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Instituto de Psicologia

Departamento de Psicologia Experimental

IRENE DELVAL

Personality development in capuchin monkeys: connecting Psychology and Behavioral Ecology

O desenvolvimento da personalidade em macacos-prego: unindo Psicologia e Ecologia Comportamental

São Paulo

2019

IRENE DELVAL

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Versão Original

Tese apresentada ao Instituto de Psicologia da Universidade de São Paulo para a obtenção do título de Doutor em Ciência

Área de Concentração: Psicologia Experimental – Comportamento Animal

Orientadora: Profª. Dra. Patrícia Izar

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Prof.(a)Dr.(a)_____

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Prof.(a)Dr.(a)_____

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Prof.(a)Dr.(a)_____

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Prof.(a)Dr.(a)_____

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

A mis padres, por enseñarme a ser libre.

ACKNOWLEDGEMENTS

First, I would like to thank my supervisor Patrícia Izar, for believe in me and for accepting to advise this thesis. Her positive comments and support along this long way were crucial for getting into a happy end.

Thanks to Gisele Zago (Gi), who was always there for solving problems (bureaucratic and from any kind), and giving moral support. Briseida, Miriam, Emma, Edu, Nicolás, Ronara, Jarka and Marco also contributed with animated talks.

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During the 18 months I have been collecting data for this thesis, I moved to Ilhéus (“Princesinha do Sul”) and met a wonderful crew that made my weekends easier after exhausting weeks of data collection. All “Asilo” people: Fabio Falcão, Christine Caselli, Tito e Ellen, Gauchinho, Victor e Balinha, Flora e Harley, Carol Cornelio, Caroleta, Marcial, Deyna, Iuri, Caio e Fer, Jhon Freddy, Vanessinha, Generoso, Lander, Luciana, Luna e Lucas... and many people around them made our almost two years in Ilhéus unforgettable. It has been an enormous luck to meet you guys, you will be always on my heart.

Fieldwork would not have been possible without the invaluable work of Robson Santos de Oliveira, Binho. Besides being the best filed assistant, responsible and interested in our particular science, he became a real friend. We shared, laughs, rainy days, mosquito biting, swamps falling and many other anecdotes.

I am also extremely grateful to Priscila Suscke, whose prior work made possible this research. Thank you, Pri, for your warm welcoming in Bahia and for all the good advices you gave us.

Back in São Paulo, after the data collection period, we re-encounter many friends. Thank you “Solimary & John” (you are like one person in two), for “sopitas” in the winter, when I was analyzing videos and writing first drafts of this thesis in the cold. Besides feeding me, Solimary had such a great patience that seated by my side and taught me how to fit mixed models in R. She always said that she “enjoys performing this kind of analysis”, but I know no one could be that masochist. I really appreciate your patience, querida.

The last months of writing of this thesis, I invaded the laboratory LAGE, in the IB-USP, where I was cordially welcomed and I found the lost concentration. Thanks to everyone there for accepting an infiltrated and desperate student.

My former roommates, Agustin and Isa, were excellent examples of high-motivated researchers, thank you as well.

Thank you to my neighbors, Nadamal and Pepela, for the good times in the garden, beer and bees, maracujá growing, and many different conversations,

all good ones. Also Bussa, Bira, Pantufa and all the Bio “turma”, that have been important figures in my integration in this terrible city.

This thesis ending have been particularly “intense” because it coincided with my son’s birth. Having a child has been the most exciting adventure in my life and the coincidence with my thesis ending could seem a mad thing. However, it helped me to relativize and gave me the peace and confidence I was lacking. Therefore, I must also thank my beautiful baby, Lino. My mother, Violeta, and my-mother-in-law, Isabel, were the Mary Poppins on this fairy tale, helping us as much as possible while we were PhD parents, both writing our thesis. Along with them is tía Peri, also willing to be a grandmother for Lino. My dad and Paz have been long-distance supporters, by Skype.

Thanks to Marcelo. We have always been a great team, professionally and domestically and, recently, it has been proven that our DNAs combine perfectly.

In addition, I am thankful to R for making easier my analyses.

I am grateful to CAPES for my doctoral grant. I feel lucky for receiving a grant during my PhD years. Today, it is hardly to believe that terrible politics are interested in destroying the scientific progress and achievements of the last years in this country. Not with my permission; we will have to fight them! No pasarán.

Lastly, I must be grateful to each of the 26 monkeys from *Principe* group at ReBio Una, for teaching me that we are all primates.

São Paulo, May 29th, 2019

Resumo

Delval, I. (2019). *O desenvolvimento da personalidade em macacos-prego selvagens: unindo a Psicologia e a Ecologia Comportamental*. Tese de doutorado. Instituto de Psicologia, Universidade de São Paulo, SP, Brasil.

O estudo da personalidade em animais é relativamente recente. Até pouco tempo atrás, na Ecologia Comportamental, as diferenças individuais consistentes eram consideradas 'ruído' em torno à estratégia ótima. Na Psicologia, evitava-se falar de personalidade em animais por temor à antropomorfização. As pesquisas têm mostrado que diferenças de personalidade se manifestam em inúmeras espécies, como formas diferentes de lidar com as pressões seletivas, com consequências para a aptidão, sendo assim uma variável muito importante em ambientes que mudam. Temperamento, Personalidade, Síndrome Comportamental ou Estilo de Enfrentamento são nomes que têm sido usados para se referir ao fenômeno dos animais exibirem "diferenças interindividuais consistentes ao longo do tempo e das situações". Porém, esses termos não são exatamente sinônimos. Ao longo desta tese, primeiro revisei o percurso histórico do estudo da personalidade em animais a partir das perspectivas da Psicologia e da Ecologia Comportamental, buscando os pontos em comum e as possibilidades de unificação das duas escolas. No segundo capítulo, avaliei se houve diferenças de personalidade, mediante a codificação do comportamento, em doze macacos-prego selvagens observados dentre 0 e 3 anos de idade. Para tanto, verificamos, usando uma análise de repetibilidade, se as diferenças individuais foram consistentes ao longo de 10 pontos de desenvolvimento, para conferir se as características de personalidade estavam já presentes logo ao nascimento ou se sofreram modificações ao longo

do desenvolvimento. Mediante análise dos componentes principais obtivemos quatro traços de personalidade: Sociabilidade-Atratividade, Ansiedade, Apertura e Atividade, achando um efeito do desenvolvimento em Sociabilidade (que diminuiu com a idade) e Ansiedade (que aumentou). Contudo, não foi possível verificar consistência intra-individual nos traços ao longo do tempo analisado. Em consonância com a literatura de personalidade e temperamento em humanos, os resultados indicaram que a estrutura da personalidade não está ainda estabelecida no começo do desenvolvimento.

Palavras chave: Personalidade, Temperamento, Traços, Desenvolvimento, Repetibilidade, Sapajus *xanthosternos*

Abstract

Delval, I. (2019). *Personality development in wild capuchin monkeys: connecting Psychology and Behavioral Ecology*. PhD thesis, Institute of Psychology, University of São Paulo, SP, Brazil.

The study of animal personality is relatively new. Until recently, in Behavioral Ecology, consistent individual differences were considered 'noise' around an optimal strategy. In Psychology, animal personality was avoided as a consequence of the fear of anthropomorphization. Research has shown that personality differences are manifest in many species, evident from different forms of dealing with selective pressures, with consequences for fitness, thus, being an important variable in changing environments. Temperament, Personality, Behavioral Syndrome, or Coping Style are names that have been used to refer to the phenomenon of animals exhibiting "consistent interindividual differences over time and across situations”. However, these terms are not exactly synonyms. Throughout this thesis, I first reviewed the historical course of the study of personality in animals, from the perspectives of Psychology and Behavioral Ecology, looking for points in common and possibilities of unification of the two schools. In the second chapter, I evaluated, through behavioral coding, if there were personality differences in twelve young wild capuchin monkeys, between 0 and 3 years-old. Then, we verified using a repeatability analysis whether the individual differences were consistent across 10 developmental points, to find out if the personality traits were already present at birth or if they were acquired during development. By means of principal component analysis, we obtained four personality traits: Sociability-Attractiveness, Anxiety, Openness and Activity, finding an effect of development on Sociability (which decreased

with age) and Anxiety (which increased). However, it was not possible to verify intra-individual consistency in the traits throughout the analyzed time. Consistent with the literature on personality and temperament in humans, the results indicated that personality structure is not yet established at the beginning of development.

Keywords: Personality, Temperament, Development, Repeatability, *Sapajus xanthosternos*

SUMMARY

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GENERAL INTRODUCTION

Irene Delval

General Introduction

Irene Delval

PRESENTATION

This thesis is more than the outcome of a four-years long research; it is the result of a long path that begun in the last year of my undergraduate studies, when I became interested in primate behavior. This interest became so important that make me took some crazy decisions, like moving to a different country, in a different continent across the sea, in order to satisfy my necessity to conduct a research with wild primates. Destiny placed Patricia Izar on my way, and she was so kind to accept two Spanish students at once (me and my partner Marcelo), that did not even speak Portuguese.

During the Master's degree, I could experience the difficulties and toughness of the fieldwork, collecting data in Carlos Botelho State Park, in São Paulo State, one of the largest remnants of Atlantic Forest. We followed several groups of *Sapajus nigritus*, with not much success because of the difficulties in finding the groups in this huge area. Fortunately, during the Master's degree, I could add data already collected by other students to my analyses, and my own data collection was used by other students from our Cognitive Ethology laboratory. After this experience, the idea of facing the PhD having problems in finding the monkeys made me decide moving to other state to guarantee the data collection. During thirteen months, we followed a wild group of *S. xanthosternos* living in Una Biological Reserve, a small remnant of Atlantic Forest in southern Bahia State. This group is monitored by radio telemetry (i.e., one adult female

wears a radio-collar), so every week we have been able to find and follow the group.

Fieldwork is a transforming experience because it is you and your co-workers, alone in the wild, under the exhaustive scrutiny of the monkeys above your head, allowing you to be a part of their lives. In the course of these thirteen months, I became an old-school naturalist, being on the field 12 hours a day, 5 days a week. Apart from collecting video recordings, I wrote a diary, thinking someday it would became a book. I cannot lie and say fieldwork was easy, because it was not: it had lots of rain, crossing rivers, swamps falling, poisonous snakes, mosquitos, a suffocating hot, and many just boring hours. However, I believe it changed my point of view and I strongly recommend every primatologist to pass through this experience. Of course, it has too unforgettable moments and very exciting wild life memories.

This thesis is about personality differences in young capuchin monkeys. I present here two main chapters, formatted as original articles. Chapter One will be submitted to an international scientific journal after the important feedback obtained from the examination board. Chapter Two has already been submitted to a special issue shared by the *American Journal of Primatology* and *Developmental Psychobiology* and is currently under review. The first chapter is a general review about the personality research science within a comparative perspective. The second chapter is properly the result of the field efforts described above, along with many hours of film transcription and data analysis on R. However, since I am not sure when the book derived for my diary will come to the light, I decide to include in this General Introduction more details about what often is not included in scientific journal articles: field conditions and

location, species description, individuals recognition, transcription process, etc. In the final concluding remarks, I briefly highlight the main results of this thesis.

UNRAVELING FIELDWORK

Who is who in this thesis

Capuchin monkeys: a smart Neotropical primate

Capuchin monkeys are Neotropical medium-size sexually dimorphic primates of the family *Cebidae* (Fleagle, 2013), with peculiar cognitive skills, such as the use of tools (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004), and high social complexity (Izar et al., 2012). At the beginning of the 20th century, capuchin monkeys were split in two groups, “tufted” and “untufted” (Elliot, 1913), but they were not recognized as differentiated genera*, Sapajus* and *Cebus*, until the studies of Lynch-Alfaro and collaborators (Lynch Alfaro, Boubli, et al., 2012; Lynch Alfaro, Silva Jr., & Rylands, 2012). These two genera represent two lineages, robust and gracile that started to diverge in the Miocene (Lynch Alfaro, Boubli, et al., 2012). Together, both genera encompasses eight species that cover a broad area of Central and South America (Lynch Alfaro, Boubli, et al., 2012; Figure 1), from Panama to the north of Argentina (Mittermeier, Rylands, & Wilson, 2013).

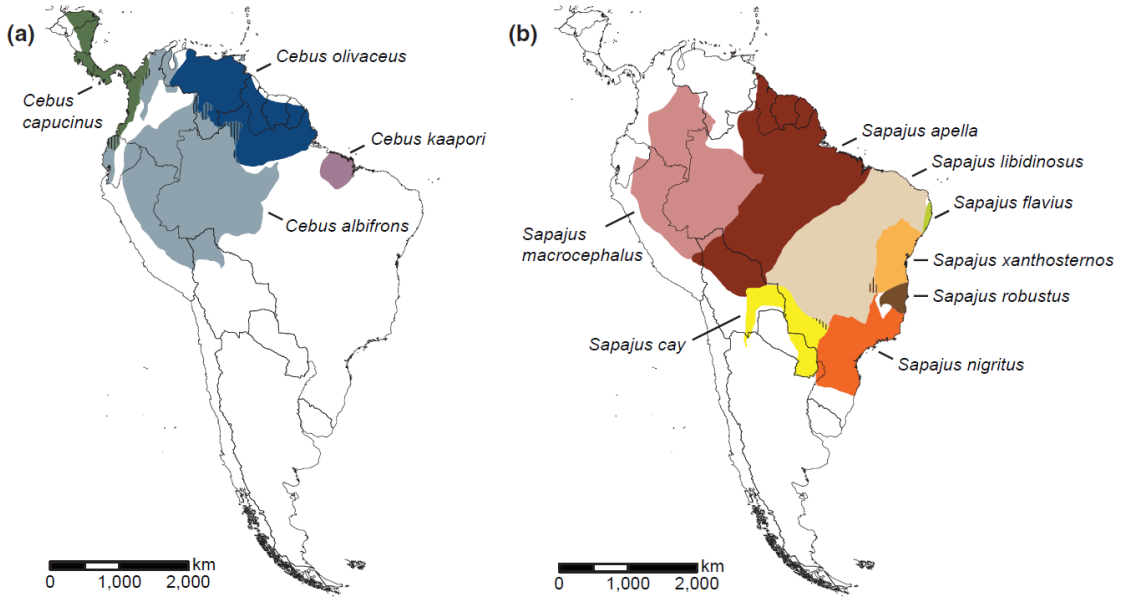

FIGURE 1. From Lynch Alfaro, Boubli, et al., (2012), Fig. 1, p. 2: "Approximate distribution of (a) *Cebus* and (b) *Sapajus* species in the Neotropics. Species distributions follow IUCN Red List maps (IUCN, 2011), with minor corrections, using the taxonomy of Silva (2001, 2002), with the addition of the newly rediscovered Sapajus flavius. Hashes symbolize intrageneric sympatry. Note the extreme overlap between (a) Cebus and (b) Sapajus species in the Amazon Basin".

Yellow-breasted capuchin monkeys: a Brazilian primate

The Yellow-breasted capuchin (*Sapajus xanthosternos*) was first described in 1826 by a German explorer, Prince Maximilian zu Wied-Neuwied, from a specimen collected in Bahia years before. This species has a limited distribution restricted to Brazil, across the states of Bahia, Sergipe, and the north of Minas Gerais, particularly, from the right bank of the Rio São Francisco to the left bank of the Rio Jequitinhonha (Coimbra-Filho, Rocha e Silva, & Pissinatti, 1991; Coimbra-Filho, Rylands, Pissinatti, & Santos, 1992; Lernould, Kierulff, & Canale, 2012, p. 72; Figure 2). *S. xanthosternos* is considered a "critically endangered" (CR) species (IUCN: Kierulff, Mendes, & Rylands, 2015), due to human hunting and habitat loss (Mittermeier et al., 2006; Suscke, 2014). The Yellow-breasted capuchin inhabits a wide variety of biomes: wet forests of the

Atlantic Forest, dry inland forests in the Caatinga and Cerrado (Canale, Kierulff, & Chivers, 2013), as well as mangroves (Beltrão-Mendes, 2015). The diet is mainly composed by fruits and invertebrates (Canale, Kierulff, et al., 2013; Suscke, 2014), but it changes according to environmental conditions, opening hard nuts by using stones as hammers in the Caatinga biome (Canale, Guidorizzi, Kierulff, & Gatto, 2009), preying lizards (Canale, Freitas, & Andrade, 2013) or porcupines (Suscke, 2014) in the wet forest, or opening crabs in the mangrove (Beltrão-Mendes, 2015).

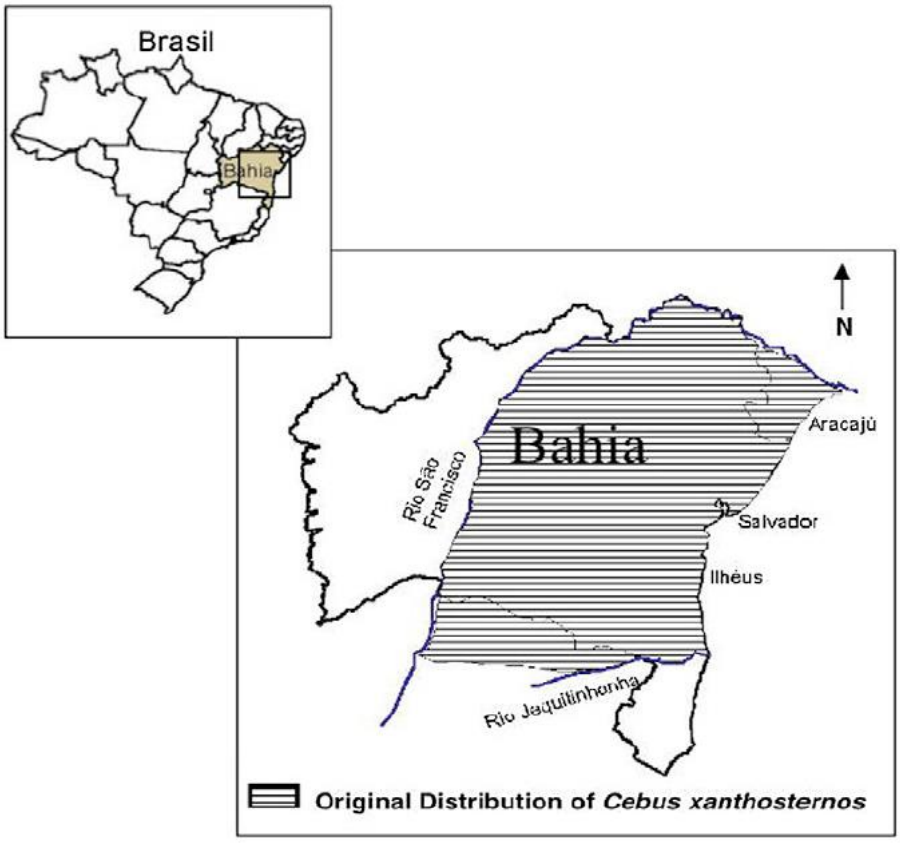

FIGURE 2. Original figure by Lernould et al., (2012, p. 72): “Original distribution of the Yellow-breasted capuchin *Cebus xanthosternos* in Brazil”. The author used the old name of the genus, currently it is called *Sapajus xanthosternos.*

Yellow-breasted capuchins from southern Bahia: **Principe** *group*

The study group, called “Príncipe”, lives in Una Biological Reserve (ReBio Una, Bahia, Brazil; 15º06’–12’S and 39º02’–12’W), a fully protected conservation unit of ca. 18500 ha, surrounded by a semi-protected area (Wildlife refuge, “Refugio da vida silvestre”, RVS) of ca. 23400 ha (Figure 3). The region is covered by lowland Atlantic Forest (Amorim, Thomas, Carvalho, & Jardim, 2008), in a mosaic of mature forest, secondary forest, and patches of rubber (*Hevea brasiliensis*) and cocoa (*Theobroma cacao*) plantations called ‘‘cabruca’’ (Figure 3) and, in lesser proportion, there are also swamp areas and old plantations of jackfruit (*Artocarpus heterophyllus*) and oil-palm (*Elaeis guineenses*). Temperature in ReBio Una averages 24–25 °C annually, and rainfall is ca. 2000 mm/year (Mori, Boom, de Carvalho, & dos Santos, 1983), with markedly dry and wet months, but not continuous wet and dry seasons (Suscke, 2009).

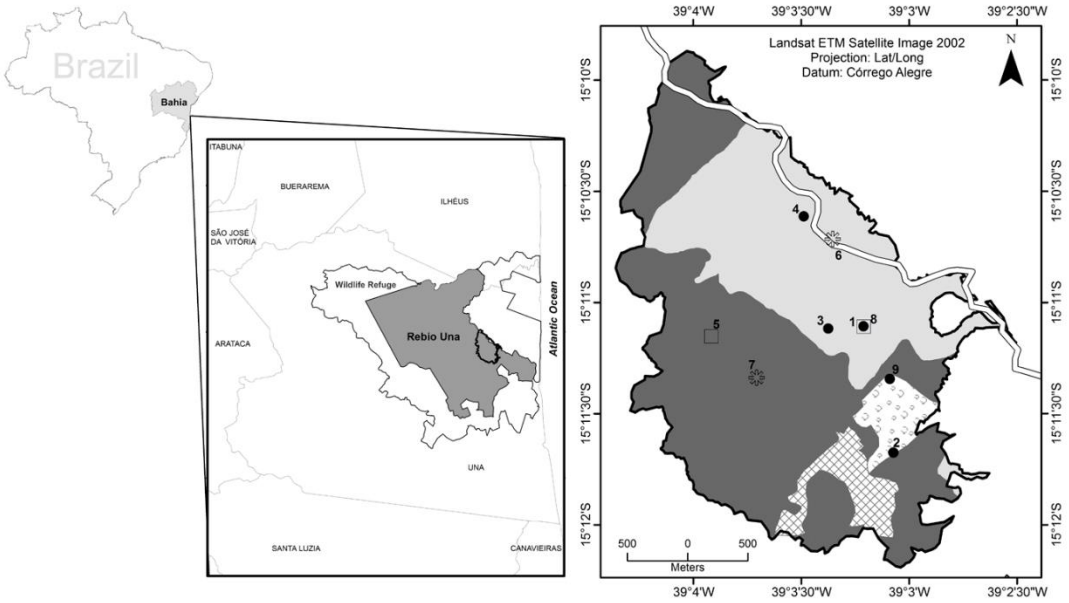

FIGURE 3. Reprinted with permission from Suscke et al. (2017, p. 144): “Localization of encounters between *Harpia harpyja* and *Sapajus xanthosternos* in different habitat types—mature forest in dark gray, secondary forest in light gray, rubber plantation in line fill, and cabruca in white with gray pattern—within the group’s home range. Black circles indicate the locations of encounters in which we observed the predator, and asterisks denote the predation attempts. White line indicates the Maruim River”.

Sympatric with *S. xanthosternos*, other primates occur in ReBio Una (see Figure 4): the “endangered” (EN) golden-headed lion tamarin (*Leontopithecus chrysomelas*, IUCN: Kierulff, Rylands, Mendes, & de Oliveira, 2008), the “vulnerable” (VU) black-handed titi (*Callicebus melanochir*, IUCN: Veiga et al., 2008), and the “near threatened” (NT) Wied’s marmoset (*Callitrix kuhlii*, IUCN: Rylands & Kierulff, 2008). The genera *Alouatta* and *Brachyteles* are currently extinct, but they could be originally present in that region (Rylands, da Fonseca, Leite, & Mittermeier, 1996). Other medium and large sized mammals have not been seen in ReBio Una for a long time, as the jaguar (*Panthera onca*), the white-lipped peccary (*Tayassu pecari*) or the tapir (*Tapirus terrestris*) (Suscke, 2014). ReBio Una has been threatened by a great hunting (Suscke, 2009, 2014) and fishing pressure that fortunately is currently diminished (personal observation).

a) b) c)

FIGURE 4. Other primate species living in ReBio Una along with *S. xanthosternos*. a) golden-headed lion tamarin (“Leontopithecus_chrysomelas.jpg” by Юкатан is licensed under CC-BY-SA-3.0); b) guigó (“Callicebus_melanochir_JJK%272.jpg” by Jacek Kisielewski is licensed under CC BY-SA 3.0); c) and Wied’s marmoset (“Callithrix_kuhlii.jpg” by Kenny Ross is licensed under CC BY-SA 2.0).

The group *Príncipe*, started to be habituated in by the end of 2003, but it was not systematically monitored until 2006, when some individuals were captured and radio-collared (Kierulff, Canale, & Suscke, 2005; Suscke, 2009,

2014). Since then, other studies have been conducted following this group: Sucke MSc at State University of Santa Cruz, UESC (2009); Sucke PhD at University of São Paulo, USP (2014), Verderane Post-Doc at USP (2019), Fernández-Bolaños PhD at USP (2019), this thesis, Delval PhD at USP (2019), Faverin MSc at USP (in progress). The radio telemetry system devices (ball-chained radio-collar) have been renewed approximately every two years, until the present time.

The *Príncipe* group had a variable number of individuals (maximum n=32, personal observation), due to migration death and births, presenting a cyclical pattern of increase in size until splitting (Suscke, 2014). The sexual ratio (male/female) was 1.0 in Suscke 2014, but went up to 1.36, calculated in our study (in August 2015). *Príncipe* group has a unique pattern of female bondedness, frequent allomothering, female-female grooming interactions, and also grooming between females and the alpha male (Suscke 2014). This group engaged infrequently in agonist interactions, presenting a relaxed non-linear dominance with a well-defined alpha male, but an alpha female occupying the second position, above the rest of other males (Fernández-Bolaños, Delval, De Oliveira, & Izar, submitted). This group is under a great predatory pressure, due to hunting by humans and to the harpy eagle (*Harpia harpyja*) attacks (Figure 3), to which the group responded performing a complex defense behavior, with markedly differentiated roles depending on age, sex and dominance (Suscke et al., 2017). Other potential predators are the cougar (*Puma concolor*), the ocelot (*Leopardus* sp.), the tayra (*Eira barbara*) and the black hawk-eagle (*Spizaetus tyrannus*), occurring in that area (Suscke, 2009).

Infants and youngsters

Chapter Two is focused in twelve individuals, who were between 0 and 36 months-old during the period of data collection (Figure 5). Although all infants were filmed since they were born, some infants did not complete 36 months at the moment we established as a limit to the video transcriptions (March 2018). Thus, just half of the sample, six individuals, completed 36 month, two individuals completed 24 months and 4 were 12 month old. This implies we include in this study infants pertaining to four different cohorts (see. Table 1, Chapter Two, p. 82).

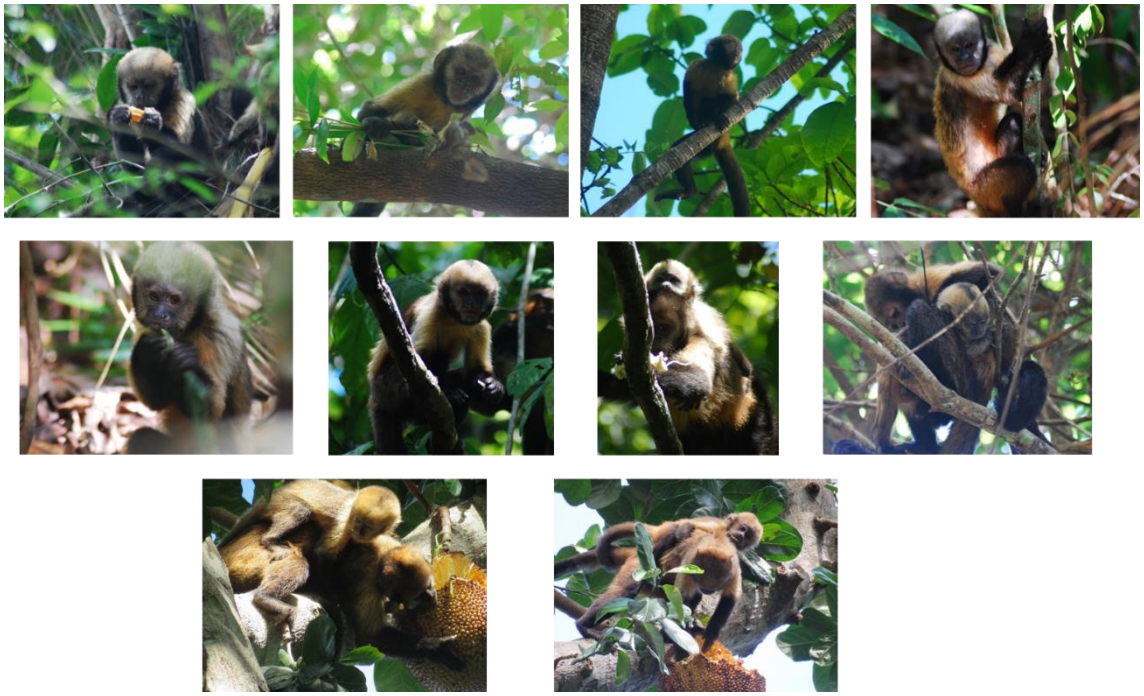

FIGURE 5. Ten youngsters of group *Príncipe* at ReBio Una. From first row upper left: Sofia, Pimenta, Rocio, Luciano, Mequetrefa, Caio, Sumo, Pigmeu, Marta e Isaque. Photos taken by the author.

Along this time, two newborns died within the first two weeks of life. One of them was on her mother's back close to the alpha male, so we suspect a case of infanticide. The mother carried her dead baby for the whole day.

Details on Collecting and Transcription Procedures

In this research, I used two sources of data: 1) video records made by the field assistant RSO (from November 2013 to March 2018); 2) video records made by ID during our fieldwork (March 2015 to March 2016). Before starting the data collection during my fieldwork, I spent two months training in the individual recognition of the 26 individuals the group had at that moment (Figure 6).

FIGURE 6. Fieldwork during the training process. From left to right: Marcelo Fernández-Bolaños, Robson Santos de Oliveira (RSO), and Irene Delval.

The huge amount of data collected implied an important investment in storage and classification. This was especially important for my research, since it is focused in development, so I needed to select videos adjusting each individual's time within each developmental stage. An additional difficulty to this task was that developmental stages were not synchronized, since individuals were born in different dates. The individuals were filmed on a focal basis. Days

were divided into two periods, morning- from 6:00 to 11:59- and afternoon- from 12:00 to 18:00. Every individual was filmed weekly in both periods (in separated days) until the sixth month of life. Then we filmed them for one period a week, altering periods every week, to avoid biases on the most typical behaviors depending on the time of the day. We planned the data collection to achieve the same amount of observation for each individual. However, the projected observation time and the real amount of video records were very dissimilar. Thus, we adjusted data during the transcription process, analyzing approximately the same amount of weekly data for each individual. Once selected, the videos were transcribed using the software Observer XT (Noldus, 1991; Zimmerman, Bolhuis, Willemsen, Meyer, & Noldus, 2009).

This was a timely demanding work (i.e., one recorded minute takes approximately ten time minutes to be transcribed, depending on the behaviors appearing in the film), that was mostly carried out by myself, and some students that I trained for this exhausting transcription process. The four observers (ID, Mariana Rímoli, Mariana Fernandes and Rosalvo Ribeiro) were trained until attained a minimum of 0.8 of congruence (*kappa* index calculated by the software The Observer XT). All the observers transcribed the same videos during the training processes, and transcriptions were compared. Finally, the data were standardized and analyzed statistically using R environment packages. The figure 7 resumes the different processes developed with data, showing the chronogram followed.

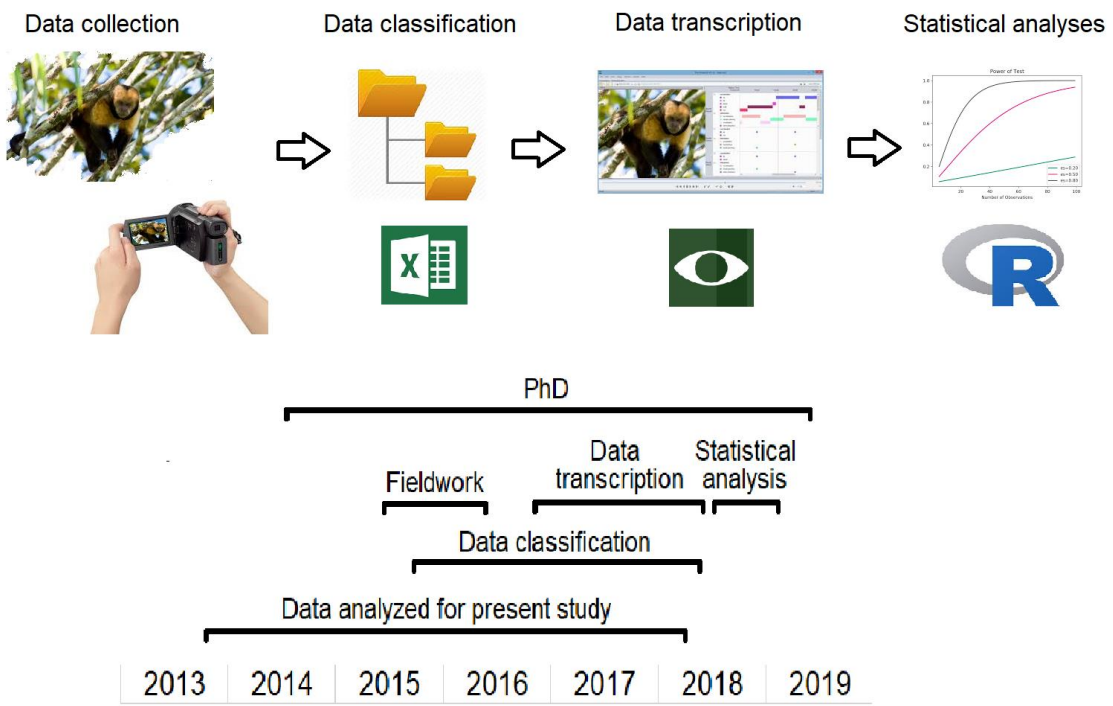

FIGURE 7. The four steps taking for obtain data in this study, showing below time devoted to each step.

I hope I have summarized here the substantial efforts made for the conclusion of this work. I believe we have found important results here, and I hope this is just the beginning of a major research. In addition, I expect I have contributed with this work to expand our knowledge about the amazing yellow-breasted capuchins.

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CHAPTER ONE

Towards an unifying concept of personality in humans and nonhuman animals

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Irene Delval, Marcelo Fernández-Bolaños and Patrícia Izar

Review article to be submitted to an international journal.

Towards an unifying concept of personality in humans and nonhuman animals

Irene Delval, Marcelo Fernández-Bolaños, Patrícia Izar

INTRODUCTION

The fact that nonhuman animals possess behavioral idiosyncratic characteristics, which may be identified as ‘personality’, has never been a secret for pet owners, veterinarians or zookeepers (Gosling & Mehta, 2013). However, for many reasons, in the psychological and biological sciences this fact has been neglected. On the one hand, biologists, inside its branch of behavioral ecology, were looking for environmental variables capable to predict regularities on behavior, ignoring individual variation. On the other hand, psychologist felt that classifying individual differences on other species by using the term ‘personality’, would fall into a risk of anthropomorphizing (but see Kwan, Gosling, & John, 2008).

A large number of animal studies, particularly in the last two decades (see Réale, Dingemanse, Kazem, & Wright, 2010), have shown that, independently from other variables such as sex, age-class or dominance rank, individuals of the same species differ systematically in their behavior. Most of this variation is nonrandom and is consistent over time and/or across contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), so it can be attributed to individual variation, it can be measurable, it shows significant cross-species generality for some dimensions (Gosling, 2008) and, subsequently, can be called ‘personality’.

Although anthropomorphism is a logical risk in comparative cross-species research, because of the extrapolation of methods from one area to another, we strongly believe that it is time to ‘animalize’ psychological research by the understanding that we are just another animal species.

Along this text, we will first explore the origins of the term and other terminological issues of personality research. Then, we will make a very brief historical review of the topic, on the basis of the most used approach, the trait theory, which is commonly applied in personality research in human and nonhuman animals’ personality research. Subsequently, we will compare results from different primate studies for, eventually, discuss if there is a common structure of primate personality.

WHAT IS PERSONALITY?

Etymological origins

Personality is an every-day usage word that comes from the Latin word *persona* (i.e. person), which originally meant ‘mask of the actor’, the ‘theatrical mask’ of a character on a performance. Although its etymological origin is not well established, *persona* is possibly related to the Latin verb *per-sonare* (literally: *sounding through*), associated to the above-mentioned theatrical mask, which often included a small megaphone (Figure 1). Other sources situate the origin of *persona* in the Etruscan word, ‘phersu’ (φersu, “mask”), derived from the Ancient Greek word *πρόσωπον* (prósōpon, literally: “in front of the face”). Through metonymy, that mask, the *persona*, became the technical term for referring a member of the theater, an actor, or to a social role, a citizen, in court. Then, in

some moment during the XIV century, the term was popularized and began to be used as a synonymous of individual.

a) b)

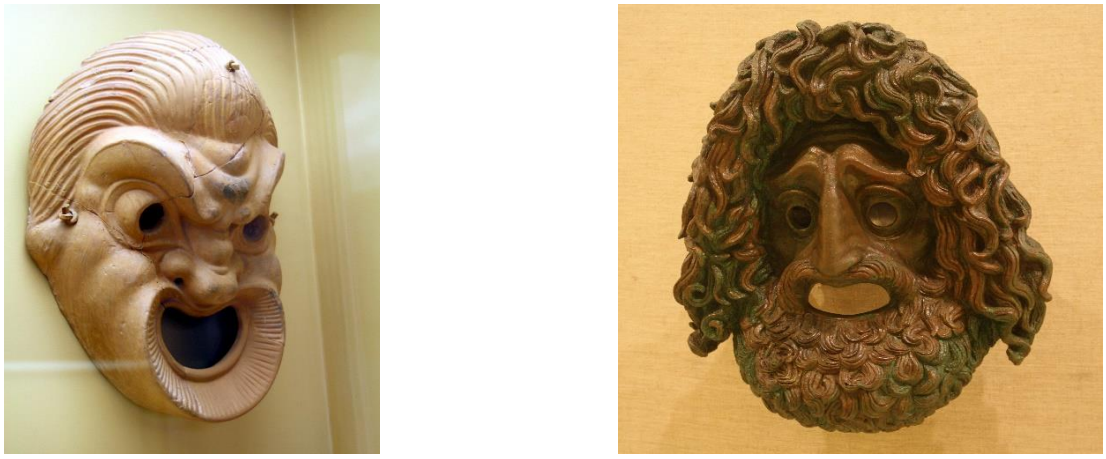

FIGURE 1. Examples of theatrical masks used on the ancient Greece. a) A terracotta comedy mask, 200-250 BCE. (Agora Museum, Athens); b) Bronze tragedy theatre mask, possibly by Silanion, 4th century BCE (Archaeological Museum of Piraeus). Photos by Mark Cartwright (2015), uploaded under the following license: Creative Commons: Attribution-NonCommercial-ShareAlike

Personality can then be interpreted as the mask someone uses to interact with the world. There are yet, however, many issues around the definition of personality that must be overcome until we get to a consensus about this term. First, as many terms in the psychological sciences, the colloquial meaning of personality blurs the significance of scientific meaning (e.g., she has lot of personality; this wine has soft personality). In addition, even within the scientific community, there are multiple definitions for this term (see Table 1), depending on the scientific framework adopted (e.g. psychoanalysis, behavioral sciences, developmental psychology, personality psychology, behavioral ecology). Finally, the etymological origins of the term personality denote a concept referring only to

our species, but, as we will see below, this is not the case. In the past decade, with the incorporation of biologists and behavioral ecologists to the study of personality, with focus in animal profiles, efforts have been made in order to get to an unanimous definition (Réale et al., 2007).

Terminological issues

Defining the concept of is also challenging due to confounding related concepts such as, temperament, copying styles, or behavioral syndromes. These concepts are not exactly synonymous to personality, but they are frequently used as if they were.

Personality:

Psychologists use the term personality to refer to human psychological qualities that contribute to an individual's enduring and distinctive patterns of feeling, thinking, and behaving (Cervone & Pervin, 2013). However, still there are many other definitions (Table 1). Pioneer on personality study, Allport (1937), evaluated 49 different definitions of the term and concluded for "the dynamic organization within the individual of those psychophysical systems that determine his unique adjustment to the environment" (Table 1). Many other definitions have been proposed since, and there is no consensus yet. Nevertheless, there are some well-established agreements: personality has traditionally been used to describe individual differences in adulthood (John, Naumann, & Soto, 2008), personality is composed by traits or domains (McCrae & Costa, 1997), personality differences are the result of selective pressures (B. R. Smith & Blumstein, 2007).

TABLE 1.

An unsystematic list of definitions for Personality, Temperament, Coping Style and Behavioral Syndrome within some different theoretical approaches.

PERSONALITY		
PERSONALITY PSYCHOLOGY	The dynamic organization within the individual of those psychophysical systems that determine his unique adjustment to the environment.	Allport 1937
	Psychological qualities that contribute to an individual's enduring and distinctive patterns of feeling, thinking, and behaving.	Cervone & Pervin, 2013
	The relatively enduring styles of thinking, feeling and acting that characterize an individual.	Costa, McCrae & Kay, 1995
	That which permits a prediction of what a person will do in a given situation.	Cattell, 1950 *apud* Ellis et al., 2009
	The commonly observable, more or less stable differences among people's behaviors.	Strelau, 1987
PSYC HIAT PY	Individual differences in the adaptive systems involved in the reception, processing, and storing of information about the environment defines 'personality'.	Cloninger 1987,
EV. PSY.	Personality differences can be conceptualized as alternative strategies for solving recurrent adaptive problems.	Buss, 2009
BEH. ECOLOGY	Between-individual differences in behavior that persist through time.	Carter et al., 2013
	Individual behavioral differences that are repeatable over time and/or across situations.	Réale et al., 2007
TEMPERAMENT		
DEVELOPMENTAL PSYCHOLOGY	A set of inherited personality traits that appear early in life [...] that are genetic in origin, like other psychological dispositions that are inherited (intelligence, e.g.) [...] and that appear in infancy-more specifically, during the first year of life.	Buss & Plomin, 1975
	The stylistic component of behavior, that is, the *how* of behavior as differentiated from motivation, the *why* of behavior, and abilities, the *what* of behavior [...] People differ in their motor activity, their intensity and equality of mood expression, their ease of adaptability, their persistence, or their degree of distractibility in the process of functioning.	Thomas & Chesss, 1977
	Relatively stable, primarily biologically based individual differences in reactivity and self-regulation assumed to have a constitutional basis.	Rothbart & Derryberry, 1981
	Individual differences in the probability of experiencing and expressing the primary emotions and arousal.	Goldsmith & Campos, 1980
	Relatively consistent, basic dispositions inherent in the person that underlie and modulate the expression of activity, reactivity, emotionality, and sociability. Major elements of temperament are present early in life, and those elements are likely to be strongly influenced by biological factors. As development proceeds, the expression of temperament increasingly becomes more influenced by experience and context.	Goldsmith et al., 1987, McCall, 1987 - synthesis
	Temperament consists of the individual differences in emotion, motor activation and attentional reaction to stimuli.	Rothbart et al., 2012
	Distinctive patterns of feelings and behaviors that originate in the child's biology and appear early in development.	Kagan, 2012

TEMPERAMENT (cont.)

COMPARATIVE PSYCHOLOGY	Behavioral styles or tendencies (rather than discrete behavioral acts) that show continuity over time and can be identified in early infancy. [..] such styles are reflected in the degree and nature (i.e., approach vs. avoidance) of responsivity to novel or stressful stimuli, and nearly all temperamental frameworks include a dimension of intensity, distress, or emotionality.	Clarke & Boinski, 1995
	Temperament is considered a construct closely related to personality, and has been defined as the inherited, early-appearing tendencies that continue throughout life and serve as the foundation for personality.	Gosling & Mehta, 2013
PERSONALITY PSYCHOLOGY	The characteristic phenomena of an individual's emotional nature, including his susceptibility to emotional stimulation, his customary strength and speed of response, the quality of his prevailing mood, and all peculiarities of fluctuation and intensity in mood; these phenomena being regarded as dependent on constitutional makeup and therefore largely hereditary in origin.	Allport, 1937
	Biologically based emotional and behavioral tendencies that are evident in early childhood.	Cervone & Pervin, 2013
	Since antiquity, the notion of temperament has been ascribed to these relatively stable differences in human behavior, which might be explained in terms of biological mechanisms.	Strelau, 1987
BEH. ECO.	Individual behavioral differences that are repeatable over time and/or across situations.	Réale et al., 2007,

COPING STYLE

ANIMAL PHYSIOLOGY	A coherent set of behavioral and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals	Koolhaas et al., 1999
	Is a response to aversive situations (i.e., escape, remove, search, wait), i.e. to situation that induce physiological stress reactions, with an activation of the sympathetic-adrenomedullary system, the pituitary-adrenocortical system, and other neuroendocrine systems	Wechsler, 1995
	The individual response to a stressor by which normally harmful physiological effects of this stressor are reduced.	Wiepkema,1991
	The suppression or reduction of deleterious effects of stress although the mismatch is objectively still present	Ödberg, 1989

BEHAVIORAL SYNDROME

BEHAVIORAL ECOLOGY	Correlation between rank-order differences between individuals through time and/or across situations and is therefore a property of a population. In contrast, a 'behavioral type' refers to the particular configuration of behaviors that an individual expresses and is therefore a property of an individual.	Bell, 2007
	Behavioral syndromes exist when the average phenotypes of individuals in one context/situation are correlated with the average phenotypes of the same individuals in a different context/situation such that populations harbor consistent individual variation in suites of correlated behaviors.	Dingemanse, Dochtermann, & Nakagawa, 2012
	Correlations between different behaviors in a population.	Herczeg & Garamszegi, 2012
	Correlations between two or more personality traits through time or across contexts.	Carter et al. 2013

Temperament:

Temperament is the preferred term for developmental psychologists (e.g., Cloninger, 1993; Goldsmith et al., 1987; Kagan, Reznick, & Snidman, 1988a; Zentner & Bates, 2008), consisting in individual differences in emotion, motor activation and attentional reaction to stimuli (Rothbart et al., 2012). Within this perspective, the basic ingredients of temperament are: early ontogenetic onset, a moderate stability, and distinctive physiological correlates (A. H. Buss & Plomin, 1984). For developmental psychologists temperament refers to the biological and physiological bases of personality (Goldsmith et al., 1987; Strelau, 1987), creating the emotional substrate of some later personality characteristics, for instance, reactivity to environmental stimuli in four-month-old infants derived into two different profiles (i.e., inhibited and uninhibited children) that could predict further anxiety (Kagan, Reznick, & Snidman, 1988b), which is usually related to Neuroticism.

In behavioral ecology, Réale and collaborators' influential work defined temperament as "individual behavioral differences repeatable over time and across situations" in (2007, p. 291). The authors, however, decided to use personality and temperament interchangeably (p. 294). Today, these authors adhered to the main-stream animal personality studies, so they use only the term personality (Montiglio, Ferrari, & Réale, 2013; Réale & Dingemanse, 2012; Réale et al., 2010).

Coping strategies:

Coping styles or coping strategies, although sometimes used as synonym of temperament or personality (e.g., Réale et al., 2007), have a more restricted meaning, referring to individual differences in the behavioral and physiological reactions to challenging or novel situations (Koolhaas et al., 1999; Wechsler, 1995). Thus, a coping style is generally linked to the idiosyncratic response to stress, and it has been proven to be related to health and illness in human (Olff, Brosschot, & Godaert, 1993) and primate research (Capitanio, 2011; Sullivan, Hinde, Mendoza, & Capitanio, 2011). Since stress response is easily studied using animal models, this term is very popular in animal welfare literature (Broom, 1991, 1997, 2001; Koolhaas, de Boer, Coppens, & Buwalda, 2010). Moreover, in the recent years, a growing interest in animal coping strategies in response to Human Induced Rapid Environmental Change-HIREC (Ferreira et al., 2016; Japyassú & Malange, 2014; Sih, 2013; Wingfield, 2013) has begun, on the basis that coping styles may have been shaped by evolution, being general adaptive responses in reaction to challenges in natural habitats.

Behavioral syndromes:

Behavioral syndrome is the term preferred by evolutionary ecologists, to whom the word ‘syndrome’ refers to a set of correlated characters (e.g., dispersal syndromes). Thus, a behavioral syndrome corresponds to a set of behaviors that are usually correlated over time and across situations (Sih & Bell, 2008; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). The most studied behavioral syndrome shows that bold individuals are usually the most belligerent

(e.g., Huntingford, 1976), resulting in the bold-aggressive behavioral syndrome. Behavioral syndromes explain the persistence in population of maladaptive behaviors, probably resulting from genetic constrains, that make behavior less flexible, according to ecological and evolutionary implications. Although considered “analogous to personality or temperament” (Bell, 2007), behavioral syndromes refer to the correlation among rank-order differences between individuals through time and/or across situations, so it is a population property not an individual one (in contrast to behavioral style).

THE SCIENCE OF PERSONALITY

The idea that every individual manifest an idiosyncratic behavioral style, from an emotional nature, was already present in antiquity. The first recognized attempt of a personality theory formulation, at least in Western cultures, occurred in the Ancient Greece. Around the fourth century BCE[1] the Greek physician Hippocrates (ca. 460- ca. 370 BCE), who is also known as “the father of medicine”, formulated the humoral theory. According to this physician, the humors were vital bodily fluids that required to be balanced for pursuing a healthy body. Later, in the Roman period, another Greek physician, Galen (129-200 CE), based upon Hippocrates’ texts, postulated that the features of people’s temperament were related to the physical humors of the body: blood, black bile, yellow bile, and phlegm, corresponding to sanguine, melancholic, choleric, and

[1] We prefer in this text the convention among English-speakers of using the expressions “Before the Common Era” (BCE) and “Common Era” (CE) to replace BC (“Before Christ”) and AD (“Year of the Lord”, from Latin expression *anno Domini).*

phlegmatic temperaments, respectively. *Dyscrasia*, or imbalance of humors, was thought to be a direct cause of sickness, while health, or *eucrasia* (= best mixture possible), correspond to equilibrated humors. Galen also recognized the influence of environmental factors, such as weather or diet, on temperament imbalance. However, since he was a physician, interested in health, he put emphasis on the relation between humors, illness and physical constitution, (Stelmack & Stalikas, 1991). Actually, some evidence that personality traits may moderate important health outcomes (e.g., cancer, heart disease, smoking) has been found (Booth-Kewley & Vickers, 1994; Eysenck, 1985; T. W. Smith, 2006; Terracciano & Costa, 2004).

In the present day, Galen's ancient formulation is considered pure folklore, however, two ideas remain alive in current theories of personality and temperament: (1) inherited biological factors are seen to underlie observable characteristics of individuals, and (2) emotions are seen as core and defining features of temperament (Clark & Watson, 2008).

A science of human personality

The scientific study of personality begins by the end of the nineteenth century with the pioneering work of Galton (1822-1911), who was the first to apply statistical methods to the study of individual differences. He was known for using questionnaires and collecting data on anthropometric features (i.e., weight, height, color of the eyes), for his research about the inheritance of intelligence. In the study of personality, Galton (1884) proposed the "fundamental lexical hypothesis", according to which personality categories are cultural universals,

defined in all languages, usually by a single word. The "lexical hypothesis" is the basis of the structural theories (i.e., personality is structured in traits) of human personality, developed after Galton by the most important personality psychologists, such as Allport (1927), Cattell (1943), and Eysenck (1967). Traits tradition represent the predominant model of empirical research in human psychology, but we cannot ignore that there are other approaches (e.g., psychoanalysis, behaviorism, cognitive approaches), including those that nearly neglect personality (e.g., situational psychology: Mischel, 1969).

Personality traits

Allport (1927, 1931) considered *trait* as the basic unit of personality, consisting in “a general and habitual mode of adjustment which exerts a directive effect upon the specific response” (Allport, 1927, p. 290). Like Allport, Cattell (1943) also relied in *trait* as the basic unit of personality, the result of correlations among variables that were further disentangled through factor analysis. Along the historical consolidation of the trait theory, different minimum number of basic traits have been proposed, from three to sixteen (Cattell, 1943; Costa & McCrae, 1992a; Eysenck, 1991, 1992; Goldberg, 1990). Currently, the most widespread taxonomies are the “Big Five” (Goldberg, 1990), which relies in a pure lexical methodology, and the "Five-Factor Model" (FFM) (Costa & McCrae, 1992a), which employs self-rating scales. Besides the methodological differences, driving to subtle divergences in the facets inside each model (e.g., warmth is a facet of Extraversion in the FFM, but it belongs to Agreeableness in Goldberg’s Big Five), both models mostly coincide in facets within each trait, and so, the scientific

community considers both taxonomies equivalent (John, Naumann, & Soto, 2008) calling them indifferently Big Five (and we do so along this text).

The basic factors of the Big Five model are Neuroticism, Extraversion, Openness to experience, Agreeableness, and Conscientiousness (remembered by the acronym OCEAN, coined by John, 1990, p. 96). Since they are the result of a factor analysis, they are hierarchically sorted by the amount of variance explained, from maximum (Neuroticism) to minimum (Conscientiousness). For a better understanding of each trait is convenient examining facets assessed by the scale (Table 2). *Neuroticism* assesses adjustment versus emotional instability; identifies individuals prone to psychological distress, unrealistic ideas, excessive cravings or urges, and maladaptive coping responses. Some authors (Goldberg, 1990) preferred this trait reversed and called it *Emotional stability. Extraversion* assesses quantity and intensity of interpersonal interaction; activity level; need for stimulation; and capacity for joy. *Openness to experience* assesses proactive seeking and appreciation of experience for its own sake; toleration for and exploration of the unfamiliar. *Agreeableness* assesses the quality of one's interpersonal orientation along a continuum from compassion to antagonism in thoughts, feelings, and actions. *Conscientiousness* assesses the individual's degree of organization, persistence, and motivation in goal-directed behavior (McCrae & Costa, 2006, pp. 46–47).

Both approaches, Big Five and FFM, proposed measurement tools that have been cross-validated in different cultures (NEO-PI: Costa & McCrae, 1992b; IPIP: Goldberg, 1999; NEO-PI-R: McCrae & Costa, 2004; McCrae & Terracciano, 2005). Recently, a six-factor taxonomy (HEXACO: Ashton & Lee, 2001) has been described in lexical studies of personality upon seven different languages (Ashton

et al., 2004), and also developing questionnaires in a short and a long version (HEXACO-60: Ashton & Lee, 2009; HEXACO-PI-R: Lee & Ashton, 2004). In practice, it includes the same Big Five taxonomy, but adds a sixth factor, Honesty-humility (Table 2), related to the facet 'straightforwardness' inside Agreeableness factor (Ashton, Lee, & Son, 2000).

Temperamental traits

As mentioned above (item 2.2, terminological issues), developmental psychologists habitually use the term temperament to refer to personality in childhood. This is not just a preference for a term but a conceptual issue. While personality psychologists are interested in getting to a reliable and broad taxonomy of the real structure of personality (i.e., a descriptive task), developmental psychologists are focused on discovering the underlying biological bases of these structures, its genetic and environmental influences and its change or stability in time (Goldsmith et al., 1987). Some authors point out that temperament manifests itself throughout development as the response to external stimuli (Thomas & Chess, 1977), mediating the influence of the environment on behavior, while others consider temperament a more static concept and focus on its inherited factors (A. H. Buss & Plomin, 1984).

Several models for temperamental traits have been proposed, most on the basis of factor analysis (see review in Rothbart & Bates, 2006). However, temperamental studies lack a common taxonomy such as the Big Five model in personality. One of the most accepted model of temperament recognizes three broad 'superfactors', that are closely related to the Big Five taxonomy: "Neuroticism/negative emotionality" (N/NE), "extraversion/positive emotionality"

(E/PE), and “disinhibition versus constraint” (DvC) (Clark & Watson, 2008). Concisely, individuals high in N/NE perceive the world as threatening, problematic, and distressing. Individuals high on E/PE are willing to engage the environment, enjoy the company of others, and approach life with enthusiasm. Finally, DvC superfactor reflects individual differences in the tendency to behave in an undercontrolled versus overcontrolled manner (Clark & Watson, 2008, p. 269). Rothbart (2007) got to a very similar broad dimensions taxonomy– Effortful control, Negative affectivity and Extraversion/surgency- (Table 2) in a comparative study of early childhood (i.e., six to seven years old) in populations from United States and China.

Temperament changes across the developmental processes, so human infants are not born with their temperamental characteristics completely established. Therefore, a variety of temperamental dimensions are detected across ontogeny (Rothbart et al., 2012). However, some regularities can predict further behavior in children (e.g., inhibition: Kagan et al., 1988b), but such consistency is not easily detected: for instance ‘effortful control’ is only noticeable in infants after 30 months (Rothbart & Ellis, 2003).

TABLE 2.

Personality and Temperament Taxonomies within different theoretical approximations*

BIG FIVE/FFM Questionnaire (NEO-PI-R) Costa & McCrae, 1992		**HEXACO** Questionnaire (HEXACO-PI) Lee & Ashton, 2004		**TEMPERAMENT** Questionnaire (CBQ) Rothbarth et al., 2001		**BEHAVIORAL ECOLOGY** Behavioral tests Reale et al., 2007	
NEUROTICISM (N)		**Emotionality (E)**		**Negative affectivity**		**Aggressiveness**	
Worrying, nervous, emotional, insecure, inadequate, hypochondriacal	Anxiety Hostility Depression Self-consciousness Impulsiveness Vulnerability	Defined by anxiety, vulnerability, sentimentality, lack of bravery, and lack of toughness, but not anger or ill temper	Fearfulness Anxiety Dependence Sentimentality	Neuroticism	Frustration/Anger Fear Discomfort Sadness Low Soothability	an individual's agonistic reaction towards conspecifics	Aggressive
EXTRAVERSION (E)		**Extraversion (X)**		**Extraversion/ surgency**		**Activity**	
Sociable, active, talkative, person-oriented, optimistic, fun-loving, affectionate	Gregariousness Activity Level Assertiveness Excitement Seeking Positive Emotions Warmth	Defined by talkativeness, energy and cheerfulness (though not by bravery and toughness)	Expressiveness Social Boldness Sociability Liveliness	Positive emotion	Activity Low Shyness High-Intensity Pleasure Smiling & Laughter Impulsivity Positive Anticipation	the general level of activity of an individual	Active vs Inactive
OPENNESS (O)		**Openness to Experience (O)**		**Effortful control**		**Boldness**	
Curious, broad interests, creative, original, imaginative, untraditional	Fantasy Aesthetics Feelings Ideas	Former known as Intellect/Imagination factor. Is one of the most controversial because of Intellect. Imagination aspect, subsuming traits such as originality and	Aesthetic Appreciation Inquisitiveness Creativity Unconventionality	Conscientousness	Attention Control Inhibitory Control Perceptual Sensitivity Low-Intensity Pleasure	an individual's reaction to any risky situation, but not new situations	Bold Docile Tame Unfearful

BIG FIVE/FFM Questionnaire (NEO-PI-R) Costa & McCrae, 1992		HEXACO Questionnaire (HEXACO-PI) Lee & Ashton, 2004		TEMPERAMENT Questionnaire (CBQ) Rothbarth et al., 2001	BEHAVIORAL ECOLOGY Behavioral tests Reale et al., 2007	
	Actions Values	creativity, appears to be a robust common element				vs Shy, Untamed, Fearful
AGREEABLENESS (A)		**Agreeableness (A)**			**Sociability**	
Soft-hearted, good-natured, trusting, helpful, forgiving, gullible, straightforward	Straightforwardness Trust Altruism Modesty Tendermindedness Compliance	Defined by good-naturedness, tolerance, and agreeableness, but also including anger and ill temper at its negative pole (different to Big Five)	Forgiveness Gentleness Flexibility Patience		an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour)	Social Sociable vs Asocial
CONSCIENTIOUSNESS (C)		**Conscientiousness (C)**			**Exploration**	
Organized, reliable, hard-working, self-disciplined, punctual, scrupulous, neat, ambitious, persevering	Self-discipline Dutifulness Competence Order Deliberation Achievement striving	Defined by such content as organization, hard work, carefulness, and thoroughness (rather than moral conscience). Therefore, this factor is almost identical to the Big Five Conscientiousness dimension.	Organization Diligence Perfectionism Prudence.		an individual's reaction to a new situation	Exploratory Neophilic vs Unexploratory Neophobic
		Honesty-Humility (H)				
		Defined by morality, sincerity or integrity	Sincerity Fairness Greed Avoidance Modesty			

*Just some representative example

A science of nonhuman personality

We can trace back the origin of animal (nonhuman) personality research to the comparative psychology of the twenty century. The Russian physiologist, Ivan Pavlov (1849-1936) observed significant individual differences in behavior in the dogs he used in his conditioning experiments (Pavlov & Petrova, 1934). Instead of ignore these differences, he decided to take them into account, calling them temperaments, in reference to Galen's proposal, and relate them to different kinds of nervous systems (i.e., choleric, sanguine, phlegmatic and melancholic dogs) (Whitham & Washburn, 2017).

Other pioneers in comparative psychology, such as Yerkes (1876-1956) and Crawford (1910-2002) were interested in our most related species, nonhuman primates. As a psychobiology professor, Yerkes founded in 1924 the Yale Laboratories of Primate Biology, and explored there among other topics, some aspects of chimpanzee personalities (Yerkes, 1939). Years later, working in the same prolific laboratories, Crawford (1938) proposed the first rating scale of chimpanzee personality, and Donald Hebb (1904-1985) established a method for testing behavioral consistency (Hebb, 1949). Despite these, and some others scattered pioneering contributions (rats' timidity: Billingslea, 1941; free-ranging baboons' emotions: Buirski, Kellerman, Plutchik, Weininger, & Buirski, 1973; chimpanzees' emotions and personality: Buirski, Plutchik, & Kellerman, 1978; captive animals' curiosity: Glickman & Sroges, 1966; stikelbacks' boldness: Huntingford, 1976; rhesus macaques' temperament: Stevenson-Hinde & Zunz, 1978), the field of animal personality did not flourish until the last decades of the 20th century.

In behavioral ecology Wilson, Clark, Coleman, and Dearstyne (1994) marked a milestone in the study of personality, being the first ones to connect some personality traits (i.e. shyness-boldness axis) to evolutionary explanations (*sensu* Tinbergen, 1963). After the publication of that seminal paper, studies in practically every taxa emerged (for an early review see, Gosling, 2001), with a striking increase in the last decade (Whitham & Washburn, 2017).

In behavioral ecology *trait* is defined as “a specific aspect of a behavioral repertoire that can be quantified and that shows between-individual variation and within-individual consistency” (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013, p. 467). However, the discussion about the basic units has never occurred (but see Réale et al., 2007), although behavioral ecologists rely in psychology to justified the analyzed traits (e.g., David S. Wilson, Coleman, Clark, & Biederman, 1993). In this tradition, researchers usually investigate one unique trait (e.g., shy-bold) within one species and its evolutionary consequences (e.g., Coleman & Wilson, 1998). Each trait is linked to ecological valid contexts, where measurements also differ according to the investigation’s goals. Thus, if a researcher is interested in ontogeny, measures around behavioral developmental changes will be taken. Alternatively, if the interest is focused in mechanisms, physiological measurements will be taken (Réale et al., 2007). Behavioral ecologists usually rely in behavioral codification in experimental situations (e.g., open field test) or natural environments for assessing the personality traits.

Behavioral ecologists are not interested in defining the whole personality structure of a given animal species (e.g., describing cockroach’s personality). Instead, they try to respond ultimate and proximate questions about traits (e.g., have bold cockroaches more mating success?). Thus, trait definitions differ from

one species to another. This lack of common definitions may seem confusing, hindering cross-species comparisons, but, on the other hand, it can be argued that, being bold is not the same for a prey than for a predator species. Gosling and John (1999), before the “explosion” of personality research in behavioral ecology, already perceived that personality assessments in animals “came in different languages; used a variety of scales, methods and notations: and varied in their scope and reliability” (p. 69).

Nevertheless, as in human personality, in behavioral ecology there has been a proposal of agreement about the number and definition of traits. This proposal (Réale et al., 2007) also refers to a five-trait model, including Boldness, Exploration, Activity, Sociability and Aggressiveness (Table 2). However, Réale et al.’s (2007) approach is not a theoretical framework describing a precise personality structure common for all animals. Instead, the authors suggested these traits, but leave to the researcher’s choice, which one would be more appropriated for the studied species and for answering the research question. Perhaps for that reason, studies using Réale et al.’s (2007) approach do not investigate exhaustively all five traits, instead they usually only account for a single trait or a few traits (e.g., exploration in Japanese macaques: Arnaud et al., 2017; boldness and docility in yellow-bellied marmots: Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013), or for suits of correlated traits, in the sense of behavioral syndromes (e.g., zebrafish: Moretz, Martins, & Robison, 2007).

Another characteristic of personality studies in behavioral ecology is that researchers usually determine the relevant traits of the targeted species based upon its typical observed behavior. For instance, great tits differ consistently in exploratory and sociosexual behavior (Carere, Drent, Privitera, Koolhaas, &

Groothuis, 2005), so artificially rearing extreme lines from wild populations in several generations may led to different responses in behavioral tests (Groothuis & Carere, 2005). To asses these species-specific individual differences (that they call personality traits) ‘standard’ behavioral tests (e.g., open-field test, novel object test) are often used. Sometimes, behavioral codification, and rarely, subjective personality ratings are also employed (for a discussion about methods in animal personality research see, Vazire, Gosling, Dickey, & Schapiro, 2007). Standard behavioral tests are tools for measuring the same traits in different taxa, but three common mistakes involving these tests have been pointed out (Carter et al., 2013): 1) a test for one species might not be appropriate for another (remembering, it is not the same being bold for a prey or predator species); 2) definitions are not yet uniform (e.g., Réale et al. (2007) exclude neophilia from boldness while others (Coleman & Wilson, 1998) include it); 3) one standard test could be measuring two or more different traits (e.g., open-field test can be a measure of boldness but also of activity level). As a consequence, Carter et al., (2013) suggested that “the indiscriminate use of ‘standard’ behavioral tests within animal personality studies may lead to the spurious labelling of personality traits” (p. 472).

PERSONALITY TRAITS IN PRIMATES

Within the young science of nonhuman personality, primates’ personality research has followed a parallel path, apart from other animal species, more closely related to the tradition of studies in human personality. As mentioned above, human personality psychologists were more concerned with getting into an exact description of personality structure rather that in answering questions

about the adaptive value of individual differences. Therefore studying closely related species is a way of fixing this lack of interest, since comparing structures can give light into the selective forces that gave rise to personality traits.

We can situate the very beginning of the interest in primate's personality after Stevenson-Hinde and Zunz's (1978) work with rhesus monkeys. Their work (1980a, 1980b; 1978) is salient for explicitly proposing a rating scale, specific for primate temperamental patterns, analyzed through principal component analysis (PCA), that was already being used in social behavior studies (Chamove, Eysenck, & Harlow, 1972; van Hooff, 1970) but not in (nonhuman) animal personality research. Although Buirski et al. (1973, 1978) were using rating scales (along with behavioral codification), they did not apply the component reduction techniques. Instead, they applied Emotions Profile Index (EPI) and assumed its structure "derived from a theory of personality which stresses the adaptive significance of emotions at all evolutionary levels" (Buirski et al., 1978, p. 123)

Along the 1980-90's, most primate personality research was conducted with captive animals, probably because there were many colonies maintained for medical research purposes. The main aim was to characterize individual differences in nonhuman primates and to test the reliability of the scales by comparing them with behavioral assessments. Furthermore, during this decade some studies evaluated the correlation of personality traits with other variables such as dominance, age and sex (e.g., Bolig, Price, O'Neill, & Suomi, 1992; McGuire, Raleigh, & Pollack, 1994), attachment style and physiological profiles (e.g., Clarke, Mason, & Moberg, 1988), and reaction to rearing conditions such as social deprivation or environmental enrichment (e.g., Schneider, Moore, Suomi, & Champoux, 1991).

As a consequence of the success of the Big Five (Costa & McCrae, 1992b; Goldberg, 1990) and its cross-cultural validation (McCrae & Costa, 1997; McCrae & Terracciano, 2005) in humans, a renewed interest on cross-species validation appeared in the middle 90's. It was suggested that a "basic" personality factor must be identifiable among nonhuman species (Zuckerman, 1992). Inspired by this criterion, a new personality rating scale was proposed, composed by 43 adjectives taken from Goldberg's (1990) adjectives list. The such called "Five-Factor Model plus dominance" (FFM + D: King & Figueredo, 1997) of chimpanzee personality was surprisingly similar to the structure found in humans. The rating scale proposed has been modified several times (King, Weiss, & Sisco, 2008; Weiss, King, & Hopkins, 2007; Weiss, King, & Perkins, 2006) until its actual form -Hominoid Personality Questionnaire- (HPQ: Weiss et al., 2009), being applied successfully to many primate species. Orangutans (Adams, King, & Weiss, 2012; Morton et al., 2013; Weiss et al., 2006), langurs (Konečná et al., 2008), chimpanzees (Morton et al., 2013; Weiss et al., 2009; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012), macaques (Adams et al., 2015; Konečná, Weiss, Lhota, & Wallner, 2012; Morton et al., 2013; Robinson et al., 2018), capuchin monkeys (Fernández-Bolaños, Delval, De Oliveira, & Izar, submitted; Morton et al., 2013; Robinson et al., 2016), bonobos (Garai, Weiss, Arnaud, & Furuichi, 2016; Weiss et al., 2015), gorillas (Eckardt et al., 2015), marmosets (Koski et al., 2017), tamarins (Masilkova, Weiss, & Konečná, 2018) and squirrel monkeys (V. A. D. Wilson, Inoue-Murayama, & Weiss, 2018) have been rated by HPQ assessments. Although there have been other questionnaire proposals (Freeman et al., 2013; Manson & Perry, 2013), definitely, this one is the most widely spread.

Using the same tool for assessing the personality structure of several primate species is an *etic*[2] approach that has the advantage of making possible cross-species comparison (e.g., Morton et al., 2013). Moreover, comparing closely related primate species might help to answer ultimate questions about the evolution of personality traits, suggesting 'when' one trait appeared during phylogeny (e.g., squirrel monkeys: V. A. D. Wilson et al., 2018) or if ecological or social variables can affect the prevalence of traits (e.g., macaques' social style: Adams et al., 2015). Finally, given that HPQ is based in human Big Five taxonomy, it can answer questions about the evolution of human personality traits.

Primate personality research is most commonly based on rating scales, similar to those applied in human personality research, whereas in other animal species it is more typical assessing traits by using behavioral codification. It has been pointed out that several methods must be combined for assessing personality in a reliable manner (Freeman, Gosling, & Schapiro, 2011; Manson & Perry, 2013), in fact, today, the majority of primate personality research relies in both, ratings and codings, to attain a validity criterion.

Uher (2018; Uher & Visalberghi, 2016) strongly criticizes the reliability of questionnaires considering that they are "retrospective memory-based judgments […] containing stereotypical biases". The author proposed an alternative method, called "behavioral repertoire X behavioral situation approach" (Uher, 2008), fully based in behavioral codification, that she applied to some primate species (Uher,

[2] The emic-etic distinction originates from linguistics, based on the distinction between phon*emics* and phon*etics* (Pike, 1967). This differentiation is now used in the behavioral sciences in reference to a more complete and exhaustive "native" (emic) perspective of behavior, to describe the object of study (in our case, personality), or an "imported" perspective of other species (etic), which allows comparisons, but loses details. This distinction is also known as bottom-up/top-down approaches (Uher, 2011).

2013; Uher & Asendorpf, 2008; Uher, Werner, & Gosselt, 2013). In fact, subjective assessment in personality research has always have been surrounded by the long shadow of *rater bias* (i.e. expectation, projections, etc.), however, multivariate techniques ensure several criteria for avoiding these sources of error: (a) inter-rater reliability, (b) inter-item consistency, (c) cross-situational consistency, and (d) cross-temporal stability are usually controlled in such personality studies (Figueredo, Cox, & Rhine, 1995). Nevertheless, several authors defend the reliability of questionnaires and maintain that both methods should lead to similar results (Gosling & Vazire, 2002; Vazire & Gosling, 2003; Vazire et al., 2007).

Using a common approach and same measurement tools for assessing primate personality is allowing comparative psychologist to obtain personality structures for several species. Further comparative research is needed in order to determine how these structures are related.

DISCUSSION

Along this text, we made a not-exhaustive review on the most remarkable problematic in personality research, both in humans and nonhuman animals. We began discussing the difficulties derived from a variety of definitions that are not exactly synonymous, thus creating confusion within the studied area. We then succinctly summarized the most important historical milestones in human and other animals personality research, and finally explored the case of nonhuman primates' personality research, as an example of a prolific field.

Temperament or personality?

The terminological issues are not completely resolved nowadays. The terms imported from other areas outside the psychological sciences (i.e., coping style or behavioral syndrome), despite have been considered equivalent to personality, are today broadly accepted in behavioral ecology as useful, more specific constructs, having their own entity apart from personality traits. The conceptual differences between personality and temperament, the first referring to a constructed result of dispositions and the second to the inherited physiological bases that develop into personality (i.e., late-emerging or basic traits), are progressively disappearing. Personality psychologists have focused for a long time only in getting to an appropriate description of the taxonomy of adult traits. Today, the most widely spread taxonomy, the Big Five, is broadly accepted and cross-cultural validated so an interest for the ultimate questions have begun. The correspondence between personality and temperament traits have been debated and empirically tested (e.g., Angleitner & Ostendorf, 1994; Kohnstamm, Halverson, Mervielde, & Havill, 1998) with better results for some traits than for others (Table 2). Moreover, both kinds of traits are today recognized as not being immune from experience, so “even if identical factors were found in infants and adults, it would not imply that infant temperament is a good predictor of adult personality” (McCrae et al., 2000, p. 183). In that sense, empirical research in humans has shown that children and adults do show rank-order continuity over time, but significant change occurs as well (Roberts & DelVecchio, 2000). This fact must be taken into account when designing ontogenetic studies of personality.

Finally, there is an unresolved debate about the more appropriate term for referring to consistent individual differences in children and animals. Whereas comparative psychologist studying animal personality advocate for the use of personality (see arguments in Weinstein, Capitanio, & Gosling, 2008), developmental psychologists consider more appropriate for children and animals the term temperament (Rothbart & Bates, 2006), but, in this case, the discussion seems just a question of labels.

Is trait theory enough for explaining personality?

Along the historical overview of personality in this text, we have only referred to the structural theories of personality. Of course, there are other very relevant approaches (i.e., psychoanalysis, phenomenology, behaviorism, person/situation debate, etc.) that we have avoided here, in order to establish limits to our review. The trait perspective has been criticized for its reductionist approach, because it seems to be opposite of humanistic psychology, that consider persons as “unified, free, conscious beings seeking self-fulfillment” (Ellis, Abrams, & Abrams, 2009, p. 219). This holistic view of the human being is very relevant in idiographic sciences, where approaches are qualitative in order to understand a relevant case of study. However, the scientific method needs to generalize and create categories for establishing laws or rules, and that is the case of personality trait psychology. The most critical approach to the trait theory is the situational personality theory (Mischel, 1969), that considers that contexts might have more predictable value on individual behavior than personality traits. Instead, psychological personality traits have the advantage of being

operationally defined and measured, allowing to establish comparisons between individuals, between populations, between cultures, between species… The trait theory, contrary to person-situation debate, attributes behavioral observable differences to underling stable personality traits, both in humans and nonhuman animals. The Big Five trait-model of human personality has allowed to make cross-cultural research (Goldberg, 1993; McCrae & Costa, 1997; McCrae & Terracciano, 2005) showing that this model is consistent with an evolutionary theory. If personality traits are adaptive, they must have been selected by natural selection and they may not be exclusive of our species (D. M. Buss, 1991; D. M. Buss & Greiling, 1999; Dingemanse & Réale, 2005). In fact, animal individual differences in personality have been shown to have consequences for evolutionarily relevant components of fitness, such as dispersal (Malange, Izar, & Japyassú, 2016), metabolic rate (Careau, Thomas, Humphries, & Réale, 2008), mating success (Both, Dingemanse, Drent, & Tinbergen, 2005), status (Perry, Godoy, Lammers, & Lin, 2017; Seyfarth, Silk, & Cheney, 2012), offspring production and parenting (Dingemanse, Both, Drent, & Tinbergen, 2004; Reddon, 2012) or cognitive performance (Carere & Locurto, 2011). In this sense, behavioral ecology- defining personality as consistent behavioral individual differences across time or/and contexts- has also embraced trait theory recognizing the prediction power of traits over contexts (since personality must be stable across contexts). The evolutionary perspective of behavioral ecology have broadened the view of traits in human personality psychology, showing the intricate relationships between personality and plasticity (Dingemanse, Kazem, Réale, & Wright, 2010; Dochtermann & Dingemanse, 2013). Correlations among

behaviors leading to personality traits might constraint evolutionary responses to environments limiting infinite plasticity (Dochtermann & Dingemanse, 2013).

The case of primates' personality research is an especial one within animal personality research. In fact, in this review, we have chosen primates not as a random example, but because it follows a more similar path to that of human personality psychology, while taking into account some of the improvements that behavioral ecology brought. It employs trait-rating methodology, but primatologist have often compared ratings with behavioral codification for validating traits (e.g., Manson & Perry, 2013). Unfortunately, the results of these comparisons are difficult to interpret since behavioral observations frequently revealed a different structure that the one obtained with ratings (e.g., Konečná et al., 2008). Behavioral observation seems to be free of biases because it relies in behavior as a unit of analysis. However, there are several 'subjectivities' that quantification techniques must confront. For instance, when quantifying in a hypothetical species foraging behavior, researchers can choose counting every food intake, or divide it into manipulation, chew and swallow, or measure the time spent foraging, or both. These decisions are sometimes arbitrary and can lead to very different frequencies of the counted behaviors, which will further modified the PCA results obtained from behavioral codings. This does not mean, of course, that behavioral coding is always biased and must be left apart. In the same way that questionnaires used in ratings must be carefully designed, tested and validated, behavioral codifications must follow a pattern, at least when measuring different populations of the same species. The fear of trait-rating methods by behavioral ecologists is unjustified and must be overcome: if the rater biases were omnipresent, inter-rater reliability would be difficult to obtain. Also, for rating an

animal, the mean rating score of every item is obtained and, then, for revealing the structure of the species, mean ratings are submitted to component reduction techniques (i.e., factor or principal components analysis), so particular rater nonsystematic deviations from the mean are eliminated (Weiss et al., 2012). The HPQ has been properly validated (Weiss et al., 2012), and has been applied to more than 15 different primate species, but it has rarely been compared with traits obtained by coding (but see Garai et al., 2016; Fernández-Bolaños et al, submitted). This pending task must be resolved with new research.

Is it possible a unified science?

Although personality research in human psychology and in behavioral ecology seem to differ substantially, mostly in research methods, they also have points in common and they have a very strong potential of becoming a unified science (Nettle & Penke, 2010). The first step for getting into a common definition of personality, useful for human and nonhuman research, has been achieved, at least inside the trait tradition. Human personality psychologists have understood that it is time to look further, overcoming their obsession with taxonomy, to answering proximate and ultimate questions (inspired from behavioral ecologists) and getting to a more complete and mature science of personality.

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CHAPTER TWO

A developmental assessment of personality in wild young capuchin monkeys (*Sapajus xanthosternos*)

Irene Delval, Marcelo Fernández-Bolaños and Patrícia Izar

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Abstract

Animal personality is defined as consistent individual differences across time and situations, but little is known about how or when those differences are established during development. Likewise, several studies described the personality structure of adult capuchin monkeys, without assessing the ontogeny of these personality traits. We analyzed the behavioral repertoire of 12 wild infant (9 males, 3 females) yellow-breasted capuchin monkeys *(Sapajus xanthosternos*), in Una Biological Reserve (Bahia, Brazil). Each infant was observed and filmed weekly from birth until 36 mo, through daily focal sampling. We analyzed the behavior of each individual in ten developmental points. By means of component reduction (PCA) we obtained 4 personality traits: Sociability-Attractiveness, Anxiety, Openness and Activity. We investigated whether there were developmental effects on those traits by fitting regression models for the effect of time on personality traits, controlling for monkey ID, sex and cohort. Sociability-Attractiveness (decreasing) and Anxiety (increasing) changed significantly along development. By means of repeatability analysis, we did not find intra-individual consistency across time in those traits. Our results show that the personality structure of capuchin monkeys is not yet established during early development, in agreement with the literature on human personality.

Keywords: behavioral coding, primates, capuchin monkeys, temperament, repeatability, differential consistency

A developmental assessment of personality in wild capuchin monkeys (*Sapajus xanthosternos*)

Irene Delval, Marcelo Fernández-Bolaños & Patrícia Izar

INTRODUCTION

Animal personality has become a trending topic in behavioral ecology and psychology along the last three decades. In fact, the number of citations and publications of this and other related terms (e.g. 'temperament', 'behavioral syndrome' or 'coping styles') in specialized journals has grown almost forty times since 1990 (Réale, Dingemanse, Kazem, & Wright, 2010; Roche, Careau, & Binning, 2016). With the incorporation of behavioral ecologists to the area, definitions became simpler, excluding unmeasurable components of personality (i.e. individual inherent [underlying] dispositions), and unifying the two main concepts: temperament and personality (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Consequently, personality became "the phenomenon that individual behavioral differences are consistent over time and/or across situations", although trait values can change across environmental conditions or age (Réale et al., 2007, p. 294).

Therefore, a growing interest in the ecological explanations of personality have recently taken the scene, focusing on how environmental factors (e.g. predation or food scarcity) can account for personality differences (e.g. aggressiveness or sociability), mostly addressing ultimate questions about fitness consequences, adaptiveness and evolution of personality traits (Dingemanse & Wolf, 2010; Nettle, 2006; Sih, Bell, & Johnson, 2004; Smith & Blumstein, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010). On the other

hand, developmental mechanisms have received less attention. Stamps e Groothuis (2010b) point as the possible cause of this lack the “erroneous assumption that personality traits are temporally stable across ontogeny” (p. 303), coming from the supposition that genes determine those traits (Bouchard & Loehlin, 2001; Sallis, Smith, & Munafò, 2018). Development is a continuous process resulting from the bidirectional interaction of genes and environment, so including the developmental perspective to the study of animal personality incorporates questions about heritability, stability and change (Caspi, Roberts, & Shiner, 2005). Following the psychological literature on humans, in the past decade, the importance of studying the developmental mechanisms underlying animal personality has been highlighted (Groothuis & Trillmich, 2011; Stamps & Groothuis, 2010a; Suomi, 1997; Trillmich & Hudson, 2011). Some studies have shown that animal personality is unstable from birth to adulthood in different species (e.g., sticklebacks: Bell & Stamps, 2004; great tits: Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002; zebra finches: Wuerz & Krüger, 2015). However, there is still a substantial lack of empirical research on a wide range of taxa.

In humans, a comprehensive meta-analysis including 152 long-term developmental studies (Roberts & DelVecchio, 2000) found that consistency in personality traits increases with maturity, probably because of the cumulative experience about the environment, and the consolidation of physiological structures. In that sense, it has been long discussed that some kinds of extreme physiological dispositions (i.e., inhibited or uninhibited children) could drive to different temperamental responses (Kagan, Reznick, & Snidman, 1988; Kagan & Snidman, 1991). Although most human studies on the development of personality

are compromised with “the child being the father of the man” (Caspi, 2000), and claim for further stability in the adulthood (i.e. at the age 30) (Costa & McCrae, 1997; McCrae et al., 2000), results are inconclusive. Actually, other researchers found evidence for personality traits changing more after the age of 30 than before (Srivastava, John, Gosling, & Potter, 2003). These inconsistent results might be reflecting differences in methods, such as the instrument used for assessing traits, the interval between measures or the age of the first test (Ardelt, 2000).

In non-human animals, due to the lack of attention paid to development (Stamps & Groothuis, 2010b) there is no such a longitudinal data basis for personality. It has long been considered that early experiences have long-term effects on the behavior of non-human animals (Harlow, 1959) but evidence for this conclusion is sparse. In a pioneering study, young rhesus monkeys were tested twice, at 1 and 2.5 years-old, showing behavioral tendencies at different ages (e.g. Activity decrease with age), but there was no individual consistency (Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980). Nevertheless, there is one meta-analysis comprising 114 studies on 98 species that compared behavioral traits across age classes (Bell, Hankison, & Laskowski, 2009). In this meta-analysis, the average across all repeatability estimates was high and significant, supporting the hypothesis that behavior is repeatable. Concerning age categories, repeatability of behavioral traits in Bell et al.’s (2009) study was lower in adults than in juveniles, a pattern opposite to that found in humans (Roberts & DelVecchio, 2000). However, the authors acknowledge the necessity to estimate repeatability of juveniles and adults of the same species. To our knowledge, there

is a considerable *lacuna* in the literature about personality early development in animals.

Here, we assess whether personality traits of yellow-breasted capuchin monkeys (*Sapajus xanthosternos*) are stable or change during early development by analyzing the behavior of wild individuals from 0 to 36 months of life (covering until half of the juvenility, Verderane, 2010).

Some researchers have pointed out the limited value of studying personality development in free ranging animals, “because it is difficult to ensure that all of the subjects in a study are observed in the same contexts, at the same ages, and across the same inter-observation intervals” (Stamps & Groothuis, 2010b, p. 304). However, studying personality development in wild populations is an important issue (Stamps & Groothuis, 2010a; Trillmich & Hudson, 2011) since standardized laboratory conditions may yield artificial effects derived from the lack of environmental heterogeneity (Groothuis & Trillmich, 2011, p. 652).

Estimates of repeatability are commonly used in behavioral ecology, applied to morphological, physiological or life-history traits (Bell et al., 2009), but this measure can be applied to any phenotypical response, such as any kind of behavior or personality trait. Repeatability is also known as ‘differential consistency’ or broad-sense repeatability, and refers to the fraction of behavioral variation in a set of measures due to the variance between individuals (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010; Stamps & Groothuis, 2010b; Stoffel, Nakagawa, & Schielzeth, 2017; Wolak, Fairbairn, & Paulsen, 2012). This means that, when within individual variation is low (i.e. multiple measures of the same individual are significantly similar) and between individuals variance is high (i.e. measures of different individuals differ significantly) the variable is

repeatable. Frequently, repeatability is used as a measure of individual consistency with individual identities being the grouping factor (Stoffel et al., 2017). In order to control whether other variables affect the repeatability estimation of a trait, ‘adjusted repeatabilities’ (Nakagawa & Schielzeth, 2010) can be estimated by using generalized linear mixed-effect models (GLMM), controlling for random and fixed effects (for a review see Bolker et al., 2009).

Measuring behavior in natural observations along several years allows determining whether the scores obtained are stable across ontogeny. If we find ‘differential consistency’ across the repeated measures on the beginning of life - which means that within individuals’ variance is low while variance between individuals is high- and this difference is maintained in time, this may mean a trait is repeatable, so we are able to claim that we found personality traits early in ontogeny of *Sapajus xanthosternos*. On the other hand, if there is no ‘differential consistency’ in our sample because there is high within-individual variation or low between-individual variation (Nakagawa & Schielzeth, 2010), the obtained traits might be not repeatable, so we cannot talk about personality early in ontogeny.

In this study, we first obtained personality traits from behavioral codification by means of principal component analysis, we then calculated regression models in order to observe developmental effects on these traits, and then calculated repeatability of personality traits, across 10 developmental stages. The devolvement of personality of *Sapajus xanthosternos* has never been studied before, and even less so in the natural setting of the species, so we face an additional challenge.

METHODS

Study site

Data were collected at Una Biological Reserve (Bahia, Brazil; 15º06'–12'S and 39º02'–12'W), a fully protected conservation unit 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 old agriculture fields called ''cabruca'' (i.e., an agroforest where cocoa trees, *Theobroma cacao*, occupy the understory forest; see Raboy, Christman, & Dietz, 2004). Other invasive species, such as jackfruit (*Artocarpus heterophyllus*) and oil-palm (*Elaeis guineenses*), are widely distributed within the secondary forest areas and old "cabruca" fields (Canale, Kierulff, & Chivers, 2013).

Study species

Capuchin monkeys (*Sapajus* spp.) are known for their cognitive skills, including the use of tools for foraging (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004) and other purposes (Falótico, Siqueira, & Ottoni, 2017; Visalberghi, Di Bernardi, Marino, Fragaszy, & Izar, 2017), and also for their social complexity (Izar et al., 2012). The genus comprises eight species widely distributed across South America (Lynch Alfaro et al., 2012). The yellow-breasted capuchin monkey (*S. xanthosternos*) is an endemic species of the northern Brazilian Atlantic Forest, restricted to southern Bahia. Due to this reduced area of distribution *S. xanthosternos* is considered a "critically endangered" (CR) species also because the "extensive habitat loss throughout its range" (IUCN: Kierulff, Mendes, & Rylands, 2015). Studying developmental processes and

personality on an endangered species allows the implementation of appropriate conservation management plans (Lynch Alfaro, Izar, & Ferreira, 2014; Malange, Izar, & Japyassú, 2016).

Studied Group and Data Collection

The studied group, called *Principe*, has been followed since 2005, when it was habituated systematically with the help of radio telemetry systems (Kierulff, Canale, & Suscke, 2005). Suscke (2009, 2014) conducted a long term study on this group, showing high predator pressure (Suscke et al., 2017) and a tight female bonded sociality with low rates of aggression (Suscke, 2014). In 2013, we started a longitudinal research on developmental processes recording weekly sampling videos of youngsters between 0 and 3 years-old on a focal basis (Altmann, 1974), thus, each individual born after 2013 was filmed weekly. During this period two researchers (ID & MFB) and one field assistant (RSO) accompanied the group from dawn to dusk, collecting also other behavioral data (5' scans sampling every 20' and all occurrences events) (Altmann, 1974). According to Verderane (2010), age classes of capuchin monkeys can be categorized as: Infant (0-1,5 years), Juvenile (1,5- 5 years), Subadult (5-7 years, only males) and Adult (males: +7 years, females: after 1st conception). Therefore, our studied sample covered the first half of juvenility of individuals.

The group had 26 ± 5 individuals, going through many changes such as dominance reversal, migration of young males, death or disappearing of elders, and permanent division. In this contribution we report data on the 12 individuals, 9 males and 3 females (Table 1), aged between 0 and 3 years (i.e. 0 and 36

months) during the time of this study and remained in the group. They were all born between 2013 and 2017, in four different breeding seasons (i.e. cohort).

TABLE 1

Youngsters of *S. xanthosternos* from *Principe* group at Una Biological Reserve in 2013-2018

	Subject		***Sex***	***Age in months in 2018***	***Birthday***	***Affiliation***	***Cohort***
1	Sofia	SOF	F	36	20/11/2013	Samantha	1
2	Pimenta	PIM	M	36	07/01/2014	Preta	1
3	Rocio	ROC	M	36	15/01/2015	Priscila	2
4	Luciano	LUI	M	36	26/01/2015	Larissa	2
5	Mequetrefa	MEQ	F	36	03/03/2015	Marcela	2
6	Caio	CAI	M	36	05/03/2015	Michele	2
7	Pigmeu	PIG	M	24	17/01/2016	Preta	3
8	Sumo	SUM	M	24	29/01/2016	Samantha	3
9	Marta	MAT	F	12	25/11/2016	Marcela	4
10	Isaque	ISA	M	12	30/11/2016	Irene	4
11	Carol	CAR	F	12	14/12/2016	Michele	4
12	Lineo	LIN	M	12	23/12/2016	Larissa	4

Ethical Note

The capuchins were observed and filmed in their natural environment, without any type of interference in their daily activities, except for the presence of human observers. 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, nº 6870180216), Brazilian legal requirements (SISBIO

permit 47501-5), and the principles for the American Society of Primatologists for the Ethical Treatment of Non-Human Primates.

Data Analyses

Video coding

We analyzed focal videos of 12 young individuals (aging between 0 and 3 years) from November 2013 to March 2018. Every week, whenever possible, each individual was followed and focal filmed during two periods (morning [6:00-12:00] and afternoon [12:01-18:00]). Among the huge video record collected for each individual, we selected 10 developmental points comprising the first three years of life: the 1st, 2nd, 3rd, 6th, 9th, 12th, 18th, 24th 30th and 36th months of life, in order to follow-up closely the developmental process. We considered one developmental point including 4-5 filming weeks. We analyzed 4828 minutes (about 80hrs) of focal films (1927 videos) using the software The Observer ® XT 13 (Noldus Information Technology, VA; Zimmerman, Bolhuis, Willemsen, Meyer, & Noldus, 2009). We transcribed 44 behaviors (Table S1), based on the literature on the typical capuchins repertoire (Fragaszy, Visalberghi, & Fedigan, 2004; Rose, 2000; Rose et al., 2003). Four trained observers analyzed the videos (see acknowledgments), after reaching 80% congruence (*kappa* confiability index 0.80), during their training period. We calculated weekly rates of behaviors for each study subject (i.e. number of observed events divided by observation time, minutes, of that individual in that specific week).

Principal Component Analyses

Weekly behavioral rates were the starting point for component reduction. We applied several criteria to our data in order to select the most accurate structure (i.e. the one explaining more variance) of personality traits from behavioral coding. Since PCA does not perform properly with infrequent events we first applied a 'minimum rate criterion' > 0.01 (i.e. at least 1 behavior every 100 minutes), which reduced the original 44 behaviors (Table S1) into 18. Using R packages *psych* (Revelle, 2017) and *paran* (Dinno, 2012) we conducted exploratory Principal Component Analysis (PCA), using the principal function in package *psych*, with varimax rotation, over the 18 remaining behaviors. Horn's parallel analysis (*paran* function) indicated that four components should be maintained, that explained 57% of cumulative variance. However, behaviors with rates close to zero were still present in the sample. We then applied a 'zero rates criterion' that excluded behaviors with more than >50% of weekly behavioral rates equal to 0. After applying the second criterion, we obtained 15 relevant behaviors (Table 2) with which we performed another PCA, varimax rotated. We choose varimax rotation because it provides orthogonal components that are independent (uncorrelated). Horn's parallel analyses (Dinno, 2009) suggested a four-component solution that explained 64% of cumulative variance (see Results, Table 3). We considered each component a different personality trait and interpreted the components according to the behaviors contained on each level.

TABLE 2

Reduced Ethogram with 15 Relevant Behaviors used in PCA.

Behavior Name	***Definition***
Eat	Monkey places food into its mouth, chews and swallows.
Forage	Monkey uses hands/mouth/feet to move food object around, does not ingest food item.
Groom	One monkey picks through or manipulates the fur of another with hands and/or mouth. (Rose, 2000)
Lipsmack	Monkey presses lips together and opens them repeatedly while making a 'p' 'p' 'p' sound.
Loc_For	Monkey locomotes while carrying food item in its hands/mouth/feet.
Move/Walk/Run	Monkey uses four limbs to locomote in any substrate.
Not_moving	Monkey is still in any substrate, being awake.
Nurse	Monkey breastfed from mother teat/Infant monkey uses mouth to suckle from mother's teat./A female suckles an infant.
Play	Two or more monkeys mutually engage in sequences of spontaneous, apparently non goal-oriented behaviors that include chasing, lunging, tagging, wrestling, rough and tumble, gentle mouthing and rolling, tickling and play biting. Many components resemble those described under 'Aggression', but are typically accompanied by a characteristic play face and performed in a relaxed manner without bodily tension or piloerection, usually without accompanying vocalizations. (Rose, 2000)
Proximity	Every time that other animal is close to the focal subject, without interacting.
Sample	Smell, poke or bite (but not consume) food (typically unripe fruit).
Scratch	Monkey itches itself. Scored every time the animal changes the limb it's using or changes the body part scratched.
Sexual	Monkey engages in behaviors such as mounting, courtship, exploration of others genitalia, etc...
Touch	One monkey puts its hand in any part of another monkey, intentionally.
Vigilant	Monkey gazes intently beyond vegetation in immediate vicinity with the head up, body stationary and slightly or conspicuously tensed. (Rose, 2000)

Scoring of individuals in personality traits

We transformed components/traits loadings into unit-weighted scores (Gorsuch, 1974), changing loadings higher than or equal to |0.4| into 1, if the behavior loaded positively into the component, or −1, if the behavior loaded negative (cf. Weiss et al., 2009). We transformed weekly rates of behavior into z-scores, in order to balance frequency differences among behaviors. We then

scored each individual in each component, multiplying the z-scores by the unit-weights, and dividing by the number of behaviors in that component. For each individual, we obtained a weekly score, and then we calculated the monthly mean and variance for every developmental point.

Statistical analyses

All statistical analyses were conducted using R software, version 3.4.0 (R Development Core Team, 2017), within the RStudio environment. We used the lme4 package for fitting the mixed-effect models (Bates, Mächler, Bolker, & Walker, 2015), the lmerTest package for quantifying *p* values for fixed effects (Kuznetsova, Brockhoff, & Christensen, 2017), the MuMIn package for model selection (Barton, 2018), and the rptR package for estimating repeatabilities (Stoffel et al., 2017).

Linear Regression

We apply generalized linear mixed-effects models (GLMM) with Gaussian distribution to analyze the relationship between each personality trait and the variables monkey ID, developmental point, sex, and cohort. The distribution of residuals was inspected visually in every model and did not show distinct deviations from normality. We first ran saturated models (SMs), one for trait, entering all variables, for testing their contribution and choosing the best model through AICc, which was calculated with function ‘dredge’ on MuMIn package. The SMs included four fixed effects (monkey ID, sex, cohort and developmental point) and their interactions. Then, we analyzed whether infants of yellow-

breasted capuchin monkeys presented differences in personality along ontogeny by controlling the monkey ID effect on personality traits. We did this in two different ways: (1) running pooled complete models (CMs) where we added developmental point as multilevel fixed factor and controlled the model for ID, sex and cohort as random effects variables, and (2) performing developmental point modelling (DPMs), so we ran one model *per* developmental point, controlling for the same random effects. We ran models in R, version 3.4.0 (R Development Core Team, 2017) using 'lmer' and 'lm' (for the SMs) functions from package lme4 (Bates et al., 2015).

Repeatability

We calculated repeatability with generalized linear mixed-effects models (GLMM) using 'rpt' function on rptR R package (Stoffel et al., 2017). The estimation models controlled for monkey ID, sex and cohort as random effects. Additionally, the CMs controlled for developmental point as a multilevel fixed effect. Statistical significance of the repeatability was tested by LRT (likelihood ratio test) of the log-likelihood of models with the random effects (monkey ID, sex and cohort). The 95% confidence intervals (CIs) and *p*-values were calculated by means of 1000 bootstrap and 1000 permutation. The rptR package applies parametric bootstrapping for the estimation of confidence intervals, but it uses randomization for inference testing (*p*-values). Consequently, sometimes *p*-values indicated significance, but the CIs included zero. We interpreted the estimates of repeatability by inspecting R coefficient, *p*-values and confidence intervals simultaneously. We considered a trait not repeatable if the CI included

zero and/or the estimation of R was below 0.1, even though the estimate of R was significant (Schuster, Carl, & Foerster, 2017).

The analyses by developmental point might seem unusual if compared to the possibility of analyzing the combined data using mixed-effects models while controlling for the repeated measures (i.e., treating developmental point as a multilevel continuous fixed factor). However, we consider this analysis adequate because our most important aim is to understand whether there is a developmental process behind personality traits, and when these changes occur during ontogeny (Krause, Krüger, & Schielzeth, 2017). The pooled analysis (i.e. all developmental points together as a fixed effect) has the advantage of reducing analysis but it disregards the moment of developmental changes. Although we perform both kinds of analyses (i.e. CMs and DPMs), we consider the latter more appropriate. The full results of repeatability by developmental point are presented in the ESM (Table S2).

We specifically tested the following questions: (1) How repeatable are the single personality traits within (DPMs) and across (CMs) ontogenetic stages, and (2) which factors influence repeatability (i.e., age, sex or/and cohort).

RESULTS

In total, we analyzed 4828 minutes (about 80 hours) of focal films of the 12 individuals aged under 3 years, at Una Biological Reserve (Bahia, Brazil). This corresponds approximately to 8 hours of focal activity *per* individual (M=482:52 min; SD= 171:29 min) (see Figure S1, supplementary material). Focal films were collected between November 2013 and March 2018.

Principal Components Analyses: Trait Definition

The results of both Horn's parallel analysis and the scree plot (Figure S2) suggested that four components should be retained, with all adjusted eigenvalues larger than 1 (3.91, 1.42, 1.11 and 1.07). The PCA revealed four components, which accounted for 64% of cumulative variance. RC1 included behavioral categories mostly related to social interactions (i.e., groom, lipsmack, proximity, touch and nurse), except for not move, forage and vigilant. Thus, this component was named Sociability-Attractiveness (see Table 2 for behavioral definitions and Table 3 for trait behavioral composition). The fact that not moving was included in this component might indicate that immatures tend to be calm while engaging in social interactions. On the contrary, the categories vigilant and forage loaded negatively to this component. This suggests that less social immatures need to be more vigilant as they keep far from the group safety, and that foraging might be a solitary activity. Because during their early development, capuchin monkeys mostly received grooming and lipsmacking, we added the suffix Attractiveness to this component. RC2 included behaviors associated to repetitive performance, such as eating and scratching, so it was named Anxiety (see Table 2 for behavioral definitions and Table 3 for trait behavioral composition). In fact scratching behavior in captivity is considered an anxious symptom that can be related to stereotypy (Aureli & De Waal, 1997; Ferreira et al., 2016). RC3 included the behaviors Playing and Sexual. In immatures sexual behavior is associated with the playing repertoire (Fragaszy, Visalberghi & Fedigan, 2004) and, as openness has a relevant "playful facet" (Weiss et al., 2009) we named this component Openness. RC4 was the Activity component, including the behavior related to locomotion.

TABLE 3

Four-component personality structure of young *S. xanthosternos*, and its loads and monthly rates in each developmental point.

Developmental point		1st	2nd	3rd	6th	9th	12th	18th	24th	30th	36th	
Sociab-Attract	load											month/beh
Vigilant	-0.61	0	0	0.02	0.05	0.03	0.08	0.04	0.08	0.08	0.12	8
Forage	-0.71	0	0.02	0.08	0.22	0.22	0.37	0.3	0.42	0.4	0.48	9
Proximity	0.75	0.76	0.79	0.71	0.67	0.65	0.61	0.49	0.54	0.27	0.38	10
Not_moving	0.58	0.5	0.47	0.55	0.31	0.21	0.15	0.11	0.12	0.13	0.09	10
Groom	0.49	0.33	0.19	0.15	0.14	0.15	0.13	0.04	0.07	0.03	0.05	10
Lipsmack	0.62	0.15	0.13	0.05	0.06	0.04	0.04	0.03	0.03	0.02	0.02	10
Touch	0.74	0.14	0.12	0.06	0.04	0.03	0.02	0.02	0.02	0	0	8
Nurse	0.56	0.19	0.13	0.12	0.13	0.08	0.05	0.02	0	0	0	7
Anxiety	load											
Eat	0.76	0	0.01	0.12	0.31	0.8	0.56	0.9	0.86	0.69	0.55	8
Loc_For	0.75	0	0.01	0.09	0.11	0.19	0.16	0.25	0.27	0.37	0.12	9
Scratch	0.64	0.03	0.21	0.3	0.37	0.44	0.47	0.35	0.42	0.36	0.31	10
Taste/Sample	0.55	0.02	0.19	0.24	0.21	0.15	0.07	0.11	0.08	0.01	0	9
Openness	load											
Sexual	0.85	0	0	0	0.04	0.01	0.02	0.03	0.03	0.03	0.03	7
Play	0.76	0	0	0.05	0.12	0.14	0.19	0.11	0.1	0.1	0.15	8
Activity	load											
Move/Walk/Run	0.92	0.32	0.63	0.71	0.62	0.56	0.71	0.44	0.45	0.53	0.58	10
beh/month		9	11	14	15	15	15	15	14	13	12	

Neither single behavioral rates (Table 3), nor personality traits scores (Figure 1) were stable across the early development of the studied capuchin monkeys. Rank order of these traits were also not stable, as indicated by the crossing of the individual curves across developmental points (Figure 1). Openness did not appear immediately after birth in ontogeny, but only after the third month of life (Table 3 and Figure 1c). In Sociability-Attractiveness (Figure 1a) monkeys were progressively converging into trait similarities from a very variable beginning. In Anxiety (Figure 1b) individuals converged at the beginning

of life in low levels of this trait, increasing the inter-individual variability in subsequent developmental points, and finally they converged again in the last developmental points measured. Activity was the most variable trait (Figure 1d).

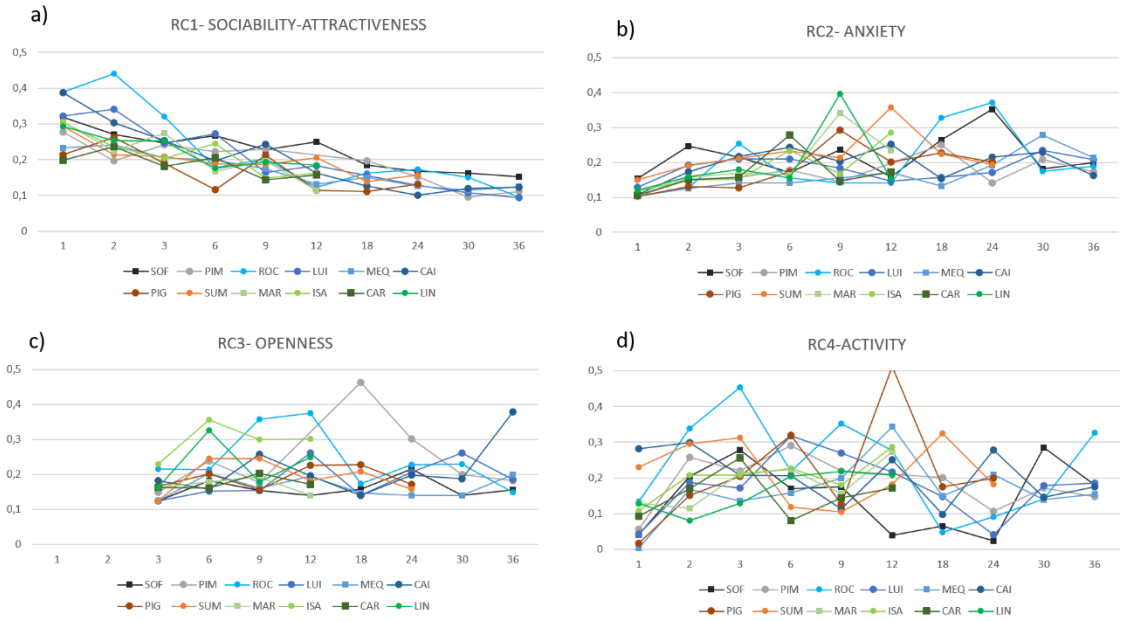

FIGURE 1. Mean scores of personality traits *per* individual across the 10 developmental points. a) Sociability-Attractiveness; b) Anxiety; c) Openness; d) Activity. Z-scores were transformed into proportions between 0 and 1.

Linear Regression

The saturated models (SMs) allowed for selecting which variables contributed to explain the variance of personality traits. The variation of RC1 (Sociability-Attractiveness) and RC2 (Anxiety) was best explained by the variables developmental point and monkey ID, but not their interactions. Sex and cohort were not included in the best models (i.e., lower AICc) of these two traits. For RC3 (Openness) and RC4 (Activity), the best models did not include monkey ID, but did include the other variables. Since we did not obtain a uniform result in

the SMs, we decided to introduce all variables in the CMs, with developmental point as a fixed effect and monkeys ID, sex, and cohort as random effects.

In the complete models (CMs) of Sociability-Attractiveness and Anxiety, the random effect variable infant ID, but not cohort and sex, contributed significantly for the regression model. Developmental point contributed significantly for both traits: Sociability-Attractiveness decreased and Anxiety increased across developmental points (Figure 2). In Openness and Activity, none of the random and fixed effects contributed to the regression models, although there was a small effect of sex.

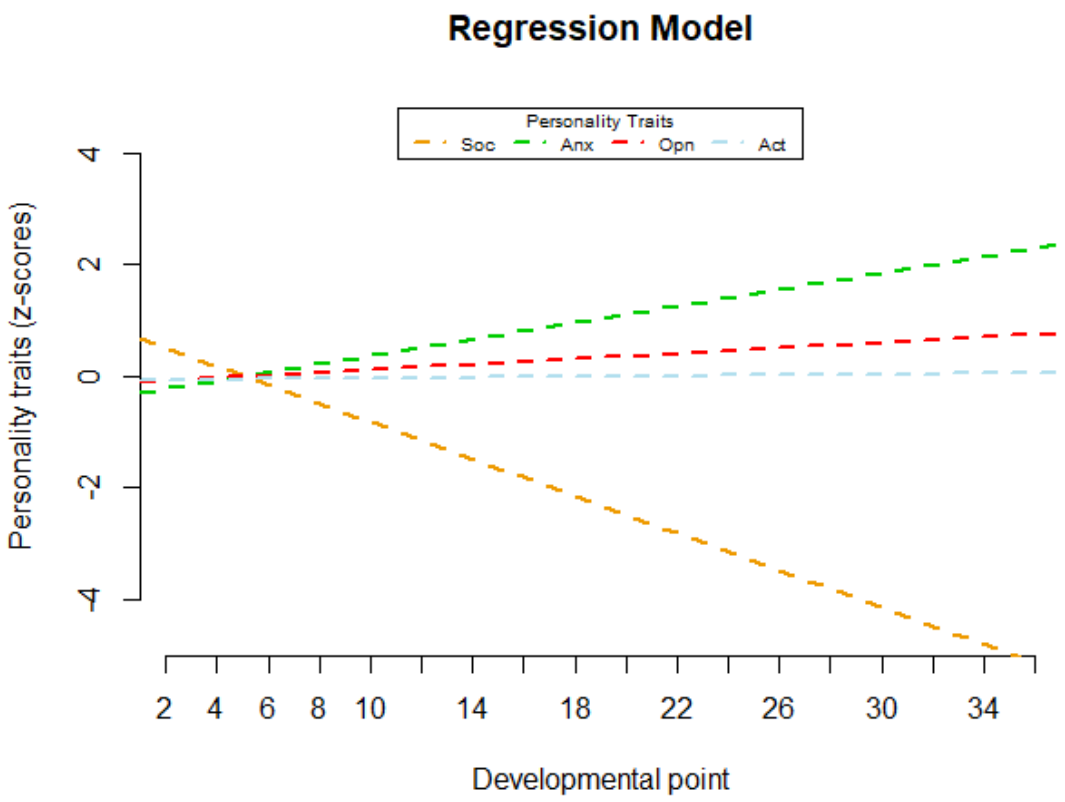

FIGURE 2. Regression model of the four personality traits with time as a multilevel fixed factor, controlling for monkey ID, sex and cohort.

Repeatability of traits

As in the regression models, based on the results of the SMs we included all variables (i.e., developmental point, monkey ID, sex and cohort) to calculate the repeatability of traits, performing both CMs and DPMs.

Repeatability of traits with complete models (CMs)

In the CMs controlling for random effects of infant ID, sex and cohort, and developmental points as a multilevel fixed effect, just Sociability-Attractiveness and Anxiety were significantly repeatable (R= 0.076, p<0.001 and, R= 0.045, p=0.01, respectively). In both traits, only infant ID affected repeatability, excluding sex and cohort (Table S2). Sex affected repeatability of both Openness (R= 0.129, p=0.01) and Activity (R= 0.052, p=0.02). Although repeatability estimates were significant, R coefficients were below 0.1, so traits were not repeatable considering the whole study period.

Repeatability of traits across developmental points (DPMs)

Besides the complete models, we performed repeatability analyses for each personality trait in each developmental point controlling for monkey ID, sex and cohort as random effects. Detailed results of these analyses are shown in ESM (Table S2). No trait was permanently repeatable across all the developmental points. Each trait followed its own ontogenetic path, which means that traits were differently repeatable in different moments: Sociability-Attractiveness was significantly repeatable from the 1st to the 6th month of life, re-

appearing as a significant repeatable trait at the 18th and 30th months of life. Anxiety emerged later in ontogeny, in the 9th month, being repeatable until the 24th month, when this trait progressively vanishes. Openness was a late appearing trait, significantly repeatable only at the 36th month, and was not detected until the 3rd month of life. Activity was inconsistently repeatable, being significantly repeatable on the first developmental points (1st and 2nd month), and then at the 18th and 24th months (Figure 3). In most cases, repeatability was below 0.4, showing that than intra-individual variance was higher than inter-individual variance.

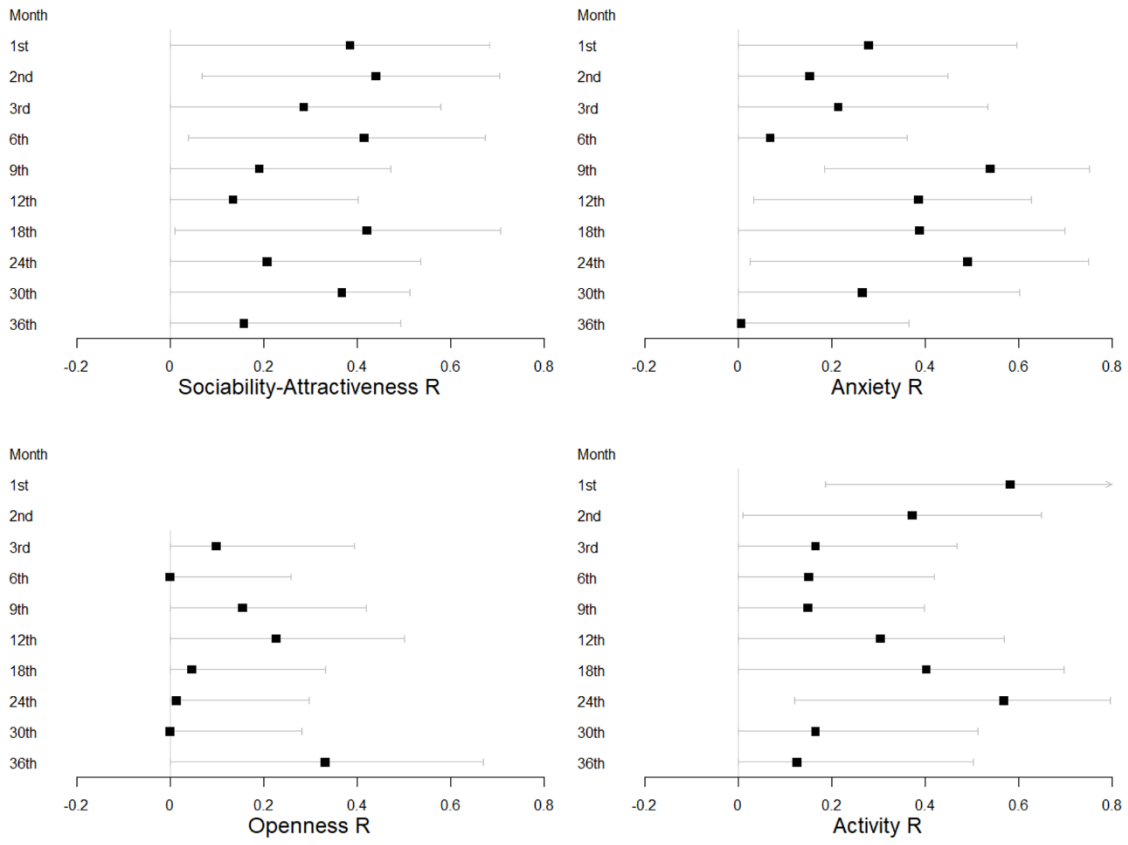

FIGURE 3. Repeatability of personality traits, with 95% confidence intervals, within and across the 10 developmental points.

DISCUSSION

In this contribution, we presented a personality structure for infants of wild yellow-breasted capuchin monkeys (from 0 to 36 months old), conformed by four traits: Sociability-Attractiveness, Anxiety, Openness and Activity. We obtained these traits by recording the daily common behavior of this species in their natural environment, quantifying it by means of behavioral coding and performing a PCA that explained a substantive quantity of variance. Additionally, we analyzed whether there were developmental effects on those traits by fitting regression models that controlled the effect of time (i.e., at 10 developmental moments), and the contribution of sex and cohort on personality traits. We found a significant effect of development on Sociability-Attractiveness, decreasing along time, and on Anxiety, increasing along time. Finally, when estimating the repeatability of those traits we did not find intra-individual consistency across time, showing that this personality structure is not yet established in early development.

Empirical research for assessing personality usually relies in two methods: behavioral coding and trait rating (Gosling, 2001). However, there is considerable debate in the literature about the adequacy of each methodology (Vazire, Gosling, Dickey, & Schapiro, 2007). Behavioral coding is considered a time consuming way of assessing personality (Freeman, Gosling, & Schapiro, 2011). However, a recent study show that this method allowed assessing personality in a reliable manner on captive cotton-top tamarins after a minimum of 5 hours of observation *per* individual (Masilkova, Weiss, & Konečná, 2018). Here we codified approximately 8 hours of focal behavioral observation *per* individual, which is a vast amount of time if we consider that we studied a wild group. It has been pointed out that it is difficult to have a complete sampling of personality in

the wild (Stamps & Groothuis, 2010b, p. 304). However, in this study we circumvented this problem by: (1) carrying out a long-term study, allowing for the repetition of contexts, (2), in a well-known population where subjects were individually recognized and their precise dates of birth were exactly known, and (3) observation intervals were well established. Studying personality development in wild populations conveys evolutionary and ecological validity to the concept.

Even though we obtained a four trait personality structure (which explained 64% of cumulative variance) of young yellow-breasted capuchins, we did not find intra-individual consistency in this traits across early development. Our results are similar to those reported for humans. In humans, personality is expected to be crystalized by the age of 30 (Costa & McCrae, 1997) and rank-order consistency reaches a plateau sometime after the age of 50 (Roberts & DelVecchio, 2000), so personality still changes even during adulthood (from 30 to 50 years), but in a modest way. Accordingly, repeatability estimations in our 12-youngster sample of wild capuchin monkeys revealed no consistency in early infancy-to-juvenility. In a meta-analysis of studies of animal personality comparing age classes, Bell et al.'s (2009) found an opposite developmental pattern, with intra-individual consistency decreasing with age. The authors claimed that longitudinal studies within the same species and groups could yield different patterns. Our results corroborate this idea.

The regression models revealed a consistent pattern of temporal changing for two of the four traits described: Sociability-Attractiveness and Anxiety. This means that, although rank-order consistency was low because each individual occupied a different position along the 10 developmental points, there was a

pattern of mean-level change for those two traits. These two concepts (i.e., rank-order consistency and mean-level change) are better understood as orthogonal constructs since they can occur simultaneously (Roberts, Walton, & Viechtbauer, 2006). In that sense, although mean-level changes appear to contradict the idea of personality stabilization with age (Costa & McCrae, 1997) this is an erroneous assumption since mean-level change refers to changes in the average trait level of a population (Caspi et al., 2005). Similar results were obtained with young rhesus monkeys, where there developmental tendencies were detected but there was no individual consistency in personality traits (Stevenson-Hinde et al., 1980).

Development of personality traits

Sociability-Attractiveness decreased across ontogeny:

Sociability-Attractiveness includes behaviors such as grooming and lipsmacking, either emitting or receiving, and nursing or proximity. We found repeatability of this trait from the 1st to the 6th month of life, and the in the 18th and 30th months of life. This is in accordance with the capuchin monkeys' social development. Frequencies of such behaviors decline with maturity, as the role of the infant changes from receptor to giver of the interaction (e.g., grooming: Fragaszy et al., 2004, p. 118). The suffix 'attractiveness' added to this trait refers to the fact that a considerable proportion of the variance in this trait could be explained by behaviors in which the individual is the recipient. Therefore, we cannot discard that the consistent decreasing pattern found for this trait is not related to personality traits of the immatures, but to changes in behavior directed to them by other group members.

Anxiety increased across ontogeny:

Anxiety comprised behaviors that are related to repetitive patterns, such as eating, scratching or locomotion while foraging (loc_for). In captivity, some of these behaviors, when performed at abnormal frequencies, are known as stereotypies, and are used as indicators of animal welfare (Broom, 1991; Ferreira et al., 2016). However, there are other nuances in this trait, since 'taste/sample' behavior could be related to novelty seeking and neophilic-like tendencies (Fragaszy, Visalberghi, & Galloway, 1997), that progressively appear in ontogeny along with increased independence from the mother, and enhancement in sensorimotor and manipulative skills (Fragaszy & Adams-Curtis, 1997). We found an increasing pattern of Anxiety from the beginning of life to the 36th month, and this trait became consistent after the 9th month, being repeatable until the 24th month. This pattern coincides with the course of maternal care and infant independency acquisition of capuchin monkeys (Fragaszy, Baer, & Adams-Curtis, 1991; Fragaszy & Bard, 1997; Verderane, 2010). Around the 9th month a point of inflection of postnatal to juvenile growth in bearded capuchin monkeys can be detected (*S. libidinosus*: Fragaszy et al., 2016) which overlaps with the middle of the infancy (that goes around 1.5 years old) for capuchin monkeys coinciding with a period of progressively independence from the mother (Verderane, 2010). Moreover, the 24th month of life is a development milestone, since it coincides with weaning in yellow-breasted capuchin monkeys (personal obs). In primates, and mammals in general, weaning is a stressful moment, as indicated by behavioral and physiological correlates (i.e., augmented endocrine response: Mandalaywala, Higham, Heistermann, Parker, & Maestripieri, 2014).

Openness and Activity do not change in ontogeny:

Openness comprised play and sexual behaviors. Such behaviors are closely related in immatures, but also in adult individuals, since play may be a part of the courtship (Carosi, Linn, & Visalberghi, 2005; Carosi & Visalberghi, 2002; Pellis & Iwaniuk, 1999). In young capuchins, both sexes engage in sexual play. Females play less often as they reach puberty, but mounting remains an important element in males' play, merging into sexually motivated behavior (Fragaszy, Visalberghi & Fedigan, 2004, p. 123). In our data, Openness was a late-appearing trait, significantly repeatable only at the 12th and the 36th month, not being detected until the 3rd month of life. This is consistent with data for the development of play in captive capuchin monkeys (Fragaszy et al., 1991). During the 4th to the 8th week of life (2nd month), the infant initiates short periods of separation from his mother for exploring the environment. Locomotor and social play (i.e., rough-and-tumble and chase play) start by the 9th week of life (3rd month) in capuchin monkeys (Fragaszy et al., 1991). Since there was high intra and inter-individual variation on this trait across the developmental points, this might indicate that personality patterns in Openness appear only later in juvenility.

Activity included only one behavioral category: 'move/walk/run'. This trait was very variable, being significantly repeatable on the first developmental points (1st and 2nd month), when the individual keeps hanging on their mother's back, and then from the 12th to the 24th month of life, but with very low coefficients, indicating lack of intra-individual consistency. Accordingly, in Bell et al.'s (2009) meta-analysis comprising 98 animal species Activity was one of the less repeatable behaviors. Activity may not be a 'true' personality trait, since

capuchins adapt their levels of activity to environmental requirements (e.g., Izar et al., 2012), and perhaps not to consistent internal dispositions.

There are some remarkable personality studies in capuchin monkeys, developed with trait rating (*Cebus capucinus*: Manson & Perry, 2013; Sapajus apella: Morton et al., 2013) or with behavioral coding (*Sapajus apella*: Uher, Addessi, & Visalberghi, 2013). The personality structure of these studies show clear convergences: the behavioral constructs arousability, impulsiveness, or anxiousness (Uher et al., 2013) fit with Neuroticism (Manson & Perry, 2013; Morton et al., 2013); the behavioral constructs “creativeness-inventiveness” or “curiousness” (Uher et al., 2013) fit with Openness (Morton et al, 2013, Manson & Perry, 2013); the behavioral constructs “aggressiveness”, “competitiveness”, or “dominance” (Uher et al, 2013) fit with Assertiveness (Morton et al, 2013) or with Extroversion (Manson & Perry, 2013); and the behavioral constructs “social orientation to conspecifics” or “gregariousness”, fit with Sociability (Morton et al., 2013) or with Agreeableness (Manson & Perry, 2013). However, none of these studies approached the development of personality, and how these personality structures are reliable with newborn-to-juvenile individuals. Our results did support the assumption of personality being fixed from the very beginning of life. In that vein, a previous study with the same group considering individuals of all ages developed a personality structure with trait rating describing three personality traits: Openness-Neuroticism, Assertiveness and Attentiveness-Sociability (*Sapajus xanthosternos*: Fernández-Bolaños, Delval, De Oliveira, & Izar, 2019). The comparison of our results on personality structure of 12 infants with the personality structure obtained including adults (Fernández-Bolaños et al., 2019) did not reveal congruence.

CONCLUSION

In sum, while we were able to classify our subjects with respect to behaviors consistent with four traits, the lack of intra-individual consistency in these traits indicates that personality is not consolidated yet during early development of yellow-breasted capuchin monkeys. To our knowledge, this one of the firsts studies on personality development on a wild primate population. There is still a substantial lack of studies analyzing the development of personality in the field or under natural conditions. In fact, compared with the number of studies on captive animals, personality has seldom been studied in the wild (Archard & Braithwaite, 2010). The implementation of more longitudinal studies on personality development can shed light to the questions about of early consistency of personality traits and developmental tendencies.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

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Supplementary Material- Chapter Two

SUPPLEMENTARY TABLES

TABLE S1. Complete capuchin monkeys' (*Sapajus xanthosternos*) ethogram used in this study

Behavior Group		Behavior Name	Definition
OUT-OF-SIGHT	10 seconds without seeing the focal subject	Out-of-sight	More than 10 seconds without seeing the focal subject (it can be hidden behind leaves, branches, other individual, etc.).
PROXIMITY	Getting within 1m close to focal individual	Proximity	Every time that other animal is close to the focal subject, without interacting.
FEEDING	Behaviors related to getting food	Forage	Monkey uses hands/mouth/feet to move food object around, does not ingest food item.
		Predation	Monkey attempts to capture vertebrate or big invertebrate prey. Includes chasing prey, pushed from nests, birds, large lizards, bats; caterpillars, grashoppers, etc.
		Eat	Monkey places food into its mouth, chews and swallows.
		Sample	Smell, poke or bite (but not consume) food (typically unripe fruit).
LOCOMOTION	Beh. involving movements or absence of movement	Not_moving	Monkey is still in any substrate, being awake.
		Rest/Sleep	Monkey rests, sitting or lying, and is not in body contact with another or performing any other behavior.
		Move/Walk/Run	Monkey uses four limbs to locomote in any substrate.
		Bipedal	Monkey stands in two feet for more than 3 seconds. It can also walk or run in two feet.
		Loc_For	Monkey locomotes while carrying food item in its hands/mouth/feet.
		Other_loc	Rest of kinds of locomotion that we are not able to categorize above.
		Groom	One monkey picks through or manipulates the fur of another with hands and/or mouth. (Rose, 2000)
		Touch	One monkey puts its hand in any part of another monkey, intentionally.

SOCIAL	Positive behs. performed towards co-specifics	Nurse	Monkey breastfed from mother teat
		Allonursing	Monkey breastfed from another female, not the mother
		Rest_in_group	Monkey rest in contact with other group members.
		Play	Two or more monkeys mutually engage in sequences of spontaneous, apparently non goal-oriented behaviors that include chasing, lunging, tagging, wrestling, rough and tumble, gentle mouthing and rolling, tickling and play biting. Many components resemble those described under ‘Aggression’, but are typically accompanied by a characteristic play face and performed in a relaxed manner without bodily tension or piloerection, usually without accompanying vocalizations. (Rose, 2000)
		Lipsmack	Monkey presses lips together and opens them repeatedly while making a 'p' 'p' 'p' sound. (http://www.living-links.org)
		Sexual	Monkey engages in behaviors such mounting, courtship, exploration of others genitalia, etc...
		Scrounge	Monkey approaches another that has a food item and try to collect and eat what the other monkey accidentally drops.
		Beg_food	Monkey approaches another that has a food item and solicits sharing by placing hand or mouth on the food, or begs with hand outstretched (see Rose, 1997).
		Allocarring	Monkey is transported in other monkey's back. It could be an adult, a young or even another infant.
		Hug	One monkey embraces another, usually front-to-front. Is more common between males.
		Indet_Soc_Interaction	Other social interaction that we can't include within above categories/Undetermined Social Interaction: Rest of affiliative interactions that cannot be categorized above.
AGRESSIVE	Behs. related to fight and agression against co-specifics.	Threat_coesp	Monkey displays threat face or display, mouth is wide opened, so that the teeth, particularly canines, are exposed, and stares at another monkey. Eye-brows can be rised up and piloerection can occur.
		Double_threat	Two monkeys in body contact, either side by side or on top of one another (= ‘overlord’, Oppenheimer, 1973) direct open-mouthed threats to one or more others. (Rose, 2000)
		Chase	Monkey chases another putting it to run.
		Fight	Two monkeys are involved in a violent battle, that can include bites, scrateches, punches.

		Indet_Agr_Interaction	Rest of agressive behaviors that cannot be categorized above
REACTION TO RISK	Risky scenarios include presence of potential predators (aerial, terrestrial), the subjective menace of the research team, another humans or domestic animals (i.e. dogs).	Vigilant	Monkey gazes intently beyond vegetation in immediate vicinity with the head up, body stationary and slightly or conspicuously tensed. (Rose, 2000)
		Get_close	When a risk is detected the monkey rapidly aproximate the risky source. Subsequently it can Threat_risk actively or just observe the potencial risk
		Threat_risk	Monkey threatens, lunges at or chases one or more individuals of another species, including humans. May include branch breaking or shaking.
		Vocalize/Alarm_call	Brief barking vocalization (= 'gyrrah', Oppenheimer, 1973) given in response to an actual or potential threat. Includes at least three distinct types of call, to large snakes, raptors, and humans or other monkey groups (see Perry, 1995). (Rose, 2000)
		Mob	A group of three or more monkeys closely approaches, bark at and repeatedly threaten one or more individuals of another species, typically a potential predator. (Rose, 2000)
		Runaway	When a menace occurs, monkey tries to get far from the source.
SELF DIRECTED		Sexual_inspection	Monkey manipulates its own genitalia.
		Annoiting	Monkey chews a substance (i.e. insect scent, mud, etc.) and rubs it into its own fur or the fur of others. (Rose, 2000)
		Urine_washing	Monkey pees on its own hands or hind legs and rubs urine on its own body.
		Auto_play	Monkey plays alone.
		Auto_groom	Monkey grooms itself.
		Scratch	Monkey scrapes or rubs lightly (as to relieve itching). Scored every time it changes the limb or body part scratched.
		Yawn	Monkey openness the mouth wide, taking a deep breath.
		Nose-wipe	Monkey touches its own nose

TABLE S2. Adjusted repeatabilities of personality traits, with their confidence intervals, across the ten developmental points and in the whole sample period, controlling for monkey ID, sex and cohort

Trait			**Sociability-Attractiveness**			**Anxiety**			**Openness**			**Activity**		
	model		**R ± SE**	**CI**	***P [LRT]***	**R ± SE**	**CI**	***P [LRT]***	**R ± SE**	**CI**	***P [LRT]***	**R ± SE**	**CI**	***P [LRT]***
CMs														
		ID	**0.076±0.045**	[0.003, 0.167]	<0.001*	**0.045±0.029**	[0, 0.105]	0.0109*	0.004±0.014	[0, 0.043]	0.399	0.001±0.008	[0, 0.028]	0.464
		Sex	0±0.023	[0, 0.082]	0.5	0±0.016	[0, 0.057]	0.5	**0.129±0.121**	[0, 0.405]	0.0106*	**0.052±0.07**	[0, 0.259]	0.0206*
		Cohort	0.089±0.082	[0, 0.303]	0.0994	0.002±0.019	[0, 0.065]	0.457	0.025±0.031	[0, 0.11]	0.147	0±0.007	[0, 0.023]	0.5
DPMs														
	1st	ID	**0.355±0.173**	[0, 0.605]	0.0158*	0.279±0.168	[0, 0.566]	0.0529	NA	NA	NA	**0.537±0.165**	[0, 0.754]	<0.001*
		Sex	0.048±0.13	[0, 0.45]	0.39	0±0.089	[0, 0.331]	0.5	NA	NA	NA	0.056±0.147	[0, 0.5]	0.397
		Cohort	0±0.112	[0, 0.402]	0.5	0±0.093	[0, 0.33]	0.5	NA	NA	NA	0±0.135	[0, 0.456]	1
	2nd	ID	0.229±0.156	[0, 0.545]	0.0753	0.153±0.125	[0, 0.435]	0.172	NA	NA	NA	**0.246±0.153**	[0, 0.527]	0.0378*
		Sex	0±0.077	[0, 0.277]	0.5	0±0.071	[0, 0.261]	0.5	NA	NA	NA	0.056±0.147	[0, 0.5]	0.397
		Cohort	0.215±0.174	[0, 0.566]	0.0998	0±0.075	[0, 0.264]	1	NA	NA	NA	0.097±0.139	[0, 0.466]	0.238
	3rd	ID	**0.286±0.161**	[0, 0.549]	0.0377*	0.202±0.143	[0, 0.472]	0.0896	0.094±0.102	[0, 0.34]	0.247	0.094±0.108	[0, 0.36]	0.247
		Sex	0±0.08	[0, 0.315]	1	0±0.075	[0, 0.28]	0.5	0.012±0.078	[0, 0.276]	0.454	0.012±0.074	[0, 0.266]	0.454
		Cohort	0±0.094	[0, 0.313]	1	0.015±0.093	[0, 0.332]	0.446	0±0.079	[0, 0.293]	0.5	0±0.69	[0, 0.242]	0.5
	6th	ID	**0.298±0.163**	[0, 0.581]	0.0185*	0.069±0.088	[0, 0.303]	0.295	0±0.062	[0, 0.215]	1	0.096±0.125	[0, 0.341]	0.186
		Sex	0±0.081	[0, 0.282]	1	0±0.064	[0, 0.239]	0.5	0.041±0.088	[0, 0.299]	0.338	0.125±0.148	[0, 0.491]	0.18
		Cohort	0.139±0.163	[0, 0.547]	0.328	0±0.054	[0, 0.182]	1	0.024±0.063	[0, 0.213]	0.365	0±0.064	[0, 0.21]	1
	9th	ID	0.132±0.106	[0, 0.356]	0.123	**0.499±0.172**	[0.052, 0.716]	<0.001*	0.13±0.107	[0, 0.361]	0.143	0.124±0.11	[0, 0.366]	0.164
		Sex	0±0.064	[0, 0.219]	0.5	0±0.097	[0, 0.349]	1	0.043±0.099	[0, 0.349]	0.346	0±0.061	[0, 0.224]	0.5
		Cohort	0.076±0.115	[0, 0.393]	0.278	0.044±0.135	[0, 0.396]	0.396	0±0.072	[0, 0.248]	0.5	0.033±0.089	[0, 0.294]	0.384
	12th	ID	0.0.135±0.108	[0, 0.362]	0.168	**0.377±0.165**	[0, 0.611]	0.0041*	0.086±0.096	[0, 0.319]	0.175	**0.305±0.149**	[0, 0.511]	0.0215*
		Sex	0±0.067	[0, 0.243]	1	0±0.099	[0, 0.364]	1	0.246±0.201	[0, 0.653]	0.061	0±0.094	[0, 0.337]	1
		Cohort	0.52±0.091	[0, 0.279]	1	0.01±0.13	[0, 0.455]	0.481	0±0.067	[0, 0.225]	1	0±0.105	[0, 0.362]	1
	18th	ID	0±0.078	[0, 0.332]	1	**0.388±0.191**	[0, 0.65]	0.0040*	0±0.065	[0, 0.223]	0.5	0.211±0.16	[0, 0.54]	0.0544
		Sex	0±0.08	[0, 0.269]	1	0±0.133	[0, 0.456]	1	0.043±0.105	[0, 0.368]	0.367	0±0.116	[0, 0.476]	1
		Cohort	**0.508±0.257**	[0, 0.829]	0.0348*	0±0.138	[0, 0.46]	1	0.1±0.124	[0, 0.42]	0.187	0.231±0.209	[0, 0.67]	0.198
	24th	ID	0.176±0.145	[0, 0.479]	0.162	**0.491±0.205**	[0, 0.695]	0.0027*	0±0.072	[0, 0.244]	1	**0.569±0.221**	[0, 0.747]	<0.001*
		Sex	0±0.097	[0, 036]	0.5	0±0.162	[0, 0.569]	0.5	0.05±0.104	[0, 0.375]	0.373	0±0.162	[0, 0.534]	1
		Cohort	0.034±0.166	[0, 0.393]	0.423	0±0.139	[0, 0.458]	1	0.135±0.142	[0, 0.491]	0.212	0±0.157	[0, 0.506]	1
	30th	ID	**0.368±0.19**	[0, 0.612]	0.0159*	0.259±0.167	[0, 0.561]	0.0677	0±0.07	[0, 0.247]	1	0.026±0.087	[0, 0.305]	0.421
		Sex	0±0.168	[0, 0.486]	1	0±0.134	[0, 0.471]	1	0.18±0.19	[0, 0.616]	0.117	0.007±0.081	[0, 0.269]	0.475
		Cohort	0±0.139	[0, 0.489]	1	0±0.136	[0, 0.482]	0.483	0±0.059	[0, 0.211]	1	0.218±0.207	[0, 0.665]	0.151
	36th	ID	0±0.069	[0, 0.242]	1	0±0.079	[0, 0.269]	1	**0.332±0.188**	[0, 0.613]	0.0247*	0.126±0.126	[0, 0.428]	0.212
		Sex	0.226±0.207	[0, 0.664]	0.126	0.052±0.119	[0, 0.433]	0.354	0±0.137	[0, 0.48]	0.5	0±0.101	[0, 0.37]	0.5
		Cohort	0.039±0.102	[0, 0.349]	0.387	0±0.077	[0, 0.25]	0.5	0±0.142	[0, 0.486]	1	0±0.114	[0, 0.4]	1

Note. Significant values are marked with * (p<0.05) in bold. R = repeatability, SE = standard error, CI = confidence interval (95%), P = error probability (P-value), LRT = likelihood ratio tests , CM= Complete model, DPMs= Developmental point models

SUPPLEMENTARY FIGURES

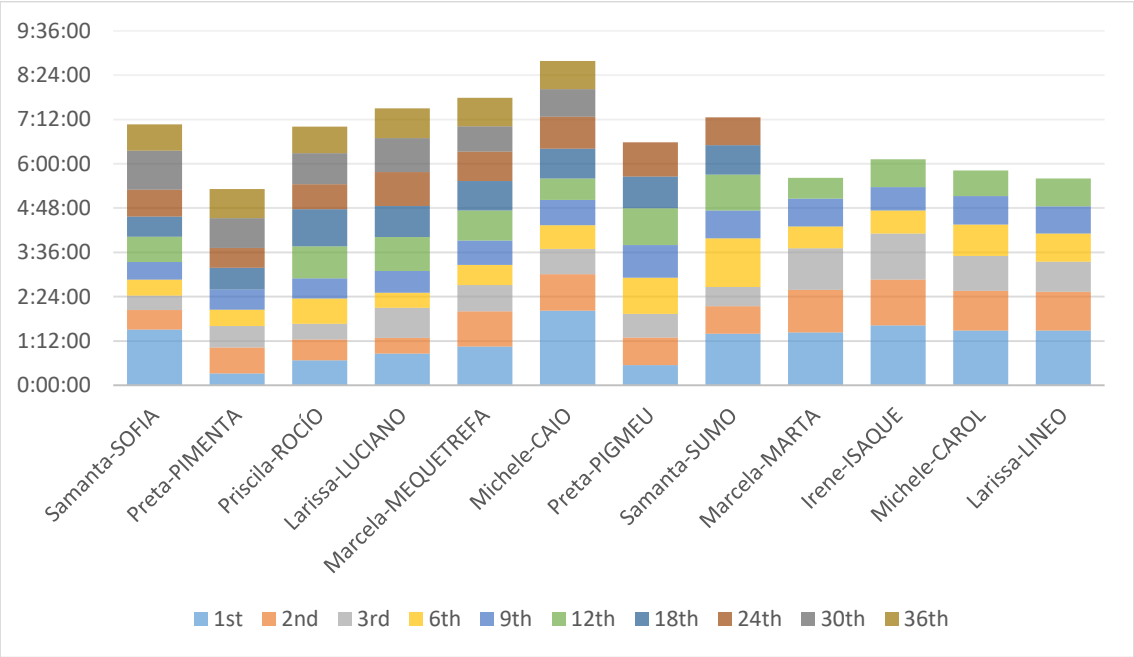

FIGURE S1 Focal video transcription effort (hours) by mother-infant dyad and developmental point

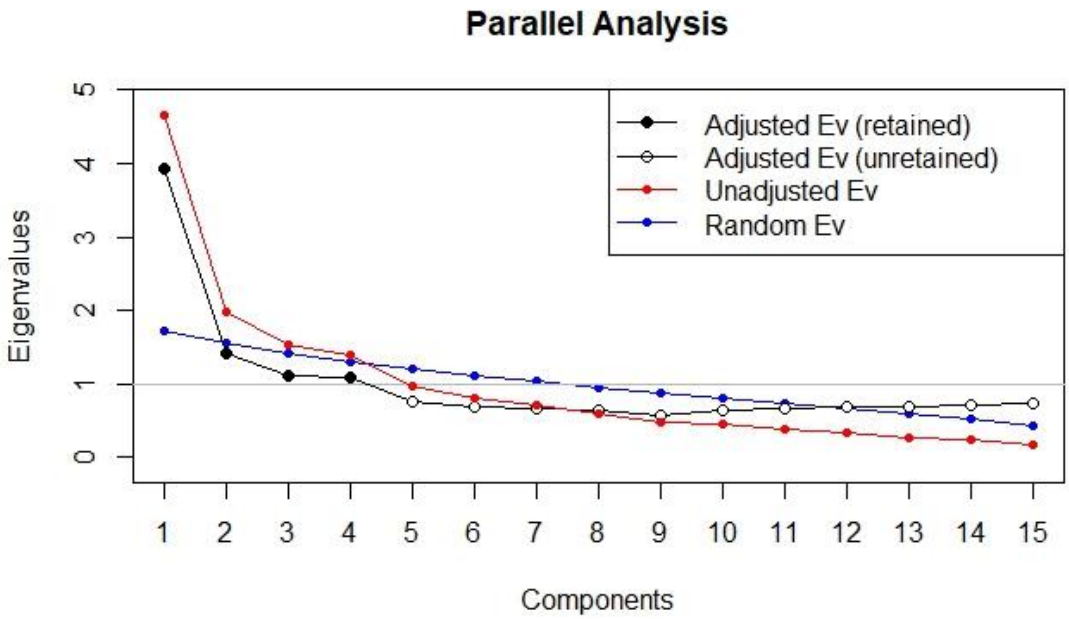

FIGURE S2 Parallel analysis scree plot with the 15 first components eigenvalues taken from unadjusted, adjusted, and random components

RESEARCH HIGHLIGHTS

-Personality is a construct that can be identified in humans and other animals.

-Trait theory has been shown useful in the explanation of personality.

-Behavioral syndrome, coping style and temperament are not exactly synonymous to personality.

-Personality research improves our knowledge about the causes of the behavior of a given species.

-Between and within-species personality research gives light about the evolutionary pathways of traits, and answering questions about environmental pressures modelling personality traits.

-Primates studies have shown that we share most traits with closely related species. However, environmental pressures also seem to act in personality, showing little differences (e.g. dominance trait in chimpanzees, but not in humans or bonobos).

-Although personality has an inherited component, in humans it is shaped across development along the first years of life. This is also expected in any animal species in order to adjust genes x environment correlations.

-Little is known about how or when individual differences in primates personality traits are established during development.

-In our research, four personality traits for young wild yellow-breasted capuchin monkeys (*S. xanthosternos*) were described: Sociability-Attractiveness, Anxiety, Openness and Activity.

-Opposite developmental tendencies on Sociability-Attractiveness and Anxiety were detected.

-Personality structure of capuchin monkeys is not yet established during early development.

-Further research would be appropriate in order to identify when personality traits stabilizes in adulthood.

-The connection of Psychology and Behavioral Ecology has already begun.

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 **Patrícia 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	Gênero: Machos e Fêmeas	Idade:	diversas	N:	15
Linhagem:	Sapajus flavius		Peso:	diversos		
Procedência:	Não aplicável					
Espécie:	Primatas não-humanos	Gênero: Machos e Fêmeas	Idade:	diversas	N:	25
Linhagem:	Sapajus libidinosus		Peso:	diversos		
Procedência:	Não aplicável					
Espécie:	Primatas não-humanos	Gênero: Machos e Fêmeas	Idade:	diversas	N:	15
Linhagem:	Sapajus nigritus		Peso:	diversos		
Procedência:	Não aplicável					
Espécie:	Primatas não-humanos	Gênero: Machos e Fêmeas	Idade:	diversas	N:	15
Linhagem:	Sapajus xanthosternos		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 Georgia, 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

Profa. Dra. Christina Abreu
Coordenadora da Comissão de Ética no Uso de Animais
Instituto de Psicologia da Universidade de São Paulo

Av. Prof. Mello Moraes, 1721 - Bloco G, 2º Andar - Sala 20 - Butantã - CEP 05508-900 São Paulo/SP - tel: 55 (11) 2648-0694 / fax: —
Horário de atendimento: 2ª a 6ª das 9h30 às 12h00 e 13h30 às 17h30 : e-mail: arietema@usp.br
CEUA Nº 6870180216