classification, for *Sapajus*: infant, from 0 to 1.5 years; juvenile,

between 1.5 and 5 years; subadult, males between 5 to 7 years old, (however, we did not had information about their real age, but we attributed this category to individuals larger than the youngsters, but without adult facial features); and adults, older than 7 years old, as indicated by the completely developed adult facial and body features. We also used a simpler classification with two categories (2cat) distinguishing between adult and non-adults individuals (subadults, juveniles and infants lumped in one category). Sex and age in *S. xanthosternos* were not evenly distributed, with more non-adult males than non-adult females, and more adult females than adult males (Table 2).

Table 2.

*Sex and age distribution of our sample with 26 wild S. xanthosternos.*

<i>sex\age</i>	<i>infant</i>	<i>juvenile</i>	<i>sub-adult</i>	<i>non-adult</i>	<i>adult</i>	<i>total</i>
<i>female</i>	1 (25%)	2 (40%)	0	3 (21.4%)	8 (66.7%)	11 (42.3%)
<i>male</i>	3 (75%)	3 (60%)	5 (100%)	11 (78.6%)	4 (33.3%)	15 (57.7%)
<i>total</i>	4 (15.4%)	5 (19.2%)	5 (19.2%)	14 (53.8%)	12 (46.2%)	

## **Dominance**

We determined the dominance hierarchies based on aggressive interactions (threatening, chasing and beating) registered in scan samplings and all occurrences records (Altmann, 1974). We applied the dominance-directed tree (Ditree) method with software Domina (Izar, Ferreira, & Sato, 2006). This method employs the win-defeat interaction between individuals, and constructs a transitive matrix by imposing to the dominance matrix a transitivity rule (that is, if A dominate B and B dominate C, then A dominates C). We established the

dominance position calculating for every individual the number of individuals reached in its Dintree. For the subsequent analyses, we categorized individuals distinguishing between dominants and subordinates. This dominance hierarchy was calculated with data collected during the study period (Dom. 2015-16), but we developed a second classification, incorporating individuals who have been dominants before or after the study period (Dom. 2010-18). Thus, in Dom. 2010-18 we included Priscila, an adult female classified as dominant during the period 12/2010-12/2013 (see Suscke, 2014), using David Dominance Index (David, 1987). In Dom 2010-18 we also included Gustavo, an adult male who became dominant in 09/2016, after a strong fight between the alpha and another male (Cassiano and Binho respectively), which resulted in the emigration of the former and the death of the last. Gustavo is still the dominant alpha male until the present moment.

## **Personality**

In a previous study (Fernández-Bolaños et al., submitted) we described the personality of the Principe's 26 individuals using the Hominoid Personality Questionnaire (HPQ; Weiss et al. 2009)<sup>3</sup>. The HPQ contain 54 items, from which

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<sup>3</sup>English original version available in [http://extras.springer.com/2011/978-1-4614-0175-9/weiss\\_monkey\\_personality.pdf](http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf)

we selected 49, and each item uses a 1 to 7 likert scale, in which 1 indicates “displays either total absence or negligible amounts of the trait” and 7 “displays extremely large amounts of the trait”. With the HPQ individual ratings we conducted a PCA analysis with satisfactory performing: adequate ICC measures, good internal consistency of components and stability, and components showing little orthogonality. The PCA structure revealed three components, and this structure was compared with the five traits described by Morton et al. (2013) with 127 captive (*Sapajus* spp.). By comparing the results of both structures and by correlating each component with the 16 behaviors (Table 1), we defined three traits: Openness-Neuroticism, Assertiveness and Attentiveness-Sociability.

In the present study, we evaluated the personality of the 26 individuals using the described three traits structure. We first transformed the components (traits) loadings into unit-weighted scores (Gorsuch, 1983), changing loadings larger or equal to  $|0.4|$  into 1 or -1 depending on its direction, following the process described by Weiss et al. (2009). Then, we multiplied the individuals' item ratings by their unit weights, and, for each trait, we added these values and divided by the number of items in that trait. After these transformations, we obtained for every individual a 1 to 7 score in the three traits (as HPQ 1 to 7 Likert scale), that we centered to zero (minimum -3.5 and maximum 3.5). Since we needed a limited number of discrete categories for developing ANOSIM analyses (see statistical analysis below), we used two reduced classifications for categorizing the individuals. The first was a scale with five categories (5cat): extreme low value, low value, indeterminate, high value and extreme high value (the first row on Table 3 indicates threshold values for each category); the second was a simple

binary classification (2cat), in which we categorized every individual as low or high comparing its value to the group median.

### **Statistical analyses**

The relations among individual variables over personality traits were analyzed conducting a multivariate analysis of variance (MANOVA) using two models: one analyzing the effect of sex, age, Dom2015-16 and the interactions of these variables over the three personality traits; the other was the same but changing Dom 2015-16 by Dom 2010-18. We transformed sex into a dummy variable, 1=female and 2=male, and considered the 2cat classification for the rest of variables. We performed Levene's test to analyze if the error of dependent variables was the same between categories. We judged significant  $p \leq 0.05$  and highly significant  $p \leq 0.005$ , one-tailed, considering p value from Sidak's post hoc test. Statistical data analyses were performed using SPSS software version 21.0 (IBM Corp, 2012).

Then, we evaluated the effect of the individual variables sex, age, rank, and personality on the behavioral similarity of *S. xanthosternos*. The procedure here employed consist in grouping individuals by similarities in the whole 16 behaviors without any *a priori* assumption, and then analyze which of the aforementioned individual variables explain better the membership to each group. Using software Primer 6 & Permanova (Clarke & Gorly, 2006) we calculated a resemblance matrix using Bray Curtis similarity index, which calculated similarities between individuals considering all the 16 behaviors. From

this resemblance matrix we developed Cluster analyses, which grouped individuals by similarity in all these behaviors. We also performed an ANOSIM analysis with 999 permutations, to test if the resemblance matrix presented significant differences according to the individual variables (sex, age, dominance, and personality traits). The ANOSIM analysis calculates the p value from the proportion of simulations with higher or lesser distribution than the observed. We considered significant  $p \leq 0.025$  and highly significant  $p \leq 0.0025$ , two-tailed.

## RESULTS

We evaluated the personality of individuals using the 5cat and the 2cat classifications (see methods). Openness-Neuroticism and Assertiveness resembled a normal distribution, but they were asymmetrical right-sided, with only 3.8% individuals with low values (table 3 and fig.1). Attentiveness-Sociability had an even more asymmetrical distribution, with 57.7% individuals with extreme high values (table 3 and fig.1). The medians, used to categorize the individuals with the 2cat classification were 0.27 and 0.58, for Openness-Neuroticism and Assertiveness, and 2.16 for Attentiveness-Sociability (Table 3 and Figure1).

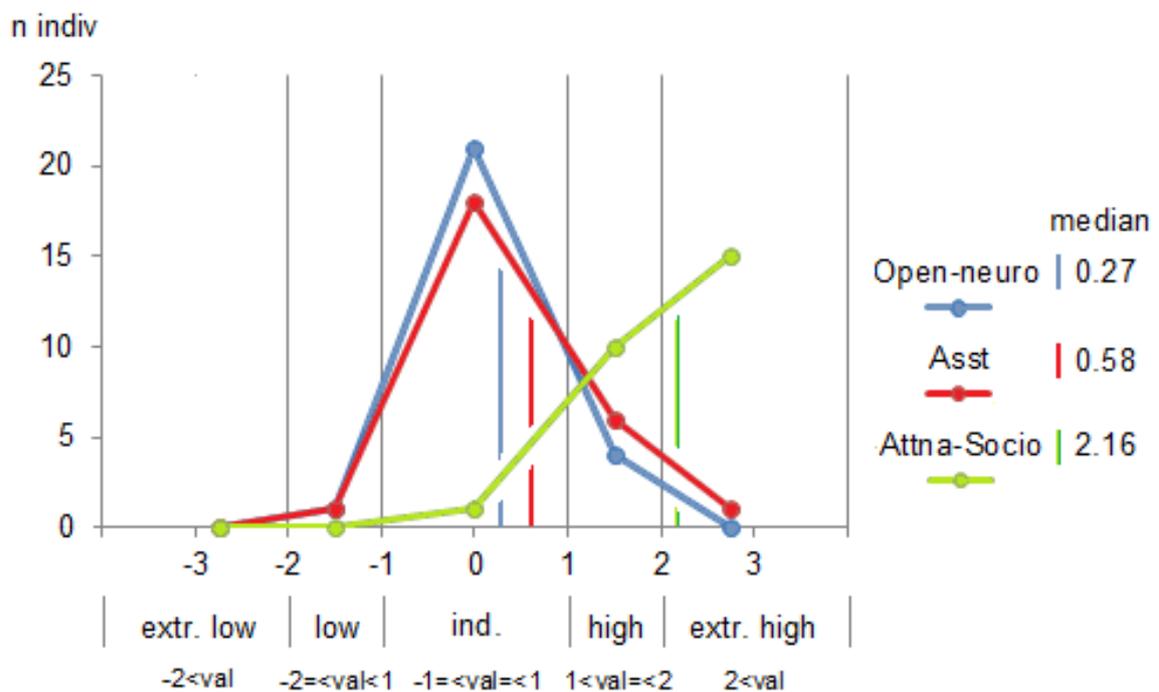
Table 3.

*Number and proportion of individuals in each HPQ trait (Openness-Neuroticism, Assertiveness, and Attentiveness-Sociability).*

Values	5cat					2cat		
	-2<val	-2≤val<1	-1≤val=<1	1<val≤2	2<val	med≥val	med<val	median
Interpretation	extr. low	low	ind.	high	extr. high	low	high	(med)
Open-Neuro	0	1 (3.8%)	21 (80.8%)	4 (15.4%)	0	13 (50%)	13 (50%)	0.27
Asst	0	1 (3.8%)	18 (69.2%)	6 (23.1%)	1 (3.8%)	13 (50%)	13 (50%)	0.58

Att-Socio	0	0	1 (3.8%)	10 (38.5%)	15 (57.7%)	13 (50%)	13 (50%)	2.16
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*Note.* First row: criteria for evaluating individuals with the 5cat and with 2cat classifications. In columns In the left side are indicated the number and percentage of individuals using the 5cat classification. In the right side are indicated the number and percentage of individuals using the 2cat classification. In the last column it is indicated the median value of the group, used for the 2cat classification.



*Figure 1.* HPQ traits frequency distribution using the 5cat classification. Vertical lines indicate the median values of each trait, used for the 2cat classification.

The dominance-directed tree (Izar et al., 2006) showed 18 individuals with the same rank position, being dominant over 24 individuals (see Table 4). This result revealed circularities in the dominance relationships, indicating that our studied group did not present a linear hierarchy. However, 3 individuals (Cassiano, Lernould and Samantha) dominated more than 24 individuals, thus, in Dom 2015-16 we considered these three individual as dominants and the other 23 we considered as subordinates (Table 4). Dom. 2010-18 had 5 dominants

(table 4) as we included two other individuals in this category (Priscila and Gustavo, see methods).

Table 4.

*Hierarchy of dominance of the S. xanthosternos Principe group.*

<i>Individual</i>	<b>Period</b>	<b>2015-16</b>	<b>2010-18</b>
	<i>n ind. Dit.</i>	<i>2cat</i>	<i>2cat</i>
<i>Naiara</i>	1	sub	sub
<i>Marcela's dau.</i>	24	sub	sub
<i>Michele's son</i>	2	sub	sub
<i>Larissa's son</i>	24	sub	sub
<i>Priscila's son</i>	1	sub	sub
<i>Henrique</i>	24	sub	sub
<i>Binho</i>	24	sub	sub
<i>Preta</i>	3	sub	sub
<i>Lernould</i>	25	dom	dom
<i>Priscila</i>	1	sub	dom
<i>Larissa</i>	24	sub	sub
<i>Marcela</i>	24	sub	sub
<i>Michele</i>	24	sub	sub
<i>Samantha</i>	26	dom	dom
<i>Cassiano</i>	28	dom	dom
<i>Irene</i>	24	sub	sub
<i>Gustavo</i>	24	sub	dom
<i>Intruso</i>	24	sub	sub
<i>Dumbo</i>	24	sub	sub
<i>Sofia</i>	24	sub	sub
<i>Lucas</i>	24	sub	sub
<i>Mingau</i>	24	sub	sub
<i>Pimenta</i>	24	sub	sub
<i>Rita</i>	24	sub	sub
<i>Marcelo</i>	24	sub	sub
<i>Bob Marley</i>	24	sub	sub
	dom	3 (11.5%)	5 (19.2%)
	sub	23 (88.5%)	21 (80.8%)

*Note.* **n ind. Dit.** (2<sup>nd</sup> column) indicates, for each individual, the number of individuals reached in its Ditree after imposing a transitive rule.

We performed a multivariate analysis of variance (MANOVA) to verify the effect of sex, age and Dom 2015-16 on the three personality traits at the same time. We accepted the null hypothesis of dependent variables covariance matrices being the same between groups ( $p= 0.177$ ), allowing us to perform the MANOVA. Observing results from the multivariate test, only age had a significant effect on the model ( $\lambda=0.114$ ,  $F_{3\ 22}=5.87$ ,  $\eta^2=0.51$ ,  $p< 0.001$ ), and the interaction age x sex had a close to significant effect ( $\lambda=0.114$ ,  $F_{3\ 22}=2.12$ ,  $\eta^2=0.3$ ,  $p= 0.08$ ).

Observing the tests of between subject-effects, there was a significant effect of age over Openness-Neuroticism ( $F_{3\ 22}=7.71$ ,  $\eta^2=0.58$ ,  $p= 0.002$ ), and observing the pairwise comparison, adults were significantly lower than infants (Sidak  $p= 0.017$ ), juveniles (Sidak  $p= 0.01$ ), and sub-adults (Sidak  $p= 0.044$ ) on Openness-Neuroticism (Figure. 2a). The proportion of individuals with high Openness-Neuroticism scores increased along development, from infant to a young stage, then it slightly decreased in the sub-adult stage, and finally it decreased drastically in the adulthood (Figure 3).

Age also affected significantly Assertiveness ( $F_{3\ 22}=7.38$ ,  $\eta^2=0.57$ ,  $p= 0.002$ ), being adults significantly more assertive than infants (Sidak  $p< 0.001$ ) and close to be significantly more assertive than juveniles (Sidak  $p=0.066$ ), and sub-adults were more assertive than infants (Sidak  $p=0.08$ ). The proportion of individuals with high Assertiveness scores increased continuously with age (Figure 3). The interaction sex x age had a close to significant effect on Assertiveness ( $F_{2\ 23}=3.53$ ,  $\eta^2=0.3$ ,  $p= 0.051$ ), indicating that adult males tended to be more assertive than young females (Figure 2b). DOM 2015-16 had a close to significance global effect on Assertiveness ( $F_{1\ 24}=3.53$ ,  $\eta^2=0.17$ ,  $p= 0.077$ ), and

observing the pairwise comparisons between categories, dominants were significantly higher in Assertiveness than subordinates ( $p= 0.001$ ) and close to be significantly higher in Attentiveness-Sociability than subordinates ( $p= 0.084$ ). When we performed another MANOVA analyzing the effect of sex, age and Dom 2010-18 over the three personality traits, the results for sex and age hold true, but Dom 2010-18 did not have any effect on personality. All dominants were adults, and males in larger proportion than females, in both Dom 2015-16 and Dom 2010-18 (Figure 2d).

In spite of a larger proportion of females than males with high scores on Attentiveness-Sociability in all age categories (Figure 2c), and, despite of differences on this trait related to age (the proportion of individuals with high Attentiveness-Sociability scores decreased until the sub-adult stage, but increased in adulthood, see Figure 3), this trait was not significantly affected by any individual variable in the multivariate analysis.

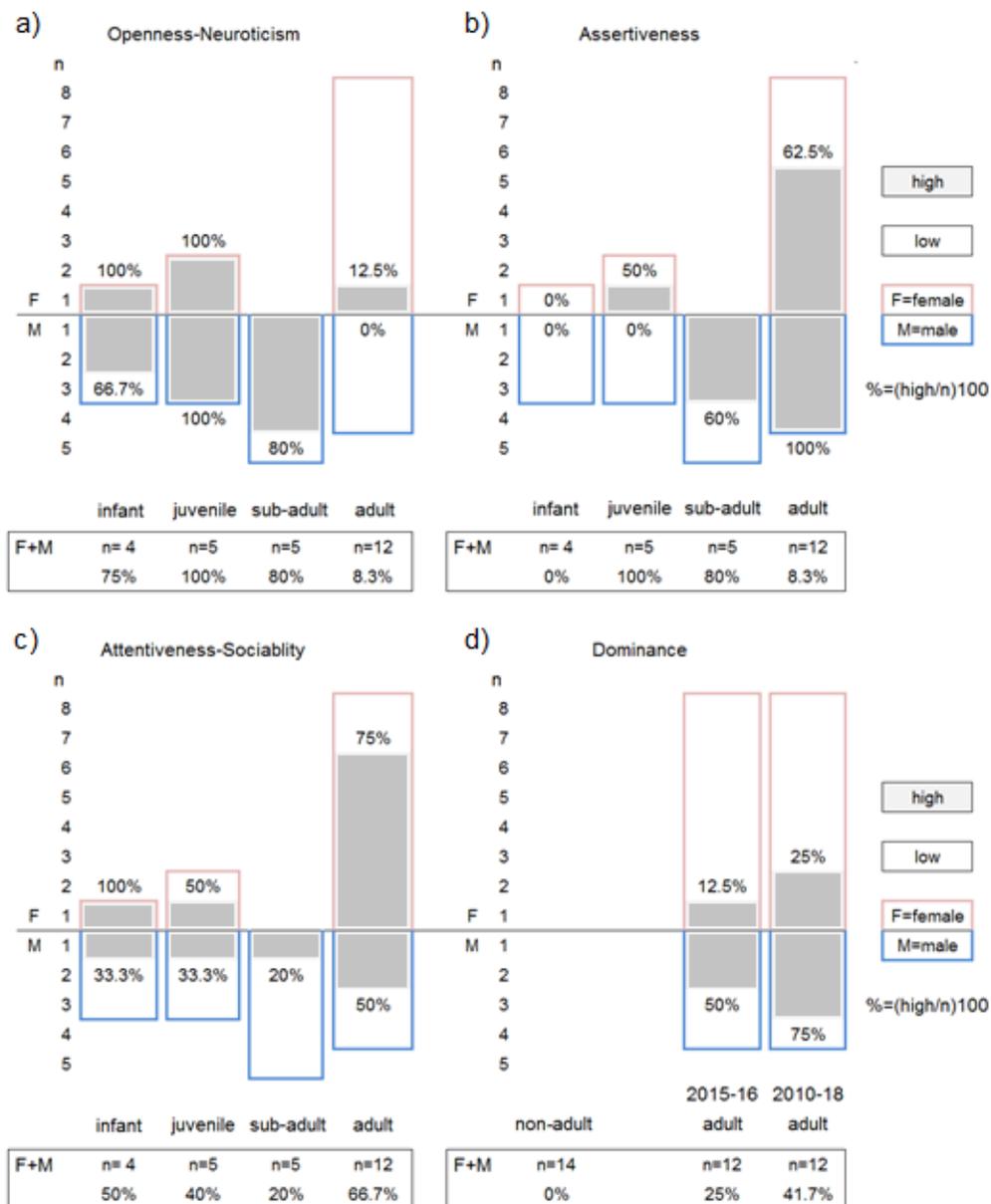


Figure 2. Sex differences across age categories in the three personality traits and in dominance.

Y-axis is divided *per sex*: up, females (F) and down, males (M); n indicates number of individuals in each category. X-axis shows four age categories: infant, juvenile, sub-adult and adult. The height of the columns indicates total number of individuals in a given sex/age category; grey shadow is indicating the percentage of individuals with high values (e.g. percentage of infant females with high values in Openness-Neuroticism over the total number of infant females). High (grey) and low (white) values were considered as above and below the median value respectively.

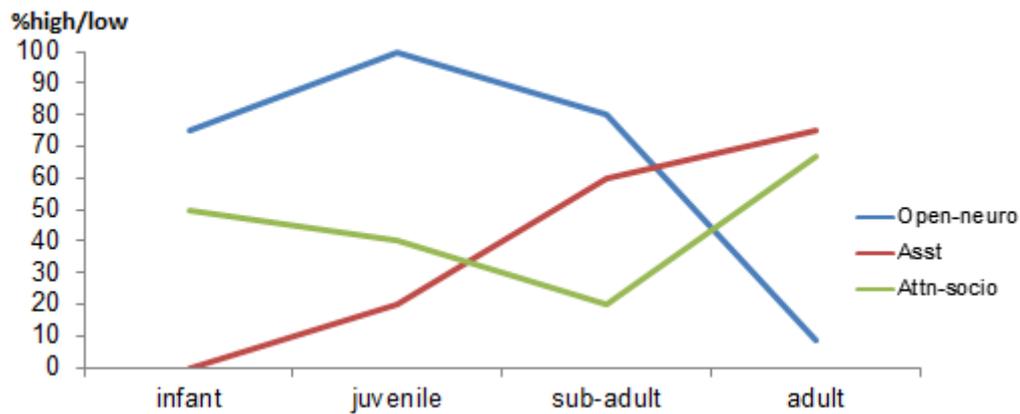


Figure 3. Percentage of individuals with high score over the total of individuals in each personality trait (Openness-Neuroticism, Assertiveness and Attentiveness-Sociability), and in each age category (juvenile, young, sub-adult and adult).

High and low values were considered as above and below the median value respectively.

The cluster analysis, based on a resemblance matrix between individuals, considering the 16 analyzed behaviors, revealed four groups (G1-G4, Figure 4). The behavioral similarity of *S. xanhosternos* individuals was significantly affected by sex ( $p=0.019$  two-tailed, Table 5).

Age affected behavioral similarity using both 2cat ( $p=0.001$  two-tailed) and 4cat classifications ( $p=0.001$  two-tailed), with significant differences between all age categories, with the exception of juvenil-subadult (Table 5). These differences can be observed in the cluster analysis: G1 was composed by Naiara, who is the oldest female in the group; G2 grouped all infants; G3 was integrated by adults, and one subadult (Henrique); and, G4 was formed only by juveniles and subadults, with the exception of the adult male Gustavo (Figure 4, 3<sup>rd</sup> column).

Dominance rank did not affect behavioral similarity of *S. xanthosternos*, neither with Dom. 2015-16 nor with Dom. 2010-18 (Table 5).

Openness-Neuroticism had a significant global effect using 2cat ( $p=0.001$  two-tailed, Table 5). This was particularly striking when inspecting the clusters: all groups were predominantly high or low in Openness-Neuroticism values (ratio low/high was: G1=1/0; G2=1/3; G3=10/1 and G4=1/9 [Figure 4, 9<sup>th</sup> column]). However, all adult individuals had high values on Openness-Neuroticism (with the exception of Samantha) and all not-adults had low values in this trait (with the exception of Michele's son), reinforcing the strong negative correlation observed between age and Openness-Neuroticism ( $r=-0.67$ ,  $p=0.001$  two-tailed, Table 5). The remaining personality traits did not have any significant effect on the behavioral patterns of *S. xanthosternos* (Table 5).

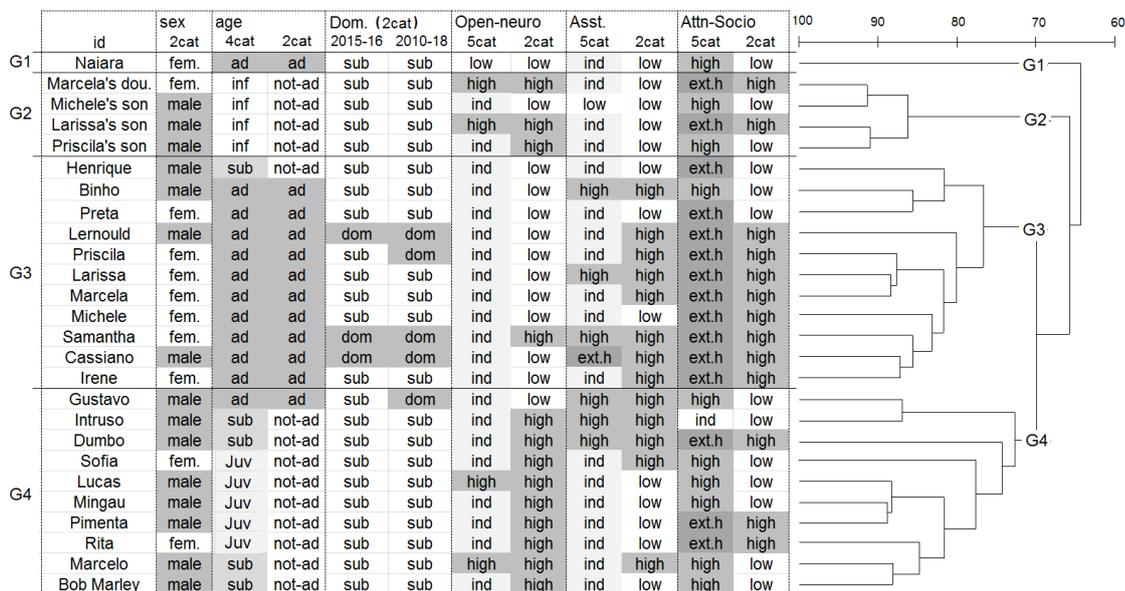


Figure 4. Cluster analysis of 26 *S. xanthosternos* individuals, grouped by similarity in 16 selected behaviors.

In the left part it is presented a table indicating the attributes of individuals using different classifications (see methods). Different categories were distinguished with different levels of grey for a better visual interpretation when compared to clusters results (right side).

Table 5.

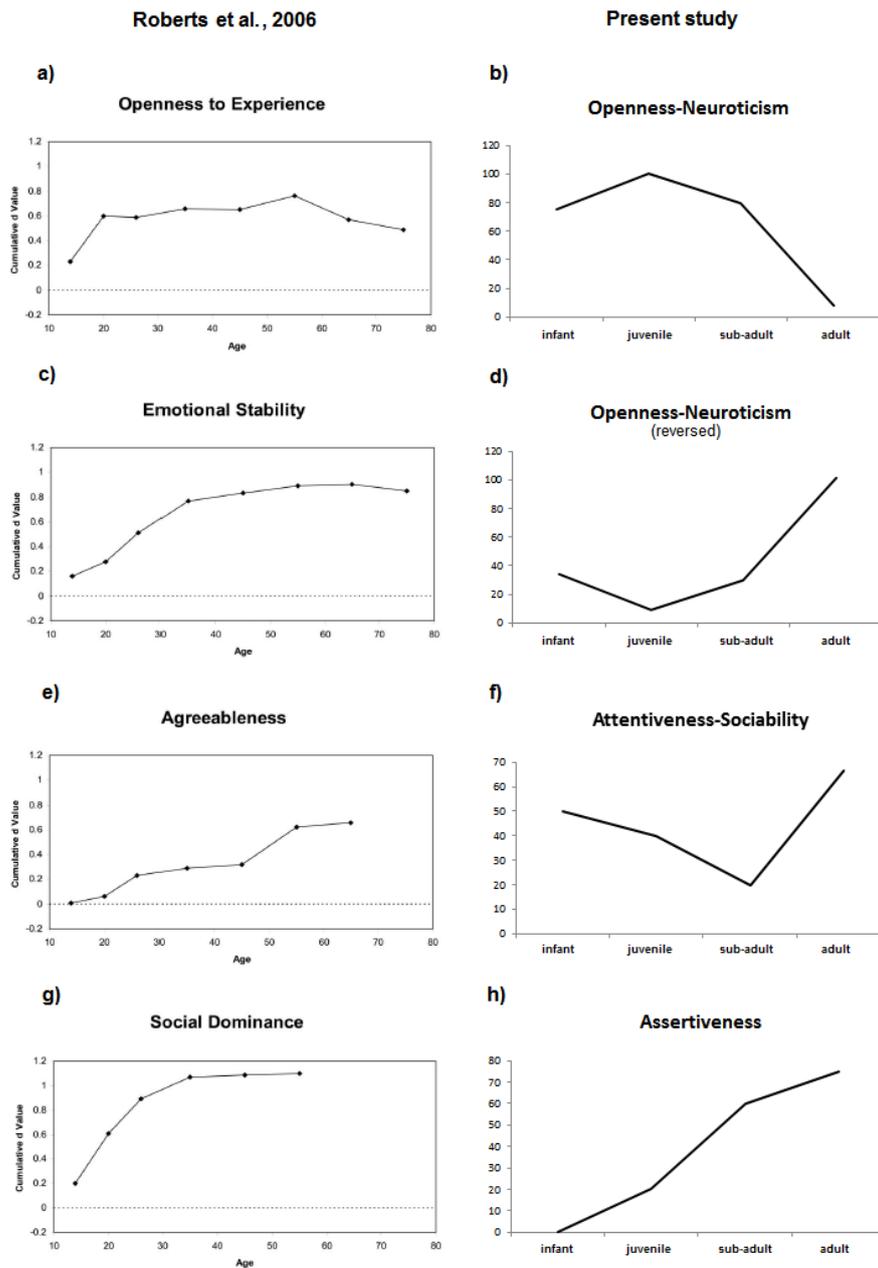
*ANOSIM results after 999 permutations, analyzing sex, age, dominance, and the personality traits.*

<b>VAR.</b>	<b>N° CAT</b>		<b>GLOBAL OR CAT-</b>	<b>R</b>	<b>P</b>
<b>SEX</b>		2cat	male vs female	0.162	0.019**
<b>AGE</b>		2cat	adult vs non-adult	0.58	0.001**
		4cat	Global	0.612	0.001**
			infant vs juvenile	0.881	0.008*
			infant vs subadult	0.869	0.016*
			Infant vs adult	0.887	0.002*
			juvenile vs subad	0.188	0.048
			juvenile vs adult	0.616	0.001**
			subad vs adult	0.512	0.004*
<b>DOM</b>	2015-16	2cat	dom vs sub	0.101	0.255
	2010-18	2cat	dom vs sub	0.119	0.135
<b>OPEN-NEURO</b>		2cat	high vs. low	0.343	0.001**
		5cat	Global	0.224	0.047
			low vs ind	0.539	0.091
			low vs high	1	0.2
			ind vs high	0.121	0.133
<b>ASST</b>		2cat	high vs. low	0.283	0.04
		5cat	Global	0.163	0.051
			low vs ind	0.242	0.158
			low vs high	0.644	0.143
			ind vs high	0.133	0.099
			ind vs ext. high	0.143	0.263
			high vs ext. high	-0.311	1
<b>ATTN-SOCIO</b>		2cat	high vs low	0.195	0.06
		5cat	Global	0.256	0.04
			ind vs high	0.093	0.455
			ind vs ext. high	0.714	0.063
			high vs ext. high	0.218	0.09

Note. \*Indicated significant  $p \leq 0.025$  two tailed, \*\*indicated significant  $p \leq 0.0025$  two tailed

## DISCUSSION

In the present study, we analyzed whether and how sex, age, and dominance affect personality, and how all those variables affect the behavioral similarity of wild *S. xanthosternos* individuals. We found an effect of age in the personality of *S. xanthosternos*, indicating that personality develops along the ontogeny of individuals. Openness-Neuroticism increased during infancy until juvenility, and then declined in adulthood. Similarly, in humans, Openness increases during infancy until adolescence and declines during adulthood (Roberts et al. 2006) and Neuroticism also declines in adulthood (Roberts et al. 2006; Srivastava et al, 2003). If we consider Emotional Stability analogous to Neuroticism (in opposite direction), and Openness to Experience analogous to Openness, we find similarities in the developmental curves of humans' traits (Roberts et al., 2006) and of *S. xanthosternos*' traits (Figure 5 a vs b, and c vs d). Other primates present similar trends: in chimpanzees and capuchin monkeys, Openness decrease during adulthood (*Pan troglodytes*: Weiss et al., 2007; *Pan troglodytes*: King et al., 2008; *C. capucinus*: Manson & Perry, 2013); in vervet monkeys the factors playful/curious and opportunistic (related to Openness-Neuroticism) decrease in adults (*Cercopithecus aethiops sabaesus*: McGuire et al., 1994). These common developmental patterns could reflect broad underlying adaptive benefits shared by humans and non-humans primates. For example, Openness should help youngsters enhancing social learning by direct interaction with conspecifics (Manson & Perry, 2013). Neuroticism is linked to fear feelings, allowing young individual to avoid potentially dangerous situations.



**Figure 5.** Comparison between human and *S. xanthosternos* development of personality traits.

Figures a, c, e and g, taken from Roberts et al., (2006) p. 15: “Cumulative d scores for each trait domain across the life course”. Figures b, d, f and h describes the evolution of *S. xanthosternos* development of personality traits found in present study (see Figure 2). Figure d was reversed to be Neuroticism in the same direction than Emotional Stability.

In *S. xanthosternos* Attentiveness-Sociability decreased until sub-adult stage and then increased drastically in adulthood. In humans (Roberts et al., 2006), Agreeableness increases at the beginning of life, but similar to *S. xanthosternos* this trait suffers a decline in the middle of life and then increases until old age (Figure 5 e vs f). In chimpanzees it has been also reported an increase of Agreeableness until the adulthood (*Pan troglodytes*: Weiss et al. 2007; King et al. 2008). We hypothesize that the increase of Attentiveness-Sociability (or Agreeableness) in human and non-human primates can be the reflection of matured social skills, which get progressively enhanced as long term relationships are being established.

Assertiveness increased gradually from infant to adult stage in *S. xanthosternos*. This trait is comparable with the human Extraversion facet Social Dominance, which also increases progressively across lifespan (Figure 5 g vs h). In chimpanzees, the personality trait Dominance, comparable with both, Assertiveness and Social Dominance, also increases until adulthood (*Pan troglodytes*: Weiss et al. 2007; *Pan troglodytes*: King et al. 2008). For both, human and non-human primates, the increasing of Assertiveness (or Dominance or Social Dominance) until adult stages should be adaptive for maintaining the social status acquired throughout life span.

The resemblance on developmental processes in the three personality traits suggests not only a common personality structure for human and non-human primates (King & Figueredo, 1997, King et al., 2008; Weiss, 2017), but also a common ontogenetic path. Further studies should address the species-specific differences on developmental processes, and how particular ecological

and social pressures interact in the phenotypic expression of personality at each life history stage.

Sex had a moderated effect on the personality of *S. xanthosternos*. The multivariate analyses of variance (MANOVA) showed a significant effect of sex x age over Assertiveness, indicating that adult males tended to be more assertive than young females, but not same aged individuals. Males are more aggressive than females in captive capuchin monkeys (*Sapajus* spp.: Uher et al., 2013) and other primates species (*Pan troglodytes*, Dominance: Weiss et al. 2007; *C. capucinus*, Extraversion: Manson & Perry, 2013) being this sex difference common across animal species, from fish to humans (Schuett et al., 2010). This between sexes difference was not evident in wild *S. xanthosternos*, in fact, it was more salient the similarity of males and females in aggressiveness (Assertiveness). This might reflect the features of their sociality, particularly that males and females share dominant positions in the hierarchy and are coalitionary partners in the rare agonistic contests within group (Suscke, 2014).

Contrary to our predictions, we did not find sex differences in Openness-Neuroticism. We cannot dismiss that for *Sapajus xanthosternos* males this trait should be helpful for migrating (Manson & Perry, 2013) and for predatory defense (Réale et al., 2007; Sih et al., 2004). However, Openness-Neuroticism has a fearful facet, which could be also adaptive for females, more vulnerable than males since they often are carrying their helpless infants or pregnant.

The dominance during the study period (Dom 2015-16) had a slightly effect on Assertiveness in multivariate analyses (MANOVA), this is an expected result, as this trait confer skills for winning fights and for establishing alliances (Morton

et al, 2013, Lefevre et al, 2014). However, considering the hierarchy during an extended period (Dom 2010-18), the dominance did not have any effect on Assertiveness, suggesting plasticity changes of personality when an individual become alpha, which are not maintained when this individual lost the dominance. On the other hand, there is some evidence indicating that dominance in *S. xanthosternos* is highly volatile and variable across time and, sometimes, guided by circumstantial or even stochastic situations. In fact, if we observe in detail the sequence of events in ReBio Una along this study some facts can be highlighted. First, the female Priscila was dominant in 2010-2013, but she occupied the lowest status during the study period (2015-2016). Second, Gustavo occupied an intermediate position during the study period, but he is the actual alpha male. The circumstances by which this male became dominant were very similar to those reported for *S. libidinosus*, in which a deadly fight between the dominants males enabled a subordinate to become the alpha male (Mendonça-Furtado et al., 2014). In our study group, the alpha male (Cassiano) disappeared and another male (Binho) died after a strong fight between them, leaving the group only with Gustavo. Finally, three over the four adult males in the group have become alpha in some moment. This high proportion suggests that, if a male reach the adulthood, in a way or in another, he will have high probabilities to become alpha in some moment, regardless of his individual qualities. More research should be conducted in order to test if individual qualities in personality (e.g. Assertiveness) or in body features (e.g. facial features: Lefevre et al., 2014) facilitate to become dominant, or if these characteristics appear after becoming dominant (e.g. via hormonal increase: Mendonça-Furtado et al., 2014).

Finally, age was, by far, the individual variable that most influenced *S. xanthosternos* behavioral similarity; for instance, the cluster constructed by behavioral similarities (Figure 4) was almost perfectly arranged by age categories. This result has implications for personality studies, since evaluating personality entails categorizing individuals by similarities on behavioral output, especially if using behavioral coding procedure. Researchers should be cautious on capturing true personality expressions, and not behavioral responses triggered by other individual variables.

While the structure of personality across capuchin species presents many parallels (Manson & Perry, 2013, Morton et al., 2013; Uher et al., 2013, Fernandez-Bolaños et al., submitted), the effect of sex, age, and dominance are still unclear. In *S. xanthosternos*, age has a striking influence in personality traits, highlighting the necessity of controlling for developmental effects. Further long-term studies should address in detail the developmental process of personality formation in capuchin monkeys, unraveling the plasticity of each trait under social and ecological process, and analyzing the differences of this process in captive and wild species.

**Ethical approval:**

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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## **CHAPTER FOUR**

### **The individual and the social structure in *Sapajus xanthosternos***

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## The individual and the social structure of *Sapajus xanthosternos*

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**Short running title:** The individual and social structure

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## **ABSTRACT**

Hinde's seminal concept of animal social structure refers to the emergent properties of the set of interactions and relationships established among group members. The social structure may be influenced by individual variables such as sex, age, dominance, and personality. These variables structure associations of individuals through homophily and heterophily patterns. Particular individuals, called keystone individuals, may also influence the social structure. Only recently some new analytical tools are being developed to allow analyzing the social structure according to Hinde's concept. The present work analyzed the social structure of a wild group of capuchin monkeys (*Sapajus xanthosternos*) observing the effect of the aforementioned individual variables and keystone individuals. We constructed a multiplex network with five layers: grooming, agonistic, proximity, coalition and play. We conducted analyses considering separately each layer, and the whole multiplex network. The social structure was quite compact, but presented a subgroup only in the play layer with the dominant male and four receptive females. Play was the layer with the highest impact on the multiplex network, placing the youngsters in the central positions. Coalition

presented a heterophily pattern with respect to sex and a homophily pattern with respect to dominance. Personality influenced the social structure, overall Openness-Neuroticism had high impact on single layers and on multiplex. The alpha male was a keystone individual. We conclude that multiplex network approach provides information which cannot be acquired with standard layer-by-layer proceed. We also concluded that the personality was an important variable patterning the social structure of *S. xanthosternos*.

*Keywords:* homophily, heterophily, muxViz, social network analysis (SNA), multiplex, layers personality

## INTRODUCTION

The study of animal social structure (Hinde, 1976), has experimented an accelerated growth linked to advances in social network analysis (SNA) techniques (Brent, Lehmann, & Ramos-Fernández, 2011). The structure and dynamics of animal societies are typically multidimensional (Finn, Silk, Porter, & Pinter-Wollman, 2018), which was the backbone of Hinde's original definition of social structure. However, most studies of animal societies analyze each association or interaction separately, ignoring crucial interdependencies among behaviors (Silk, Finn, Porter, & Pinter-Wollman, 2018). Multiplex networks can help to overcome this caveat; in these networks, the interactive behaviors are represented in different layers connected by individuals participating in more than one layer (Finn et al., 2018). Recently, new analytical tools have emerged, allowing the analysis of the whole multiplex including its structural properties, and the relationships between layers (De Domenico, Porter, & Arenas, 2015). The

use of multiplex network analysis in biological systems, although still infrequent, has great potential for describing animal societies, and particularly, the complex primate social systems (Papio cynocephalus ursinus: Barrett, Peter Henzi, & Lusseau, 2012; Ateles geoffroyi: Smith-Aguilar, Aureli, Busia, Schaffner, & Ramos-Fernández, 2018).

In his seminal work, Hinde (1976) highlighted the relevance of attributes or characteristics of individuals (“individual variables” hereafter) such as sex, age and dominance status, in shaping the social structure. For example, through homophily, the tendency of same-category individuals to associate between themselves, or through the opposite pattern, heterophily, where individuals of different classes tend to associate. Homophily is a fundamental principle of human association, structuring marriage, friendship, work, and several other contexts of life (McPherson, Smith-Lovin, & Cook, 2001). Similarly, other animals associate based on similarity of individual variables like age, sex, or dominance status: mammals, like dolphins (*Tursiops* spp.: Lusseau & Newman, 2004), marmots (*Marmota flaviventris*: Wey & Blumstein, 2010), feral horses (*Equus ferus*: Bouskila et al., 2015), or primates (e.g., *Ateles geoffroyi*: Ramos-Fernández, Boyer, Aureli, & Vick, 2009; *Macaca sylvanus*: Sosa, 2016), and also reptiles, like lizards (*Ameiva corax*: Eifler, Eifler, Malela, & Childers, 2016). Heterophily is observed, for example, in capuchin monkeys preferential female-male coalitionary and grooming relationships (Izar, 2004; Izar et al, 2012) that can reduce the risk of infanticide (Izar, Stone, Carnegie, & Nakai, 2009). Homophily and heterophily can be context-dependent; for example, in capuchin monkeys (*Sapajus xanthosternos*), females prefer to groom other females but also prefer to remain spatially close to males (Suscke, 2014). For this reason, it

is relevant to investigate homophily and heterophily patterns using a multiplex network approach that allows analyzing the effect of individual variables considering the different interactions and associations together.

Animal personality refers to the underlying behavioral tendencies that are different across individuals and consistent within individuals over time, which affect the behavior expressed in different contexts (Stamps & Groothuis, 2010). Although still poorly studied, there is some evidence pointing towards the tight connection between social structure and personality. In humans, for example, SNA based algorithms applied on Facebook predicted personality traits more accurately than human judgment (Youyou, Kosinski, & Stillwell, 2015). In non-human primates, homophily based on personality has been described: chimpanzees “friends” are similar in Sociability and Boldness traits (*Pan troglodytes*: Massen & Koski, 2014), capuchin monkeys with similar Neuroticism scores have higher affiliative relationships, and individuals with similar Sociability scores have higher quality relationships (*Sapajus* spp.: Morton, Weiss, Buchanan-Smith, & Lee, 2015). Personality is divided in a discrete number of traits (McCrae & Costa, 1997; Weiss, 2018), and each trait is more likely to be expressed in a particular social context, for example Sociability in the grooming network, or Aggressiveness in the agonistic network. However, traits can be correlated, and should be studied together rather than as isolated units (Sih, Bell, & Johnson, 2004), thus, a multiplex network approach is suitable for analyzing the effect of personality on social structure.

Some individuals, called keystone, have an important role on the network occupying a central role interconnecting other individuals (Krause, James, & Croft, 2010), with essential contribution to the information flow or mediating the

group stability. For example, knockout studies in macaques have shown that some individuals have the role of “policers”, as their absence provokes an increase in conflicts (*Macaca nemestrina*: Flack, Girvan, de Waal, & Krakauer, 2006). In capuchin monkeys, alpha males are also keystone individuals, as the dispersal of an alpha male has relevant consequences at the group level, e.g. an increase in infant mortality (*Cebus capucinus*: Jack & Fedigan, 2018). A multiplex network approach allows for analyzing the impact of keystone individuals from a holistic perspective. For example, in a baboon troop (*Papio cynocephalus ursinus*: Barrett et al., 2012), the disappearance of the alpha female had a negligible effect on the female grooming network, but the proximity network became more clustered, groups of females became tightly connected between them, but weakly connected with the others). By adopting a multiplex approach, the authors could corroborate that the absence of the alpha female had important repercussions on the global network.

In the present study we analyzed the social structure of a wild group of capuchin monkeys (*S. xanthosternos*) constructing a multiplex network with five layers: grooming, agonism, proximity, coalitions and play. We assessed the effect of sex, age, dominance and personality on the social structure of *S. xanthosternos*. Individual variables are fundamental for understanding the animal social structure (Hinde, 1976), as the kind of associations or interactions shared by two individuals is affected by their attributes. With this analysis, we examined which associations or interactions are common to each individual variable category (for example, if dominant individuals tended to participate in agonist contests but also in grooming associations, but not in coalitions). Particularly, we analyzed the effect of personality in the way individuals interact (Krause et al,

2010). Finally, by using a multiplex network approach, we could assess how these variables affect the global social structure.

We conducted interlayer correlation analyses to explore between-layer patterns of interaction and association. With these analyses, we can enhance our understanding about *S. xanthosternos* sociality, exploring how individuals are related among them through different associations and interactions, and the tendencies of hubs (highly interconnected individuals) to be socially active in different associations and interactions.

We analyzed the community structure in each layer and in the multiplex network, assessing if sets of *S. xanthosternos* individuals are more tightly connected among them than with the rest of the group, or if connections among individuals are evenly distributed. The community structure has crucial implications in the animal social structure, mediating in the information flow, relevant for learning dynamics (Cantor & Whitehead, 2013; Coelho et al., 2015) or spread of diseases (Altizer et al., 2003).

Third, we conducted a motif analysis (Milo et al., 2002) looking for triadic structures of inter-layer relationships occurring more often than expected by chance. These triadic structures may reveal essential patterns about *S. xanthosternos* social structure, as motif analysis describes how individual relationships are mediated by a different kinds of interactions or associations, (Smith-Aguilar et al., 2018), considering not only direct connections, but also the indirect relationships established through a third individual.

In addition, we analyzed the homophily and heterophily patterns on *S. xanthosternos*, which are fundamental principles of animal association (Bouskila

et al., 2015; Eifler et al., 2016; Lusseau & Newman, 2004; Ramos-Fernández et al., 2009; Sosa, 2016; Wey & Blumstein, 2010) (Lusseau & Newman, 2004; Eifler et al., 2016; Wey & Blumstein, 2010; Bouskila et al., 2015; Ramos-Fernández et al., 2009; Sosa, 2016). The results were compared with previous studies with the same capuchin monkeys group (Suscke, 2014) (Suscke, 2014), giving the opportunity for analyzing if the patterns of *S. xanthosternos* sociality are stable thought time.

Finally, we analyzed the existence of keystone individuals conducting a “topological knockout” (Flack et al., 2006). In this procedure, we removed the associations and interaction of individuals with the highest centrality, observing changes on social structure. With these analyses we tested if *S. xanthosternos* social structure is resilient (i.e., maintains structural similarity after changes in their membership composition) or if it is weakly connected, suffering in the cohesiveness in the absence of keystone individuals. Finally, we tested if dominants are keystone individuals, as was previously found in *C. capucinus* (Jack & Fedigan, 2018) (Jack & Fedigan, 2018).

## **METHODS**

This study was conducted at the Una Biological Reserve, (Bahia, Brazil), a fully protected conservation area of ca. 18500 ha. The region is covered with lowland Atlantic Forest (Amorim, Thomas, Carvalho, & Jardim, 2008), in a mosaic of mature forest, secondary forest, and patches of agricultural fields called “cabruca” (i.e., an agroforest where cocoa trees—*Theobroma cacao*— and jack fruit occupy the understory forest; see Raboy, Christman, & Dietz, 2004).

The group of *S. xanthosternos*, called “Principe”, has been studied since 2005, when it was habituated and monitored systematically with the help of radio telemetry technology (Kierulff, Canale, & Suscke, 2005). In the present study we analyzed the period from April 2015 to March 2016, for a total of 115 days, distributed in three sampling weeks every month. During the study period two researchers (ID & MFB) and one field assistant (RSO) accompanied the group during 3 to 5 days per week, from dawn to dusk (on average 11h 37' (697') per day; SD= 2h14' (134') per day. MFB collected behavioral data at 5' scans sampling every 20', recording all occurrences (Altmann, 1974).

## **Individual variables**

### ***Sex and age***

We considered four age categories based on Verderane (2010) classification for *Sapajus*: infant, from 0 to 1.5 years; juvenile, between 1.5 and 5 years; subadult, males between 5 to 7 years old, (although we did not have information about their real age, we included in this category individuals larger than the youngsters, but without adult facial features); and adults, older than 7 years old, as indicated by the completely developed adult facial and body features. During the study period, the group had a minimum of 24 individuals and a maximum of 28 individuals, but here we focused on 26, which stayed in the group the whole period. Sex and age were not evenly distributed, with more adult females than adult males and more young males than young females: 12 adults (4♀/8♂), 5 sub-adults (0♀/5♂), 5 juveniles (2♀/3♂), and 4 infants (1♀/3♂).

### ***Dominance***

In a previous study, (Fernandez-Bolaños, Delval & Izar, 2018, in prep.) we calculated dominance hierarchies in the Principe group with the dominance-directed tree (Ditree) method using software Domina (Izar, Ferreira, & Sato, 2006). There were circularities in the dominance relationships. We established the dominance position calculating for the number of individuals reached in each individual Ditree. Based on these results, in the present study, we distinguished between subordinates (n=5), intermediates (n=18) and dominants (n=3) (Table S1).

### ***Personality traits***

We analyzed the personality of the 26 capuchin monkeys in a previous study (Fernández-Bolaños, Delval, De Oliveira, & Izar, 2018 submitted), using behavioral coding and the Hominoid Personality Questionnaire (HPQ; Weiss et al., 2009). We defined three traits: 1) Openness-Neuroticism, defined as fear and curiosity tendencies, and engaging in behaviors with impulsive, volatile and lack of calmer disposition, such as playing, 2) Assertiveness, defined as aggressive tendencies and lack of anxiety or fear, linked to anti-predatory defense behaviors, but also with certain prosocial tendencies, reflected in grooming behaviors, and, 3) Attentiveness-Sociability, defined as high prosocial tendencies, reflected in huge frequencies of grooming behaviors. We scored the 26 individuals in the three personality traits using a -3.5 to 3.5 scale.

## Interaction indices

The multiplex network had two directed interaction layers (grooming and agonistic), in which one actor directs a behavior towards a receiver, and three undirected associations layers (proximity, coalition and play) with no actor or receiver roles between individuals (table 2). However, since the five layers were analyzed together in the same multiplex network, we considered all five layers as if directed interactions. In that way, for example if individual A and B were playing, we considered that A directed play towards B, and B directed play towards A. Thus, we duplicated the information of undirected associations changing the order of individuals (A-B to B-A). For every layer we sum the events registered in the scan sampling with the events registered in all occurrences (this was not necessary with the proximity layer, as only was registered with scan sampling, table 2). With the resulting sum we calculated the Simple Ratio Index (Cairns & Schwager, 1987) modified for directed interactions:

$$\frac{A \rightarrow B}{A \rightarrow + \rightarrow B - A \rightarrow B}$$

Where  $A \rightarrow B$  is the number of events that A directed towards B,  $A \rightarrow$  is the number of events that A directed towards any individual in the group, and  $\rightarrow B$  is the number of events directed towards B from any group member. Once calculated, the five interaction indices were standardized by dividing them by the maximum value for each index. Thus, all indices were transformed to the same scale.

Table 1.

*Description of the five layers employed in present study*

Layer	directed/ undirected	Definition	Sampling
<i>Grooming</i>	directed	Picking through or manipulate the fur of another monkey with hands and/or mouth (Rose, 2000)	Scans+AO
<i>Agonistic</i>	directed	threat, chase or beat to a conspecific	Scans+AO
<i>Proximity</i>	undirected	Individuals registered within 1 m. each other	Scans
<i>Coalition</i>	undirected	Collaborating with other partners in an agonistic episode	Scans+AO
<i>Play</i>	undirected	Engaging in sequences of spontaneous, apparently non-goal oriented behaviors (Rose, 2000)	Scans+AO

Note: AO – all occurrences

## Network construction

Next, we entered the standardized interaction indices on *MuxViz*, an open-source visualization and analysis tool developed specifically for multilayer networks (De Domenico, Porter, et al., 2015), which runs on the R programming environment (R Development Core Team, 2017) with a graphical user interface. In the multiplex network, every layer represents a different association or interaction and, in each layer, every node represents a different individual. Layers are connected by individuals who participate in more than one layer (state nodes), we built an “edge-colored graph” without any *a priori* attribution of costs for changing from one layer to another, different from other kind of multiplex networks (i.e., “multilayer interconnected networks”: Solé-Ribalta, De Domenico, Gómez,

& Arenas, 2016). The multiplex network was a weighted one, in which the strength of edges (connections) was determined by the standardized interaction index of each pair of individuals in each layer. We constructed a figure representing the five-layer multiplex network, in which size of edges was proportional to strength, and size of nodes was proportional to eigenvector centrality of individuals.

### **Interlayer correlation**

In order to assess structural relations between layers in the multiplex network, we calculated edge overlap, which estimates whether individuals tightly connected in one layer, are also tightly connected in another layer (Boccaletti et al., 2014). We also calculated the Spearman correlation of node strength, which estimates whether hubs (individuals with many connections to other individuals) in one layer, are also hubs in another layer (Boccaletti et al., 2014). Furthermore, we calculated the Spearman correlation of node in-strength (receptions) and out-strength (emissions), which contribute with relevant information for the directed interaction layers. For example, the Spearman correlation of node out-strength might inform us if the individuals who emitted more grooming, are the same individuals who emitted more agonistic interactions.

### **Community structure (modularity)**

Communities (modules or cliques) are densely connected groups of individuals, with sparser connections between groups (Newman, 2004, 2006). With *MuxViz* we can search for communities on single layers using infomap algorithm, which performs random walk simulations on each layer, and identifies

modular structures in which speed flow slows down. With *MuxViz* we can also search for communities in the whole multiplex network using multiplex infomap algorithm (De Domenico, Lancichinetti, Arenas, & Rosvall, 2015), with similar proceed than infomap algorithm, but performing interlayer random walk simulations. For the multiplex infomap method a “relax rate” defines the probability for the random walk to move between layers, ranging from 0 (constraining the random walk in only one layer) to 1 (maximum probability of interlayer movement). We selected relax rate following method described by Smith-Aguilar et al. (2018): taking the intermediate value between those which rendered the maximum and the minimum number of communities. We performed the multiplex infomap algorithm with 1000 random walks.

### **Motif analysis**

Motifs can be defined as “recurring, significant patterns of interconnections” (Milo et al., 2002, p. 824). In multilayer networks, motif analysis can reveal relationships between layers and how nodes are associated through different kinds of interactions (Smith-Aguilar et al., 2018).

In the present study we looked for motifs connecting three individuals by any association or interaction represented on each of the five layers. For example, two usual playmates could exchange frequent agonistic interactions with a third individual and, if this triadic pattern occurred more often than expected by chance, this was detected as a motif involving two different layers (play and agonistic). *MuxViz* searches for triadic motifs based on randomizations of the network. We used 1000 randomizations, and a cutoff value of  $p < 0.01$  to identify

motifs. In addition, we only considered motifs representing at least 1% of the motifs in our empirical (non-randomized) multiplex network.

### **Effect of individual variables on single layers and on the multiplex**

Social networks could present assortative patterns in which individuals associate according to individual variables (Lusseau & Newman, 2004). In the present work, we analyzed the effect of sex, age, dominance, and personality traits on single layers and on multiplex network. Node versatility refers to the centrality of a node across layers in a multiplex network, a versatile node is highly active in many associations or interactions (in different layers) connecting many nodes in the multiplex network, for example, versatile nodes play an important role in the information transmission, as they are active in different communication channels (De Domenico, Solé-Ribalta, Omodei, Gómez, & Arenas, 2015). First, we conducted Pearson correlation analyses to assess the relationship between individual variables, eigenvector of single layers, and eigenvector versatility. Eigenvector is a centrality measure, which considers how well connected is an individual considering the connections of its neighbors. Among the several commonly used centrality indices, we chose Eigenvector centrality, because this index has good performance with small and densely connected networks, is suitable for weighted edges and in multiplex networks can inform about the influence of individuals in the whole network (Smith-Aguilar et al., 2018; Sueur et al., 2011; Voelkl & Kasper, 2009).

We conducted a multiple regression linear model analyzing the influence of sets of individual variables over eigenvector of single layers and eigenvector

versatility. Both the, Pearson correlations and multiple regression analysis were computed in R (R Development Core Team, 2017), considering a significance value of  $p \leq 0.05$  one-tailed.

Then, we conducted Mantel tests for assessing patterns of homophily (i.e. preferential association between same-category individuals) and heterophily (i.e. preferential association between different-category individuals) with respect to the aforementioned individual patterns (sex, age, dominance, and personality traits). In this analysis we used a binary classification of individual variables, thus, we transformed sex into a dummy variable (1=female and 2=male); in age we distinguished between adult and non-adults individuals (subadults, juveniles and infants lumped in one category); in dominance we distinguished between dominant individuals and the rest (table S1); and in the three personality traits we distinguished between low or high comparing its value to the group median. Mantel test calculates the p value from the proportion of simulations with lower or higher distribution than the observed; we considered a two-tailed significance value of  $p \leq 0.025$ . We conducted the Mantel test with 1000 permutations with the software SOCPROG (Whitehead, 2009).

### **Keystone individuals' analysis**

In multiplex analysis, we can analyze the influence keystone individuals, not just on particular networks, but also in the Social Structure. We selected the individual with the highest eigenvector versatility (indicating the greatest influence on multiplex) and conducted a topological knockout exercise (Flack et al., 2006), creating a new multiplex network without that individual (and therefore removing

all its associations and interactions from the data). We then observed how the knockout affected certain network characteristics which describe group cohesiveness. We observed changes in density (i.e. the proportion of individuals connected with respect to the maximum number of possible connections), diameter (i.e. the longest of the shortest paths connecting two individuals) and mean in path length (i.e. the mean of the shortest paths connecting two individuals). In addition, we used the knockout sample to conduct the of community analyses described in the section *Community structure (modularity)*, in order to observe the changes in communities found in the whole sample.

## RESULTS

The five-layered multiplex network of *S. xanthosternos* (Figure 1) presented 1729 intra-layer edges, and the 26 individuals appeared in all layers, with the exception of one adult female (LAR) who was not present in the play layer. The proximity layer was the most cohesive, presenting the higher density, the smaller diameter, and the smaller mean path length among all layers (Table 2). The other four layers were much less cohesive than the proximity layer, with lower densities, diameters and mean path lengths, and showing similar index values (Table 2)

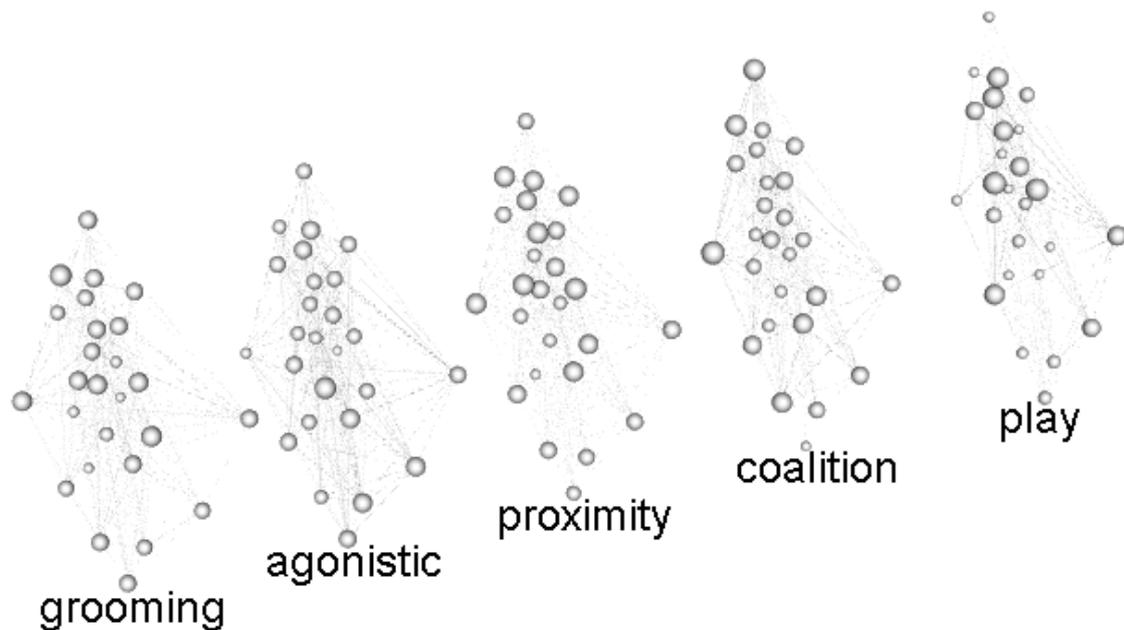
Table 2.

*Descriptive information of five layers representing interactions and associations between 26 capuchin monkeys S. xanthosternos*

Multiplex layer	Mean index	Mean weight	Min-max (weight)	Nodes	Edges	Mean degree	Density	Diameter	Mean path length
Grooming	0.04 ±0.04	2.4±1.1	0.26-4.98	26	257	19.8±7.8	0.40	0.3	1.7
Agonistic	0.04±0.03	4.3±1.7	0.81-8.09	26	232	17.8±7.6	0.36	0.7	1.7
Proximity	0.03±0.04	3±1	0.46-4.59	26	590	45.4±6.1	0.91	0.1	1.1

Coalition	0.08±0.06	4.9±2.2	0.23-9.35	26	356	27.4±10.6	0.55	0.3	1.5
Play	0.05±0.05	4.1±3.4	0-10	25	294	22.6±13.4	0.45	0.5	1.6

*Note.* Mean index and Mean weight columns, indicate values before normalization. Values following  $\pm$  are standard deviations.



*Figure 1.* Multiplex network on five layers of association and interactions of 26 capuchin monkeys (*S. xanthosternos*). Node size is proportional to layer eigenvector, edge size is proportional to edge strength.

### Interlayer correlation

To analyze interlayer similarities, we first calculated the weighted edge overlap between layers. The multiplex network had 2.3% mean edge-overlap between all layers. Proximity (the denser layer) was highly overlapped with all layers, with the exception of the agonistic one, indicating that individuals who were spatially close to each other, also groomed each other, participated in

coalitions and played together more frequently, but were not aggressive towards each other (Figure 2a). The agonistic and play layers were the most distinct, with the lower edge overlap values with the other layers (Figure 2a).

To analyze node similarities across layers, we calculated the Spearman correlation of node strength between layers. The strength of nodes was highly correlated in the coalition and grooming layers, indicating that individuals who participated in more coalitions also groom more each other than other individuals (Figure 2b), thus leading to more similarity between the grooming and the coalition layers. The play layer was more distinct; the strength of nodes in the play layer was negatively correlated with the grooming and coalition layers, indicating that individuals who engaged in more playing associations, engaged in less grooming and coalitions (Figure 2a).

Individuals who received more grooming interactions participated in more coalitions and received less agonistic interactions (Figure 2c). Individuals who received more agonistic interactions participated in more play associations but less in coalitions (Figure 2c). Individuals who directed grooming more frequently, participated in more coalitions but less in play associations (Figure 2d). Individuals who directed more agonistic interactions directed more grooming interactions, were spatially close to other individuals and participated in more coalitions (Figure 2d).

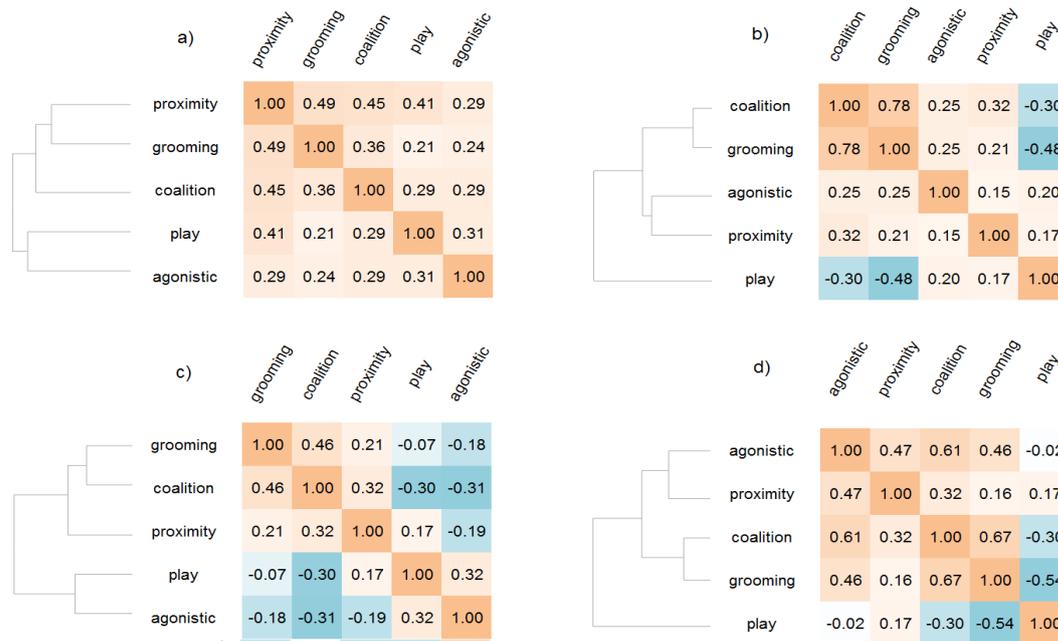


Figure 2. Node overlapping and Interlayer correlation in the *S. xanthosternos* multiplex.

a) Node overlapping, b) Spearman correlation of edges strength, c) Spearman correlation of edges in-strength, d) Spearman correlation of edges out-strength. In the left of each figure, the cluster analysis of individuals made with Jensen–Shannon distance matrix, which groups layers by similarity in related metrics. Colors from white to dark red indicated the degree of node strength (a) and positive Spearman correlation coefficient (b, c and d), and from white to dark blue negative Spearman correlation coefficient (b, c and d).

## Community structure (modularity)

We look for communities on single layers using the infomap algorithm. Results were very similar in the five layers, showing a unique single-layer community encompassing all individuals. As an exception, the play layer distinguished between five individuals and the rest. These individuals were the dominant male (CAS) and four adult females (IRE, PRE, PRI and SAM), so, in the play main component there were only two adult females (MIC and NAI), as LAR was absent in that layer (Figure 3b).

We also looked for communities in the whole multiplex network using the multiplex infomap algorithm. The maximum possible number of communities was 6, reached with a relax rate of 0.01, and the minimum number of communities was 1, with a relax rate of 0.208; thus we selected the middle value between these relax rates, that was 0.154. With a relax rate of 0.154 the 26 individuals pertained to a unique community encompassing the five layers, with the exception of LAR in the play layer (Figure 3b).

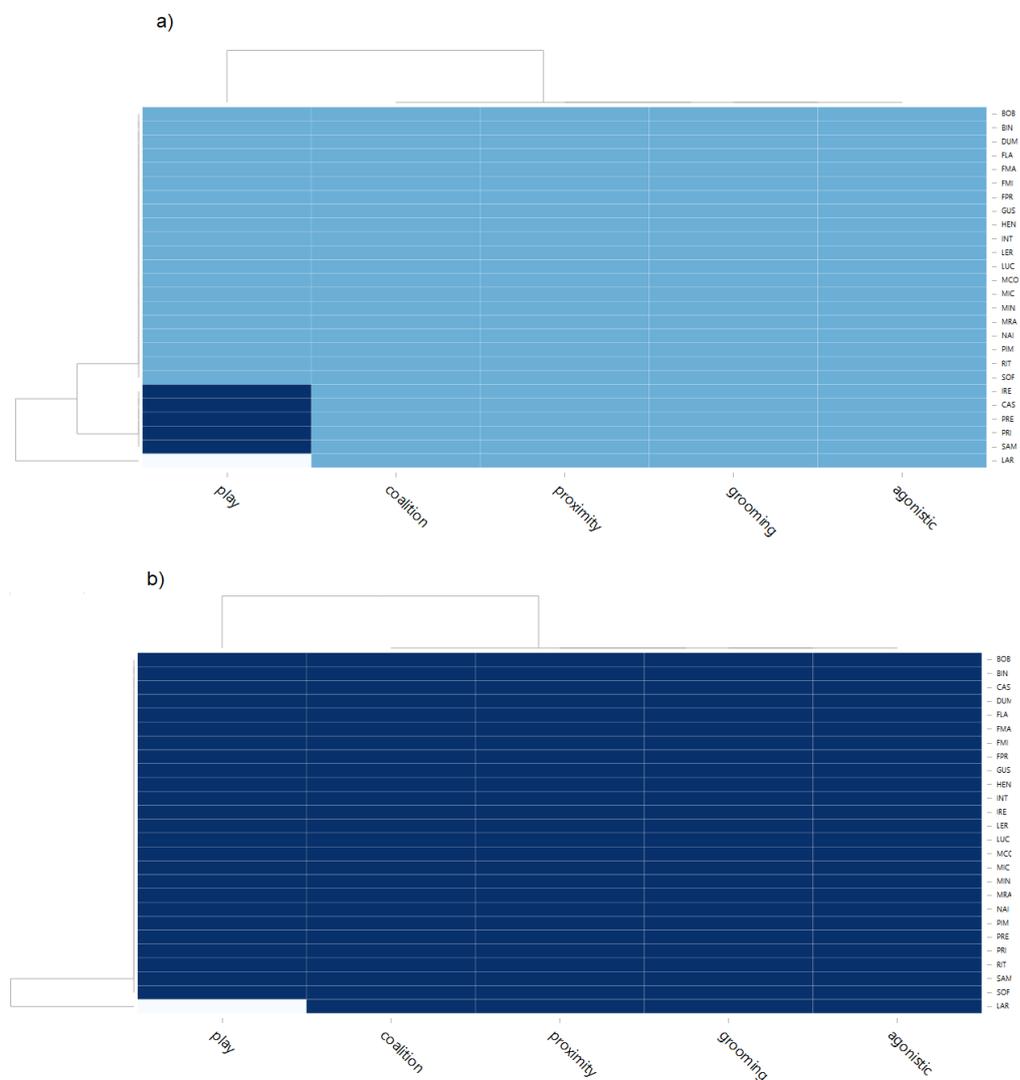


Figure 3. Communities in *S. xanthosternos*.

Communities in each layer calculated with the infomap algorithm (a) and communities in the multiplex network calculated with the multiplex infomap algorithm with relax rate 0.154 and 1000 runs (b). X-axis represents, in the bottom, the five layers of multiplex network, and in the top, the cluster analysis of layers made with Jensen–Shannon distance matrix. Y-axis represents, in the right, the 26 *S. xanthosternos* individuals, and in the left, the cluster analysis of individuals made with Jensen–Shannon distance matrix. Different blue colors indicate which individual pertain to each community, color white indicates absence of an individual in a layer.

## Motifs

Motif analysis identified nine triadic substructures that occurred more frequently than expected by chance ( $p \leq 0.01$ ) and which represented at least 1% of all empirical substructures (Figure 4). These nine motifs represented 69.4% of all triadic substructures, the two most frequent represented together 36.6%. The directed interaction layers (grooming and agonistic) were not present in any motif. The most frequent motif was a triangle fully connected by play interactions. This indicates that the most common triadic substructure was made by three habitual playmates, in which each possible pair engaged frequently in playing, but not necessarily the three at the same time. The second most frequent motif (14.7%) was a fully connected triangle composed of three different interactions: play, coalition and proximity. There were other two intra-layer motifs, both in the coalition layer, in the first the three individuals were usual companions in coalitions (7.3%), in the second two individuals were habitual coalition companions with a third, but they were not habitual companions between them (1%). In general, motif analysis revealed that individuals were frequently connected (directly or through a third individual) by playing, secondly by coalitions, and thirdly, combining these two associations and proximity.

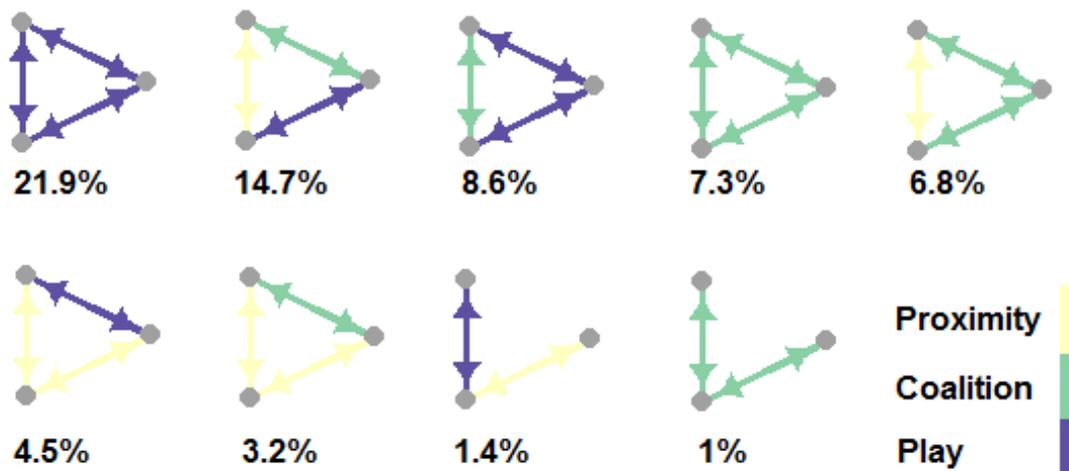


Figure 4. Motifs in the *S. xanthosternos* multiplex.

Triadic structures that occurred more often than expected ( $p < 0.01$ ) when compared to 1000 randomizations of the network, and had frequencies above 0.01 in the empirical network.

### Effect of individual variables on single layers and on versatility

From Pearson correlation, we could determine that individual variables (sex, age, dominance, Openness-Neuroticism, Assertiveness, and Attentiveness-Sociability) were not independent. Age was significantly correlated with the three personality traits (Table 3), indicating that adult individuals were lower in Openness-Neuroticism ( $r=-0.67$ ,  $p<0.001$ ), but higher in Assertiveness ( $r=0.67$ ,  $p<0.001$ ) and Attentiveness-Sociability ( $r=0.42$ ,  $p=0.033$ ) (Table 3). Males were lower in Attentiveness-Sociability ( $r=-0.46$ ,  $p=0.018$ ), and dominants higher in Assertiveness ( $r=0.65$ ,  $p<0.001$ ) (Table 3).

Play eigenvector was significantly influenced by all individual variables, with the exception of dominance (Table 3). Individuals with high eigenvalues in the play layer were mostly: youngsters ( $r=-0.92$ ,  $p<0.001$ ), males ( $r=0.46$ ,  $p<0.017$ ), with high Openness-Neuroticism scores ( $r=0.72$ ,  $p<0.001$ ), but low

Assertiveness ( $r=-0.63$ ,  $p<0.001$ ) and low Attentiveness-Sociability scores ( $r=-0.39$ ,  $p=0.048$ ) (Table 3). Conducting a multiple linear regression model with these five individual variables predicting eigenvalues of play layer, only Attentiveness-Sociability did not have a significant contribution to the model (Table 4, Mod. 4).

Individual variables affected versatility eigenvector, in a similar trend as these variables affected play eigenvector: individual with high multiplex eigenvector were youngsters ( $r=-0.81$ ,  $p<0.001$ ), with high Openness-Neuroticism scores ( $r=0.76$ ,  $p<0.001$ ), but low Assertiveness scores ( $r=-0.47$ ,  $p=0.016$ ) (Table 3). Conducting a linear model with these three individual variables predicting eigenvalues of multiplex, only Openness-Neuroticism contributed significantly to the model (Table 4, Mod. 5).

Individual variables had a similar effect on proximity eigenvector, than observed in versatility and play eigenvector: individuals with high proximity eigenvectors were young ( $r=-0.52$ ,  $p=0.006$ ) and with high Openness-Neuroticism scores ( $r=0.54$ ,  $p=0.004$ ) (Table 3). However, these two individual variables did not contribute significantly to the linear model predicting proximity eigenvalues (Table 4, Mod. 2).

Both, dominants and Individuals with high Attentiveness-Sociability score had high coalition eigenvalues ( $r=0.58$ ,  $p=0.002$ , and  $r=0.67$ ,  $p<0.001$ , respectively, Table 3), both variables contributing significantly to the linear model (Table 4, Mod 3).

No individual variable correlated significantly with eigenvalues of the agonistic layer.

Finally, the eigenvector values of layers contributed significantly on the eigenvector versatility, but specially the eigenvector of the play layer (Table 4, Mod. 6).

Table 3.

*Pearson correlation of individual variables and eigenvector of layers and versatility eigenvector.*

	age	sex	Dom	Open-Neuro	Assert	Attn-Socio	
age	1.00	-0.31	0.24	-0.67**	0.67**	0.42*	
sex	-0.31	1.00	0.16	0.31	-0.02	-0.46*	
Dom	0.24	0.16	1.00	0.26	0.65**	0.36	
Open-Neuro	-0.67**	0.31	0.26	1.00	-0.11	-0.16	
Assert	0.67**	-0.02	0.65**	-0.11	1.00	0.33	
Attn-Socio	0.42*	-0.46*	0.36	-0.16	0.33	1.00	LINEAR MODELS:
Groom	-0.04	-0.32	0.24	0.07	0.15	0.49*	Mod. 1: Groom. ~ Attn-Socio
Agon.	-0.19	-0.01	-0.09	0.19	-0.20	-0.35	
Proxim.	-0.52*	-0.02	0.15	0.54**	-0.18	0.18	Mod. 2: Prox. ~ age + Open-Neuro
Coalit.	0.33	-0.30	0.58**	0.01	0.34	0.67**	Mod. 3: Coalit. ~ Dom + Attn-Socio
Play	-0.92**	0.46*	-0.17	0.72**	-0.63**	-0.39*	Mod. 4: Play ~ age + sex + Open-Neuro + Assert + Attn-Socio
Versat.	-0.81**	0.26	0.07	0.76**	-0.47*	-0.14	Mod. 5: Versatility~ age + Open-Neuro + Assert

*Note.* Indicated in the left side the predictor variables of linear models (Table 4) correlations. \* $p \leq 0.05$ , \*\*  $p \leq 0.005$

Table 4.

*Linear model of individual variables predicting the four layers eigenvectors (Mod. 1-4) and versatility eigenvector (Mod.5) and the four layers eigenvectors predicting versatility eigenvectors (Mod.6)*

Mod. 1 Groom. ~	Estimate	Std. Error	t value	Pr(> t )	Mod. 2 Prox. ~	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.13	0.16	0.8	0.434	(Intercept)	0.75	0.16	4.53	0.000***
Attn-Socio	0.2	0.07	2.73	0.012*	age	-0.06	0.05	-1.23	0.23
Res. SD <sub>24</sub> : 0.22, Mult. R <sup>2</sup> : 0.24, Adj. R <sup>2</sup> : 0.21, F <sub>1 24</sub> : 7.48, p: 0.016					Open-Neuro	0.13	0.09	1.53	0.139
Mod. 3 Coalit. ~	Estimate	Std. Error	t value	Pr(> t )	Res. SD <sub>23</sub> : 0.21, Mult. R <sup>2</sup> : 0.34, Adj. R <sup>2</sup> : 0.28, F <sub>2 23</sub> : 5.9, p: 0.009				
(Intercept)	-0.08	0.12	-0.71	0.488	Mod. 4 Play. ~	Estimate	Std. Error	t value	Pr(> t )
Dom3	0.16	0.06	2.71	0.012*	(Intercept)	0.62	0.16	3.96	0.000***
Attn-Socio	0.2	0.06	3.63	0.001**	age	-0.14	0.05	-2.91	0.009**
Res. SD <sub>23</sub> : 0.16, Mult. R <sup>2</sup> : 0.58, Adj. R <sup>2</sup> : 0.54, F <sub>2 23</sub> : 15.87, p: 0.000					sex	0.17	0.05	3.31	0.003**
Mod. 5 Versat.~	Estimate	Std. Error	t value	Pr(> t )	Open-Neuro	0.17	0.06	2.75	0.012*
(Intercept)	0.79	0.16	5.06	0.000***	Assert	-0.12	0.05	-2.71	0.014*
age	-0.06	0.05	-1.24	0.2301	Attn-Socio	0.04	0.05	0.81	0.43
sex	0	0.05	-0.01	0.9901	Res. SD <sub>20</sub> : 0.11, Mult. R <sup>2</sup> : 0.92, Adj. R <sup>2</sup> : 0.9, F <sub>5 20</sub> : 45.76, p: 0.000				
Open-Neuro	0.18	0.07	2.79	0.0109*	Mod. 6 Versat..	Estimate	Std. Error	t value	Pr(> t )
Assert	-0.05	0.05	-1.02	0.3188	~	0.01	0.02	0.63	0.533
Res. SD <sub>21</sub> : 0.12, Mult. R <sup>2</sup> : 0.75, Adj. R <sup>2</sup> : 0.71, F <sub>4 21</sub> : 4.32, p: 0.000					(Intercept)	0.01	0.02	0.63	0.533
***=p<0.001; **=p<0.01, *=p<0.05					Groom	0.08	0.03	2.91	0.009**
					Agonist	0.24	0.02	12.73	0.000***
					Prox.	0.16	0.03	4.77	0.000***
					Coalit.	0.29	0.02	12.38	0.000***
					Play	0.54	0.02	28.75	0.000***
					Res. SD <sub>20</sub> : 0.02, Mult. R <sup>2</sup> : 0.99, Adj. R <sup>2</sup> : 0.99, F <sub>5 20</sub> : 639.2, p= 0.000				

There were patterns of homophily in the play layer with respect to age, Openness-Neuroticism and Assertiveness (Mantel test: p=0.001, p= 0.001, and

$p=0.006$ , respectively, all two-tailed, Table 5). In the coalition layer there was homophily with respect to dominance and Openness-Neuroticism (Mantel test:  $p=0.013$ , and  $p=0.006$ , respectively, all two-tailed), but heterophily with respect to sex (Mantel test:  $p=0.954$  two-tailed), indicating that coalitions were mostly formed by males and females together (Table 5). In the agonistic layer there was homophily with respect to Assertiveness (Mantel test:  $p=0.004$  two-tailed, Table 5)

Table 5.

*Mantel test with 100 permutations conducted in the five layers, with considering the individuals variables, age, sex, dominance and personality traits.*

	age	sex	Dom	Open-Neuro	Assert	attn.Socio
Grooming	0.294	0.434	0.105	0.168	0.422	0.068
Agonistim	0.074	0.08	0.327	0.004*	0.188	0.832
Proximity	0.552	0.358	0.871	0.102	0.24	0.956~*
Coalition	0.084	0.954*	0.013*	0.006*	0.924	0.514
Play	0.001**	0.02*	0.174	0.001*	0.006*	0.506

Homophily: \* $p \leq 0.025$ , \*\* $p \leq 0.0025$ , and ~\* close to significance  $0.05 \geq p < 0.025$ .

Heterophily: \* $p \geq 0.975$  and ~\* close to significance  $0.950 \geq p < 0.975$ . All correlations two-tailed

Individual variables are binary (non-adult vs adult, female vs male, subordinate vs dominant; and low vs high).

### Key stone individual analysis

The individual with highest versatility eigenvalue was an infant male (FLA), presenting also the highest eigenvalue in the play and in the proximity layer, and high eigenvalue in the grooming layer (Table6). The second and third individuals with highest versatility eigenvalue were two juvenile males (PIN and LUC) with high eigenvectors in the play and in the proximity layers (Table 6).

We performed a topological knockout excluding from multiplex all associations and interactions of the individual with highest eigenvalue (FLA), observing the effect on different layers. This procedure did not change substantially any metric of any layer (Table 7). After, we conducted with the knockout sample an intra-layer analysis of communities, with the infomap algorithm, and an inter-layer analysis of communities, with the multiplex infomap algorithm using the same relax rate employed with the whole sample (0.154). With both proceeds results were identical than observed with the whole sample (Figure 3 vs Figure S1).

Then we conducted a topological knockout with the alpha male (CAS), who was the fourth individual with highest eigenvector versatility, presenting the highest coalition eigenvector, and high eigenvector values in the proximity and in the grooming layers (Table 6). In the absence of CAS, an adult female (PRI) disappeared from the play layer (female LAR was also absent, even in the whole sample), indicating that PRI was only registered playing with CAS during the study period (Table S2). The absence of CAS also influenced the diameter of the agonistic layer, increasing 50% (Table 7), indicating that CAS was an individual who maintained the cohesiveness in the agonistic layer. The intra-layer analysis of communities show some differences when compared with same analysis made with the whole sample: the subgroup observed in the play layer made by (CAS, IRE, PRE, PRI and SAM) dissapeared (Figure 3a vs Figure S2a)

Finally, we conducted a topological knockout with the alpha female (SAM), who was the fifth individual with highest eigenvector versatility, presenting the highest grooming eigenvector, and high eigenvector values in the proximity and

in the coalition layers (Table 6). The absence of SAM did not produce any substantial difference in the cohesiveness measures (Table 7), and the analysis of communities were identical to that observed with the whole sample (Figure 3 vs Figure S3)

Table 6.

*Individual variables and eigenvector of each individual sorted by eigenvector versatility.*

ID	sex	age	Dominance	Openness-Neuroticism	Assertiveness.	Attentiveness-Sociability	Versatility	play	proximity	grooming	coalition	agonism
FLA		inf	int	1.08	-0.13	2.19	65.3	1.00	1.00	0.83	0.40	0.41
PIM		juv	int	0.80	-0.25	2.31	64.9	0.79	0.72	0.73	0.54	0.64
LUC		juv	int	1.18	0.25	1.88	64.0	0.82	0.77	0.51	0.39	0.66
CAS		ad	dom	0.20	2.38	2.75	63.7	0.05	0.76	0.74	1.00	0.08
SAM		ad	dom	0.34	1.97	2.50	62.9	0.03	0.85	1.00	0.82	0.30
FMA		inf	int	1.16	-0.47	2.25	62.8	0.83	0.83	0.68	0.41	0.73
MIN		juv	int	0.90	-0.34	1.63	62.8	0.71	0.61	0.44	0.63	0.54
MCO		sub	int	1.26	0.63	1.56	62.1	0.67	0.69	0.15	0.45	0.53
RIT		juv	int	0.86	0.31	2.56	61.6	0.62	0.55	0.55	0.61	0.84
MIC		ad	int	-0.20	0.31	2.63	61.6	0.02	0.81	0.62	0.76	0.80
SOF		juv	int	0.92	0.97	1.44	61.1	0.35	0.82	0.61	0.54	0.54
GUS		ad	int	0.04	1.31	1.63	60.3	0.23	0.46	0.47	0.45	0.77
FPR		inf	sub	0.42	-0.66	1.56	60.1	0.95	0.91	0.70	0.25	0.33
BOB		sub	int	0.34	0.56	2.00	59.3	0.58	0.46	0.38	0.49	0.48
FMI		inf	sub	0.04	-1.06	1.13	58.8	0.72	0.92	0.66	0.34	0.44
IRE		ad	int	-0.18	0.88	2.63	58.5	0.10	0.52	0.59	0.74	0.29
LER		ad	dom	-0.24	0.97	2.69	58.3	0.06	0.48	0.68	0.90	0.45
LAR		ad	int	-0.32	1.41	3.06	58.3	0.00	0.78	0.92	0.74	0.46
HEN		sub	int	-0.20	0.56	2.13	55.7	0.35	0.34	0.12	0.35	0.52

MRA	ad	int	-0.12	1.00	3.13	55.6	0.01	0.64	0.80	0.53	0.27
PRI	ad	sub	0.00	0.59	2.81	55.4	0.00	0.59	0.67	0.60	0.50
INT	sub	int	0.38	1.28	0.75	55.1	0.19	0.26	0.32	0.18	1.00
BIN	ad	int	-0.32	1.81	1.75	52.1	0.23	0.33	0.57	0.03	0.59
PRE	ad	sub	-0.52	0.41	2.06	51.0	0.03	0.29	0.58	0.42	0.43
DUM	sub	int	0.70	1.19	2.19	49.0	0.18	0.30	0.06	0.24	0.05
NAI	ad	sub	-1.48	-0.72	1.56	44.5	0.01	0.06	0.08	0.21	0.40

Note. blue = males, and with pink = females

Table 7.

*Descriptive information of five layers after three knock-out analyses: without the individual with highest eigenvector in multiplex (FLA), without the alpha male (CAS) and without the alpha female (SAM).*

Without FLA	Nodes	Edges	Density	Diameter	Mean path length
Grooming	25 (-1)	238 (-19)	0.4 (0.00)	0.4 (+0.01)	1.7 (0.0)
Agonistic	25 (-1)	220 (-12)	0.37 (+0.01)	0.7 (0.0)	1.7 (0.0)
Proximity	25 (-1)	544 (-46)	0.91 (0.00)	0.1 (0.0)	1.1 (0.0)
Coalition	25 (-1)	330 (-26)	0.55 (0.00)	0.3 (0.0)	1.5 (0.0)
Play	24 (-1)	262 (-32)	0.44 (-0.01)	0.5 (0.0)	1.6 (0.0)
Without CAS	Nodes	Edges	Density	Diameter	Mean path length
Grooming	25 (-1)	229 (-28)	0.38 (-0.02)	0.3 (0.00)	1.7 (0.0)
Agonistic	25 (-1)	210 (-22)	0.35 (-0.01)	1.4 (+0.7)	1.7 (0.0)
Proximity	25 (-1)	544 (-46)	0.91 (0.00)	0.1 (0.00)	1.1 (0.0)
Coalition	25 (-1)	308 (-48)	0.51 (-0.04)	0.3 (0.00)	1.5 (0.0)
Play	23 (-2)	280 (-14)	0.47 (+0.02)	0.1 (-0.4)	1.5 (-0.1)
Without SAM	Nodes	Edges	Density	Diameter	Mean path length
Grooming	25 (-1)	221 (-36)	0.37 (-0.03)	0.3 (0.0)	1.7 (0.0)
Agonistic	25 (-1)	209 (-23)	0.35 (-0.01)	0.8 (+0.1)	1.7 (0.0)
Proximity	25 (-1)	542 (-48)	0.90 (-0.01)	0.1 (0.0)	1.1 (0.0)
Coalition	25 (-1)	314 (-42)	0.52 (-0.03)	0.3 (0.0)	1.5 (0.0)
Play	24 (-1)	286 (-8)	0.48 (+0.03)	0.5 (0.0)	1.6 (0.0)

Note. Between parenthesis results of subtracting the whole sample value to the knock-out sample value.

## DISCUSSION

In the present study, we developed a five-layer multiplex network, enabling a holistic analysis of the social structure of a wild capuchin monkey group. Proximity was much more cohesive than the other four layers. In this layer, individuals were highly interconnected, reflecting that spatial associations are much more frequent than, for example, coalitionary associations. A similar effect was found in a six-layered multiplex network with spider monkeys (*Ateles geoffroyi*; Smith-Aguilar et al., 2018) with the layer “association”. In both studies, these differences in layer density reflect a biological reality about animal behavior. However, the higher density of proximity layer does not mean necessarily that *S. xanthosternos* socialize principally through proximity. In the remaining analysis that considered the weights of connections, reflecting the magnitude of relationships, not just number of individuals connected, proximity was less important. For example, in the motif analysis, the most frequent triadic structure did not reflect proximity associations.

In the community structure analysis, we have shown that connections were evenly distributed among individuals, without the formation of sub-groups. By using a multiplex approach, we have shown this pattern, not only in single layers, but in the whole social structure. The absence of modular patterns is usual in animal societies with a reduced number of individuals (Borgatti, Everett, & Johnson, 2018). Sometimes in these reduced groups, a modular structure reflect a transitional state before fission (Zachary, 1977). Our study group underwent changes in social organization, increasing gradually the number of memberships until fusion (Suscke, 2014). In fact, 18 months after the end of this study (in

September 2017) the group split. It is possible that the analysis of community here developed was too early for capturing modular differences.

As an exception, the play layer showed a subgroup composed by four adult females and the dominant male. These females were receptive during the study period, the other females were carrying too young infants, and another female was too old (NAI). In the study period, we observed only CAS, the dominant male, courting three females, all three belonging to the play subgroup. In addition, some of the playing events between CAS and these females occurred within the same day that the courtship happen. Capuchin monkeys present a complex courtship behavior (Carosi, Linn, & Visalberghi, 2005; Visalberghi, Di Bernardi, Marino, Fragaszy, & Izar, 2017), with many parallels with play. It is possible that in *S. xanthosternos* the adult male-female play signalize sexual receptivity, on the other hand, play between adults occurring in non-sexual social contexts could be a byproduct of its use in sex (Pellis & Iwaniuk, 2000).

The present study assessed the effect of individual variables on the social structure of *S. xanthosternos*. Sex had an effect on play, being males more central in that layer. In addition, there was a heterophilic pattern in coalition layer with respect to sex. In *S. xanthosternos* male and female dominance relations are quite egalitarian (Suscke, 2014), thus, for alpha males and females should be adaptive helping each other in maintaining their hierarchies. Supporting this, there was a homophilic pattern in coalition with respect to dominance. Interestingly, we found different patterns in relation to those described for the same group in a previous study (Suscke, 2014): male-female preference association in grooming, female-female preferential association in proximity, and

male-male agonistic interactions. This indicates that the social structure of *S. xanthosternos* is flexible, and probably affected by changes in social organization (*sensu* Kappeler & van Schaik, 2002).

Age affected the play layer: youngster individuals were more central in this layer. Play was the layer that most affected the whole multiplex network, what was observed in different analysis (motif analyses, community analysis, and eigenvector versatility). Using multiplex network approach, we could capture the relevance of play in *S. xanthosternos* social structure, using standard SNA methodology it may be not possible arrive to this result. The relevance of play in *S. xanthosternos* whole multiplex network highlights the role of play in the construction of social structures suggested for some authors (Beckoff & Byers, 1998; Fagen, 1981; Resende, Izar, & Ottoni, 2004).

Openness-Neuroticism and age had similar effects on the network, for example, both provoked a homophily pattern in the play layer. Youngsters had higher Openness-Neuroticism scores than adults, what could suggest the effect of Openness-neuroticism as a byproduct of age. Nevertheless, in some cases the effect of Openness-Neuroticism on network was higher than age. This was the case of versatility eigenvector, indicating that, having high scores of Openness-neuroticism was the principal characteristic of individuals occupying the central positions in the whole social structure of *S. xanthosternos*. In addition, individuals presented homophily patterns in coalition and agonism networks with respect to Openness-Neuroticism, patterns that were absent when considering the variable age. This trait has an homophily effect in three over the five layers considered, high and low Openness-Neuroticism individuals kept separated in play, in the

coalition and in the agonism layer. In that way, we can conclude that *S. xanthosternos* sociality is highly influenced by this trait. Openness has a “playful facet” (Weiss et al., 2009), so, open playful individual are the most usual playmates and may frequently play between them. The homophily in coalition and agonistic layers has a less straightforward explanation, and motivates future research.

Attentiveness-Sociability also influence on *S. xanthosternos* social structure, individuals with high values on this trait where more central on the grooming and coalition layers. From interlayer correlations, we observe that coalition hubs tended to be also grooming hubs, overall grooming emitter hubs. The role of grooming in establishing alliances and agonistic support is well known (e.g., Schino, 2007). Here we show for the first time that this association might reflect personality tendencies. Future studies should address the role of pro-social facet of personality, like Attentiveness-Sociability or similar traits (Sociability: Weiss et al. 2009; Agreeableness: Costa & McCrae, 1992).

Assertiveness was the trait personality with the most reduced influence on social structure. However, it had a slight effect on the play layer, individuals with high Assertiveness rarely engage in playing. In addition, an homophily pattern, high and low Assertiveness individuals tend to play separately. Perhaps assertive individuals have different kind of plays, a future hypothesis to be tested is, if assertive individuals engage more frequently in “play fighting” (Aldis, 2013).

Our results supported the hypothesis that personality affect social networks, in accordance with previous evidence with humans (Youyou et al., 2015) and non-human primates (Massen & Koski, 2014; Morton et al., 2015),

2014). We advanced these previous studies by showing this effect in the whole social structure, by adopting the multiplex analysis. This appeared to be a promising paradigm, motivating more studies in that direction.

We analyzed the existence of keystone individuals. Retiring, FLA, the individual with the highest centrality in the whole social structure (highest eigenvector versatility) did not provoke any substantial change. The relevance of FLA in the network was explained by its centrality in the proximity and in the play layer. On the one hand, the proximity layer was highly cohesive, and so resilient to structural changes. On the other hand, from motif analysis we observed that the most frequent substructure was made by three habitual playmates, so, if FLA is one of these playmates, its disappearance will not have great impact, as the other two playmates are directly connected.

We also tested if dominants were keystones individuals, the alpha male, CAS, seem to be, but not the alpha female, SAM. In the agonism layer, the absence of CAS provoked a decrease in cohesiveness, particularly in diameter, we can consider that CAS was a “broker” in the agonist layer (*Tursiops* spp: Lusseau & Newman, 2004). In the play layer the absence of CAS has the opposite effect, the subgroup to which it belonged joined to the main group. These opposite effects can be explained by the topology position of CAS in the network: in the agonist layer CAS was highly central in the group, and its absence made the others less connected; in the play layer CAS was highly central in the sub-group, and its disappearance made the other subgroup members join to the main group, though weaker connections to main-component members. The role of the dominant in capuchin monkeys has been previously reported (C.

*capucinus*, Jack & Fedigan, 2018), in fact, some authors propose that dominant individuals should be considered intrinsically key individuals (Sih, Hanser, & McHugh, 2009).

In conclusion, we highlighted the importance of Hinde's concepts (1976), and studied the social structure in its widest sense. We have shown results that would not be possible with standard layer-by-layer SNA. New analytical tools, particularly *Muxviz* (De Domenico, Porter, et al., 2015), facilitate the complex analysis, highlighting the importance of incorporating network multiplex in SNA.

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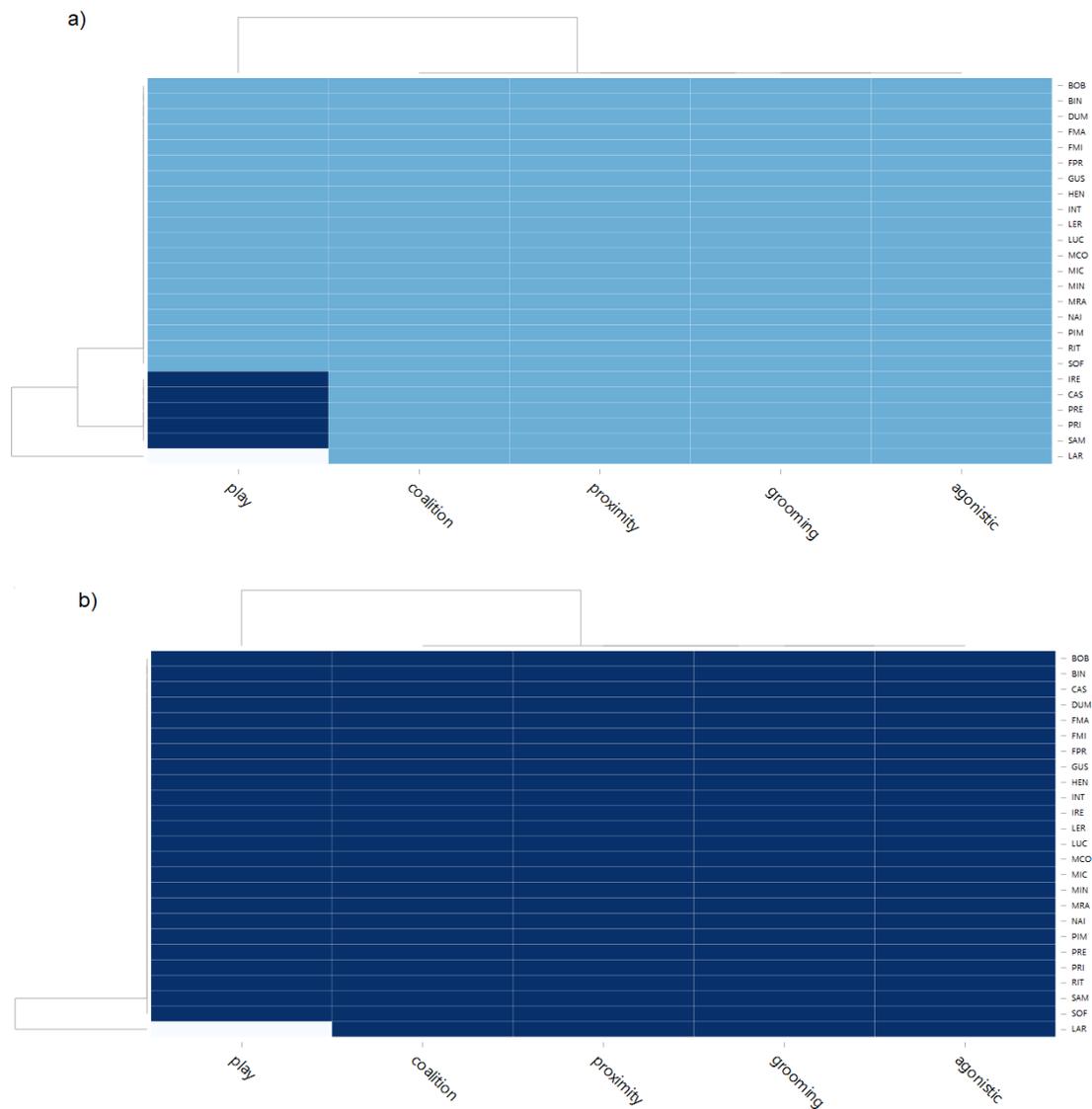
## Supplementary material- Chapter Four

Table S1.

*Hierarchy of dominance of the S. xanthosternos Principe group*

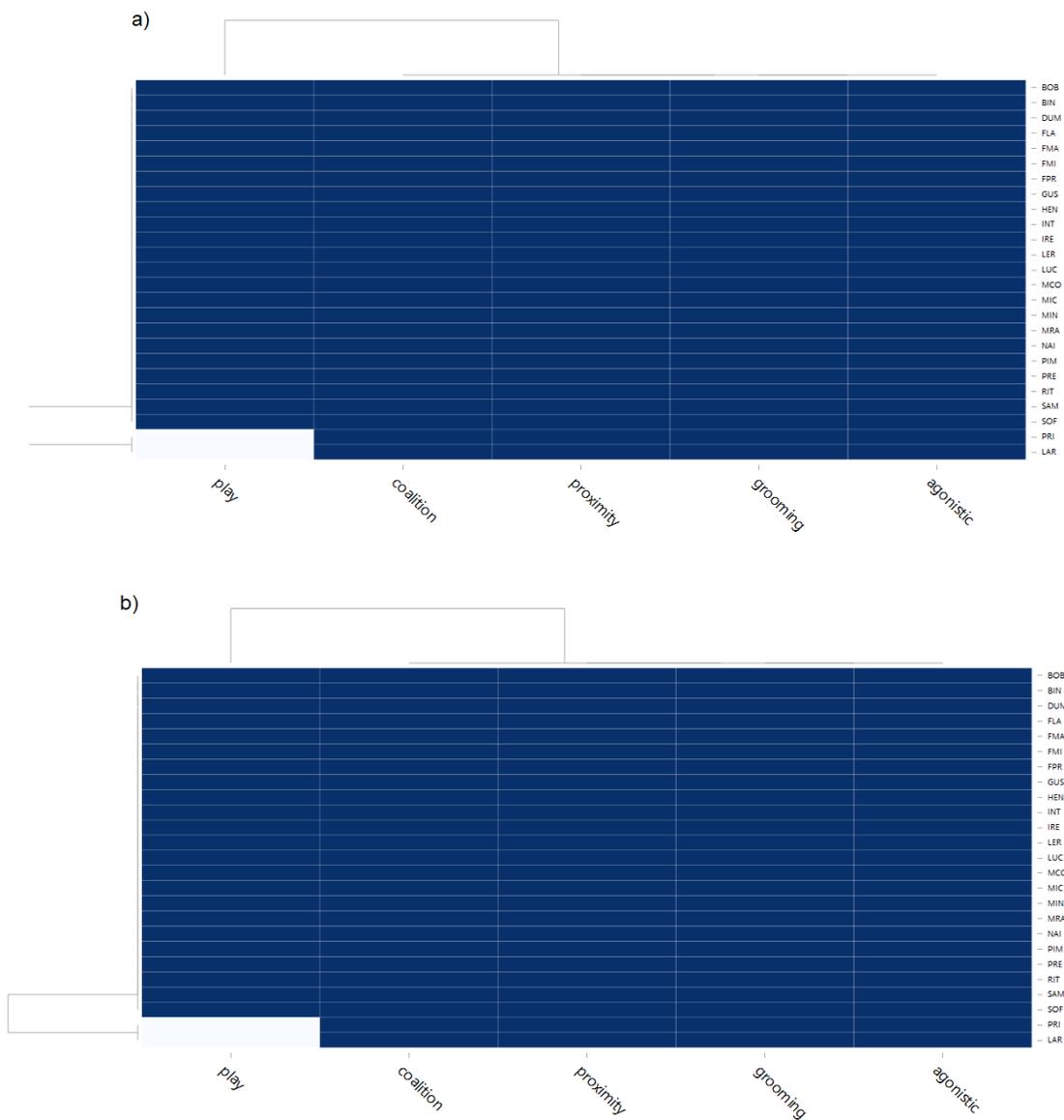
id	n ind. Dit.	3cat	2cat
NAI	1	sub	sub
FMA	24	int	sub
FMI	2	sub	sub
FLA	24	int	sub
FPR	1	sub	sub
HEN	24	int	sub
BIN	24	int	sub
PRE	3	sub	sub
LER	25	dom	dom
PRI	1	sub	sub
LAR	24	int	sub
MAR	24	int	sub
MIC	24	int	sub
SAM	26	dom	dom
CAS	28	dom	dom
IRE	24	int	sub
GUS	24	int	sub
INT	24	int	sub
DUM	24	int	sub
SOF	24	int	sub
LUC	24	int	sub
MIN	24	int	sub
PIM	24	int	sub
RIT	24	int	sub
MAR	24	int	sub
BOB	24	int	sub

*Note.* **n ind. Dit.** (2<sup>nd</sup> column) indicates, for each individual, the number of individuals reached in its Ditre after imposing a transitive rule. Binary classification (2cat) used in Mantel test.



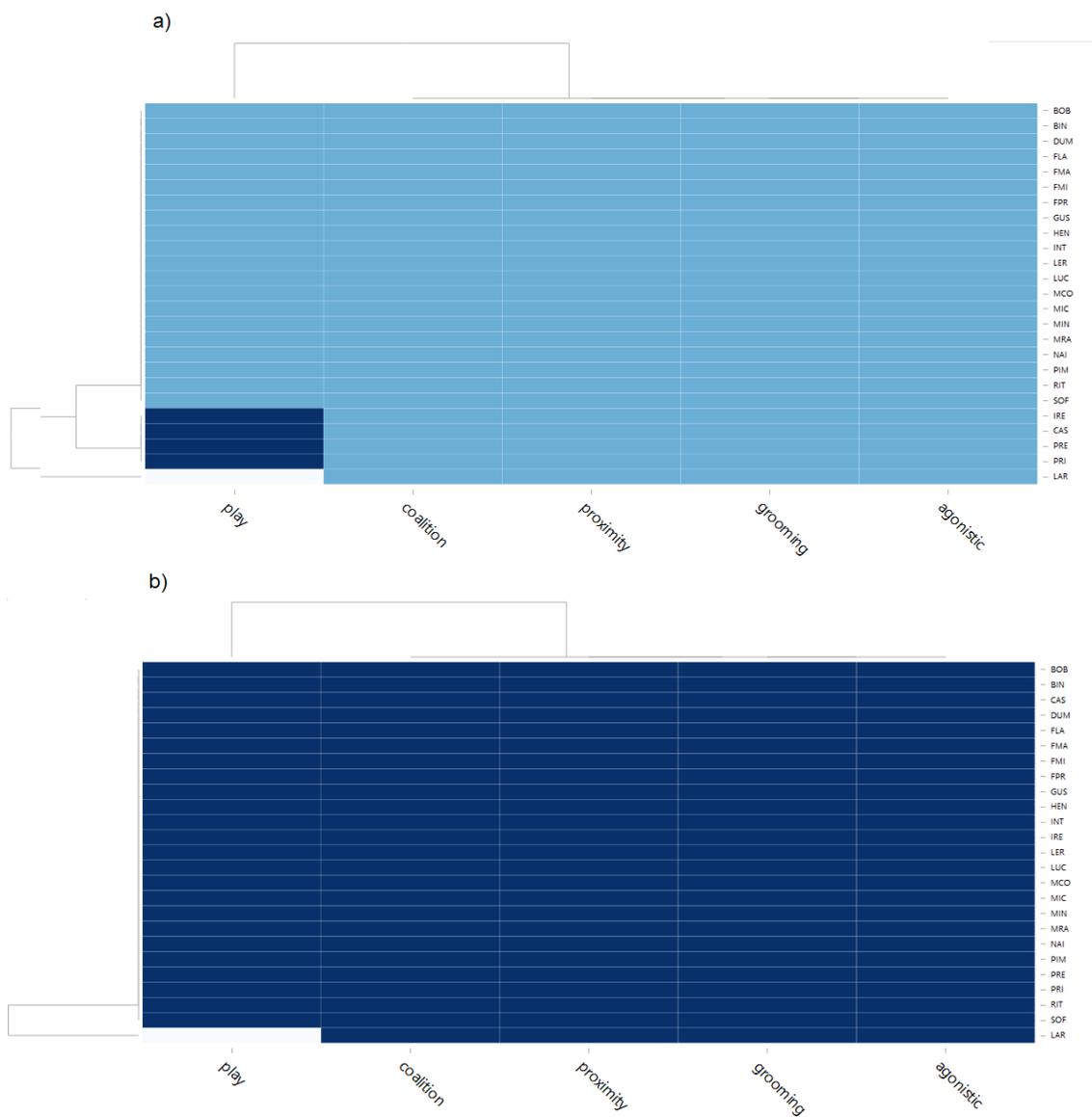
*Figure S1. Communities in S. xanthosternos after FLA knockctout.*

Communities in each layer calculated with the infomap algorithm (a) and communities in the multiplex network calculated with the multiplex infomap algorithm with relax rate 0.154 and 1000 runs (b). The x-axis represents, in the bottom, the five layers of multiplex network, and in the top, the cluster analysis of layers made with Jensen–Shannon distance matrix. The y-axis represents, in the right, the 26 *S. xanthosternos* individuals, and in the left, the cluster analysis of individuals made with Jensen–Shannon distance matrix. Different blue colors indicate which individual pertain to each community, color white indicates absence of an individual in a layer.



*Figure S2. Communities in S. xanthosternos after CAS knockctout.*

Communities in each layer calculated with the infomap algorithm (a) and communities in the multiplex network calculated with the multiplex infomap algorithm with relax rate 0.154 and 1000 runs (b). The x-axis represents, in the bottom, the five layers of multiplex network, and in the top, the cluster analysis of layers made with Jensen–Shannon distance matrix. The y-axis represents, in the right, the 26 *S. xanthosternos* individuals, and in the left, the cluster analysis of individuals made with Jensen–Shannon distance matrix. Different blue colors indicate which individual pertain to each community, color white indicates absence of an individual in a layer.



**Figure S3.** Communities in *S. xanthosternos* after SAM knockout.

Communities in each layer calculated with the infomap algorithm (a) and communities in the multiplex network calculated with the multiplex infomap algorithm with relax rate 0.154 and 1000 runs (b). The x-axis represents, in the bottom, the five layers of multiplex network, and in the top, the cluster analysis of layers made with Jensen–Shannon distance matrix. The y-axis represents, in the right, the 26 *S. xanthosternos* individuals, and in the left, the cluster analysis of individuals made with Jensen–Shannon distance matrix. Different blue colors indicate which individual pertain to each community, color white indicates absence of an individual in a layer.

## **CHAPTER FIVE**

### **Conclusion**

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Marcelo Fernández-Bolaños

Along the previous chapters, we have analyzed several issues about the individual and the social structure of wild *S. xanthosternos*.

We started analyzing the personality of the studied individuals using trait rating with questionnaire HPQ (Weiss et al. 2009). We developed a personality structure, which was compared with the structure of captive 126 *Sapajus* spp. (Morton et al., 2013), and with behavioral coding traits. We described three personality traits: 1) Openness-Neuroticism, defined as fear and curiosity tendencies, and engaging in behaviors with impulsive, volatile and lack of calmer disposition, such as playing; 2) Assertiveness, defined as aggressive tendencies and lack of anxiety or fear, linked to anti-predatory defense behaviors, but also with certain prosocial tendencies, reflected in grooming behaviors; and 3) Attentiveness-Sociability, defined as high prosocial tendencies, reflected in high frequencies of grooming behaviors. We concluded that trait rating was more suitable than behavioral coding for capturing *S. xanthosternos* personality, but personality description from trait rating enhanced when compared with single behaviors. Through comparison with other studies, we hypothesized that the traits Openness, Neuroticism, Assertiveness and Sociability, could be the core elements of capuchin monkeys personality.

Secondly, we analyzed whether and how the individual variables, sex, age, and dominance affect personality of *S. xanthosternos*, and results showed high effect of age. We also tested which of these individual variables (including personality) have the greatest impact on *S. xanthosternos* behavioral similarity, and, again age was the most relevant variable. These results highlights the need for controlling for the developmental effects on personality studies. The

developmental curves were compared with other primate species, revealing striking parallels, especially with humans, suggesting a typical developmental process of personality in the Primate order.

Finally, we described the social structure of *S. xanthosternos* using an innovative multiplex network approach, analyzing five layers: grooming, agonistic, proximity, coalition and play, but also the whole network structure considering the five layers. We investigated the effect of the individual variables sex, age, dominance, and personality on single layers and on multiplex network, and the effect of particular individual (keystone individuals). Results showed that play was the layer with greatest impact on the whole multiplex network, placing the youngsters in the central position. The social structure of *S. xanthosternos* was compact, without internal community divisions, but the play layer had a subgroup including the dominant male and four receptive females. Coalition tended to be made by males and females, with a homophily pattern with respect to dominance, suggesting that alpha males and females supported each other maintaining their hierarchies. The patterns described in a previous study with the same group (Suscke, 2014) were not replicated in our study, suggesting that the social structure of *S. xanthosternos* is flexible across time. Personality had a relevant effect on the social structure of *S. xanthosternos*. Overall the trait Openness-neuroticism affected several layers and the whole multiplex network. Agonism, coalition, and play presented homophily patterns with respect to Openness-Neuroticism, and this trait had the greatest impact on centrality in the whole social structure (eigenvector versatility). The alpha male was a keystone

individual, as its topological absence created a decrease in cohesiveness in the agonistic layer, and caused the disappearance of the play subgroup.

As a closure conclusion, we emphasize the importance of considering personality in primates, and other animal studies of behavior, the need for controlling for developmental effects on studies of personality, and the importance of studying animal social structure from a holistic perspective, following the path pointed by Robert Hinde more than 40 years ago.

# ETHICAL COMMITTEE APPROVAL



INSTITUTO DE PSICOLOGIA  
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Comissão de Ética no Uso de Animais  
Universidade de São Paulo

## CERTIFICADO

Certificamos que o Projeto Intitulado "Plasticidade fenotípica de macacos-prego (gênero Sapajus): Investigação sobre o efeito de trajetórias ontogenéticas distintas e de ativação contexto-dependente.", protocolado sob o CEUA nº 6870180216, sob a responsabilidade de Patricia Izar - que envolve a produção, manutenção e/ou utilização de animais pertencentes ao filo Chordata, subfilo Vertebrata (exceto o homem), para fins de pesquisa científica ou ensino - está de acordo com os preceitos da Lei 11.794 de 8 de outubro de 2008, com o Decreto 6.899 de 15 de julho de 2009, bem como com as normas editadas pelo Conselho Nacional de Controle da Experimentação Animal (CONCEA). Este projeto foi aprovado pela Comissão de Ética no Uso de Animais do Instituto de Psicologia da Universidade de São Paulo (CEUA/IPUSP) na reunião de 25/02/2016.

We certify that the proposal "Phenotypic plasticity of tufted capuchin monkeys (genus Sapajus): effect of different ontogenetic trajectories or of context-dependent activation?", utilizing 70 Non-human primates (males and females), protocol number CEUA 6870180216, under the responsibility of Patricia Izar - which involves the production, maintenance and/or use of animals belonging to the phylum Chordata, subphylum Vertebrata (except human beings), for scientific research purposes or teaching - is in accordance with the Law 11.794 of October 8 2008, Decree 6899 of July 15, 2009, as well as with the rules issued by the National Council for Control of Animal Experimentation (CONCEA). This project was thereby approved by the Ethic Committee on Animal Use of the Psychology Institute of the University of São Paulo (CEUA/IPUSP) in the meeting of 02/25/2016.

Vigência da Proposta: de 03/2016 a 10/2020

Laboratório: Psicologia Experimental

Procedência: Não aplicável

Espécie: Primatas não-humanos

Linhagem: Sapajus flavius

Gênero: Machos e Fêmeas

Idade: diversas

N: 15

Peso: diversos

Procedência: Não aplicável

Espécie: Primatas não-humanos

Linhagem: Sapajus libidinosus

Gênero: Machos e Fêmeas

Idade: diversas

N: 25

Peso: diversos

Procedência: Não aplicável

Espécie: Primatas não-humanos

Linhagem: Sapajus nigritus

Gênero: Machos e Fêmeas

Idade: diversas

N: 15

Peso: diversos

Procedência: Não aplicável

Espécie: Primatas não-humanos

Linhagem: Sapajus xanthosternos

Gênero: Machos e Fêmeas

Idade: diversas

N: 15

Peso: diversos

Resumo: A literatura em comportamento animal evidencia interesse crescente na ideia de plasticidade fenotípica como fator crucial na evolução. Dentre os primatas não humanos, o gênero Neotropical Sapajus constitui modelo ideal para investigar hipóteses sobre plasticidade comportamental como adaptação a diversidade de contextos ambientais. Assim, o objetivo deste projeto é investigar fatores subjacentes à variabilidade comportamental observada entre populações de Sapajus. Buscaremos responder se essa plasticidade resulta de flexibilidade reversível contingente a mudanças ambientais (plasticidade ativacional) ou de trajetórias ontogenéticas distintas desde o desenvolvimento inicial das diferentes populações (plasticidade ontogenética), por meio da relação entre variância intra e entre populações ao longo de diferentes fases do desenvolvimento. Também investigaremos, por meio de uma análise genômica e de análises de covariação fenotípica e genética por modelos mistos, a hipótese nula de que a variabilidade é resultado de variação genética. Para tanto, serão comparados, por meio de filmagens semanais de um dia inteiro, indivíduos de quatro populações selvagens de espécies irmãs (*S. nigritus*, *S. libidinosus*, *S. xanthosternos* e *S. flavius*), do nascimento até os 36 meses de idade, bem como variáveis ecológicas e características dos sistemas sociais, e genótipo, comportamento e perfil hormonal de todos os indivíduos dos grupos estudados. Este projeto é multicêntrico, envolvendo pesquisadores brasileiros da USP (IP e IB), UNESP Botucatu, UFABC e UFRN, norte-americanos, das Universidades da Califórnia, Los Angeles, da Geórgia, Athens, e de Medicina e Biociências de Kansas, europeus, do Instituto de Ciência e Cognição de Roma, Itália e da Universidade de Veterinária de Viena, Áustria, e um pesquisador do Instituto Politécnico Nacional do México.

São Paulo, 25 de fevereiro de 2016

Prof. Dra. Christiane Assis Izar  
Coordenadora da Comissão de Ética no Uso de Animais  
Instituto de Psicologia da Universidade de São Paulo

