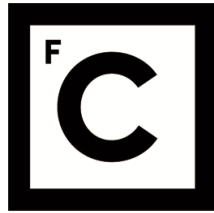


UNIVERSIDADE DE LISBOA  
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**Ciências  
ULisboa**

**A Neurodevelopmental Approach to the  
Phylogeny and Ontogeny of Primate Personality**

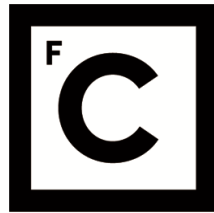
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**Doutoramento em Biologia**  
Especialidade Etologia

Ângela Catarina Calero Brandão

Tese orientada por:  
Professor Luís Matos Vicente  
Professora Maria Augusta da Gama Antunes

Documento especialmente elaborado para a obtenção do grau de doutor



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## NOTA PRÉVIA

A presente tese contém capítulos já publicados (capítulo 2) e outros preparados para ser submetidos (capítulos 1, 3, 4 e 5) de acordo com o Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, e com o Despacho N.º 4624/2012 do Diário da República II série nº 65 de 30 de Março de 2012. A candidata realizou os trabalhos em colaboração, mas liderou e participou integralmente na concepção dos mesmos, desde a obtenção dos dados, análise estatística, discussão dos resultados e redação dos manuscritos.

Lisboa, 21 de Fevereiro de 2021

Ângela Catarina Calero Brandão

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## **List of general nomenclature and abbreviations**

<b>Abreviattion/Symbol</b>	<b>Description</b>
FFM	Five Factor model
PFC	Pre-Frontal Cortex
OFC	Orbitofrontal Cortex
MAPK	Mitogen-activated Protein Kinases
IQ	Intelligence quotient
HPA	Hypothalamic-pituitary-adrenal
REM	Random Effect Model
CI	Complexity Index
PI	Predictability Indices
PIns	Predictability Non-Social Index
PIsi	Predictability Social Initiating Index
PIsr	Predictability Social Receiving Index
UTI	Unusual Transition Index
UTIns	Unusual Non-Social Transition Index
UTIsi	Unusual Social Initiating Transition Index
UTIsr	Unusual Social Receiving Transition Index

SNAP	Single Nucleotide Polymorphism
MFS	Mean Flexibility Scores
IBI	Interval Interbirth
SDI	Species Diversity Index
SDIns	Diversity Index for Non-Social Behaviours
SDIsi	Species Diversity Index for Social Initiated Behaviour
SE	EthoSeq schematic matrices
SFIsr	Species Diversity Index for Social Received behaviours
SFIsp	Species diversity Index for social proximity
SUTI	Species Unusual Transition Index
SPI	Species Predictability Index
SPIns	SPI Non-Social
SPIsr	SPI Receiving Social Behviours
SUTIns	SUTI Non-Social behaviours
SUTIsi	SUTI Initiating Social Behaviours
SUTIsr	SUTI Receiving Social Behaviours

## **Glossary of central terms**

This glossary is intended to provide the author's definitions of the central terms introduced and explored in this thesis. Specific aspects of each concept may be explored in different parts of the thesis and we advise the reader to consult this glossary to understand the underlying meaning across contexts and any time doubts might emerge.

**Personality:** This term refers to the neuropsychological process of organization of information-cum-activity that is personally relevant for the individual. What motivates the choice of information includes an epistemic (knowledge about the world) motivation and a self-interest (what is good or bad for the individual) motivation. The valuation of information is always a relative process, which changes with time and contexts. Consequently personality is considered to be a dynamic process of continuous change by assimilation and accommodation (or feedback-feedforward networks in neurological terminology). This neuropsychological process of organization creates an internal model used to make predictions and to interact with the environment. For each person, the internal model tends to stabilize over time by the continuous accumulation of evidence. What normally are considered traits or phenotypes, in other conceptions of personality, are in this view seen as the byproducts of this organizational process -- the forms of behavioral, cognitive and emotional stability that are created over time.

**Diversity:** This term refers to a quality of a group, namely the differences that can be observed across individuals within the group in durations and frequencies of behaviors. For example, all individuals may exhibit aggressive behaviors, but some individuals show more frequent instances of, or persist longer in, aggressive behavior than others. It is considered that such differences are quantifiable and can be compared. The significant differences found among individuals in a group represent the group's diversity. One group will be considered to have more diverse personalities among its members, if, when compared to another group, the first group shows a larger variety of behaviors with significant differences in frequency. One species will be considered to have more diversity than another species, if, one species' groups show more behaviors with significant differences among its members, than the other species' groups. More information about the proposed way of measuring frequencies of individuals' behaviors and diversity of groups can be found in chapters 3, 4 and 5.

**Flexibility:** This term refers to variation in individual behavior over time. For example, the frequency and duration of aggressive behavior exhibited by one individual might vary from day to day. It is considered that these variations are quantifiable and can be compared across individuals. Individuals whose behaviors vary more over time are considered to be more flexible. Groups may also be considered to vary in flexibility depending on differences

among their members. A group will be considered to be more flexible when the personalities of its members show greater variability over time than those of another group. Similarly, one species can be considered to be more flexible when the personalities of its members show greater variability over time than those of another species. More information about the proposed way of measuring and comparing individuals, groups and species can be found in chapters 3, 4 and 5.

**Complexity:** This term refers to differences among individuals in how many patterns of behavioral sequences they exhibit consistently over time. It is considered that these differences are quantifiable (for example, by using the EthoSeq program that attributes conditional probabilities to each behavior). A sequence  $A \rightarrow B$  is considered a pattern if, when A occurs, 25% or more of the times it is followed by B. Comparing patterns across individuals, one individual may exhibit the pattern  $A \rightarrow B$  but not  $A \rightarrow D$ ; a second member may exhibit only the pattern  $A \rightarrow D$ ; a third member may exhibit both patterns. Individuals with more complex personalities will be the ones that present more alternative patterns when compared with others that present fewer patterns, for example:

Individual 1 (most complex)	Individual 2	Individual 3	Individual 4 (least complex)
$A \rightarrow B$ 25%	$A \rightarrow B$ 40%	$A \rightarrow B$ 60%	$A \rightarrow C$ 100%
$A \rightarrow C$ 25%	$A \rightarrow C$ 30%	$A \rightarrow D$ 30%	
$A \rightarrow D$ 25%	$A \rightarrow E$ 25%		
$A \rightarrow E$ 25%			

Groups can also be compared in terms of complexity based on the complexity

of the personalities of their members. A group is considered more complex if its members, when compared to those of another group, show more behavioral patterns overall. Similarly, the relative complexity of personality among species can be compared. One species is considered to be more complex than another species if when their respective groups are compared, one species' groups contain more individuals with high complexity among their members, than the groups of other species. More information about the proposed way of measuring and comparing individuals, groups and species can be found in chapters 3, 4 and 5.



## **Acknowledgments**

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Finally, I would like to say a few words about personality. It is my firm conviction that personality is not predetermined and that we all become "what we are" through a process. In each individual's process of becoming, we are all responsible as society. Each one of us contributes to the transformational process of the other even when we don't necessarily know that other. The transformational process that we all undergo throughout our lives is the one that allows real change to happen. In the process of fighting for a better world, we have to fight for a better us. Thank you!"

Angela Catarina Calero Brandão

## **Abstract**

This thesis proposes a new theory of personality in human and nonhuman primates, integrating neuroscience with ontogenetic and phylogenetic developmental perspectives. In this theoretical proposal, the most important goals for the study of personality are to understand: a) the ontogeny of personality, including the development of individual differences; b) the phylogeny of personality, including the common brain areas and functions that underlie personality ontogeny across primate species; and c) how individual differences regarding idiosyncratic aspects of individuals' personalities reflect adaptations to the individuals' life-histories that brought them about. Three essential premises are at the core of this theory: first premise: Personality is a dynamic structure, changing through the individual's ontogeny; second premise: Personality organizes interactions with the external world into a complex internal model; and third premise: Personality evolved through primates' phylogeny along with the brain structures that sustain it. At the empirical level, the hypotheses were that animals with higher cognitive abilities related with the referred brain areas, would have more diverse, flexible and complex personalities. A group of species covering the main branches of the primate phylogenetic tree were studied: a) Strepsirrhines: red-ruffed lemurs (*Varecia rubra*) and ring-tailed lemurs (*Lemur catta*), b) Haplorrhines - Platyrrhines: squirrel monkeys (*Saimiri boliviensis*) and tufted-capuchin monkeys (*Sapajus apella*), and c) Haplorrhines - Catarrhines: mandrills (*Mandrillus sphinx*) and white-handed gibbons (*Hilobates lar*). The choice of species was limited to access availability. Data were collected via direct observation of behavior of animals from the Lagos' Zoo, Badoca Park and Maia's Zoo. Data were analyzed statistically and mathematically to obtain information on three personality aspects: 1) Diversity, 2) Flexibility, and 3) Complexity. The personality study methodology used was innovative. The data obtained are a first corroboration of the hypothesis defended. Further studies with other groups, species, and outside the context of captivity are required.

**Keywords:** personality; diversity; flexibility; complexity; primates.

## Resumo

Esta tese propõe uma nova teoria da personalidade em primatas humanos e não-humanos, que integra a neurociência com as perspectivas desenvolvimentistas ontogenéticas e filogenéticas. Nesta proposta teórica os objectivos mais importantes para o estudo da personalidade são: a) a ontogenia da personalidade, incluindo o desenvolvimento das diferenças individuais; b) a filogenia da personalidade, incluindo as áreas cerebrais e as funções comuns às diferentes espécies de primatas e subjacentes à ontogenia da personalidade; e c) e como as diferenças individuais, referentes a aspectos idiossincráticos dos indivíduos, reflectem as adaptações derivadas das suas histórias de vida. São três as premissas essenciais que estão no cerne desta teoria. Na primeira premissa assume-se que a personalidade é uma estrutura dinâmica que muda ao longo da ontogenia do indivíduo. Na segunda premissa assume-se que a personalidade organiza as interacções do indivíduo com o mundo externo num modelo interno complexo. E a terceira premissa assume-se que a personalidade evoluiu ao longo da filogenia dos primatas pela evolução das estruturas cerebrais que a sustentam.

A teoria proposta considera que personalidade é uma estrutura dinâmica que organiza as interacções com o exterior num complexo modelo interno. Este modelo é utilizado como uma fonte de informação para as funções executivas, incluindo a tomada de perspectiva (tomada de perspectiva cognitiva – “teoria da mente”, e emocional – “empatia”), envolvidas no processo de tomada de decisão. O córtex pré-frontal, em especial a área orbitofrontal, e o córtex cingulado, têm um papel central na estrutura e funcionamento da personalidade. Durante o desenvolvimento do indivíduo, as experiências vividas contribuem para a formação do modelo interno – ou seja, a personalidade, e para a estrutura e fisiologia do córtex orbitofrontal assim como das restantes áreas pré-frontais. Postula-se que as diferenças filogenéticas destas áreas cerebrais são responsáveis pelas diferenças nas capacidades de tomada de decisão das várias espécies. Ao nível neuronal, a personalidade é compreendida como um modelo de teste de hipóteses de tipo Baysiano. Consequentemente, as diferentes espécies de primatas, tendo diferentes capacidades de processamento da informação, tanto em termos de quantidade como de velocidade, terão igualmente diferenças na personalidade.

No contexto desta tese, ao nível empírico o trabalho centrou-se no comportamento animal. Como hipóteses consideram-se que os animais com capacidades cognitivas superiores relacionadas com o funcionamento do córtex pré-frontal teriam personalidades mais diversas, flexíveis e complexas. Para testar estas hipóteses foram estudados um conjunto de espécies representando os ramos principais da árvore filogenética dos primatas: a) para a subordem dos estrepsirrinos: o lémure-vermelho (*Varecia rubra*) e o lémure-de-cauda-anelada (*Lemur catta*), b) para a subordem dos haplorrinos, parvordem dos platirrinos: o macaco-de-cheiro-boliviano (*Saimiri boliviensis*) e o macaco-capuchinho (*Sapajus apella*), e c) para a subordem dos haplorrinos, parvordem dos catarrinos: o mandril (*Mandrillus sphinx*) e o gibão-de-mãos-brancas (*Hilobates lar*). A escolha das espécies dependeu também da disponibilidade. Os dados foram recolhidos pela observação dos animais do Zoo de Lagos, do Badoça Safari Park e do Zoo da Maia (todos em Portugal). Os dados foram obtidos por observação directa do comportamento e foram analisados utilizando a estatística e a teoria matemática dos grafos, de forma a avaliar três dimensões da personalidade: 1) a diversidade (quantas categorias comportamentais apresentaram diferenças significativas entre os membros de um grupo), 2) a flexibilidade (quão flexível é a utilização de uma categoria comportamental específica em situações/condições ambientais diferentes), e 3) a complexidade (quão complexos são os padrões comportamentais gerados por cada indivíduo de um grupo). A metodologia utilizada para estudar a personalidade foi inovadora. Os resultados obtidos corroboraram as hipóteses defendidas e podem ser vistos como uma primeira abordagem com resultados positivos. São necessários mais estudos com outros grupos e espécies, incluindo grupos que não estejam em cativeiro, para avaliar melhor estas hipóteses.

Esta tese está organizada em capítulos. O “Capítulo 1 – Introdução”, consiste numa introdução extensa à proposta de enquadramento teórico desta tese. Esta introdução está organizada na forma de um longo artigo, e uma versão abreviada do mesmo já foi preparada para submissão. O “Capítulo 2 – Uma nova metodologia para o estudo da personalidade”, está organizado na forma de um artigo e apresenta a abordagem metodológica proposta. Este artigo foi intitulado “Using behavior observations to study personality in a group of capuchin monkeys (*Cebus apella*) in captivity.”, e foi publicado na revista científica Behaviour 156 (2019) 203–243. O artigo também inclui

os resultados do estudo da personalidade em macacos-capuchinhos, realizado com os dados recolhidos no contexto deste trabalho de tese. O “Capítulo 3 – A aplicação da nova metodologia ao estudo da personalidade em *Man drilus sphinx*: uma espécie ainda não estudada”, está também organizado na forma de um artigo pronto para submissão. Neste capítulo demonstra-se o valor desta metodologia para o estudo de uma espécie ainda não estudada ao nível da personalidade. O estudo realizado revela, ao nível do indivíduo, a riqueza da informação que é possível obter a respeito da personalidade, ao mesmo tempo que contribui para a compreensão da dinâmica de grupo. O “Capítulo 4 – Explorando a utilidade da metodologia para a comparação entre espécies”, está também organizado na forma de um artigo preparado para submissão. O objectivo deste artigo é demonstrar que esta metodologia pode ser útil na comparação entre espécies, sendo um bom instrumento para a exploração das três dimensões de personalidade propostas, ao nível da espécie. As duas espécies de lémures foram escolhidas para esta comparação, devido à falta de informação sobre a personalidade em lémures, e porque esta comparação poderia contribuir para a teoria evolutiva do desenvolvimento cerebral anteriormente proposta para os estrepisirinos. O “Capítulo 5 – Resultados preliminares corroboram a abordagem neurodesenvolvimentista da filogenia e ontogenia da personalidade”, também está organizado na forma de um artigo preparado para submissão. Este capítulo consiste nas conclusões da tese, e inclui a apresentação dos resultados e a explicação de como estes resultados podem ser interpretados ao nível teórico. Este capítulo demonstra como a teoria proposta nesta tese pode ser utilizada para articular numa única explicação as duas teorias principais da evolução do cérebro nos primatas – a “teoria do cérebro social” e a “teoria ecológica”.

O “Capítulo 6 – Epílogo-Prólogo” é o capítulo final desta tese. Está organizado como uma reflexão de carácter mais filosófico, sobre o que o autor espera ser a contribuição da sua tese para o trabalho teórico e empírico em biologia. Este capítulo defende que as implicações teóricas da teoria neurodesenvolvimentista da personalidade têm o potencial de modificar as perspectivas actuais da personalidade. A teoria proposta torna possível responder às quatro questões essenciais no estudo do comportamento de Niko Tinbergen's (1963): 1) Como funciona a personalidade? A personalidade funciona como um modelo de decisão; 2) Como se desenvolve? A personalidade desenvolve-se através da aprendizagem das relações entre o indivíduo e o ambiente; 3) Qual é a sua função? A função da personalidade é organizar a informação e tornar o indivíduo mais capaz de

gerar predições correctas; e 4) Como evoluiu ao longo da filogenia dos primatas? A personalidade evoluiu através da adaptação a ambientes progressivamente mais complexos.

O Capítulo 6 mostra o carácter multidisciplinar do presente trabalho e reivindica que entender o fenómeno da personalidade não é conseguido através do estudo de uma só disciplina. Portanto, esta teoria da personalidade tem implicações em várias áreas, incluindo aquelas disciplinas mais próximas da biologia, tal como a psicologia, bem como disciplinas mais distantes, como por exemplo a inteligência artificial. Esta teoria da personalidade coloca importantes questões filosóficas com implicações sociais. Desafia igualmente, as fronteiras comuns estabelecidas entre humanos e não-humanos, assim como o âmbito da nossa responsabilidade social enquanto humanos. Em tempos de grande mudança social e ambiental, a perspectiva teórica neurodesenvolvimentista da personalidade fornece uma “lente” com a qual poder reflectir sobre um número maior número de temas, em contraste com os considerados pela maioria das anteriores teorias de personalidade.

O capítulo 6 também apresenta uma revisão da contribuição ao nível empírico do trabalho desta tese. A teoria proposta permite o estudo da personalidade em que é respeitada a idiossincrasia dos indivíduos em estudo, enquanto minimiza o enviesamento através das observações directas do comportamento e utilizando categorias comportamentais com elevado valor facial que requerem níveis mínimos de inferência. A simplicidade metodológica na recolha de dados também permite a utilização de bases de dados pré-existentes que contêm dados que não foram inicialmente recolhidos no âmbito do estudo da personalidade. A autora espera que este trabalho empírico funcione como um prólogo para investigações empíricas futuras do estudo da personalidade em primatas e eventualmente em outros taxa. Compete aos futuros investigadores avaliar a relevância e utilidade da presente metodologia para os seus próprios objetivos de investigação.

**Palavras-chave:** personalidade, diversidade, flexibilidade, complexidade, primatas.

# **Chapter 1 - Introduction**

# **A Neurodevelopmental Approach to the Phylogeny and Ontogeny of Primate Personality**

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## **Abstract**

This article proposes a new theory of personality in human and non-human primates, integrating neuroscience with ontogenetic and phylogenetic developmental perspectives. The proposed theory considers personality as a dynamic structure that organizes interactions with the external world into a complex internal model. Self-other distinction and perspective-taking capacities represent important executive functions involved in decision-making. These capacities are considered as essential aspects of the dynamic nature of personality. At the brain level the orbito-frontal cortex is an area understood to play a central role in personality structure and function. At the neuron level the brain is understood as a Bayesian hypothesis-testing mechanism. Increasing processing and storage capacities are related with personality phylogeny. The theory proposed here constitutes a pathway for overcoming limitations of previous theories by integrating these various levels of analysis in approaching the ontogeny of primate personality structure as well as its phylogeny.



**Keywords:** persobality, primates, neurodevelopment, phylogeny, ontogeny, self-other distinction, perspective-taking. Prefrontal cortex, orbitofrontal cortex, cingulated cortex.

## **Introduction**

Interest in systematic research regarding personality started about a century ago in the context of psychology. In the field of individual psychology, Allport, in 1937, presented over 50 different existing definitions of personality, demonstrating that the operationalization of this concept is by far not easy and the choice of definition nonconsensual. For the moment, let us start with the definition of personality endorsed by Gosling (2001),: “Those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving”.

Several students/theorists of human psychology with approaches ranging from Freud’s psychoanalytic theory to Maslow’s organismic theory, developed various approaches to theorizing and developing research regarding personality. Many of these authors understood that researching was as important as theorizing but also were confronted by the difficulties regarding operationalization, observation and measurement that pose a challenge for this research area even today. The study of personality in nonhuman primates is a somewhat more recent phenomenon. Although, between 1930 and 1940 primatologists started discriminating individual differences in monkeys and apes, after that decade individual differences were largely ignored except by Jane Goodall in her work at Gombe National Park (Weiss et al. 2011). Only in the 60’s a few articles about primate personality started to be published, and then between the 80’s and 90’s the number of publications grew exponentially and then stabilized through the 21st century (Freeman et al. 2011).

One of the influential authors in human personality psychology who also had a large impact in research on personality in non-human primates was Eysenck. He believed that different dimensions of personality were associated with biological or anatomical differences between individuals (Miles & Hempel 2003). He developed a factorial theory applied to personality measurement (Eysenck 1950), in an attempt to overcome difficulties comparing and analyzing research derived from different theoretical

orientations. While highly influential, even until today, this supposed atheoretical approach to personality has itself become adopted as a theory, known as the Five Factor Model. Adopting this factorial model as a theory confuses some aspects of the interpretation of research on personality with causality theory. Stemming from this confusion, efforts to link genetic findings with traits derived from factor analysis have been made in research with both humans (Rushton, Bons, and Hur 2008; Figueredo and Rushton 2009; Power and Pluess 2015) and non-human primates (King and Figueredo 1997; Freeman and Gosling 2010; Freeman et al. 2013).

Theoretical and methodological problems derived from these factorial approaches are not usually fully considered. Nevertheless Jana Uher's deep and extensive work explores underlying theoretical assumptions regarding personality measurement and taxonomy of the different perspectives, as well as the methodological problems and constraints related with those approaches (Uher 2013, 2014b, 2015; Uher and Visalberghi 2016; Uher, Addessi, and Visalberghi 2013; Uher 2014b, 2014a; Trofimova et al. 2018; Uher 2018; Uher et al. 2018).

Research about personality has continued to develop within different areas of psychology and biology. In our view, the most important difference in the work developed so far is between two focal sets of concerns. On the one side are concerns about the measurement of individual differences and the categorization of different personality types (Eysenck and other researchers using the FFM are included in this group). On the other side are concerns about a) the ontogeny of personality, b) the common mechanisms underlying it and in particular the development of individual differences; and c) the description of such individual differences regarding idiosyncratic aspects of individuals' personalities and the adaptive, functional histories that brought them about.

When we consider the present panorama in the study of personality, we find a multiplicity of theories and methodological approaches. Many fields contribute directly or indirectly to personality research. But what stands out is the lack of a common theoretical approach that integrates different perspectives and research findings. Such diversity of sources creates a need for a theory capable of fully integrating the immense

body of knowledge generated -- something current theories, taken by themselves, fail to do.

A proposed solution to take advantage of the diversity of theories and methodological approaches to the study of personality is the development of a framework that can integrate the several theoretical approaches and the results derived from them into a coherent theory that makes use of various conceptual and empirical inputs in complementary ways. We propose to generate a theory to accomplish this goal. It is important to clarify three essential premises that are at the core of this theory. The first premise is that personality is a dynamic structure and not a fixed immutable structure inherited by the individual. Personality changes through the individual's ontogeny via similar assimilation-accommodation processes as described by Piaget (1952) for the ontogeny of intelligence. The second premise relates to the role that personality has in the individual's life as an organizing structure of the social and non-social environment and the individual's role in it. The third premise is that personality evolved through primates' phylogeny along with the neuronal structures that sustain it.

This article will clarify our Developmental Brain-Based Primate Personality Theory and how it can be used to integrate findings in various areas of research on human and non-human primates.

### **The ontogeny of personality**

In scientific discourse about concepts such as mind or intelligence, there is strong consensus that the underlying organ that allows those abilities is the brain. With respect to the concept of personality, this linkage with the brain which we think should be equally obvious does not appear in a clear and explicit way in most theories. Few have doubts about the importance of genetic factors in the development of intelligence, but an extreme importance, especially in the case of humans, is given to all the other factors contributing, through the life-spans of individuals, to the actualization of the intelligence potential of each individual. In the theory that we propose personality is considered in this same way.

Considering the brain as the organ that allows the existence and the development of personality we propose that as the brain develops, personality forms and continues to develop as well. The ontogeny of personality can be best understood using a developmental model similar to that described by Piaget (1952) for the ontogeny of intelligence in which changes occur via assimilation-accommodation processes. In developmental theories like in Piaget's, development is understood as resulting from a complex set of processes involving the interaction of underlying genetic information with ongoing interactions with the environment. Within these processes, structures emerge over life cycles and generations, each of which has its own emotional, cognitive and behavioral manifestations. Both developmental biology and developmental psychology consider phenotypic traits as manifestations of processes of developmental dynamics in which regulation mechanisms operate in complex and in simultaneous ways at different levels of the organism-environment system (Lickliter & Honeycutt 2003).

We can see and analyze the changes during the ontogeny of an organism's brain at the following different levels: 1) the molecular and cell, 2) the organization of neuronal circuits, which range from small neuronal circuits to anatomical areas (e.g. orbitofrontal cortex area) and their connections, and 3) behavioral, cognitive and emotional organizations, and the interactions of the individual with the external world (social and non-social aspects). All these levels are interacting as well as interrelated (the levels represent conceptually distinguish parts of a continuum).

### **The brain changes with experience and the brain needs experience to change**

Primates may be considered to have more "open" behavioral programs than other animals (Mayr 1974). In primate species, individuals' ontogeny depends on experience. That means the brain at birth has a very immature organization compared to the adult brain. For the brain to adequately develop it needs experience. The brain, through its development from conception to maturity, and continuing through life, is subject to the effects of experience. According to Sweatt (2013), experience (which includes a vast number of aspects such as environmental toxins, maternal behavior, psychological or physical stress, learning, drug exposure, and psychological trauma) interacts with genes

through epigenetic mechanisms<sup>1</sup> in the central nervous system. Furthermore, the brain is known to have significant capacity to change through postnatal experience. Experience can modify neural growth and gene expression leading to changes in neural circuits, behavior repertoires associated with them, and cognitive abilities (LaMantia 2012). While debate remains regarding the ages in different species at which the brain is said to “mature,” mature brains still maintain some degree of plasticity through changes in synaptic connections as new skills and memories are formed and as some older memories disappear with time (LaMantia 2012).

The individual’s personality changes as result of his or her experience. S/he uses learning derived from experience to organize his/her internal representative models and behavioral repertoire (assimilation). When s/he discovers that his/her knowledge is in some way insufficient, the individual uses this external information to adjust his/her own models and repertoire (accommodation). Personality can be seen as assimilation-accommodation process in which the social environment is internally organized in a model that reflects his/her current knowledge about it and his/her role in it. But at the same time, this model is permeable to learning, if changes or novelties in the environment cannot be adequately assimilated by the existent model. The degree of permeability will vary intra and inter-species.

### **Emotional, cognitive and behavioral organization: The internal model**

Piaget’s (1952) theory of the sensory-motor origin of cognition is central for understanding the origin of adult mental and behavioral organizations. This origin implies a mind-body-world interconnection, in which in the sensory-motor operations of perception and action lead to the development of the logic of the world and to the logic of the mind. The *logic of the world* consists of the rules and structure by which the individual understands and organizes the world he/she is in. The *logic of the mind* consists of the rules and structure by which the understood outside world is integrated

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<sup>1</sup> “Epigenetics refers to the ensemble of mechanisms that concurrently modify the chromatin to stabilize or dynamically modulate gene expression, without affecting the DNA sequence itself. These mechanisms primarily involve DNA methylation (DNAm), histone posttranslational modifications (HPTMs), and small noncoding RNAs (sncRNAs).”(Bohacek et al. 2013).

with the present and past information of the individual's own internal set of rules and structure constructed. In other words, the individual constructs an *internal model* of the world in which he/she integrates the external information. This process of integration of the external information into the internal model is continuous; the information changes the internal model and this model shapes the individual's subsequent reactions to the external world.

These logics organize the sensory-motor activities while the activities remain central components of the logics. Therefore cognition is *embodied* in the material interactions of the organism. See Laakso's (2011) review article for further discussion of the "embodied cognition hypothesis" in contrast to the study of "disembodied cognition" within cognitive science. This hypothesis tightly intertwines experiences of perception and emotion in the emergence of cognitions. Thelen (2000) explicitly proposes that the mechanism of embodiment continues through life in a dynamic manner: "therefore, cognition depends on the kinds of experiences that come from having a body with particular perceptual and motor capabilities that are inseparably linked and that together form the matrix within which reasoning, memory, emotion, language, and all other aspects of mental life are embedded" (p. 5). Consequently, for each specific individual body (and brain), there will be specific associated capabilities strongly dependent on the particular body that mediates the experiences lived.

Neuroscientists have begun to investigate the processes in the brain that accompany sensory-motor activity. What was referred to above as logics that organize sensory-motor activities can be understood at the brain level as comprising sensory-motor neuronal circuits. Those circuits can be reinforced by the individual's own actions. Moreover the recognition of similar actions by another individual may also trigger those same sensory-motor circuits. This process represents a form of generalization of learning. For example, when an individual observes another individual performing an action, mirror neurons fire and trigger the sensory-motor neuronal circuitry *as if* the animal itself was performing the action (Ferrari and Rizzolatti 2014). This process is referred to as "motor mimicry". When the action performed is an expression of an intense emotion, and the individual reacts as if it were experiencing the same emotion, this is referred to as "emotional contagion". Emotional contagion can be seen as a precursor for the development of social capacities (Prochazkova and Kret 2017).

Imitation of actions in humans is seen by Chaminade et al. (2005) as involving two components. One component entails an individual directing attention toward the apparent goal of an observed action. The second component entails an individual directing attention toward the means by which the goal is achieved. Imitation is a creative reconstruction of the observed act which occurs when the two components are integrated (Chaminade et al. 2005).

The connections established during the imitation process depend on associations made between sensory *experiences of observing* movements and motor *experiences of executing* those movements (Heyes 2001). Imitation requires separate visuospatial representations both of an observed model and of one's body schema (Chaminade et al. 2005). Similarly, social learning of emotional responses in humans depends on associations between experiences of observing emotional responses of others and bodily experiences of one's own emotional reactions (Lamm and Majdandžić 2015).

Mirror neuron mechanisms have roles in both “empathy“ and “theory of mind” even when the motor component of imitation is not explicit (Schulte-Rüther et al. 2007). In the case of empathy, although the individual empathizing is not observed to be acting overtly, motor, somatosensory and cognitive processes play roles (supported by distinct neural pathways) in the evocation of an empathic response (Lamm and Majdandžić 2015). The empathizer experiences within him/her body, expressions of the emotions that the observed individual is experiencing. While “empathy” is affective perspective-taking (i.e., perspective-taking to understand affect), “theory of mind” is cognitive perspective taking (i.e., perspective taking to understand thoughts) (Lamm and Majdandžić 2015). Based on the particular brain areas where mirror neurons were found both in human and non-human primates, it has been suggested that the development of the motor areas of the brain has allowed increasingly complex social functions (Ferrari & Fogassi, 2012).

In sum, the idea that internal models have sensory-motor origins (i.e. “embodied cognition”) becomes clearer when we analyze the brain structures underlying the mechanisms of imitation and perspective-taking. The sensory and motor components are essential for the construction of an internal model in which the experiences of observing and executing are integrated and serve as a basis for subsequent behavior.

This internal model is used by the individual both in simple actions like motor mimicry as well as in more complex tasks, including tasks like perspective taking in which the social component is evident.

### **Self-other distinction**

Founded on brain structure, development of personality depends on the intimate relationship of the individual with the surrounding environment. In humans, personality is a central component of “who we are” as individuals -- an intimate and idiosyncratic aspect of our identity (Gosling et al. 2003), and “who we are in relation to the other” -- our roles in our social contexts. Humans form their conceptions of their own personalities through a process of comparing their behavior patterns to those of others.

Comparison with others requires making a self-other distinction. The capacity for comparing oneself to another, implies the capacity of distinguishing oneself from the other. The ontogenesis of this capacity also depends on sensory-motor organization. Beginning at what Piaget (1952) called the “sensory-motor level” the brain creates organizations, or “models” which entail interconnections of sensory-perceptual, motor and emotional experiences, and *differentiations between self and other*. In the beginning of life, action, perception, and emotion experiences are tightly intertwined but cognitive representations and concepts are not yet present. The latter two emerge from the sensory-motor experiences to which they refer. As the organism continues to develop, sensory-motor activity remains tied to representations and concepts in various ways. As discussed earlier, this process has been called embodiment and continues through life in a way in all mental activities (Thelen 2000).

Expanding the previous example of the imitation process, if a human baby in a developmental phase in which he/she still cannot differentiate between self and other, is faced with a simple behavior performed by another person (e.g., sticking out his/her tongue) the behavior will be imitated – motor mimicry, and if the baby is faced with some intense emotion like another baby crying, it will cry too – emotional contagion. The capacity for self-other distinction does not eliminate these reactions in human adults. The common human experience of being near to someone who yawns and



feeling an “uncontrollable” impulse to do the same behavior reflects motor mimicry. The process of containing automatic motor mimicry is accomplished by imposing self-focus (Spengler et al. 2010). In this process, containment is achieved by diverting some of the attention given to the object imitated and focusing it on oneself. The self-focus is achieved by the intervention of the *medial prefrontal cortex* (Spengler et al. 2010). As we mentioned before, the medial prefrontal cortex has a role in the neural pathways involved in perspective taking -- both emotional (empathy), and cognitive (theory of mind).

Unlike emotional contagion, empathy requires perspective-taking using representations of the others’ emotions, including distress. It has been shown that, in human adults, representations of distress activate similar but not equal neuronal networks to those activated in self-distress. Empathy requires making a self-other distinction. Since empathy is different from emotional contagion because in the latter self-other merging exists (Jackson et al. 2006b). Empathy is more than an identification-through-similarity process, it is possible to feel empathy for someone different from us through activation of the same neural circuits as with someone similar to us (Lamm et al. 2010). In the case of empathy the areas activated include the anterior insula, the *anterior cingulate cortex*, the parietal operculum, the posterior cingulate, the precuneus, the right temporoparietal junction, and the *ventromedial frontal cortex* (Jackson et al. 2006a; Schulte-Rüther et al. 2007; Lamm, Meltzoff, and Decety 2009; Olsson and Phelps 2007; Olsson, Nearing, and Phelps 2007). In the case of theory of mind (cognitive perspective taking), the areas activated include the amygdala, the *anterior cingulate cortex*, the temporal pole, the superior temporal gyrus, the temporal parietal junction, and the *prefrontal cortex (PFC)* (especially the *orbitofrontal cortex (OFC)* and the *medial areas*) (Frith 2001; Johnson 2005). The areas in italics represent overlaps in brain location between the neuronal circuitry referred to as underlying empathy and the circuitry underlying theory of mind.

Now we would like to focus attention on the connection between personality and the overlapping brain areas discussed above. In humans, lesions in the *OFC* or *ventromedial prefrontal cortex* have been found to be associated with lack of “empathy” and often

with diagnoses of antisocial personality disorder, especially psychopathy<sup>2</sup> (Shamay-Tsoory et al. 2010). It has been claimed that these symptoms are the results of an impaired “theory of mind” (especially the affective perspective taking component). Other recognized dimensions of human personality have also been claimed by researchers to be associated with the ventrolateral PFC and medial PFC. These include “pro-social behavior” and “self-control” (Telzer et al. 2011). It also has been claimed that in general, for primates, the frontal cortex is involved in social behaviors that have been labeled as “cooperative”, “altruistic” or “spiteful,” as a result of the activation of the reward system (Chang, Gariépy, and Platt 2013). The reward system is constituted by the *orbitofrontal cortex*, the *anterior cingulate sulcus*, and the ventromedial striatum. This last region might be responsible for the pleasant feelings elicited by prosocial behaviors (Chang, Gariépy, and Platt 2013; Telzer et al. 2011).

The *anterior cingulate cortex*, the third common area involved in the emotional and cognitive perspective-taking circuits, as well as in the reward circuit, is also a prefrontal sub-region and its function is related with attentional control. Research on the anterior cingulate area has suggested that it is involved in reward anticipation, decision-making, empathy, emotional state attributions, impulse control, error detection, conflict monitoring and modulation of emotional responses (Critchley 2005; Botvinick et al. 2004; Etkin et al. 2011; Bush et al. 2000; Jackson et al. 2006b; Schulte-Rüther et al. 2007; Lamm et al. 2009). The anterior cingulate cortex plays roles in monitoring goal-oriented actions, maintaining sustained attention and avoiding distracters, and performing the executive function of adjusting cognitive control (Newman, Creer, and Mcgaughy 2015; Newman and Mcgaughy 2011).

In sum, the self-other distinction appears to be central to the capacity for perspective-taking. This capacity, together with attentional control, is part of the executive functions. The executive functions are implicated in managing decisions and their consequences. As we just explained, the common brain areas (orbitofrontal, ventromedial PF, and anterior cingulate cortices) involved in 1) the cognitive

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<sup>2</sup> Psychopathy is considered to be a developmental disorder with emotional and behavioral impact. The individuals with this diagnosis present insensitivity towards others, impulsivity, poor behavioral control, and diminished capacity for experience of remorse (Shamay-Tsoory et al. 2010). Antisocial Personality Disorder is a diagnosis of DSM-V (F60.2; DSM, 2013) recognized by ICD-10 by the name Dissocial Personality Disorder (F60.2; ICD-10, 2016) in which psychopathy is the extreme form.

perspective-taking circuit, 2) the emotional perspective-taking circuit, and 3) the reward circuit can be considered to be the brain areas supporting personality. We propose that personality is an organizing mechanism that organizes all the information regarding the individual and the overall environment, and builds on ongoing learning -- both social and nonsocial, with the function of deciding what is best for the individual.

### **Personality as a dynamic organizing structure**

As we mentioned earlier, the mind integrates the external information into its internal model in a continuous way. The information changes the internal model and this model determines the individual reaction to the external world. We are proposing that personality is this internal model — a dynamic self-organizing structure.. We are further proposing that regarding the ontogeny of this dynamic self-organizing structure, experience plays a continuous role in building, maintaining and changing personality. Thus while being a “structure” implies a degree of stability, dependence on experience implies permeability to novelty with makes significant personality change a continuous possibility.

According to developmental psychologists, the ontogeny of all self-organizing dynamic structures is due to the ongoing role of experience, and includes a variety of patterns, continuities and rapid changes (Fogel and Thelen 1987; Fischer and Bidell 2006). As we try to conceptualize how personality as a dynamic self-organizing structure functions and develops, it may be helpful to keep in mind the distinction. Fischer and Connell (2003) proposed regarding two motivational systems that underlie the dynamic process. They called these “epistemic motivation and “self-organizing motivation”.

We understand *epistemic* motivation to refer to a process that through interaction with the world ultimately leads to the fullest possible understanding. It has its roots in circular reactions, described by Piaget as beginning in infancy and continuing through life. We come to know the world through organizing it into our own activity. We repeat cycles of activity over and over again, each time incorporating more of our environments. Consider the grasping schema in infancy: the infant grasps the objects s/he sees at every opportunity. When the environment is incorporated as expected, this

completes the “circle” and triggers the repetition of the action. When the environment does not respond as expected, the structure must be modified to incorporate the new data before it is repeated. For Piaget every encounter simultaneously entails assimilation and accommodation. In the example of the infant’s grasping, the accommodation is the infant’s learning more ways of positioning the fingers to grasp new object and learning about new textures. But assimilation predominates insofar as the infant faces no problem in repeating the grasping over and over again. When the infant faces a real problem, e.g. the thing that s/he grasps bites him/her, accommodation dominates over assimilation because the new information forces a reorganization of the schema to predict when grasping will be painful. Circular reactions promote the development of skills and knowledge of the world.

Based on Fischer and Connell's (2003) description of *self-organizing motivation*, we prefer to call it *self-interest motivation*. It is a process of continuously monitoring our interactions with our environment to detect what is good/bad for ourselves and to organize stable patterns of activities based on these attributions. To summarize the co-action of these two motivational systems, makes structures like personality continually changeable. Working through processing constant feedback from activity patterns get transformed by experience, so as to more fully represent the world (internal and external), with the goal of self-preservation,

This mechanism is very important from a survival perspective. Individuals need to process a huge amount of information every second. If each individual would process the information arriving to him/her in a “vacuum”, without past information to relate with, this individual would face two problems: 1) s/he would need too much processing time, which would pose the danger of being too slow in responding; and 2) s/he would take the risk of making systematic mistakes. In other words, if an individual does not have mechanisms by which s/he can correct predictions based on previous past information, s/he would also be at risk of committing serious mistakes, either by repeating the wrong choice or by persisting in a negative situation. For example, if a past choice of feeding in a particular place always had been a good choice until the last time, when something in the environment changed and made it threatening, an individual must be able to incorporate this crucial information in future decisions, to

increase the likelihood of survival. So, the more dynamic this system can be in quickly integrating new information the more advantageous it will be to the individual.

Furthermore, when we think about information, we have to take into account social information, which is as important as non-social information. For example, 1) being able to have a clear distinction between oneself and another, 2) being able to understand the other, cognitively and emotionally, and 3) being able to anticipate the other's reactions, all have clear survival value. It has been suggested by Bergmüller and Taborsky (2010) that at even a more basic level, being different from others of one's group (i.e., having a different personality), even if in the absence of the capacity for self-other distinction, probably also has the value of decreasing competition.

Some of the neurological mechanisms involved in dynamic self-organizing processes are already known. Neuronal learning based on the association of stimuli with distinct levels of hedonic value entails the activity of the *orbitofrontal cortex (OFC)*. This type of learning is characterized by quick learning and equally quick reversibility (Rolls 2006). This learning mechanism allows the OFC to generate: 1) flexible responses -- responses that depend on details in ambiguous situations, 2) adjustments of predictions or models of environmental reward (Rushworth et al. 2007) and 3) instrumental choices based on expectations of results (Baxter & Browning 2007; Stalnaker et al. 2007; Saddoris et al. 2005; Cardinal et al. 2002). In practical terms this type of learning can be understood by the following example. If a primate finds a tree with green apples and his/her previous learning history informs him/her that green apples are sweet, but then on this new tree the type of apple is different and the green color is due to immaturity and the apple tastes bitter, s/he will in a single experience learn that to be green is not enough to ensure sweetness, and his/her model of good apples will get updated to a more complex one that distinguishes these two types of apples. The management of different types of rewards in diverse situations, relates to an action-reward learning process in which the OFC area uses past information to make the next selection, especially in ambiguous situations (Roesch & Schoenbaum 2006; Schultz & Tremblay 2006; Rushworth et al. 2007; Volz et al. 2008; Walton et al. 2010).

The capacities of the OFC are also implicated in social learning (Kringelbach & Rolls 2003), including facial and vocal emotion-recognition (Hornak et al. 1996). In humans,

patients with lesions in the OFC exhibit dysfunctions of these capacities, including being incapable of using information from negative emotional expressions in making social judgments (Willis et al. 2010). According to Brand & Markowitsch (2006) patients with lesions in the larger area of the *ventrolateral PFC* (which includes part of the OFC) demonstrate difficulties “making socially appropriate decisions”, and present significant changes in “personality” according to their relatives, and in their “interpersonal and social relations”. Moreover, OFC is involved in affect information processing, namely autobiographical memories for both positive and negative episodes, and in its retrieval (Markowitsch et al. 2003; Piefke et al. 2003). Patients with ventral prefrontal lesions (including the OFC) demonstrate amnesia for details of their own autobiography (such as specific events and their associated mental states. They have difficulties re-experiencing past autobiographical episodes, but their recollection of episodes not related to them personally were not impaired (Levine 2004). Evidence suggests the involvement of the ventromedial PFC in self-referential cognitive processes and self-reflection (Zysset et al. 2003; Argembeau et al. 2007; Schmitz, Kawahara-baccus, and Johnson 2004). Additionally, the ventral and dorsal anterior medial PF cortex, , specifically the dorsoposterior was involved the self-referential processing entailed by perspective-taking (Argembeau et al. 2007).

In sum, the capacities for making adequate decisions, taking into account past and present information, and managing ambiguous situations, are used in both non-social and social situations. In social situations the mechanisms of cognitive and emotional perspective-taking (“theory of mind” and empathy), self-other distinctions and autobiographical memories are useful in making the most adaptive social decisions. All of these capacities are aspects of the dynamic structure of personality for species that possess these capacities.

### **The internal model at the neuron level**

At a micro-level of analysis, that of the neuron, one way to consider how personality operates as a dynamic structure is by conceptualizing the brain as a hypothesis-testing or “Bayesian” mechanism (Friston 2012). This conceptualization starts from the assumption that neural connections encode a model of the world. This model is

necessary for to make inferences from sensory inputs received (Friston 2012). Following this assumption, the increase of the brain's potential for association is directly related to the increase of the potential complexity of the predictive models that the brain's neural connections can encode. In other words, as the complexity of the neuronal connections increase, the models used for associating inputs, making inferences, and predicting outcomes become more complex. Understanding of the brain in this way implies understanding connectivity and functional integration as capacities of the brain.

More concretely, the OFC receives and integrates information from several sensory modalities, such as olfaction, taste, visceral afferents, somatic sensation and vision (Araujo and Simon 2010; Rolls, 2006; Öngür, Ferry, and Price 2003; Öngür and Price 2000). For integrating the information the orbitofrontal cortex has several specialized neurons. Rolls (2006) describes the variety of neurons that can be found in the OFC. Some neurons are only fire in response to specific stimuli (e.g., sweet taste) while others respond to a variety of stimuli (e.g. visual and somatosensory stimuli). This means that some have the property of a unimodal response (e.g., olfactory) while others have the property of a multimodal response (different combinations of taste, olfactory, somatosensory, and visual stimuli), allowing a variety of combinations of associations. There are also conditional reward neurons, which are neurons that give information about the current reinforcement status of particular stimuli. This implies that the reward value can change, as it does for instance when an animal is approaching satiation. The reward system communicates the satisfaction felt in the moment the stimulus is encountered as input to the conditional reward neurons. There are also neurons that detect non-reward when a reward was expected but not received. (This can be understood as an "error" in the model's prediction.) These neurons have been suggested to be the part of the brain mechanism that allows task- or context-specific reversal to occur (Rolls, 2006). This would mean that some learned associations can be corrected in a few experiences or even in a single experience (one-trial learning) that contradicts the previous expectation. Some neurons respond to novelty, and their response fades after a few experiences. Finally, there exist face-selective neurons, which respond to facial gestures or movements. This variety clearly demonstrates the important role of the OFC in managing the information (both social and non-social) used in the predictive models of the brain.

All the neurons described and their capacities are used to build association networks, that encode the internal model. They serve the function of optimizing the organization of perception and decision-making (Friston 2012). It has been observed that neurons encode information about sensory uncertainty in the form of probability distributions (Knill & Pouget 2004). This is the “Bayesian Mechanism” to which Friston refers. The simple choices made based on that information can be predicted by differential firing rates of neurons encoding different actions (Hollerman et al. 2000; Rolls 2006).

The way this learning process occurs at the intra-neuronal level is largely still a mystery. Hebbian modification of synapses (the mechanism by which reinforcement of synapses happens through repetition) is most likely involved in the establishment of pattern association networks (sequences of synapses previously reinforced through repetition) (Rolls, 2006). What we do know is that mechanisms of molecular “development” of cells (occurring in embryonic or fetal development) used to regulate cell division and to differentiate and perpetuate cell phenotypes, (e.g., growth factor regulation, mitogen-activated protein kinases (MAPK) signaling, and epigenetic mechanisms), are conserved in the adult central nervous system to serve long-term plasticity and memory formation, as means of consolidating and stabilizing cognitive-behavioral memories (Day & Sweatt 2011). Even though there is not clear evidence that epigenetic mechanisms are necessary for ongoing storage of memory (Sweatt 2013), several studies point in this direction (Miller et al. 2010; Lattal and Wood 2013; Rosales-Reynoso et al. 2016).

The pattern association networks constitute the brain’s internal model that we have been exploring in this article. At the neuronal level, when something is learned it means a set of patterns of firing is established. Let us use the previous example of the green apples for explaining how a set of patterns is established by learning at the neuronal level. The monkey eats for the first time one apple, it was a *red* apple and s/he likes it (it will function as a reward). A neuronal network is established with the information red apples taste good (association red with food-apple with taste). After that s/he eats a *yellow* apple and a parallel association occurs. A new related neuronal network is established in this case with the information yellow apples are good. Next s/he eats a *green* apple, and the same process occurs. In this moment a pattern association network is established. This is called an attractor network. An attractor network is a network with excitatory



recurrent collateral connections with some neurons having high rates of firing while others have low rates and in which each pattern of firing is associated with itself (“autoassociation network,” Rolls, 2006). So in the example an apple will trigger all the networks established, for red, yellow and green, regardless of the stimulus in question. The term attractor is used because patterns related to the ones learned will attract the association network into firing. For example, if a more yellow-brownish type of apple were presented the network would fire too. In this way a rule is created. In our example the rule would be “apples are good”, entailing a strong association between the stimulus apple and the reward value associated to it. There is a bias established in this way. The bias can be seen as the neuronal base for the *self-interest motivation* previously explained. When our monkey tastes the immature green apple with a bitter taste his/her OFC error-neurons would fire. There was a mismatch between his/her expectation (sweet flavor) and the actual outcome (bitter flavor). The error-neurons will activate the inhibitory neurons, extinguishing the attractor network and leading to the emergence of a new rule (Rolls, 2006) -- in our example: “some apples are good but not all apples are good; some green apples are not good.” Adaptations of the synapses and neurons cause a new attractor network to be established. In this process, our monkey will have experienced through one-trial learning: “those green apples are not good”. His previous simpler model, “apples are good,” thereby becomes developmentally transformed into a more complex one “some apples are good but not all apples are good; some green apples are not good-” We might speculate that after a series of experiences of observing color changes and related taste-changes in apples, our monkey may form a general understanding that apples mature over time, and that that apples are fruits with different degrees of maturity. With this further transformation, a new even more complex pattern attraction network as well as new rules for choosing the best times to eat particular applies can be expected to develop. This entire process can be understood as the neuronal process associated with *epistemic motivation* as discussed above.

The brain as a hypothesis-testing mechanism can be said to maximize the efficiency of decision-making by continually coordinating information drawn from successive trials (the evidence) with internal representations (the models) used for decision-making (Friston 2012). The cumulative trial-by-trial hypothesis testing (Bayesian) model of brain functioning explains a) how evidence can be integrated over time in structuring the personality, b) why personality structure is not rigid or fixed but rather dynamic, c)

why over the course of the animal's life, after the juvenile period, personality becomes more stable (with the progressive accumulation of evidence, the neuronal foundation of the dynamic structure has become strengthened), and d) why increases in personality diversity (animals becoming more different from each other in a given group/species and complexity (use of more complex internal models) across primate species could be expected over the course of phylogeny. The topic of the phylogeny of the dynamic structure of personality in primates will be the focus of discussion in the next section.

### **The phylogeny of personality**

Several behavioral reactions develop through maturation process. When we compare baby primates of different species, including human babies, we observe similar patterns of development, suggesting a common origin for primate development (Matsuzawa, 2001). This common origin is related with common neuronal maturation processes that are equivalent across species insofar as the species' brains comprise the same brain areas. The time and experiences needed to fully develop a particular brain area varies from species to species. Moreover larger maturation periods are normally associated with greater cognitive capacities.

One of the major phylogenetic changes evident in the comparative observation of several extant primate species is that primates with larger brains tend to have higher total lifespan years as well as larger numbers of years of infancy and juvenile periods (Charnov & Berrigan 1993; Kaplan & Robson 2002). Longer periods of maturation tend to correlate with increased cognitive abilities across primate species, (e.g., to master complicated foraging tasks and to master social skills, in ecological and social domains respectively) (Walker et al. 2006). Chimpanzees (Lonsdorf 2013) and capuchin monkeys (MacKinnon 2013) are examples of species with longer periods of maturation where social learning happens and is needed for the acquisition of complex skills, when compared to other Catarrhini (old world monkeys) and Platyrrhini (new world monkeys) respectively. Compared to other primates, great apes were found to have both greater cognitive abilities and larger ratios of brain size to body size (Kringelbach & Rolls 2004).

Humans are at the extreme longer end of the range of maturation periods. The cerebral cortex of an infant born at term has only one third of the total surface area; post natal cortical expansion is non-uniform and the areas of lateral temporal, parietal and frontal cortices expand nearly twice as much as other areas by the age of 12 (Hill et al. 2010). Chimpanzees have one third of the absolute brain size of humans, but both species triple their brain size from neonate to adult (3.26 times in humans and 3.20 times in chimpanzees), which demonstrates the importance of post-natal development and experience (Matsuzawa 2007).

We can conclude that several capacities develop after birth during the brain maturation period. For example, PFC is one of the areas that develops most after birth, needing experience to fully achieve its cognitive potential; the related capacities will be less developed in the species with shorter periods of maturation. Moreover, in the species in which the PFC area is less complex (with fewer sub-areas) it is expectable to see less developed capacities for a) distinguishing self from other, b) perspective-taking, and c) decision making, even to the degree of the capacities being completely absent. In the following sections we will try to explore the phylogenetic changes in the PFC, especially OFC area, as well as the implication of these changes for these capacities.

### **The phylogeny of the self-other distinction**

The capacity of distinguishing oneself from the other is not equal for all primates or even all mammals. During evolution, there has been an increasing capacity for making a self-other distinction (de Waal 2012; de Waal 2019). Probably all mammals show some degree of behavioral or emotional contagion. As we explained before in the discussion of motor mimicry and emotional contagion, neither requires the capacity for self-other distinction.

De Waal (2012) proposed, in his “Russian Dolls” model, that *coordination and shared goals*, which depends on coordinating behaviors (e. g. movements, collective responses and communications about resources or dangers), and *sympathetic concern* and *consolation*, would be intermediate evolutionary states of the self-other distinction process. *True imitation* (following several steps of a role-model in an exact way) and

*emulation* (achieving a goal by following a role-model though not following the exact same steps, as in master-apprentice relationships), represent the final stage in the evolution of “theory-of-mind” or cognitive perspective-taking. The final stage in emotional perspective-taking is evidenced in *target helping* (see de Waal, 2019 for an explanation of this concept and its relationship to emotional perspective-taking). De Waal (2019) views different species as spread along a continuum in the evolution of self-other distinction capacities, and views humans as one of the most developed species.

Social learning both by imitation (observed body movement) and/or emulation (observed object movement) has been observed in some primate species (Kumashiro et al. 2003; de Waal 2012; van de Waal et al. 2013). Further, there is evidence that great apes (chimpanzees, bonobos, orangutans, and gorillas) are capable of making a self-other distinction when the “mirror self-recognition test” is used, with only some doubts about gorillas’ capacity for self-recognition (Suarez and Gallup 1981; Robert 1986; Walraven, van Elsacker, and Verheyen 1995; Westergeerd and Hyatt 1994; Allen and Schwartz 2008; Posada and Mentserrat 2007).

However, these capacities are not limited to primates. Other animals like avian species, whales, killer whales, and dolphins exhibit imitation behaviors too (Abramson<sup>a,b</sup> et al. 2013; Allen et al. 2013; Heyes 2001). Several species such as dolphins, killer whales, elephants, pica pica birds, passed the “mirror self-recognition test” (Marten and Psarakos 1995; Delfour and Marten 2001; Reiss and Marino 2001; Plotnik, Waal, and Reiss 2006; Prior, Schwarz, and Gu 2008). Although there have been some arguments about how much the mirror self-recognition test, imitation, emulation, consolation or target helping instances, reflect a fully developed self-other distinction capacity (e. g. Lagattuta & Thompson, 2007), there is a consensus that the animals that present all those behaviors correspond to the ones with relatively long maturation periods and greater cognitive abilities.

Some developmental psychologists claim that the mirror self-recognition test only represents *physical self-recognition* -- a limited form of self-awareness (Lagattuta & Thompson, 2007). Human developmental studies have demonstrated that the development of self-conscious emotions (experiences of pride, guilt, shame and

embarrassment) happen at the end of the second year or the beginning of the third year, and imply a *self-awareness with temporal permanence* (beyond the here and now) and between the ages of 4 and 5 full self-evaluation and comparison with the others -- a *meta-cognitive self-awareness* develops (Rochat 2003; Lagattuta & Thompson, 2007).

When chimpanzees were presented with a free-drawing test task entailing chimpanzee faces sketched on white sheets of paper without eyes, noses and mouths, the chimpanzees exhibited a strong tendency to draw on top of what was already drawn, rather than on white space (Matsuzawa 2012; Saito et al. 2014). Human children less than 3 years old showed a similar tendency, but older children, as well as a few with 2.5 years, tended to fill in the missing details (eyes, nose, and mouth). These results have been interpreted as a product of a) the development of imagination through social interaction, b) human children's ability to internalize others' differing viewpoints and c) strong motivation to share socially (Saito et al. 2014). Although not denying the roles of factors a-c, we believe that the differences between human children after 2.5-3 years old and chimpanzees are due largely to the emergence of self-awareness with temporal permanence, which implies the consciousness of the missing physical details independently of time.

A case study reported by Matsuzawa (2012) in which one chimpanzee was diagnosed at the age of 24 with spinal cord inflammation that paralyzed his body, as may illustrate the difference between our interpretive framework and Matsuzawa's. The chimpanzee was taken care of by humans for 6 months during which s/he slowly recovered. Matsuzawa's team observed that s/he did not show any changes in his mood such as depression or anxiety signs during the time s/he was cared for, from the time s/he was paralyzed until s/he recovered limited movement capacity. Matsuzawa and his colleagues' interpretation was that s/he had limited capacity for time and space travel, which limited his imagination of the future. Our interpretation is that having no self-awareness with temporal permanence s/he could not see "himself now" and compare it with "himself before", and consequently s/he could not imagine "himself in the future".

In sum, the emergence of the capacity for self-other distinction probably evolves through phylogeny following similar steps to the ones described for the emergence of self-awareness in human children (see Rochat 2003, for more details). A phylogenetic

continuum can be observed ranging from primate species only exhibiting awareness of a *self-world differentiation* and how their own body is situated in relation to other entities, to primates that exhibit a *physical self-recognition* -- the more limited form of self-awareness, to primates exhibiting a fuller *self-awareness with temporal permanence* and *meta-cognitive self-awareness*. The last capacities have only been convincingly demonstrated in humans thus far.

### **The phylogeny of perspective-taking**

Dunbar (Dunbar & Shultz 2007; Dunbar 2009) observed that in primates, there is a strong relationship between social group size and brain size, and postulated his “social brain hypothesis”, based on this observation. The theory argues that in larger groups the needs for processing social information are increased, and the brains of primates who live in such groups would increase in size in response to these processing needs. The “cultural intelligence hypothesis”—a more differentiated and integrated elaboration of Dunbar’s hypothesis, was supported by the work of Pasquaretta et al. (2014). They found that the size of primate social groups does significantly correlate with measurements of the efficiency of their social networks. However they also found that species consensually considered to be more *intelligent* (with more cognitive capacities) and *more tolerant* (with more emotional capacities) were found to have significantly higher levels of social networks efficiency (Pasquaretta et al. 2014). Highly developed capacities for individual social learning, as occurs in species capable of developing and transmitting cultural traditions, give social and ecological survival advantages through behavioral flexibility. Pasquaretta et al. (2014) “study highlights the inter-play between social networks and information flow through social learning and the development of neocortex ratio” (p.6). Social tolerance fosters individuals’ learning, together with responsiveness to objects and motivation to engage in new activities. All of these qualities are necessary conditions for learning complex activities (Visalberghi and Faagaszy, 2012). It is in especially tolerant social contexts (in which much physical closeness is accepted) that the capacities for imitation or emulation emerge, and complex activities as nut-cracking can be learned. Chimpanzees are an example of a species with this type of learning (Hopper, Marshall-Pescini and Whiten, 2012).

Nevertheless it is known that less tolerant primate species, like macaques, are still capable of learning by observation of the other, a learning process particularly enhanced by observation of the other's errors (Monfardini, Hadj-Bouziane, and Meunier 2014). They are also capable under experimental conditions of learning systems of rules (Smith et al. 2011) and of learning the symbolic meaning of tokens (Bevacqua et al. 2013). Some of these skills are quite complex but macaques' cognitive capacities are lesser than those of capuchin monkeys or chimpanzees. Macaques' vicarious learning is normally limited to simple behavior-reward associations. Macaques, although less tolerant than Capuchins or Chimpanzees, exhibit some behaviors that could be described as expressing "sympathetic concern". These behaviors are very important in creating a physically and emotionally safe environment. In such an environment, some degree of learning from observation can occur. Several studies of various macaque species as well as baboons have demonstrated that grooming has a tension-reduction function. It alleviates distress, measured both behaviorally (rates of self-directed behaviors, such as pulling ones own hair; compulsive self-licking) and physiologically (heart rate; fecal corticoid and salivary glucocorticoid levels) (Aureli & Fraser 2012).

What are the major differences between more and less tolerant primate societies? In the former, individuals are able to acquire through vicarious learning more complex skills that depend on at least two conditions being met: 1) an intrinsic motivation to learn skills that take years to master (very delayed "reward") and 2) a very high tolerance from adults toward children and adolescents. For this tolerance capacity to exist we know some form of emotional perspective-taking is needed, even if a full empathic capacity might not exist.

We now consider cognitive-perspective taking capacity, which is an important part of executive functioning. It enables individuals to form representations of social and ecological situations. These representations are used to create potential future social scenarios, and to anticipate changes in environmental conditions -- both of which help individuals to deal with uncertain situations (Geary 2005). To form representations of social and ecological scenarios some form of cognitive-perspective taking is needed, even if full "theory-of-mind" capacity might not exist. The term "social brain" implies the capacity for "mentalistic understanding" of the another's behavior (Johnson 2005).

The capacity to represent mental states of others' and attribute intentionality to others' minds, have been inferred from the capacity to follow gaze direction and discover inconspicuous things. For instance, the recognition of the direction of visual attention of other individuals ("following gaze direction"), is a common capacity throughout primate phylogeny including lemurs, new world monkeys and old world monkeys (Ruiz & Santos 2012). But the capacity for using the direction of others' gaze to discover inconspicuous things has been documented only in a few primates (Tomasello et al. 2001; Ruiz & Santos 2012). The capacity to make inferences about goals by following gaze direction was demonstrated among great apes using an experimental paradigm (Kano and Call 2014). Using the same experimental paradigm with 11-month-old human infants, similar results were obtained (Cannon and Woodward 2012).

In comparison with a fully developed "theory-of-mind," what the apes and the human 11-month-olds could do can be understood as a not-fully-mature developmental step named "a theory of rational action" or the capacity to interpret actions as means to goals (Gergely and Csibra 2003; Kano and Call 2014). At this step, the individual can make interpretations and predictions regarding others' goal-directed actions, but s/he may not yet be able to represent others' minds and attribute intentional mental states to them (Gergely and Csibra 2003; Kano and Call 2014). Until the early 2000's there was a consensus that the capacity to represent mental states and intentions and to attribute them to others' minds develops around 4 years old in humans (Southgate, Senju, and Csibra 2007). However these findings were based on verbal tests. With a non-verbal test -- the "anticipatory looking false-belief test", 2-year old children demonstrated the ability to attribute mental states to others (Southgate, Senju, and Csibra 2007). In this test, the subject, in the role of an observer, is required to anticipate (anticipation is measured by eye movement tracking) what an actor will do upon returning after s/he leaves an object in one place and in the actor's absence, a third-party moves it to a different place. The "false-belief" refers to the actor's expectation that the object will be found where s/he left it.

The capacity to reason about the false beliefs of others' was tested using a similar method in rhesus macaques. Researchers concluded that although rhesus macaques were able to represent relations among agents, objects, and goal-directed actions as well as knowledge or ignorance about how the situation was altered in the agents' absence.



However, they were not able to represent agents' beliefs and make specific predictions based on those beliefs (Marticorena et al. 2011). More recently, experiments using the same anticipatory looking false-belief test discussed above have shown that great apes (bonobos, chimpanzees and orangutans) were able to anticipate that the other would act according to his/her false beliefs (Kano et al. 2017).

Human developmental psychologists continue to discuss how to interpret the results of Southgate, Senju, and Csibra's (2007) study with 2-year old children. One explanation that we find parsimonious and consistent with what we know about long maturation periods of PFC ontogeny is that offered by Baillargeon, Scott, and He (2010). They postulate that 2-year-olds fail in elicited-response verbal tasks because executing simultaneously the three component processes required to succeed at the task overwhelms their limited resources, and/or because the connections between the brain regions (right temporo-parietal junction, anterior cingulate and PFC, and frontal and temporal brain regions) that serve these processes are still inefficient. The processes required to succeed at the verbal task include: 1) false-belief-representation, 2) response-selection, (naming the possible responses and choosing the one that would result from the false belief) ( and 3) response-inhibition (to inhibit the selection of the response that would be based on his/her own greater knowledge) This perspective would explain the differences in human performances on the verbal vs. non-verbal tests and the parallel performances on non-verbal tests by great apes.

In sum, species with more efficient social networks are those that are more tolerant and intelligent and have more developed perspective-taking capacities. Species with less efficient networks will not exhibit those perspective-taking capacities. As is the case with the self-other distinction, each primate species would have a position on a continuum from total absence of capacities to represent others' knowledge, to full *perspective-taking capacity* (making a clear distinction, both emotional and cognitive, between the self and the other). Intermediate points on the continuum include the capacity to *represent others' actions*, and the capacity to *represent the others' beliefs*.

## **The phylogeny of the brain areas underlying personality**

The previous sections have discussed the relationship personality evolution with brain evolution. Understanding how and why the brain areas involved in personality have evolved through primate phylogeny is important for understanding the process of personality phylogenesis and the survival value of personality.

The neocortical areas of the brain, especially those related to the PFC, are the main areas involved in personality structure and function. As argued previously, we see evolution in the capacities for cognitive and emotional perspective-taking and the self-other distinction as related to the executive functions. Through these executive functions, personality, as a dynamic organizing structure, organizes the relationship between the individual's activity/experience and the external world. How the brain has evolved throughout primates' phylogeny has implications for how this dynamic structure can develop for each primate species.

When comparing brains of primates with other mammals, it is possible to say that primate brains tend to be larger in proportion to body size, as well as that they tend to have unusually large neocortices (Striedter 2005). One of the most significant changes produced during the evolution of primates, along with the significant development of the visual cortex, is the evolution of the primate PFC which has been more deeply researched only in these last few decades. For personality, it is the evolution of this brain area that has greatest relevance. The following sections assume the consensus depicted in Figure 1.1

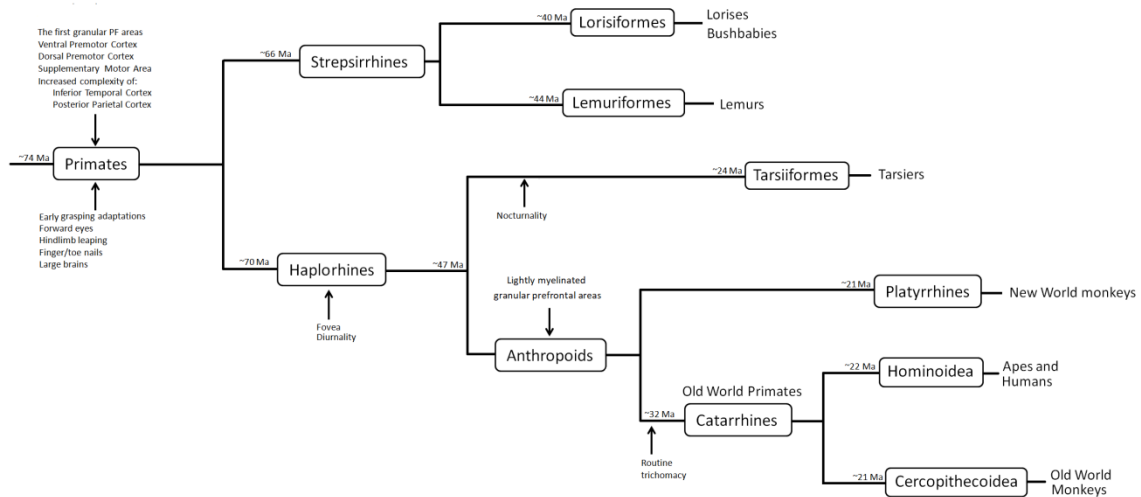


Figure 1.1 Simplified phylogenetic tree for primates, representing a selection of key lineages. Divergence-time estimates were based on Pozzi et al. (2014). Some of the evidence for the morphological changes and time estimates is derived from the analysis of fossils of extinct primates and some from molecular-clock analysis. In the figure, PF represents the prefrontal cortex. We thank Steven Wise for his advice in constructing this figure

## 1) The evolution of the PFC in Strepsirrhines

The evolution of the PFC started in other mammals that pre-dated primate phylogeny. Primate prefrontal cortices are composed by neurons whose cytoarchitectonic structures range from no apparent structural organization (agranular) to being well-organized into distinct layers (granular). Although the agranular PFC areas could be considered unique to primates, including Strepsirrhines, homologous areas may exist in other mammalian vertebrates' brains. Animals such as rodents have areas that include the infralimbic, prelimbic, agranular insular, agranular orbital and anterior cingulate cortex, and lie adjacent to other allocortex areas like the olfactory bulb; nevertheless there is no evidence that nonmammalian vertebrates have agranular PF cortices (Passingham & Wise 2012).

As with agranular PF cortices, it is only with the early primates, including Strepsirrhines, that the first granular PFC areas emerge. There is some controversy about whether areas homologous to granular PFC areas can be found in other animals like rodents. However, Passingham and Wise (2012), Preuss (2007) and Laubach et al. (2018), in their reviews of these controversies, state that on the basis of current evidence

we can conclude such homologs do not exist and that granular PFC areas emerge only with primates. What has been called the rodent medial PFC correspond to locations associated with the primate anterior cingulate cortex (Laubach et al. 2018). This confusion has its origin in the fact that in rodents, points from rostral (front) to caudal (back), are contained within a horizontal plane, while in the extant primates brains are curved.

Some extinct basal primates, the plesiadapiforms, had linear brain plans similar to living rodents, but a shift in brain organization occurred in the first euprimates (Long, Bloch, and Silcox 2015). The increased of PFC tissue volume, with the development of granular cytoarchitecture, led to a displacement of the anterior cingulate cortex along and a curvature of the corpus callosum in primates (Laubach et al. 2018).

One part of the PFC that is particularly central to personality is the OFC. Although in evolutionary terms it is an ancient structure of the brain, cytoarchitectonic differences in its organization as well as in its size and complexity can be observed to dramatically increase in primates in comparison to rodents (Kringelbach & Rolls 2004; Rolls & Grabenhorst 2008). The emergence of the granular areas of this cortex occurred simultaneously with considerable reorganization of the connections among different cortical areas. In primates the granular PFC including new PFC areas, as well as the granular OFC project to the dorsal striatum rather than to the ventral striatum as is the case with rodents (Passingham & Wise 2012). Also, sensory and autonomic inputs to the granular OFC are received indirectly, first being processed in the agranular area (Passingham & Wise 2012). In contrast, in rodents all processing occurs in the areas that receive such inputs. These differences between primates and rodents have important implications such as increasing capacities for goal achievement, for encoding food value, and for flexible neurophysiologic regulation.

## **2) The evolution of the PFC in the Haplorhines**

Further changes in the PFC occurred throughout primate phylogeny. This section will focus on the changes first seen in Haplorhines. Preuss & Goldman-Rakic (1991) affirm that contrary to prior belief, the granular PFC area has evolved significantly during

primate evolution. They compared this cortical area in the *Galago* (normally known as bushbaby) which is a small brain strepsirrhine, with the *Macaca* which is an anthropoid Haplorhine. They concluded that although an important part of their frontal cortices, namely the premotor, orbital, and medial regions, appear to be very similar, in the granular frontal cortex there were near twice as many areas in *Macaca* as in *Galago*. Many of these were additional and more rostral areas with no obvious homologs in *Galago*. Furthermore, *the Galago* lacked a cortex resembling the distinctive, lightly myelinated cortex of the *Macaca* principal sulcus. The areas unique to the *Macaca* include the mid-lateral PFC, the dorsomedial PFC, the ventral PFC and the polar PFC. One possible explanation offered by the authors is that these areas evolved as an answer to new ecological and social pressures, namely 1) the change to a diurnal life which involves an increase of predation and competition, and 2) the enlargement of social groups as an evolution strategy for lowering predation risk (Passingham and Wise 2012).

Dunbar's (Dunbar 2009; Dunbar & Shultz 2007) "social brain hypothesis" argues that the increase in size of social groups is a factor contributing to brain evolution because of the increased cognitive demands of social life in larger groups. The social brain hypothesis also suggests that in larger social groups the generalization of bonding from reproductive to non-reproductive relationships occurs. Consequently, the increasing sizes of social groups may have fostered more complex social relations (complex networks) to which brain development may have been an evolutionary response. More recent research has supported ecological, and evolutionary-developmental hypotheses that increase of brain size is predicted more by diet, (especially a change from folivory to frugivory) than by social group size (e.g., DeCasien, Williams, and Higham 2017). This diet change would have required increased spatial information storage and better retrieval abilities, more complex cognitive capacities for 'extractive foraging' of fruits and seeds, to which may have been an evolutionary response. Moreover, this diet would provide more energy which would be available to the fetus for its brain growth (DeCasien, Williams, and Higham 2017). While controversy was generated by this more recent research, the role of social complexity remains unclear, since social group size is not an adequate proxy for social complexity (Bergman and Beehner 2015). We view it as very likely that both ecological and social factors, contribute to phylogenetic brain increase in size and in complexity.

To further understand the evolution of the PFC in the Haplorhines, we can turn to the foundational work on brain mapping conducted by Broadman in 1912 and 1913. He compared cortical surface areas of brains in the following species: human, chimpanzee, gibbon, mandrill, baboon, macaque, capuchin monkey, marmoset, black lemur and dwarf lemur (Elston & Garey 2013; Passingham & Wise 2012). He concluded that during primate phylogeny the granular PFC areas expanded proportionately more than other cortical areas. It is important to note, considering the small brain sizes of the early catarrhines and platyrrhines fossils, that much of the expansion of the brain Broadman described occurred after the split between new world and old world primates. Also, it is important to note that recently it has been suggested that cerebral complexity and encephalization could have evolved independently, from two types of selective pressures: one for increased complexity (through gyrification, also known as cortical folding) and the other for volume (encephalization) (Rogers et al. 2010). At least in old world monkeys, cerebral complexity preceded encephalization (Gonzales et al. 2015). Although evolution occurred independently in the Old World and the New World primates (Passingham & Wise 2012) ecological pressures leading to brain expansion that Broadman found in both may have been similar in the environments for both lineages. Food shortage, the need to improve the use of cues and signs to predict location of high-quality foods, the need to predict which trees would produce food and when, and the need to recognize predictor events, for predation risk, were presumably some of these common pressures (Passingham & Wise 2012).

In sum, there seem to be two important functional consequences of the evolution of the anthropoid brains. One is the ability to adapt to new situations by a new learning process that allows quick learning (with one trial or very few trials). Second is the increasing capacity to predict upcoming events through learning (both social and non-social). These new granular PFC areas are responsible for these capabilities.

### **3) The evolution of the PFC in Hominids**

There are no doubts that humans have larger cerebral cortices in comparison to other primates. There has been a significant debate about whether the PFC, is

disproportionally larger in humans, some claiming yes (Chaplin et al. 2013; Kaas 2013; Preuss 2011; Smaers et al. 2017), others no (Barton and Venditti 2013; E. C. Bush and Allman 2004; Semendeferi et al. 2002; Semendeferi and Damasio 2000), and others say no when it comes to volume but yes regarding the absolute number of neurons (Gabi et al. 2016). A more recent work has shown that previous research used a methodology that substantially underestimates PFC size, especially in humans, and that the proportion of grey matter occupied by PFC in humans is greater than in chimpanzees, and that the disparity is even larger for the proportion of white matter occupied by the PFC (Donahue et al. 2018).

Human (*Homo*) and chimpanzee-bonobo (*Pan*) lineages diverged from a common ancestor approximately 7.6 million years ago (Pozzi et al. 2014). The common ancestors' brains had approximately one-third the size of modern humans (humans living over the past 40,000 years). Kaas (2013) claims that, especially over the last two million years, the brains of our ancestors increased extremely in size, from the 400 – 600 cm<sup>3</sup> range to the 1200 – 1600 cm<sup>3</sup> range of modern human. He asserts that the prefrontal, posterior parietal, lateral temporal, and insular regions accounted for much of this increase in size. In contrast, Semendeferi and Damasio (2000) state that a linear relationship has been observed in hominids between the size of the PFC and the overall brain size, during roughly the same period. Bruner & Holloway (2010) propose that this linear relationship could be the result of a lateral reallocation of the neural mass during encephalization, i.e. an enlargement of the maximum endocranial width (that is, at the upper temporal areas). In thinking about relevant findings we should keep in mind Semendeferi & Damasio's (2000) caution that we have to be careful in how we interpret data when there is a significant variability intra- and inter-species of certain parts of the brain, and few specimens have been studied. But even taking this caution into account, it's important to recognize that because temporal areas are related to memory processing, the enlargement of the temporal areas (relative to the growth of the PFC as a whole) that has been observed might be connected with the increased capacities for time perception and for conceptualizing the histories of the lived experience of self and others. Although these capacities are managed by PF areas, the PF areas may not have needed to grow at the same rate as earlier in primate evolution.

Connecting the observations of hominids discussed above with previous observations regarding primate brain evolution in general can lead to the conclusion that as Preuss (2007) states, primates in comparison to other mammals have additional brain areas. These areas constitute new divisions of the parahippocampal cortex (an important part of the temporal cortex). Preuss (2007) suggests that these new structures may underly the development of the capacity to form long-term memories. This increased capacity for forming memories, facilitate forming and holding in mind at least three different concepts of the self: 1) the self in the present, 2) the self in the past, and 3) the self in the future. As we discussed in self-other evolution section this capacity of self-awareness with temporal permanence is the basis for developing a meta-cognitive self-awareness -- the capacity for conscious self-evaluation and comparison with the others (Rochat 2003; Lagattuta & Thompson, 2007). In conclusion, the differences between human brains and those of other primates are not just a matter of volume, but they include substantial organizational changes that allowed changes in complex capacities as executive functions to emerge (Preuss 2011; Smaers et al. 2017).

### **Neuronal microstructure evolution**

In this section, we change focus from the evolution of larger brain structures to microstructure evolution. Brain expansion and cellular reorganization through primate evolution have entailed changes in the number of spines of the pyramidal cells. Pyramid cells or pyramid neurons, are multipolar neurons found in areas including the cerebral cortex, the hippocampus and the amygdala. These neurons are the primary excitatory elements of the PFC and were first discovered by Santiago Ramón y Cajal (1894). Pyramid cells are the basic neuronal building block of the cerebral cortex. They comprise over 70% of all neurons in the cortex (Elston et al. 2006). Moreover, in the granular PFC the average number of spines in the basal dendritic trees of pyramidal neurons is more than 10.000, which is much higher than the average number of spines of dendritic trees of pyramidal cells in other cortical areas (e.g., primary visual area 1 pyramidal cells have an average of 600 spines) (Elston & Garey 2013). These regional differences in pyramidal cell morphology contribute to area-specific aspects of cellular



and systems function, such as propagation-potential properties and divergent synaptic plasticity (Elston, Benavides-Piccione, and DeFelipe 2001).

Research has suggested that long-term information storage in neural tissue could be primarily related with selective addressing of synaptic contacts. In other words, highly branched dendritic arbors may result in a significant increase in the capacity for learning and memory (Poirazi and Mel 2001). Consistent with Poirazi and Mel's interpretation, a recent study with humans found that more intelligent individuals present larger and more complex dendrites of pyramidal neurons, faster action potential kinetics, and more efficient information transfer from inputs to output within cortical neurons (Goriounova et al. 2018). In addition, Goriounova et al. found that temporal and frontal cortical thickness are related with IQ (intelligence quotient -- a widely used measured of intelligence). Temporal areas are associated with memorization, frontal areas are associated with learning and information management.

Humans and non-human primates are born with a large number of supranumerary synapses. In the course of activity some of these synapses are eliminated while others are strengthened and stabilized. This change with experience is a core mechanism for generating diversity across individuals' neuronal connections. In humans' PFC, a substantial elimination of synaptic spines continues beyond adolescence and throughout the third decade of life before stabilizing (Petanjek et al. 2011). This long maturation process highlights the importance of experience and the impact of environment on both cognition and emotion. This maturation process appears to be essential for developing complex functions such as affect modulation, self-conceptualization, mentalization, cognitive flexibility, and working memory (Petanjek et al. 2011). As we previously mentioned, humans, compared to other primates, have the longest maturation period and the most complex cognitive capacities. These differences are a product of neuronal variations between humans and non-human primates.

In fact, Ramón y Cajal already observed in 1894 that the morphology of pyramid cells was different in different mammal species. The more basal species in the phylogenetic tree had less differentiated, less numerous, shorter and less ramified dendritic spines. Despite the importance of these observations, they were not further explored until recently, when Elston, Benavides-Piccione, and DeFelipe in 2001 described this same

morphological variety in primates. When comparisons among prosimians, new world monkeys, old world monkeys, and humans are made, differences in PFC cells are observed. PFC cells of humans have more branches and spines than PFC cells of the other species ( Elston & Garey 2013 Elston 2011; Elston et al. 2005; Elston, Benavides-Piccione, and DeFelipe 2001; Elston et al. 2006). Furthermore, there are differences among the other primates studied indicating that the PFC expansion of the granular tissue occurs not only by increases in the total number of neurons, but particularly by increases in the number of those more complex neurons that have more branches and spines (Elston et al. 2006, 2011). In addition, these differences are related to differences in computational capacities, which suggests that they are responsible for variations in planning, prioritizing, and conceptualization capacities that are normally related to the PFC area (Elston et al. 2006, 2011).

It is very interesting to note, that as it happens with humans, in other primates there are marked inter-individual differences in the average number of dendritic spines in the basal dendritic trees of the neurons of the PFC. Elston et al. (2011) compared different primates of different species, in terms of the number of spines in the “average neuron”. Their report stated

“While we would expect to find some degree of interindividual variation in cell structure, that observed in the gPFC is unprecedented. We found, for example, a 56% difference in our estimates of the total number of dendritic spines in the basal dendritic tree of the average neuron...” (p.12).

The relevance of the individual differences discussed above to personality is as follows: Personality as we see it is a dynamic structure that manages information about the social and physical environment. Individual experience shapes the nature and complexity of brain structure, especially that of the PFC. Differences among individuals’ personalities are a reflection of these differences. Personality shapes cognitive and emotional aspects of decision-making and it changes and reorganizes itself in response to novel experience.

We have suggested that an essential aspect of primate brain evolution entails increased ability for very quick learning, even one trial learning. At the cell level, learning is based on the establishment of new synaptic contacts by association, followed by their

strengthening and stabilization through a Hebbian mechanism<sup>3</sup> (Chklovskii et al. 2004). It is reasonable to assume is that the greater potential of association that comes from increased number and complexity of neurons in the granular PFC area has evolved through the primate phylogeny and has increased brain processing speed and capacity. These observations support the assumption of the increased brain processing speed and capacity through phylogeny.

As stated before we view the increasing of information processing speed as an essential aspect of primate PFC evolution. The appearance of von Economo neurons, during neuronal evolution of the granular PFC, can be seen as another evolutionary step in the increase of processing speed. Von Economo neurons are a relatively large bipolar type of neurons. Their simple dendritic structure suggest that they send basic information at high speed, while the pyramid cells discussed previously send more detailed information (Ibegbu et al. 2014). Von Economo neurons have been observed to be concentrated mainly in the anterior cingulate cortex and the fronto-insular cortex, and have been more recently observed concentrated in the granular frontal area, in the dorsolateral PFC and in the medial frontopolar cortex (Fajardo et al. 2008; Ibegbu et al. 2014; González-Acosta et al. 2018).

Von Economo neurons have been found in the hominids (humans and great apes). They also have been discovered in large species with very different evolutionary histories like African and Asian elephants (*Loxodonta africana*, *Elephas maximus*; Hakeem et al. 2009), as well as several large marine mammals (cetaceans including mysticetes and odontocetes) (Butti et al. 2009; Hof & Van Der Gucht 2007). The emergence of von Economo neurons in highly intelligent mammals with large brains have been considered as a case of convergent evolution (Hakeem et al. 2009).

Butti et al. in 2011 (2013) estimated that von Economo neurons first appeared in hominid primates 16 million years ago and suggested that they were associated with social conscience and interoception mechanisms. More recently these neurons have been found also in Macaques, located in the anterior insular cortex and in the anterior

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<sup>3</sup> A Hebbian mechanism (proposed by Hebb, 1949) is a repeated and persistent stimulation of a postsynaptic cell by a presynaptic cell which leads to an increase in synaptic efficacy. This mechanism is an explanation of how synaptic plasticity occurs.

cingulate cortex, which suggests that they emerged when cercopithecids and hominoids diverged around 25 million years ago (Evrard, Forro, and Logothetis 2012). The greater concentration and size of these neurons in hominids is compatible with the idea of a spectrum of self-consciousness (Critchley & Seth 2012).

Von Economo neurons represent a very small proportion of the neurons in cortical-layer V<sup>4</sup>. Only about 15% of the post-natal number of neurons are present in the human newborn. By approximately age four the remainder have appeared (Allman et al. 2005; Ibegbu et al. 2014; Butti et al. 2013). This is precisely the age of meta-cognitive self-awareness emergence (the capacity for full self-evaluation and comparison with the others). There is a sharp increase of these neurons at around eight months of age that coincides with the emergence of self-awareness and separation-individuation from the mother (Butti et al. 2013). The stranger anxiety reaction and the “no” gesture are typically considered evidence of this separation-individuation process. This period corresponds to the time of recognition of one’s physical body — a limited form of self-awareness (Rochat 2003). It has been suggested that von Economo neurons have a role in the integration of bodily feelings, emotional regulation, and goal-directed behaviors, as well as in fast intuitive evaluation of complex social situations (Butti et al. 2013; Ibegbu et al. 2014). In these functions, physiological states of the body including the input of the autonomic nervous system are used to guide behavior choices as von Economo initially suggested (Butti et al. 2013).

In sum, the analysis of neuronal microstructural evolution of primates PFC (which includes OFC) and anterior cingulate cortex suggests that computational and speed capacities increased through primates’ phylogeny. These increasing neurological capacities potentiate the emergence and development of distinguishing self from other, perspective-taking, and decision-making (including cognitive and emotional processes). These, in turn, lead to progressively more complex and quick solutions to social and non-social problems. We have explained how crucial experience is for the ontogeny of PFC of several primate species. Especially in hominids, brain ontogeny relies progressively more on experience in the early years of individuals’ development. The emergence of von Economo neurons in PFCs of hominids is consistent with what we

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<sup>4</sup> Cortical brain tissue can be agranulated (without observable organization) or granulated with organization in layers. These layers are represented by roman numerals ranging from I (bottom) to a maximum of VI (top).

said regarding the importance of embodiment in the ontogeny of the internal model. The optimal development of all the capacities that we have discussed depend on post-natal brain maturity. Consequently different individuals of the same species will have different brains, even at the neuronal level, which will translate into differences in the way they process information (both social and non social) and in their emotional, cognitive and behavioral responses. Moreover, with the increasing of neuronal computational and speed capacities through primates' phylogeny there is an increase of inter-individual differences in brains among the individuals, leading to more diverse and complex brains.

In sum, brain evolution cannot be seen merely a matter of enlargement. It involves changes at various levels of organization. Each individual's brain creates an idiosyncratic internal model of the surrounding world (social and non-social). Each individual takes decisions informed by his/her model's predictions. The diversity of internal models within a species depends on the neuronal computational capacities of the species' brains, particularly their PFCs, as well as on the diversity of experiences among species members. This internal model is what we call personality.

### **Some factors that influence personality ontogeny**

In this final section we will give an example (see figure 2) of how personality is formed. We select just a few aspects to illustrate the complexity involved in personality organization. In this example we are not intending to be exhaustive. Our main goal is to illustrate the cyclic character of the processes that lead to the establishment of the dynamic structure of personality. We also want to underline with our example how this structure is sensitive to external influence, and how some influences have a transgenerational impact.

Having demonstrated how the dynamic structure of personality is dependent on the brain, we claim that its ontogeny starts with brain ontogeny, in the moment that brain development begins. Embryology studies make clear that the influences on brain

development are numerous. These influences act initially in the form of inductive signals<sup>5</sup>, either promoting or blocking certain changes. Multiple signals interact with what are called “cell precursors” in a complex way to form future nervous cells and neural circuits (Purves et al. 2012). External influences on the signals an embryo receives include genetic or epigenetic information inherited through the mother or the father as well as environmental or behavioral events that alter what passes from the mother through the chorion.

The existence of epigenetic inheritance through the germline has been progressively established through studies with rats, demonstrating transmission via oocyte cells and sperm cells of epigenetic modifications of RNA (Dias and Ressler 2014; Champagne and Curley 2009; Bohacek et al. 2013; Franklin et al. 2010; Franklin, Saab, and Mansuy 2012; Chen et al. 2016; Henry-Berger et al. 2018). Adaptations that occur in response to social and environmental changes in an individual’s life can be inherited by subsequent generations. But the inheritance is not irreversible. They may be reversed in a future generation by environmental influence, in what can be considered to be “soft inheritance.” In this neo-Lamarckian perspective, heritable epigenomic<sup>6</sup> changes can pass through a few generations but are ultimately reversible (Sweatt 2013). We have to consider the transgenerational epigenetic effects on brain functions, namely the impact of early stress (Champagne and Curley 2009; Champagne 2008; Weaver et al. 2004; Bohacek et al. 2013; Franklin et al. 2010; Franklin, Saab, and Mansuy 2012).

Evidence suggests that highly stressful experiences at different stages in life can have transgenerational effects (Bohacek et al. 2013). DNA methylation changes induced by stress can be maintained across several generations and induce specific behavior alterations (phenotypic changes) (Franklin et al. 2010). This means that highly stressful

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<sup>5</sup> Inductive signals is a term used in embryology to refer to substances, like folic acid, that have a role in the development of the embryo. These substances either promote changes (like formation of new cells, e.g. the presence of a Leucocyte Inducing Factor near neural crest progenitor cells induces the formation of sensory neurons, while a Stem Cell Factor near the same neural crest progenitor cells induces the formation of melanocytes) or block changes (which leads to the formation of other types of cells -- for example, in neurogenesis, the presence of the blocking factor Notch and the inducing factors bHLH lead to the formation of neuronal precursors and ultimately to the formation of neurons). For further information please read Purves et al (2012).

<sup>6</sup> The epigenome consists of chemical compounds and proteins that when attached to DNA direct actions such as turning genes on or off and controlling the production of proteins. These modifications do not change the sequence of the DNA, just DNA’s instructions. These epigenomic changes sometimes are passed through cell division, from cell to cell, and sometimes from one generation to the next. <https://www.genome.gov/about-genomics/fact-sheets/Epigenomics-Fact-Sheet>

experiences of progenitors induce neuroepigenetic changes in the progeny. The progeny will have changes in the epigenome of its central nervous system. In other words, the brain of the progeny will have stress-responses expressed physically and behaviorally (anxious responses) even if the stressors that originate the changes in the progenitor's epigenome are not present in the progeny's environment.

In the example represented by figure 1.2 we consider two situations. Figure 1.2, # 1 represents the neo-natal brain ontogeny in a normal stress situation of the progenitors, in which neuroepigenetic changes do not occur. In figure 1.2, # 2 represents the opposite situation, neuroepigenetic changes do happen and the neo-natal brain ontogeny carries inherited neuroepigenomic changes. In this second case we have the conditions for a phenotypic trait of anxiety (and other behavioral changes) to be expressed; the newborn will tend to react in anxious ways regardless of the surrounding environment. If no further changes happen in this individual ontogeny, this can become a personality characteristic. We will return to this aspect later.

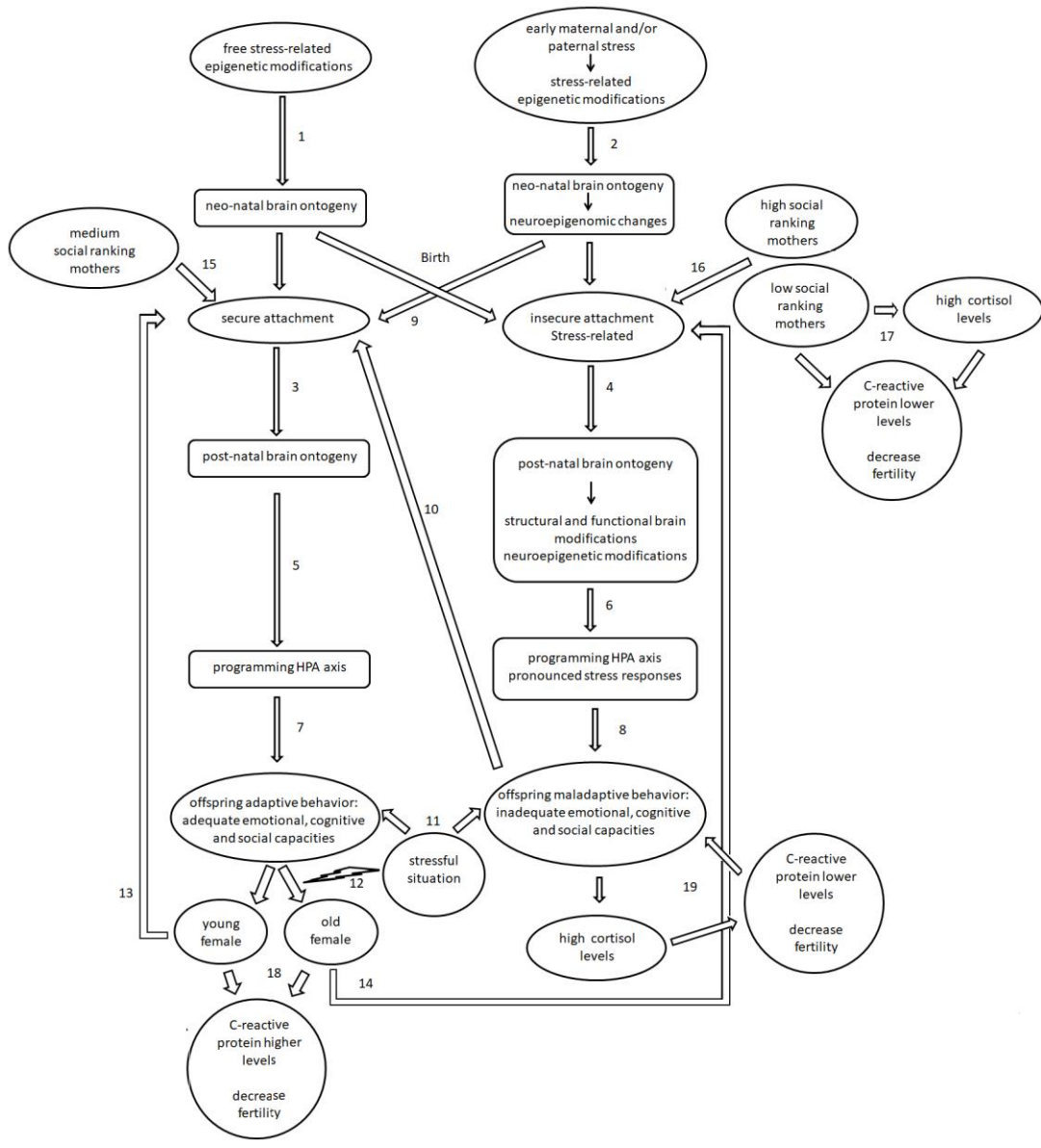


Figure 1.2 Illustration of how various factors affect the emergence of personality structure. In the diagram, variables such as stress, attachment, C-reactive protein, and cortisol, as well as their complex interrelationships, are illustrated in the way they influence and are influenced by personality. The number boxes 1-19 are explained in detail on the text.

Once the main brain structures are established after # 1 and # 2, the major sources of influence act on the brain circuits, which are known to be very plastic even in the mature brain. Personality gets progressively structured after birth. This development lasts several months or years depending on the time a given primate species needs to achieve brain maturity. The specific brain areas more directly involved in personality



function are located in the PFC, which is the area that takes the longest maturation period of all brain areas (Sowell et al. 1999; E. E. Nelson and Guyer 2011; O'Donnell et al. 2005; Gogtay et al. 2004). Specifically the OFC and ventromedial PFC are linked with the development of valuation (the process of associating emotional value with stimuli), inhibition of responses, the acquisition and generation of rule use (“learning the contingencies of behavior in different contexts”), “theory-of-mind” (cognitive perspective-taking), self-other distinction and empathy (emotional perspective-taking). These processes only reach level of full development after the adolescent period, by which time those brain areas achieve full maturity (Frith 2001; Jhonson 2005; Jackson et al. 2006a; Olsson, Nearing, and Phelps 2007; Nelson and Guyer 2011). This means that there is a very long period of potential impact of experience in the way these areas develop.

Studies in rats suggest that *stress factors* also have a strong impact on developmental processes provoking amygdala hypertrophy (by dendritic morphological changes), as well as atrophy of the hippocampus and PFC<sup>7</sup> (by decreasing spinal density in the prelimbic and orbitofrontal cortices), and changes in their functions (Negrón-Oyarzo, Dagnino-Subiabre, and Muñoz Carvajal 2015; Negrón-Oyarzo et al. 2013; Vyas, Pillai, and Chattarji 2004; Gourley, Swanson, and Koleske 2013; Liston et al. 2006). After a stress recovery period, both the hippocampus and the prefrontal cortex, recover in their structure and function (Negrón-Oyarzo, Dagnino-Subiabre, and Muñoz Carvajal 2015; Liston et al. 2006; Vyas, Pillai, and Chattarji 2004). There is a open question about which areas of the PFC might not recover completely (Negrón-Oyarzo, Dagnino-Subiabre, and Muñoz Carvajal 2015; Gourley, Swanson, and Koleske 2013; Liston et al. 2006). The changes due to stress occur even when the rats were already adults, due to neuronal plasticity (Liston et al. 2006).

This type of research demonstrated the profound changes in the morphology of neurons due to stress. The impact on dendritic structure and functioning happens through experience-dependent plasticity mechanisms (Moench and Wellman 2014). The impact is felt both when the animal has not yet arrived at the end of the maturation period and after maturity has already been achieved. We can reasonably assume that similar

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<sup>7</sup> Accurately we cannot talk about homologous of granular PFC areas in rodents. Please consult the discussion in the section about evolution of the PFC in Strepsirrhines for an adequate interpretation of the presented results.

processes happen in the dendritic spines of pyramidal neurons of anterior cingulate cortex and the PFC of primates. In this early developmental period, highly stressful experiences provoke changes at the levels of brain structure and , but also trigger persistent epigenomic changes in the brain (Champagne and Curley 2009; Franklin et al. 2010; Franklin, Saab, and Mansuy 2012; Sweatt 2013; Gudsnuk and Champagne 2012).

It is in this precise period of development when attachment occurs. It is well established that in the early stages of ontogenetic development in primates, the attachment process is crucial for the optimally adaptive development of the individual. A secure attachment (Figure 1.2, # 3) becomes the basis for the development of effective emotional regulation, which implies stress management abilities and social cognition, as has been made clear by the work of Bowlby and Ainsworth and their followers on humans (Bowlby 1982;1969; Ainsworth 1991; Bretherton 1992; Mikulincer et al. 2003). Infants with secure attachment experience low stress levels, due to the confidence that they will be protected by their mothers (or, in the case of humans, other family members with whom they have a secure attachment too).

In contrast, infants with insecure attachment experience high stress levels and they do not feel confident in their attachment figures' protection (figure 1.2, # 4). An insecure attachment has strong and long lasting effects on individuals' reactions over the life-span that might only be possible to reverse in some cases (Bard 2012; Maestripieri 2003; Sperling & Berman 1994; Ainsworth 1991; Ainsworth & Bowlby 1991).

The few longitudinal studies with nonhuman primates that studied victims of early maternal rejection one year later, (summarized by Fairbanks & Hinde 2013) have shown significant behavioral differences from peers. We consider these differences to be important aspects of personality ontogeny. For juvenile vervet monkeys who have been rejected by their mothers' exhibit lower novelty-seeking scores, higher rates of social play for males, and higher rates of affiliation for females; rejected rhesus monkeys show lower rates of solitary play; rejected Japanese macaques show fewer fear reactions when being approached by other monkeys as well as less post-conflict scratching (anxiety indicator) after an aggressive encounter. In contrast to the few longitudinal studies, there is an extensive literature showing the more dramatic effects of the absence of maternal care or the receipt of substandard care (Machado 2013). In Macaque monkeys, these

experiences initiated a flow of events leading to social withdrawal, abnormally aggressive or fearful behavior, and a tendency to exhibit repeated and self-directed motor stereotypies (e.g. pulling out one's own hair) (Machado 2013).

The first months of a primate's life, during which the attachment process is most affected by maternal care and contact, corresponds to the time period in which many neuronal structures are being developed. For example, in macaque monkeys, the synaptic contacts between the amygdala and its "downstream" and "upstream" brain regions are established and then myelinated over more than three months before the neural connections resemble those of adult macaques (Machado 2013). Another important brain structure, the orbitofrontal cortex, develops the majority of its connections to other cortical areas by the seventh week after birth. Although by the first to the second month of life these connections resemble those in adults' brains, by observing the myelination process it's possible to conclude that these connections only reach functional efficiency by the end of the first year for the posterior OFC and by the end of the second year for the anterior OFC (Machado 2013).

Chimpanzees brains at birth have 40% the size of adults (in our species it is about 28%). During development and maturation, interactions with caregivers are crucial and early atypical experiences have serious consequences on cortical and subcortical organization (Bard and Hopkins 2018). Significant long-term effects were found in gray-matter in nuclei such as caudate, putamen, accumbens, as well as in the rectus gyrus, and the orbital prefrontal cortex. These results were similar to those found in institutionalized children, for whom cortical gray-matter volume was smaller than in non-institutionalized children (Sheridan et al. 2012; Nelson et al. 2011).

Similarly, humans' PFC's develop extensively through changes that include synaptogenesis, pruning, and myelination during childhood (Farah & Noble 2005). Disturbances in these ontogenetic processes have clear personality consequences that are especially observable when children become adults. As Damasio (1994) summarizes, these consequences include a) rigidity, perseverance and stereotypy in the way these adults approach others, b) lack of creativity and originality, c) decreased ability to feel pain or pleasure, d) a high tendency to exhibit an inflated self-image in initial interactions, and e) decreased capacity for constructing a theory of mind.

Research has examined the impact of institutionalization of children and the concomitant deprivation of parental care on neurological development. It was found that disruptions to neurological development occur due to poor stimulation, have been associated with lower IQ, deficits in language use, executive function, impairments and delays in a variety of social-emotional domains and a very high prevalence of mental health problems (Sheridan et al. 2012).

Personality development is affected by early experience. In the case of abandonment, early-life stress and insecure attachment, the individual is going to have difficulties in learning and decision-making processes, in cognitive and emotional perspective-taking, difficulties in the self-other distinction, and difficulties in the embodiment processes – including self-awareness of emotions.

In a recent review of early-life social adversity by French and Carp (2016) that focused on marmosets, squirrel monkeys, and macaques, the authors underlined the short- and long-term consequences of such adversity. Diverse developmental outcomes regarding affect, social behavior, cognitive and attentional processes were found to vary according to the degree of early-life social adversity. These emotional, cognitive and behavioral changes were found to be related to variations in the underlying neural substrates which include changes in the anterior cingulate, prefrontal and orbitofrontal cortex, and in the hypothalamic–pituitary–adrenal (HPA) axis response. In other words, they result from changes in central and peripheral regulatory processes. It becomes clear that even at peripheral regulatory processes, the effect of early post-natal stress is highly impacting. In fact HPA activity is increased and that increment can be measured by the increased basal of cortisol levels (Pryce et al. 2011; Birnie et al. 2013). Globally, these findings, taken together suggest a central role of development in programming the HPA axis as well as in other neuroendocrine systems (Flinn et al., 2011).

The next part of Figure 1.2 demonstrates the influence of attachment processes. Primate offspring who establish secure attachments tend to develop adequate neuronal structures and functions, with no long-lasting epigenetic changes induced by stress, and with a normal-functioning HPA and other neuroendocrine systems (figure 1.2, #5). In contrast, primate offspring who establish insecure attachments tend to develop differences in neuronal structures and neuroendocrine systems (figure 1.2, # 6). A securely attached

individual will be likely to exhibit adaptive behavior with adequate social, cognitive and emotional capabilities. These capacities will translate into the capacities for effective decision-making, cognitive and emotional perspective-taking, and self-other distinction that are expectable for his/her species (figure 1.2, #7). In contrast, an insecurely attached individual (as well as individuals who have experienced other highly stressful situations such as food deprivation or an environment with high levels of aggression), will have modifications of neuronal structures and functions with long-lasting neuroepigenetic modifications induced by stress, and with an altered HPA and other neuroendocrine systems activity (figure 1.2, # 6). Such an individual will tend to exhibit maladaptive behavior with inadequate social, cognitive and emotional capabilities. These capacities will be translated into difficulties in decision-making, cognitive and emotional perspective-taking, and self-other distinction, in comparison with what is expectable for his/her species (figure 1.2, # 8).

It has been hypothesized that the role of neuroepigenetic mechanisms in the settlement and maintenance of the functional changes exposed before. While we have been discussing maladaptive epigenomic changes, it is also true that experiencing of or exposure to environmental changes could trigger heritable epigenomic changes that improve survival over a few generations. As with the maladaptive changes, adaptive changes are also eventually reversible because they are based on epigenomic changes and not upon a direct change of offspring's DNA nucleotide sequence (Sweatt 2013; Champagne 2008; Weaver et al. 2004; Champagne and Curley 2009; Dias and Ressler 2014; Bohacek et al. 2013; Franklin et al. 2010). In sum, negative experiences in early life and their epigenetic consequences can be maladaptive or adaptive depending on the environmental context. They are more likely to be adaptive when they lead to increased behavioral flexibility in aversive conditions, increasing resilience (Gapp et al. 2016)

Figure 1.2, #9 refers to the possibility of reversing neuroepigenomic changes inherited via transgenerational transmission. Such changes, though they have been claimed to be ultimately reversible (Sweatt 2013), have until recently only been demonstrated to be reversible under very specific pharmacological conditions in studies of mice (Weaver et al. 2004; Curley et al. 2011). Nevertheless, recent research, also with mice, has shown that reversibility can happen through environmental stimulation (Weaver et al. 2017; Gapp et al. 2016) without pharmacological intervention. Increasing sensory, cognitive and

motor stimulation promotes brain plasticity, preventing long term structural consequences like changes in the grey matter. It is possible to observe the prevention of structural gray matter consequences of attachment disruption by adequate early stimulation of chimpanzees' development (Bard and Hopkins 2018). In institutionalized human children recovery via the increase of the white matter can be observed (Sheridan et al. 2012). In addition it was observed that marmosets who were experimentally separated from their families to disrupt attachment, recovered from HPA changes following family reunions (Taylor et al. 2015; Birnie et al. 2013). These researchers also observed that the presence of a family member buffered the effect of HPA stress response. In human studies, there is considerable evidence that an insecure attachment might change into a secure attachment (and vice versa) if the necessary conditions are present. Research also shows that institutionalized children, after being adopted, might develop a secure attachment if there is a parental sensitivity (rapid and adequate responses to the child emotional needs) (Veríssimo and Salvaterra 2006; Schoenmaker et al. 2015). For exemplification purposes we indicate this possibility in Figure 2 by #10, but that item in the figure would correspond to any situation which would give individuals the opportunity to restructure their neurological and psychological organizations in response to environment stimulation. In other words, an individual could carry epigenetic changes as a result of a traumatic experience, (e.g., early deprivation of caring as in cases of maternal abandonment or negligence) but after this traumatic initial experience the individual could experience stimulation that counteracted such changes (e. g. ., in cases of cross- fostering).

Early events experienced by individuals start the process of personality development. From good, pleasant experiences, an individual will learn to trust and feel confident about him/herself and/or another individual or group; from bad, unpleasant experiences, the individual will learn the opposite. The degree of differentiation of both good and bad experiences into learning specific associations with other individuals or situations, will depend on two aspects: 1) the variety of experiences lived, and 2) the brain processing capacities. If the experiences are negative and tend to be repeated, the individual will tend to generalize and react in very similar ways to different individuals or situations. If the individual belongs to a species with limited brain processing capacities, the degree of differentiation of experiences memorized and processed will be

smaller, consequently the diversity of reactions and the complexity of them will be small.

Regardless of whether individuals' experiences are good or bad, species processing capacities have implications for the development of diversity of personalities across members of the species. In a species with low processing capacities the individuals will tend to react similarly to similar situations (not showing a large differentiation of responses for the same situation). In species with greater processing capacities, the degree of personality diversity will be larger, incorporating more elements of information from previous experiences. To the extent that the variety of experiences lived are limited, the degree of diversity among personalities will be less. Individuals and species will be distributed over a continuum with respect to brain process.

Stress as a psychophysiological experience will not be determined purely by objectively describable environmental events (Figure 1.2, # 11). Stress will also be influenced by the internal model (personality) that the individual uses to make sense of the events. Capitanio and colleagues found that personality differences in monkeys, as measured by observer ratings of adjectives used to describe human personality, correlated with different stress responses to similar environmental events with implications for the immunological system (Capitanio et al. 1999; Capitanio et al., 2008). Capitanio (2011) stated that personality probably affects the functioning of HPA and the sympathetic-adrenal-medullar systems, although it is not clear yet in which way.

The effect of personality of HPA and sympathetic-adrenal-medullar system functioning is important because the cortisol hormone, which increases in stress reactions, will have different impacts in the attachment process depending on the mother's age (Figure 1.2, #12). The cortisol hormone enhances arousal and responsiveness to infant stimuli in young, inexperienced female primates (Figure 1.2, # 13), but it decreases the adequacy of maternal behavior in older, more experienced mothers (Figure 1.2, # 14) (Saltzman & Maestripieri 2011). Several other hormones and neurotransmitters also play a role in the attachment process. These hormones include estrogen, prolactin, oxytocin, and cortisol.

Social ranking can be a source of stress connected with food and sex access. According to Fairbanks and Hinde (2013), adequacy of maternal care (for developing secure

attachment) is a U-shaped function of mothers' rankings in their social hierarchy. Low-ranking (marginal to the group) mothers and high-ranking mothers are more rejecting toward their offspring (Figure 1.2, #15 and #16). The authors argue that in the case of the low-ranking mothers the rejection results from energetic stress, while for the high-ranking mothers, the rejection results from a "strategy" of shortening the inter-birth interval to maximize the number of offspring. Social ranking in human beings is reflected in the difference in children's environments. Farah & Noble (2005) cite studies showing that differences in child-rearing environments have profound consequences. When people are compared based only on whether their incomes are below (less advantaged) or above (more advantaged) the poverty line, large and significant effects on the development of language and executive function brain systems are found. It is possible to observe from more extreme examples of early social adversity that environmental deprivation disrupts neurological development, with the serious consequences discussed above.

In sum, within the attachment process in primates (human and non-human), complex relationships among variables are involved. Disruptions to the process of establishing healthy, secure attachments usually have consequences not only for the development of individuals throughout their life-cycles but also for their offspring.

Early stress also has consequences for reproductive success. The relationship of C-reactive protein to pregnancy is an example of how this influence may occur. Clancy (2013) summarized the research on C-reactive protein which is involved in the inflammatory process necessary for pregnancy to happen. He reports an inverted U-shaped curve in the graphic representation of the relationship between the amount of C-reactive protein present in women and their fertility. Both lower and higher levels of protein are associated with fertility decrease (Figure 1.2, # 17 and #18). Chronic childhood stress associated with problematic family environments and traumatic social events (such as sexual or physical abuse or parental drug and alcohol problems) lead to elevations of cortisol, which suppresses the immune system and reduces inflammation (Figure 1.2, #19). These events are important predictors of future menstrual disturbances, suppressed reproductive functioning, and high morbidity (Flinn et al. 2011; Clancy 2013).



In summary, the previously-mentioned variables -- C-reactive protein, attachment, environmental stress (including resources like food deprivation), social ranking, age -- were selected and examined to illustrate the non-linear and complex relationships among variables in the ontogeny of the individual personality. Many other variables may have a direct or indirect impact on development, including other hormonal factors (besides cortisol), the nutrition and the immune system information that children receive through breast-feeding, interaction with both males and females, culture, etc. The discussed factors demonstrate how environmental influences have a broad, even intergenerational, impact. The analysis of these factors moves the debate regarding nature versus nurture to a completely different level. If experience affects the nature of brains and brains effect the nature of experience, it is more appropriate to discuss nature-nurture cycles than nature versus nurture. Some of our examples may have suggested implications of this kind of analysis of the interaction of genetic and environmental process for biology, psychology and other scientific approaches, as well as for important ethical and social-political questions. While space doesn't allow a systematic discussion of these implications, we do believe that they warrant both reflection and political and social change, especially when we think about humans (Combs-Orme, 2013; Rothstein, Cai, & Marchant, 2009; Rothstein, Cai, & Marchant, 2009; Wright, Ralph, Ohm, & Anderson, 2013; among others).

### **Final remarks**

Our hope in writing this article is to transcend the limits of most current theories of personality and to provide a general theoretical framework that can explain personality ontogeny in both human and non-humans primates. In our Neurodevelopmental Approach to Primate Personality one of the central foci is the role of brain. We consider the brain to be the physical foundation of personality as a dynamic structure – an internal model that organizes information and activity and that changes over time as it adapts to its environment.

Personality is a mechanism that organizes all the information regarding the individual and the overall environment, and builds on ongoing learning -- both social and

nonsocial (*the epistemic motivation*), and generates decisions regarding what is best for the individual (*the self-interest motivation*). The capacities for making adequate decisions, taking into account past and present information, and managing ambiguous situations, are used in both non-social and social situations. These capacities are called executive functions. The executive functions are implicated in managing decisions and their consequences. In social situations, the mechanisms of cognitive and emotional perspective-taking (“theory of mind” and empathy), self-other distinction, and autobiographical memory are useful in making the most adaptive social decisions. All of these capacities are aspects of the dynamic structure of personality for species that possess these capacities. The common brain areas (orbitofrontal, ventromedial PF, and anterior cingulate cortices) involved in 1) the cognitive perspective-taking circuit, 2) the emotional perspective-taking circuit, and 3) the reward circuit, can be considered to be the brain areas supporting personality.

Personality ontogeny is directly dependent on brain ontogeny and subject to the pressures that directly or indirectly influence brain development. In every species, characteristics of brain structure constrain the possibilities for the development of this dynamic organizing structure in that species. By personality phylogeny we refer to the process by which these constraints are removed as the brain evolves in response to environmental and social pressures. In primate phylogeny, primates’ brain changes allow increases of *environmental responsivity* and *prediction capacity*. These two capacities are “social-cognitive” in the sense that what is being responded to and predicted includes both the social and physical environment.

*Environmental responsivity* refers to the capacity of the brain to change in response to information from the environment in ways that result in rapid yet long-lasting changes in behavior. *Prediction capacity* refers to the capacity of the brain to change in ways that increase over time the ability to accurately predict events in the physical and social environments based on past information. Specifically in relation to social environments, learning how other individuals behave and in what ways we can predict their behavior and adapt to it, is an extension of the ability to make quick yet long-lasting changes. Individuals include in their internal models not only behavior patterns identified among surrounding group members (necessary for prediction capacity) but also response

patterns for adapting to other members .These response patterns create a personal role for the individual within the group (an aspect of environmental responsivity).

Each individual will have his/her idiosyncratic, continually changing, internal model of the surrounding world and its behavior will depend on this internal model. With time particular cognitive organizations of the environment, both social and nonsocial, become consolidated and therefore more stable within the dynamic structure that we propose to call “personality.” It is considered a dynamic structure because the processes discussed above make the structure susceptible of change by new learning, even after its components have been consolidated. We can expect that change in the environment will bring about more transformational changes in personality, while stability in the environment will lead to further consolidation of existing personality structure. In our view, the increase of cognitive abilities over the course of primate phylogeny allowed for an increase of diversity and complexity in personalities.

We hope the example in Figure 1.2 makes clear how a research model for primate personality could be developed. A huge amount of data and a large number of factors which are inter-related can pose a practical management problem. A good way of attempting to solve this potential problem is to build a computer model based on the compilation of the knowledge we have about the roles of different factors. A computer model has the advantage of: 1) being able to compile and organize a very large quantity of data (big data analysis) and 2) being able to test hypotheses in a much less reductionist way than studies of the relationships of just a few variables.

We hope that our proposal will interest researchers and scholars from a variety of fields of study who can help make the theory more differentiated and integrated. Further differentiation and integration of the theory will provide a fuller understanding of primate personality phylogeny and ontogeny.

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## **Chapter 2 – A New Methodology for Studying Personality**

**Using behaviour observations to study personality in a group of capuchin monkeys  
(*Cebus apella*) in captivity**

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**Abstract**

This article presents a novel approach to the study of primate personality and illustrates it with a study of capuchin monkeys. While most personality studies with capuchin monkeys have used rating questionnaires, the research method of this study relies instead on direct behavior observations. In an effort to capitalize on the full richness of behavioral observation data, we used both statistical and non-statistical methods to analyze data from behavioral observations of a group of capuchin monkeys in captivity. Interest in capuchin monkeys as a species has increased due to their cognitive capacities, behavioral flexibility and complex social structure, as well as many similarities with great apes in dimensions of personality. In this study we focus in three aspects of personality: diversity, flexibility and complexity. Our results provide a detailed picture of these aspects of capuchins' personality, including the degree of "predictability" and "unusualness" of individual capuchins' behavior.

**Keywords:** personality; capuchin monkeys; diversity; flexibility; complexity; behavioral transitions; predictability index; unusual transitions index.



## Introduction

Personality research describes individual differences in behavior, feelings and cognition which tend to be stable across time and conditions (Gosling, 2001), providing important clues to understanding population adaptability and evolution (Roche, Careau, & Binning, 2016). Differences in behavior across individuals in a given population can be summarized by reference to each individual's "average behavioral display." Furthermore, in any given population, individuals tend to respond to moment-to-moment changes in the environmental conditions in different ways. This behavioral response variation across individuals within a population is called phenotypic plasticity (Dingemanse & Wolf, 2013). Increasing evidence suggests that also the behavior of some individuals shows more moment-to-moment variation than that of others. We can refer to this phenomenon as "between-individual differences in plasticity". These two aspects of individual differences -- between-individuals differences in plasticity and between-individual differences in average behavioral display -- can be considered complementary components of an individual's phenotype (Dingemanse et al., 2010).

Lehner (1996/2007, pp. 440-464) discusses how the analysis of both intra- and inter-individual sequences of behaviors represents an important component of studying behavior that goes beyond the analysis of individual differences in various simple behavioral categories, coded element by element. Long behavioral sequences formed by easily identifiable small actions are more interesting because they reveal more behavioral plasticity than the stereotyped behavioral sequences (Japyassú et al., 2006). The main goal of studying behavioral sequences is gathering information about idiosyncrasies of each individual's behavioral choices. Some sequences involve social interactions while others do not. Individual differences can be found in both types of sequences. This method allows us to address the questions of what are the typical reactions of each individual when facing specific social or non-social situations and how different those reactions are from the ones observed to be most typical within his/her group<sup>8</sup>. For the study of personality, we believe that the analysis of behavioral sequences, especially during social interaction, is important for understanding the uniqueness of an individual. From the beginning of the study of human personality,

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<sup>8</sup> With the study of sequences we are not answering questions of who is the most sociable individual, or who interacts most with whom.

differences in patterns of how individuals interact with others has been seen as central, and from the beginning of psychotherapy, changing such patterns through novel interactions has been seen as equally central.

This study explores the three dimensions of individual personality previously explained: 1) *diversity*, as the differences in the average behavioral display (i.e. different individuals presented distinct repertoires of behavior), 2) *flexibility*, as variability across observations of the behavioral responses (i.e. different individuals presented different capacities for variation over time with respect to one or more particular behaviors), and 3) *complexity*, as variability in the specific sequences of behavior (i.e. more complex individuals present more similarly strong consistent combinations of sequences of behavioral responses, for example having two or three similarly behavior alternatives of response with similar probabilities for being chosen, than do less complex individuals, which might have for example only one highly probable response).

The distinction between nomothetic and idiographic approaches is critical for understanding the history of the study of human personality (Cone, 1986; Uher, 2015). Nomothetic approaches treat what they are studying as objective phenomena subject to universal laws and attempt to derive those laws. Ideographic approaches treat what they are studying as the activity of specific, unique subjects and attempt to understand the meaning of commonalities and differences that are observed as contingent on various combinations of factors. In the study of personality nomothetic approaches have focused on the the measurement of individual differences and the categorization or the taxonomy of different personality types. Ideographic approaches have focused on ontogeny, including the common mechanisms underlying the ontogenetic process, as well as the description of individual differences regarding idiosyncratic aspects of individuals' personalities and the adaptive, functional histories that brought them about (Uher, 2015).

In the exponential increase in studies of personality in non-human primates that has occurred since the 80's various methodological approaches have been used (Freeman et al. 2011). While most works on personality in non-human primates have used nomothetic approaches (e.g. trait models) there are some exceptional examples of research adopting more ideographic approaches. One example is Jane Goodall's work on chimpanzees at Gombe National Park, which included descriptions of individual

personalities that can be described as both rich and deep. With the term, “rich”, we refer to the level of detail in which what is unique to an individual is described. With the term “deep”, we refer to the description of organizational structures of personality in which some less observable difference may be claimed to underlie and explain more superficial differences that are easier to recognize. In our view, more ideographic, or mixed approaches, are necessary to understand the richness of personality that we can find in the individuals of a given group, and to find finer differences between groups and even between species.

The current study of a group of capuchin monkeys in captivity conceptualizes personality as individual-specific patterns of behavior and aims to identify such patterns. The group of monkeys in our study appeared to be brown capuchin monkeys, *Sapajus apella*, first mentioned by Kerr, 1792 (Kress & Conley, 1978), but later referred to as *Cebus apella*. More recently evidence has suggested that two different species exist, *Sapajus apella* and *Cebus apella*; however, as *Sapajus apella* has expanded its territory, considerable hybridization of the two species has occurred (Alfaro et al., 2012; Alfaro, Silva, & Rylands, 2012). This matter of taxonomy continues to be the focus of intense debate in the scientific community. Because the group we studied was in captivity, hybridization is especially likely, so our choice to use the name *Cebus* is somewhat arbitrary.

The genus *Cebus* and *Sapajus* are different from all other platyrrhines: both morphologically and behaviorally. Capuchins present an exceptional cognitive level (demonstrated by the capacity for complex tool use and possibly traditional culture), great behavioral flexibility and complex social structure (e.g., Byrne & Suomi, 1996; Perry, 2011; Ottoni, 2015; Fragaszy et al., 2017). Recent evidence suggests that the personality structure of brown capuchins (from genus *Cebus and Sapajus*) partially overlaps with that of great apes (Uher, Addessi, & Visalberghi, 2013; Morton et al., 2013).

Morton and colleagues (Morton et al., 2013; Morton, Lee, & Buchanan-Smith, 2013), reported Assertiveness, Openness, Neuroticism, Sociability and Attentiveness as dimensions of individual differences in a group of captive brown capuchin monkeys.

They derived these constructs using “Principal Component Analysis” of ratings<sup>9</sup> by 25 researchers and 3 caretakers concerning 127 capuchin monkeys. Later, these authors collected behavioral data regarding (or ‘on’, or ‘based on observations of’) 14 capuchin monkeys (between 7 and 12 months after the ratings) during their participation in an experiment entailing cognitive tasks. Similarly, Robinson and colleagues (2016) found Assertiveness, Openness, Neuroticism and Agreeableness as dimensions of individual differences in a group of 100 brown capuchin monkeys. These authors also used rating questionnaires and PCA analysis but did not follow up with any further behavioral observations.

On the other hand, Uher and colleagues (2013), by using a ‘Behavioral Repertoire x Environmental Situations Approach’ (operationalizing behavioral measurements through behavioral observation and applying behavioral tests – standardized experimental ‘situations’), reported 20 non-lexical emic personality constructs as dimensions of individual differences (e.g. aggressiveness, arousability, anxiousness, competitiveness,) in 24 capuchins in captivity (see Table 2.1). In a subsequent study of capuchins, Uher and Visalberghi (2016), found significant differences in the conclusions drawn about capuchins’ behavior observation and those derived from raters’ assessments. They concluded that raters assessment was biased<sup>10</sup> due to “raters’ mental abstractions and stereotypic beliefs about animals” (p 77). In addition, these authors have found fewer age and sex differences in individual-specific behavior described through systematic behavioral observation, in comparison to the differences found using ratings of personality constructs. Specifically, the authors found that some of the raters’ assessments differed substantially from the behavioral data (e.g., compared to females, males were scored as less anxious, more excitable, more vigilant, more competitive, more curious and impulsive in the raters’ assessments; but in behavioral data those tendencies were not found; moreover, in the behavioral data, there were only very slight age, sex or rearing-related differences in the capuchins individual-specific behaviors.).

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<sup>9</sup> Raters produced these ratings by making assessments of each individual primate guided by a trait assessment questionnaire. For an example of such a questionnaire: [http://extras.springer.com/2011/978-1-4614-0175-9/weiss\\_monkey\\_personality.pdf](http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf) . For a better understanding of how rating questionnaires are used in research on human and non-human primates, consult Weiss (2017); for an example of such application, see Freeman et al. (2013).

<sup>10</sup> To better understand the limitations of the ratings approach consult Uher (2013, 2014); to see an illustration of these limitations with another primate species consult Uher, Werner, & Gosselt (2013).

Table 2.1 Comparison between outcomes (individual differences found) in studies of differences among capuchin monkeys' personalities (all groups were captive).

<b>Study</b>	<b>Method</b>	<b>Components/outcomes</b>
Robinson et al., 2016	Rating (Hominoid Personality Questionnaire and Manson and Perry Questionnaire for white faced capuchins)	Assertiveness, Openness, Neuroticism and Agreeableness
Morton et al., 2013a)	Behaviour within task performance and Rating (Hominoid Personality Questionnaire*)	Assertiveness, Openness, Neuroticism, Sociability and Attentiveness
Uher et al., 2013; Uher and Visalberghi 2016	Rating (five-point rating scale to judge raters own familiarity with the capuchins), behavioural tests and behavioural observation	Aggressiveness to conspecifics, Aggressiveness to humans, Arousability, Anxiousness, Competitiveness, Creativeness/inventiveness, Curiosity, Distractibility, Dominance, Food orientation, Gregariousness, Impulsiveness, Physical activity, Persistency, Playfulness, Self-cleanliness, Social orientation to conspecifics, Social orientation to humans, Sexual activity and Vigilance.

Comparing the outcomes produced by the studies described in Table 2.1, it is evident that the methods used by Uher and colleagues (2016) yielded more constructs beyond those that formed the basis for constructing of the rating questionnaires themselves. Because relying exclusively on rating scales constrains from the outset what might be observed, it places a limitation to the understanding of capuchins' personality that can be achieved from such research. Uher and colleagues' methods transcend this limitation.

For the reasons discussed, we made the methodological choice for the current study to use direct observation data as our starting point. The method we employed in this study, which we will describe below, yields evidence related to individuals' idiosyncrasies. We tried to minimize subjectivity by not using the rating methodology commonly used in studies of animal personality. Instead, we asked our observers to observe categories of behavior described in the species' ethogram, without making any attributions of value.

In another study of capuchins, Byrne and Suomi (2002) integrated physiological, behavioral, and ratings-based personality data and found relationships among ratings of individual personality traits, specific behavior patterns, and cortisol reactivity in juvenile brown capuchins. In order to rate each capuchin the authors considered the 25 personality traits measured using the Behaviour Rating Questionnaire by Stevenson-

Hinde and colleagues (1980) for rhesus monkeys. The authors found that individuals with high cortisol levels tended to play and explore less than others, to seek more social proximity and to display more self-directed behavior. They also found a positive correlation between high cortisone levels and traits such as Apprehensive, Fearful, Insecure, and Submissive.

To summarize, this study explores the three dimensions of individual personality previously explained: 1) *diversity*, 2) *flexibility*, and 3) *complexity*. In the current study we collected observational data as a starting point for attempting to yield complex qualitative and quantitative descriptions of the individuals' personalities.

## **Material and Methods**

For this study we observed a group of 14 capuchin monkeys (*Cebus apella*), 11 females and 3 males, from the Lagos' Zoo in Algarve, Portugal. The group lived on two artificial islands connected by a bridge and a rope, with artificial structures (such as stairs, swings and little houses) connected by ropes, and some arboreal vegetation. In the same lake there are other nearby islands, not connected with the capuchins' ones, on which other species lived. The small houses could be used by the capuchin monkeys as night shelters since they did not sleep in an indoor facility. The animals can have direct views of visitors who could stand at a minimum of 3 meters from the islands' shores. Sometimes other animals like ducks enter the area of the islands and their surrounding water and the capuchins interact with them (e.g., try to hunt them). The capuchin monkeys were fed twice a day (morning and afternoon); the keepers had to cross the moat by wading to deliver the food.

The capuchin monkeys were observed in sessions of 10 minutes each. Observation occurred between February and May 2015. The number of sessions per individual ranged from 59 to 83. The differences across individuals in number of observation sessions were due to factors external to the study design (e.g., baby's birth). Because this study was designed to compare adult personalities and not as a developmental study in which age would be considered an important variable, we followed MacKinnon's

(2013) developmental stages of *Cebus capucinus* and our research subjects comprised the group members in the categories of adult female (typically aged 5 to 6 or older), adult male (typically 10 years and older), and subadult male (typically 7 to 10 years old).

We built an identification sheet with characteristics of each subject. Prior to the observations, we constructed a complete ethogram for the species (based on literature review: Manson, 1999; Carosi & Visalberghi, 2002; Serbena & Monteiro-filho, 2002; Visalberghi, Valenzano, & Preuschoft, 2006; Leonardi et al., 2010; Machado, Costa, & Ribeiro, 2014), and a data sheet with 14 behavioral categories (e.g. self-grooming; affiliation) derived from the complete ethogram. The complete ethogram comprises too many behaviors for an observer to observe and record simultaneously, so some selection and organizing was necessary. We started by excluding some behaviors that our literature review suggested were more a function of other variables than personality differences. For example, eating behavior was excluded because access to food is closely related to hierarchical position. Sleeping was excluded because it is closely related to factors such as time of day and environmental conditions. Then, the remaining behaviors were organized into the 14 categories each of which included several specific behaviors. More information about the behaviors included in each category can be found in the supplementary data (Supplementary materials, Table S1).

We distinguished the selected behaviors between events (i.e., behaviors which lasted 1-second) and states (i.e., behaviors that lasted more than 1-second). Events were measured in terms of number of occurrences. States were measured by the number of seconds they lasted<sup>11</sup>. The 14 behavioral categories observed can be classified as non-social or social behaviors. Within the agonistic social behaviors, two subcategories were distinguished: ritualized non-physically aggressive behaviors (e.g., showing teeth) and effective physically aggressive behaviors (e.g., biting). Similarly, submission behaviors were classified into ritualized and effective types (see Table 2.2).

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<sup>11</sup> See Paul Martin and Patrick Bateson (2007/2010) and Philip Lehner (1996/2007) for literature on sampling behavior and definition of "states vs. events".

Table 2.2 Table depicting the organization of the 14 behavioral categories derived from the ethogram for capuchin monkeys. Each row of the table corresponds to one of the behavioral categories derived from the ethogram

<b>Behavioral categories</b>	<b>State initiated by the focal individual</b>	<b>Event initiated by the focal individual</b>	<b>State received by the focal individual</b>	<b>Event received by the focal individual</b>
<b>Non-social behaviors</b>	Self-grooming Scent Marking Solitary Play Urine Wash	Solitary Play event		
<b>Social behaviors</b>	Affiliation Initiator Sex Initiator Play Initiator Ritual Agonism Initiator Aggression Initiator Ritual Submission Initiator Effective Submission Initiator Parental Behavior	Affiliation Initiator Event Play Initiator Event Ritual Agonism Initiator Event Aggression Initiator Event Ritual Submission Initiator Event Effective Submission Initiator Event	Affiliation Receiver Sex Receiver Play Receiver Ritual Agonism Receiver Aggression Receiver Ritual Submission Receiver Effective Submission Receiver	Affiliation Receiver Event Play Receiver Event Ritual Agonism Receiver Event Aggression Receiver Event Ritual Submission Receiver Event Effective Submission Receiver Event
<b>Abnormal Behaviors</b>	Abnormal Behavior	Abnormal Behavior Event		
<b>Arms Reach</b>	Arms Reach			

In addition to coding the behavioral categories, we recorded all the moments in which an individual was observed in the proximity of conspecifics (proximity was defined as a distance closer than the measure of a fully stretched arm and the behaviors were coded in a category named (Arms Reach). For analytic purpose, we divided these observations into 6 extra variables ranging from arms reach 1 -- being within arm reach of one conspecific, to arms reach 6 -- being within arm reach of six or more conspecifics. All observations were video-taped using cameras attached to the observers' heads. The observers recorded events by making line strokes on an observation sheet, and measured states using a stop-watch and writing length of time on the observation sheet. When there was any doubt about what behavior occurred or how long it lasted, the videotape



was viewed and discussed by the entire research team and decisions were made by consensus. Two observers participated in data collection. A prior test of the Inter-observer reliability of these two observers resulted in a correlation above 90%. Data obtained was analyzed using IBM computer program SPSS, Version 24 (2016) and the EthoSeq program (Japyassú et al., 2006)

In total, 40 variables were analyzed, combining the behavioral categories (separating initiator, receiver and event or state for each category) and the arm reach categories. We explored the three following dimensions of personality.

### *Diversity*

"*Diversity*" refers to differences among all individuals' average behavioral display (i.e. different individuals presented distinct repertoires of behavior). Following Dingemanse and colleagues' (Dingemanse et al., 2010; Dingemanse & Dochtermann, 2013; Dingemanse & Wolf, 2013) proposal to quantify individual variation, the Random Effect Model (REM) was applied to each behavioral category. For each category, the time spent on all the constituent behaviors was treated as the dependent variable. Event-behaviors were treated in the same way as state-behaviors, for each event-behavior assumed to last 1 second. The two variables treated as independent were 1) which individual was engaging in the behavior, and 2) whether it was the first, second, third, etc. observation session. REM is a hierarchical linear model that allows for individual effects, under the assumption that the individual specific effects are not correlated with other independent variables. Mixed-effect modeling approaches in which REM is included are preferable to other classic statistical analysis because the former allow direct estimation of both between- and within-individual variances, do not require a balanced/complete sampling, and allow for calculation of repeatability of traits with non-Gaussian error distributions (Dingemanse & Dochtermann, 2013).

### *Flexibility*

"*Flexibility*" refers to variability across observations of the behavioral responses (i.e. different individuals presented different capacities for variation over time with respect

to one or more particular behaviors). The group variance for each behavioral category represents the variability observed in the group.

The variance of each behavioral category  $B$  is the expected value of the square deviation from the mean of  $B$ ,  $\mu = E[B]$ :

$$\text{Var}(B) = E[(B - \mu)^2]$$

In this calculation are included all the observations made for all the individuals of the group for each behavioral category  $B$ .

The individual variance for each behavioral category represents the flexibility each individual has for any behavioral category. Equally to the group variance, in the individual variance is applied the same formula but for this calculation only are included the observations made for each the individual of the group for each behavioral category  $B$ .

### *Complexity*

“*Complexity*” refers to variability in the specific sequences of behavior (i.e. more complex individuals present more similarly strong consistent combinations of sequences of behavioral responses than less complex individuals). Using the EthoSeq program (Japyassú et al., 2006), we analyzed the behavioral patterns that we could find for each individual observed. EthoSeq uses mathematical Graph Theory in its analysis of behavior sequences (it is not an inferential statistical method). This program identifies sequences of behaviors that occur frequently in the set of observations, analyzing each behavior as potentially the start of one or more frequently occurring sequences. For every behavior, Ethosec calculates, and reports, the relative probabilities (based on the full data set) of it being followed by various possible “next behaviors.” These calculations may be completed based on relatively small sets of data or based on much larger data sets.

EthoSeq uses what are called “transition matrices” for providing input for its calculations. The transition matrix lists all possible behaviors along both the main row and the main column. Each input corresponds to a transition by specifying the behavior that comes first and the behavior that follows it. In our study, each observation session was considered to be a sequence. Consequently each behavioral transition observed in

the session was inserted in the matrix. The first transition entered (let us name it “ $xy_1$ ” for example purposes) corresponds to the one from the first behavior observed (e.g. “ $x_1$ ”) to the behavior which followed it (e.g. “ $y_1$ ”), and the last transition entered (let us name it “ $xy_n$ ”) was the one from the next-to-last behavior of the session (“ $x_n$ ”) to the behavior which followed it (“ $y_n$ ”). It is the EthoSeq program that extracts the sequences within the inputted data in an *a posteriori* probabilistic mathematical analysis. Observers solely observed behaviors as they happened, without any preconceptions regarding sequences.

If a research design preconceptualized sequences, and asked observers to find instances of their occurrence, this would require subjective decisions by someone regarding what constitutes a reasonable beginning and end of a sequence. This is the kind of decisions we chose our research method in order to avoid. Furthermore, if sequences were conceptualized in this *a priori* fashion, then in our case, when an observation session started an ongoing sequence might be presumed to pre-exist and when our observation ended, a sequence might be presumed to extend beyond the end of the observation period. But our main reason for choosing an *a posteriori* approach like EthoSeq is that if observers were to be trained in advance to recognize sequences, bias would be created towards only recognizing the sequences that were anticipated. This would not include all the potential sequences that might occur in the individuals’ behavior. These sequences could be very meaningful especially if they are unknown, uncommon and/or more unique to some individuals of the group. Because of these arguments, we decided to consider the starting and ending points of an observation session to serve as arbitrary starting and ending points for sequences.

The EthoSeq program allows behavioral sequences of different individuals to be compared because the sequences EthoSeq recognizes do not depend on the beginning and end time of behavior (as do other programs, e.g., Theme software from Magnusson, 2000; Japyassú et al., 2006). For discriminating those sequences assumed to be obtained by chance from those that are not, EthoSeq allows for the use of chi-square testing prior to the EthoSeq calculation of behavioral trees. In such testing, “an iterative chi-square test (see Brown, 1974) with a user-specified significance level can be performed in order to highlight above- and below-chance transitions” (Japyassú et al., 2006; p.550).

In our study, we chose a significance level of  $\alpha=0.01$ .

Using our observational data, the program found sequences of behaviors for each individual. The complexities of the sequences ranged from 2 to 5 behavioral transitions. Each transition can be from the one pre-transition behavior to one of 19 post-transition behavior possibilities, with different probabilities associated with each of the 19 possible sequences. For the purpose of EthoSeq analysis we considered only 20 distinct behavioral categories -- we did not distinguish state categories from identically named event categories. The detailed analysis of these transitions, given their complexities, is beyond the scope of this paper (for more details *EthoSeq Outputs and Behavioral Sequences* can be consulted in supplementary materials, Tables S4 and 5, and outputs form SE1 to SE15).

### *3.1 The Nine Indices*

Based on the EthoSeq outputs we constructed nine indices that were calculated for each of the individuals in the capuchin monkeys' group. For all 9 indices, we focused exclusively on the data regarding the first transitions of each sequence in order to compute the indices.

#### *3.1.1 The Complexity Index (CI)*

Complexity is operationally defined in our study as the number of similarly strong consistent combinations of sequences of behavioral responses after a given first behavior in the sequence that the individual demonstrates, across all behavioral categories. Consequently, the personalities of individuals with more alternative patterns are considered to have a higher degree of complexity than those of the individuals with fewer alternative patterns. The mathematical process of calculating the Complexity Index described below reflects our effort to describe such differences using only the data regarding first transition in EthoSeq-identified sequences. In most transitions from a specific first behavior, a specific individual tends to transition to one, two, or three possible second behaviors. Rarely, but sometimes, an individual may have more than three recurring transitional patterns following a particular first behavior. The probability

for an individual of each second behavior, given a first behavior, is calculated by EthoSeq from the full set of observations and is expressed as a percentage. For calculating the CI we considered only the three most probable second behaviors (because more than three transition patterns is highly unusual). The formula for calculating CI entails a series of mathematical operations on conditional probabilities. The probabilities are represented by x's in the formula. The subscripts for each x refer to the category of the first behavior in the sequence (represented by Arabic numerals) and to the order of likelihood of the 2<sup>nd</sup> behavior for which the probability is being calculated (represented by lower case Roman numerals). For example, x<sub>1i</sub> represents the probability of the 1<sup>st</sup> most likely 2<sup>nd</sup> behavior when the first behavior is category 1 (self-grooming); x<sub>1ii</sub> represents the probability of the 2<sup>nd</sup> most likely 2<sup>nd</sup> behavior when the first behavior is 1 (self-grooming); x<sub>1iii</sub> represents the probability of the 3<sup>rd</sup> most likely 2<sup>nd</sup> behavior when the first behavior is 1 (self-grooming).

See Table 2.3 for further examples.

Table 2.3 Arabic numerals (1,2,3, ..., y) refer to the line on the list of behavioral categories of the first behavior of the sequence (y corresponds to the total number of categories found to start sequences -- in the case of our group, 20; x refers to the probability, expressed as a percentage and calculated by EthoSeq, that a given individual will follow that first behavior with a particular 2<sup>nd</sup> behavior; and lower case roman numerals refer to order of likelihood (from highest "i" to lowest "iii") of a category of 2<sup>nd</sup> behavior, following the 1<sup>st</sup> behavior indicated by the Arabic numeral, for that individual

<b>1st most likely 2<sup>nd</sup> behavior</b>	<b>2<sup>nd</sup> most likely 2<sup>nd</sup> behavior</b>	<b>3<sup>rd</sup> most likely 2<sup>nd</sup> behavior</b>
x <sub>1i</sub>	x <sub>1ii</sub>	x <sub>1iii</sub>
x <sub>2i</sub>	x <sub>2ii</sub>	x <sub>2iii</sub>
x <sub>3i</sub>	x <sub>3ii</sub>	x <sub>3iii</sub>
...	...	...
x <sub>yi</sub>	x <sub>yii</sub>	x <sub>yiii</sub>

Formula for calculating each animal's CI:

$$CI = \frac{(\sum_{i*1})/y + (\sum_{ii*2})/y + (\sum_{iii*3})/y}{3}$$

Where:

$$\sum_i = \sum X_{1i}, X_{2i}, X_{3i}, \dots, X_{yi}$$

$$\sum_{ii} = \sum X_{1ii}, X_{2ii}, X_{3ii}, \dots, X_{yii}$$

$$\sum_{iii} = \sum X_{1iii}, X_{2iii}, X_{3iii}, \dots, X_{yiii}$$

And 3 represents the number of different second behaviors used for calculating this index.

In applying the above formula to the calculation of individual capuchin monkeys' CIs' any x lower than 25% was changed to zero. We did this because any second behavior that has a probability of less than 25% is more likely to be due to chance rather than corresponding to a stable pattern within the animals' personality.

### *Predictability Indices*

The *Predictability Index (PI)* was calculated using the probability for an individual of the most probable second behavior (as represented above as "x<sub>i</sub>").

Formula for calculating each animal's PI:

$$PI = \frac{\sum X_{1i} + X_{2i} + X_{3i} + \dots + X_{zi}}{z}$$

Where **z**, whose value differs from one individual to another, corresponds to the total number of categories found to have consistent subsequent behaviors in that particular individual. Consistency is defined similarly to above as having a probability  $x \geq 25\%$ .

The *Predictability Non-Social Index (PIns)* was calculated as was the PI, however we considered for PIns only the first most probable second behavior for non-social first behaviors.

Formula for calculating each animal's PIns:

$$\mathbf{PI}_{ns} = \frac{\sum X_{1i} + X_{2i} + X_{3i} + \dots + X_{z(ns)i}}{z(ns)}$$

Where  $\mathbf{z(ns)}$  corresponds to the total number of non-social categories found to have consistent subsequent behaviors in that individual. The abnormal behavior category was excluded because it is unclear when such behavior is or is not social.

The *Predictability Social Initiating Index (PI<sub>si</sub>)* was calculated as was the PI, however we considered for PI<sub>si</sub> only the first most probable second behavior for first behaviors by that particular individual that fell within categories of “initiation of social behaviors”.

Formula for calculating each animal’s PI<sub>si</sub>:

$$\mathbf{PI}_{si} = \frac{\sum X_{1i} + X_{2i} + X_{3i} + \dots + X_{z(si)i}}{z(si)}$$

Where  $\mathbf{z(si)}$  corresponds to the total number of “initiation of social behaviors” categories found to have consistent subsequent behaviors for that individual. The abnormal behavior category was excluded because it is unclear when such behavior is or is not social.

The *Predictability Social Receiving Index (PI<sub>sr</sub>)* was calculated as was the PI, however we considered for PI<sub>sr</sub> only the first most probable second behavior for first behaviors by that particular individual that fell within categories of “receiving social behaviors”.

Formula for calculating each animal’s PI<sub>sr</sub>:

$$\mathbf{PI}_{sr} = \frac{\sum X_{1i} + X_{2i} + X_{3i} + \dots + X_{z(sr)i}}{z(sr)}$$

Where  $\mathbf{z}(\mathbf{sr})$  corresponds to the total number of “receiving social behaviors” categories found to have consistent subsequent behaviors for that individual. The abnormal behavior category was excluded because it is unclear when such behavior is or is not social.

### 3.1.3 The Unusual Transition Indices

The *Unusual Transition Index (UTI)* measures how often a particular individual transitioned from a first behavior to a second behavior that was unusual, in the sense of rarely occurring as a subsequent behavior to the first behavior within the group as a whole. For calculating the UTI we considered to be unusual only transitions for which the probability of occurrence across all observations of the group was less than or equal to 15%.

Formula for calculating each animal’s UTI:

$$\mathbf{UTI} = \frac{\sum X_{1u} + X_{2u} + X_{3u} + \dots + X_{wu}}{w}$$

Where the subscript  $\mathbf{u}$  means that  $\mathbf{x}$  refers to the probability of an unusual second behavior, and  $\mathbf{w}$  corresponds to the total number of categories found to have unusual second behavior within the group (in our sample  $w = 19$ ).

The *Unusual Non-Social Transition Index (UTIns)* is calculated similarly to the UTI but only considers non-social categories of first behaviors.

Formula for calculating each animal’s UTIns:

$$\mathbf{UTIns} = \frac{\sum X_{1u} + X_{2u} + X_{3u} + \dots + X_{w(ns)u}}{w(ns)}$$



Where  $w(\mathbf{ns})$  corresponds to the total number of non-social categories found to have unusual second behavior within the group (in our sample  $w(\mathbf{ns}) = 3$ ). The abnormal behavior category was excluded because it is unclear when such behavior is or is not social

The *Unusual Social Initiating Transition Index (UTIsi)* is calculated equally to the UTI but only considers “initiation of social behaviors” categories of first behaviors.

Formula for calculating each animal’s UTIsi:

$$\mathbf{UTIsi} = \frac{\sum X_{1u} + X_{2u} + X_{3u} + \dots + X_{w(\mathbf{si})u}}{w(\mathbf{si})}$$

Where  $w(\mathbf{si})$  corresponds to the total number of “initiation of social behaviors” categories found to have unusual second behavior within the group (in our sample  $w(\mathbf{si}) = 8$ ). The abnormal behavior category was excluded because it is unclear when such behavior is or is not social.

The *Unusual Social Receiving Transition Index (UTIsr)* is calculated equally to the UTI but only considers “receiving of social behaviors” categories of first behaviors.

Formula for calculating each animal’s UTIsr:

$$\mathbf{UTIsr} = \frac{\sum X_{1u} + X_{2u} + X_{3u} + \dots + X_{w(\mathbf{sr})u}}{w(\mathbf{sr})}$$

Where  $w(\mathbf{sr})$  corresponds to the total number of “receiving social behaviors” categories found to have unusual second behavior within the group (in our sample  $w(\mathbf{sr}) = 7$ ). The abnormal behavior category was excluded because it is unclear when such behavior is or is not social.

## Results

### *Diversity*

The REM analysis showed significant individual differences for 27 variables. In the light of the fact that we measured individual differences by considering a large number of behavioral categories, for avoiding Type 1 errors we applied a Benjamini-Hochberg correction to our data. As can be seen in Table 4, this correction resulted in decreasing the number of significant personality-related differences to 24.

Table 2.4 The table presents a summary of the results of the REM analysis. The columns represent sequentially: 1) the variables analyzed, 2) the population variance, 3 and 4) the results of the REM, and 5) the critical p-values after the Benjamini-Hochberg correction. P values less than 0.01 are marked with \* and values less than 0.001 are marked with \*\* (Continued on the next page).

<b>Behavioral Categories</b>	<b>Group Variance</b>	<b>Random Model F</b>	<b>Effect Sig.</b>	<b>REM control Critical value (Benjamini-Hochberg)</b>
Self-grooming	0.001	3.549	0.000**	0.001*
Scent Marking	0,000	0.433	0.511	0.011
Solitary Play	0.002	12.66	0.001*	0.001*
Solitary Play event	0.000	7.716	0.006*	0.004
Urine Wash	0.000	74.090	0.000**	0.001*
Affiliation Initiator	0.046	89.751	0.000**	0.001*
Affiliation Initiator Event	0.000	51.816	0.000**	0.001*
Sex Initiator	0.000	3.724	0.068	0.008
Play Initiator	0.003	9.916	0.002*	0.002*
Play Initiator Event	0.000	10.625	0.001*	0.001*
Ritual Agonism Initiator	0.000	4.197	0.049	0.007
Ritual Agonism Initiator Event	0.000	26.902	0.000**	0.001*
Aggression Initiator	0.000	22.771	0.000**	0.001*
Aggression Initiator Event	0.000	37.477	0.000**	0.001*
Ritual Submission Initiator	0.000	1.559	0.219	0.011
Ritual Submission Initiator Event	0.000	17.753	0.000**	0.001*
Effective Submission Initiator	0.000	21.570	0.000**	0.001*
Effective Submission Initiator Event	0.000	34.612	0.000**	0.001*
Parental Behavior	0.056	1.567	0.211	0.01
Affiliative Receiver	0.038	107.545	0.000**	0.001*

Behavioral Categories	Group Variance	Random	Effect	REM control
		Model	Sig.	Critical value (Benjamini-Hochberg)
Affiliative Receiver Event	0.000	35.504	0.000**	0.001*
Sex Receiver	0.000	3.276	0.071	0.008
Play Receiver	0.002	6.518	0.014	0.005
Play Receiver Event	0.000	9.512	0.002*	0.002*
Ritual Agonism Receiver	0.000	2.809	0.094	0.009
Ritual Agonism Receiver Event	0.000	6.689	0.012	0.004
Aggression Receiver	0.000	8.383	0.004*	0.003
Aggression Receiver Event	0.000	28.943	0.000**	0.001*
Ritual Submission Received	0.000	0.000	0.996	0.012
Ritual Submission Received Event	0.000	11.767	0.001*	0.001*
Effective Submission Receiver	0.000	2.599	0.112	0.009
Effective Submission Receiver Event	0.000	68.230	0.000**	0.001*
Abnormal Behavior	0.000	4.869	0.028	0.006
Abnormal Behavior Event	0.000	4.942	0.026	0.006
Arms Reach	0.000	183.978	0.000**	0.001*
Arms Reach 1	0.000	354.230	0.000**	0.001*
Arms Reach 2	0.000	44.7830	0.000**	0.001*
Arms Reach 3	0.000	44.857	0.000**	0.001*
Arms Reach 4	0.000	21.432	0.000**	0.001*
Arms Reach 5	0.000	7.840	0.005*	0.003
Arms Reach 6	0.000	1.647	X	X

In figure 2.1 each colored line represents the personality profile of a different individual by considering all behavioral-categories for which individual differences were found. Moreover, Figure 2.1 illustrates the diversity of personalities within the group (for more details on descriptive statistics consult supplementary materials A).

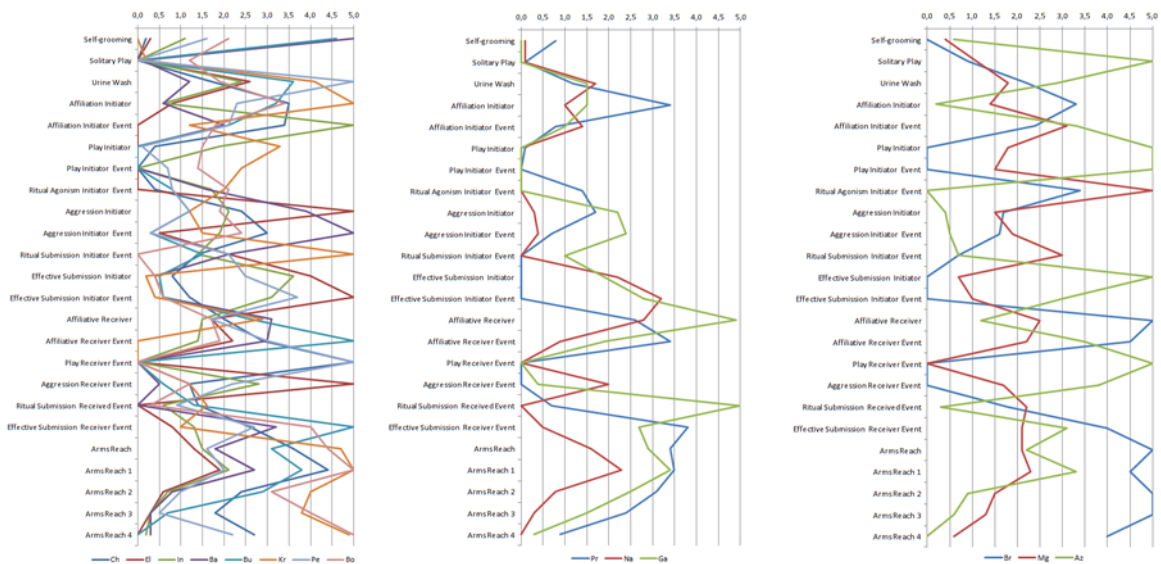


Figure 2.1 For convenience, we divided the results for the 14 individuals in our group into 3 graphics. The first graphic represents the profiles of the 8 females without babies. The second graphic represents the profiles of the 3 females with babies. The third graphic represents the profiles of the 3 males of the group. To facilitate comparison, the results for each behavioral category were transformed into a 0-5 ratio scale, in which 5 represents the highest mean value obtained in the group and 0 represents a complete absence of instances of that behavioral category.

Examining figure 2.1 we can see that the different females have different profiles. Ba and El have profiles that on the whole are very similar, but our method reveals interesting differences between them. For example, both are aggressive adult females (the two most aggressive members in the group, Ba scored 3.9 points and El scored 5.0 points in the 0-5 ratio scale and they are ranked the second and first among the group in aggressiveness), but while Ba has low level of submissive behaviors (0.4 and 0.6 points), El has a high level of submissive behaviors (4.0 and 5.0 points). Looking at the arm reach data, Ba stays more frequently in the proximity of other group-members compared to El; this result suggests that Ba could be more sociable compared to El (see various levels of arms reach in figure 1). Compared to the group as a whole Ba and El make less affiliation efforts (Ba 0.6 and El 0.8 for time spent initiating affiliation and Ba 2.0 points and El 0.0 points for affiliation initiation events). They both receive moderate levels of affiliation attempts from the other members of the group, although Ba receives more (3.1 and 3.0 points for affiliation receiver and affiliation receiver event respectively) than El (1.7 and 2.2 points). However, Ba tends to receive more submissive (3.2 points) and less aggressive behaviors (0.5 points) from other group members compared to El (submissive behaviors 0.8 points; aggressive behaviors 5.0

points); moreover, Ba engages in more self-grooming behavior (5.0 points) than El (0.2 points). El usually does not receive submissive behaviors (0.8 points), does receive very high levels of aggressive behaviors from others (5.0 points) and engages in less self-grooming behavior (0.2 points) than Ba.

In our group, the male Br and the female Pr, conversely to their fellows, never performed submissive behaviors. This suggests their possible highest-ranking positions; this evidence is in line with what is expected to occur in wild groups (Izawa, 1980). Pr and Br are frequently surrounded by other members of the group (see various levels of arms reach in figure 1). They both present low levels of aggression (Pr and Br both with 0.7 for initiating aggression and Pr 0.7 and Br 1.6 points for initiating aggression events). They both present high levels of affiliation in (Pr 3.4 and Br 3.3 points for time spent initiating affiliation and Pr 0.8 and Br 2.4 for initiating affiliation events). Our methods also let us see how the group differentiates individuals through their reactions, even in the case of similarly behaving individuals in equally high hierarchical positions. In the case of Pr and Br, they received very different levels of affiliation (Pr 2.6 and Br 5.0 points for time spent receiving affiliation and Pr 3.4 and Br 4.5 points for events of receiving affiliation). They also received different levels of submission (Pr 0.7 and Br 1.8 points for receiving ritual submission events and Pr 3.8 and Br 4.0 for receiving effective submission events).

To give one final example, in the males group we can observe one very unusual individual, Az (adult). He is an extremely playful individual (see playing categories in graphic 1), he shows frequent submissive (5.0 and 3.0 points for effective submission initiator and effective submission initiator event, respectively) and rare aggressive behaviors (see ritual agonism and aggression categories). He receives moderate-high levels of agonistic behaviors (3.8 points) and, at the same time, moderate levels of submissive behaviors (3.1 points).

## Flexibility

Individual differences also exist in the consistency with which a specific individual behaves across observation sessions. Flexibility refers to the relative absence of consistency – (i.e. the amount of intra-individual variance across observation sessions for each behavioral category, see figure 2.2). Some individuals do not show much flexibility (measured by variance), acting in very similar ways across sessions, while others change their behavior more frequently according to the situation. The group (inter-individual) variance differs across the behavioral categories. Some behavioral categories did not show any significant inter-individual variance while other categories did (see group variance in Table 2.4). But taken together, flexibility in more categories indicates a more flexible behavioral repertoire for some individuals in comparison to others.

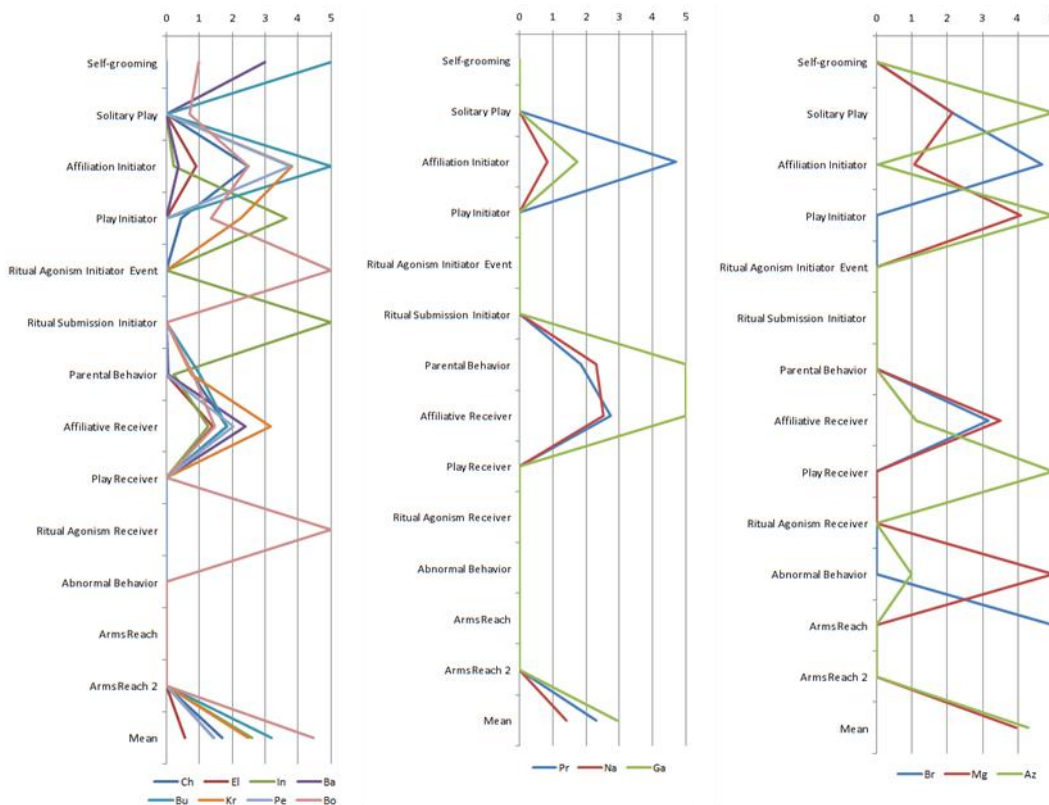


Figure 2.2 For convenience, we divided the results for the 14 individuals in our group into 3 graphics. The first graphic represents the flexibility profiles of the 8 females without babies. The second graphic represents the flexibility profiles of the 3 females with babies. The third graphic represents the flexibility profiles of the 3 males of the group. For each behavioral category, flexibility reflects the extent to which the frequency of that behavior varied

for an individual across observation sessions. To facilitate comparison, the results for variance in each behavioral category were transformed into a 0-5 ratio scale, in which 5 represents the highest variance value obtained by any individual for that behavioral category, and 0 represents no variance across all the observation sessions. An individual's Mean Flexibility Score corresponds to the mean variance for that individual across all behavioral categories, after each variance score was transformed in the 0-5 ratio scale.

In terms of Mean Flexibility Scores, the most flexible individuals of the group are Br (5.000 points in a 0-5 ratio scale) and Bo (3.125 points), while the less flexible individuals are El (0.575 points) and Na (1.422 points).

To illustrate our results regarding flexibility, consider Ba and El discussed above. They are both aggressive adult females. Initiation of aggressive behaviors did not show flexibility in any individuals within the group with the exception of one individual who showed flexibility for the category of initiating ritual agonistic events. Similarly, for the subcategories of submissive behavior, there was no flexibility in most subcategories. Only for the subcategory of initiating ritual submission did just one individual in the group show flexibility. Thus Ba and El, like most other group members, do not show changes across days and situations in aggression or submission. In contrast, initiating affiliation is a category in which many members of the group did show intra-individual variation. Ba's flexibility score was 0.357 (very low) and El's score was 0.893, still less than 1/5 of the highest score. On the other hand, Ba, who as mentioned above receives moderate degrees of affiliation efforts from the other individuals, also varied across sessions considerably in the receipt of affiliation behaviors from others (2.394 points), meaning that her social context was not stable in this respect. El, who contrary to Ba receives low levels of affiliative behavior, experiences this more consistently from her social surrounding with considerably less change across time (1.408 points). Finally, self-grooming behaviors which are low for El, do not show changes through time (0.000), while Ba, shows moderate levels of flexibility (3.000) with respect to this behavior.

Again in terms of Mean Flexibility Scores, Br, the dominant male of the group, is the most flexible individual. Pr, the dominant female of the group, has a much lower score in flexibility (2.321 points). Although both Br and Pr showed equally high scores relating flexibility in affiliation efforts (4.702 points), Br has a more variable social environment with oscillating affiliation efforts by others (3.169 points) than Pr (2.746),

and Br also shows a huge amount of variability in social proximity (5.000 points for arms reach) in comparison to Pr (0.000 points for arms reach). Az the unusual adult male, showed a high Mean Flexibility Score (4.292 points), with the highest scores in the 3 behavioral categories related with playing behavior (5.000 points). We interpret this score as indicating that he adapts his playing behavior to different situations and days, and also that others oscillate considerably in their interest in playing with him. In contrast, he is the most inflexible individual in the group with respect to affiliation efforts (0.060 points), meaning he only very minimally adapts these behaviors to the environment. With respect to affiliation, the other members of the group also act in consistent ways toward him, not changing much their efforts to affiliate across days and situations (1.127 points).

These examples show how detailed flexibility information complements diversity information in allowing rich, complex analyses of individual personality patterns. At the same time, calculating Mean Flexibility Scores allows for the appreciation of how flexible each individual is in comparison to other group members.

### *Complexity*

Individual differences were also found in the complexity of behavior. Complexity can be described as variability in the specific sequences of behavior within an individual's behavioral repertoire. Individuals with more complex personalities are understood as those who, for a greater number of initial behavior demonstrate greater strong consistent combinations of sequences of behavioral responses than individuals with less complex personalities. We can generalize from our data regarding complexity that for most behavioral categories there are transitions to one or two other categories of behaviors which are similarly characteristic for most individuals (with the exception of few behavioral categories for which EthoSeq found present three or even four common behavioral choices, see supplementary materials for more details, Table S5).



Figures 2.3 and 2.4 show how different individuals are with respect to the nine indices calculated. Analyzing the graphics we can see that all individuals show moderate to high complexity. Also, predictability is moderate to high (see figure 2.3). However, regarding predictability, if we look separately at the indices for sequences in which a) the first behaviors are non-social behaviors, b) the first behaviors are “initiation of social behaviors” by the focal individual and c) the first behaviors are “receiving of social behaviors” by the focal individual we observe that in some individuals of the group the differences among the three indices are small (less than 1 point) while in an approximately similar number of others the differences among the three indices are large (around 2 points).

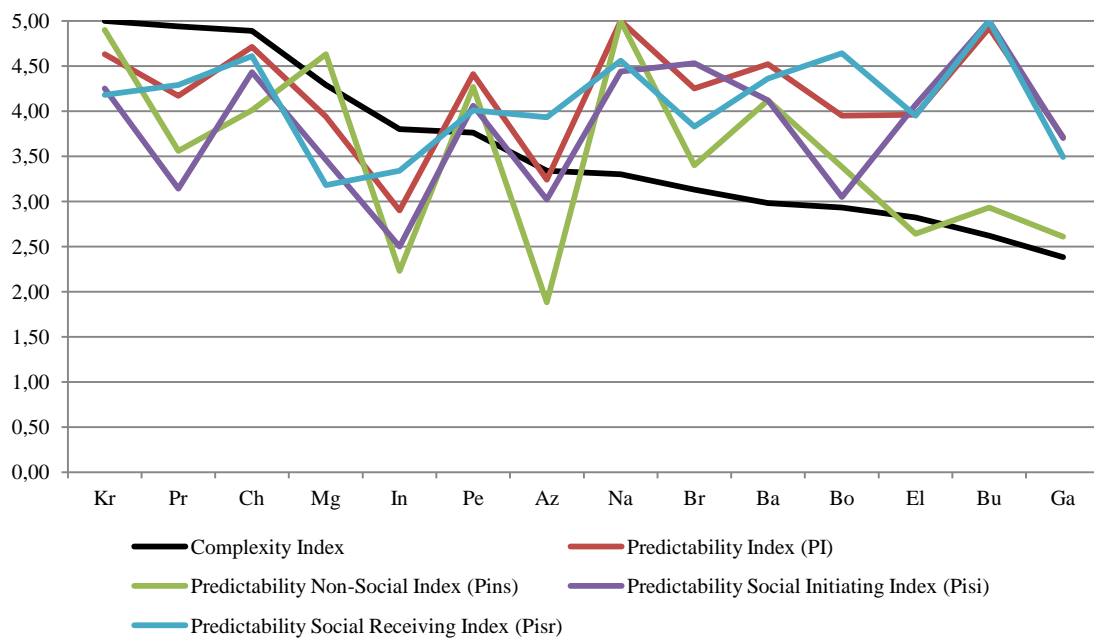


Figure 2.3 The graphic represents the results for the complexity index and for the four predictability indexes calculated. For comparison purpose the results were transformed into a 0-5 ratio scale, in which 5 was the highest value obtained in the group for each index.

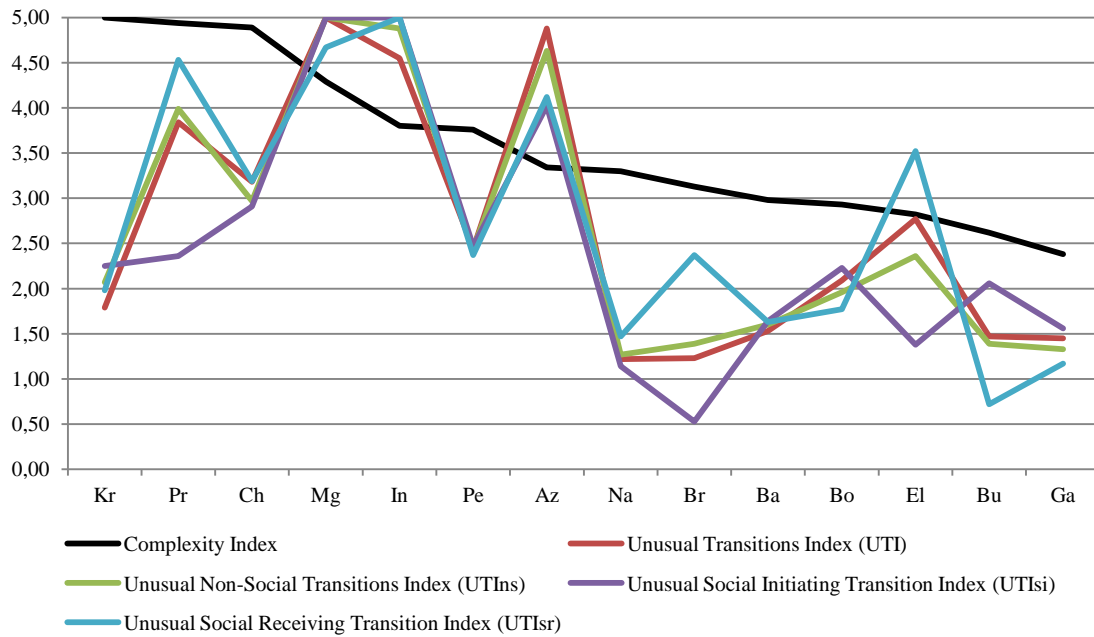


Figure 2.4 The graphic represents the results of the complexity index and the four “unusual” indices calculated. For comparison purpose the results were transformed into a 0-5 ratio scale, in which 5 was the highest value obtained in the group for each index.

With respect to the Unusual Transitions Index, some individuals have low rates of unusual behavioral responses emitted or received, while others have high rates (with differences of more than 4 points between individuals). Unlike with predictability indices, the three unusual transition indices tend to be relatively close for most individuals of the group (less than one point for 10 individuals).

Following the examples of diversity and flexibility, we will examine the results of the generated indices with the same individuals chosen for previous examples. Ba and El, adult females, both show moderate degrees of complexity (2.98 and 2.82 points, respectively). Moreover Ba is very predictable in her behavioral sequences (predictability index - *PI* 4.52 points) which means that for most members of the group she tends to be reliable and also the social environment tends to be stable with her; more specifically she is very reliably in both in sequences started by non-social behaviors (*PI<sub>ns</sub>* 4.12 points) as in sequences started by her behavior (*PI<sub>si</sub>* 4.12 points), sequences where the behavior is started by another member of the group are even more predictable (*PI<sub>sr</sub>* 4.36 points). El in contrast is less predictable in her behavioral sequences (*PI* 3.96

points) which means that for most members of the group she tends to be less reliable and also the social environment tends to be less stable with her; more specifically she is not very predictable in sequences started by non-social behaviors (*PI<sub>ns</sub>* 2.64 points), is more predictable in sequences started by her behavior (*PI<sub>si</sub>* 4.07 points), in contrast sequences where the behavior is started by another member of the group are less predictable (*PI<sub>sr</sub>* 3.95 points).

EthoSeq provides more detailed information about differences between individuals, even when their personalities appear on the surface to be similar in some ways (for more details on behavioral trees from EthoSeq output consult supplementary data, from SE1 to SE15). For example, when Ba is aggressive, 46.15 % of the time she receives an effective submission as a response. The remaining occasions either she receives a variety alternative responses from others, none of which occurs 25% or more of the time, or she follows her direct aggression with a variety of other behaviors, again none of which occurs 25% or more of the time. When she performs ritualized agonism she receives affiliation from others 50% of the time. The remaining 50% of the time, the next behavior in the sequence, whether by Ba or others, is one of a variety of behaviors, none of which occurs 25% or more of the time. In contrast El who has similar frequencies of aggressive behavior than Ba, in half of the times in which she is aggressive she receives affiliation and in the other 50% of the times she follows her aggressive behavior with effective submissive behaviors. We interpret these data as suggesting that she does not intimidate others, but rather ends up either behaving submissively towards others or being pacified by receiving affiliative behaviors from others. Although El sometimes expresses ritualized aggression toward others, EthoSeq did not recognize any behavioral sequence that consistently follows such ritualized aggression. The way Ba and El react to receiving aggressive behaviors by other member of the group is also very different. When Ba receives a direct aggression she always responds by initiating affiliation (100%) which makes her be highly predictable and reliable. In contrast, when El receives a direct aggression she responds in effective submissive ways in 54.55% of the times, which makes her not as predictable as Ba. When Ba receives ritualized agonism in 50% of the situations she is aggressive back in a non ritualized manner, while in the other 50% of the times she ritualizes submissive behaviors. When El receives ritualized agonistic behaviors she always responds with urine wash (100% of the times); only one other member of the group Kr responds in this

way and she only does it 50% of the times, which makes El a quite unique member with respect to response. These examples demonstrate how EthoSeq can be useful for understanding how individuals differ regarding their behavior. In this case aggressive behavior can be described in a detailed manner, considering both the focal individual's pattern behavior, as well as the usual patterns common in the group as a whole.

Using complexity and predictability indices, we can also see differences between the two dominant members of the group, Pr and Br. Pr, the dominant adult female of the group, had an extremely high complexity index (4.94 points), while Br, the dominant adult male was scored lower (3.13 points). Pr is overall slightly less predictable than Br (*PI* 4.17 vs. 4.25 points), being more predictable in her non-social behaviors (*PI<sub>ns</sub>* 3.56 vs. 3.40), less predictable regarding behavioral sequences initiated by her behavior (*PI<sub>si</sub>* 3.14 vs. 4.53), and more predictable regarding sequences initiated by another member (*PI<sub>sr</sub>* 4.29 vs. 3.83 points).

Finally, let's consider the predictability of Az, adult male – the individual in the group who is unusual in his high degrees of playfulness. His sequences are quite unusual because he plays in many situations in which this behavioral response is not expectable from group norms (see supplementary materials for details, Table S5 and EthoSeq output SE1). He presents moderate levels of complexity (3.34 points for the complexity index), and presents lower levels in all predictability indices than Ba, El and Pr (For, Az, *PI*= 3.24 points; *PI<sub>ns</sub>* =3.02 points; *PI<sub>si</sub>* =3.02 points and *PI<sub>sr</sub>* =3.93 points). Az's score is just slightly higher than Br for *PI* and *PI<sub>sr</sub>* indices (*PI* 3.24 and *PI<sub>sr</sub>* 3.93 respectively for Az vs. *PI* 3.13 and *PI<sub>sr</sub>* 3.83 points for Br). Another characteristic of Az is that after initiating effective aggressive behaviors he always receives effective submissive behaviors (100%); this sequence is only equal in frequency to those one other individual -- Bu. Every time Az receives aggressive behaviors he responds with submissive behaviors (100%). Every time he receives ritual submissive behaviors, he subsequently always receives ritual agonistic behaviors (100%). He is the only individual exhibiting this specific sequence. In sum, although Az has some very predictable sequences, his behavior is on the whole very unusual compared to the group and relatively unpredictable. Figure 4 shows that Az has the second highest score on the unusual transition index – *UTI* (*UTI* 4.88 points, Mg adult male is the highest), reflecting the very unique aspects of his personality.

Data regarding *UTI* scores also provide evidence of how different the two dominant individuals are from each other. Br (the dominant male) presents the second lowest score on the *UTI* (1.23 points) while Pr (the dominant female) has the fourth highest score (*UTI* 3.84 points). In the unusual transition index for non-social behaviors – *UTIns* Br received 1.39 points (Pr received 3.99 points on the *UTIns*). For social behaviors, in sequences initiated by the individual's own social behaviors the majority of the behaviors that followed are the expected ones for Br (unusual transition index for social initiated behaviors – *UITsi* 0.53 points, whereas for Pr the same index is *UITsi* 2.36), but for sequences initiated by others' social behaviors Br's unusualness is higher than for sequences he initiates (unusual transition index for social received behaviors – *UITsr* 2.37 points (while Pr received an even higher score of *UITsr* 4.53 points). So it is possible to conclude that Br's behavioral sequences are mainly constituted by the typical behaviors of the group, while Pr has a much higher level of unusualness in her behavior.

The previous examples illustrate how information about complexity enriches the conceptualization of individuals' personality patterns.

## **Discussion**

Our results have demonstrated that different individuals have very distinct repertoires of behavior. Moreover, using observations of behavior as the basic methodology allows us to explore several important ways in which individuals' personalities differ: diversity, flexibility and complexity.

## *Diversity*

Our results demonstrate the existence of considerable diversity in behavioral profiles in this group of capuchin monkeys. The individuals presented distinct repertoires of behavior. A detailed review of Table 2.4 shows that for 19 behavioral categories (excluding arms reach categories) there were significant individual differences within the group, representing personality differences between the individuals. Such behaviors included non-social behaviors (self-grooming, solitary play and urine wash), as well as social behaviors (affiliation, play, ritual and effective agonism, ritual and effective submission, by both actors and receivers). Personality differences were also found regarding the “arms-reach” category, which reflects the individual’s usual degree of proximity to other (up-to-four) conspecifics.

According to Dall and colleagues (2004) species adaptation and survival in a changing environment is related to the richness of inter-individual variation. Adaptive challenges result in such variation, and species that have developed inter-individual variation may have a selection advantage when the environment changes or varies. In fact, capuchin monkeys have a widespread habitat distribution, including extreme habitats and even edge habitats (Lehman, 2004). Their habitats, demand a generalist diet, fluctuate accordingly to the seasons, and according to MacKinnon (2013) are subjected to potential anthropogenic disturbance. Feeding and ranging patterns in this species seem to diverge accordingly to fruit availability and distribution in order to meet nutritional needs (Robinson & Redford, 1986; Zhang, 1995; Di Bitetti, 2001; Wright, 2007). Even in captivity, capuchin monkeys are known to reproduce and maintain a good welfare (Visalberghi & Riviell, 1987; Bicca-Marques & Gomes, 2005). Such diversity in personality differences may be in fact an evolutionary strategy to cope and thrive in such harsh environments and contexts, providing the species an ecological advantage.

## *Flexibility*

The literature on Capuchin monkeys (e.g, G Byrne & Suomi, 1996; Perry, 2011; Ottoni, 2015; Frigaszy et al., 2017), describes evidence of a high level of behavioral flexibility, reflected in 1) their complex social structure entailing cooperation among individuals and 2) their elaborate foraging techniques (e.g., tool use), making this species resilient. It is possible that within-species flexibility has arisen because individual differences in behavior within a group may decrease competition (Bergmuller & Taborsky, 2010). Using our methods which equate flexibility with intra-individual variation, our results show that different levels of individual flexibility among individuals can be observed in some behavioral categories. Within these categories some individuals can be recognized as showing more variability across observation sessions than others. Consistent with our results, other authors have predicted that behavioral flexibility would not be consistent across individuals (Boyce & Ellis, 2005; Sih & Bell, 2008). In addition to demonstrate variation in flexibility in general our data indicated that for several behavioral categories, individuals who were not necessarily the most flexible in general showed the highest level of flexibility for each of those categories. We see the evaluation of each Capuchin's flexibility in relation to the group as a whole as important because it sheds light on the question of which individuals of the group have greater potential for adaptability to specific environmental changes.

## *Complexity*

Another important aspect of individual personality differences is in the ways the individual responds to the behavior of others, or integrates its own sequential behavior with the responses of others. This is part of what we investigate when we focus on the sequences of behavioral transitions. We consider behavioral complexity as a measure of the variety of consistent patterns of combinations or sequence of behavior. The analytic methods applied here (detecting behavior transitions using EthoSeq) do not entail inferential statistics. Instead they focus on identifying, and describing the probability of,

various patterned behavioral sequences. Our method offers a different perspective on primate personality from approaches which focus on finding statistically significant differences in more gross aspects of individual differences. It thereby allows for improved description and understanding of each primate's unique patterns of organization of behavioral sequences. This method is consistent with our view of personality as referring not only to quantitative differences, but also to qualitative differences related to preferred patterns of behavior.

Using the EthoSeq analysis, we were able to extract very rich information about the different individuals of the group. First we were able to differentiate the most complex individuals – the individuals exhibiting more alternative behavioral responses in their sequences -- from those individuals who tend to respond in more fixed ways or more disorganized ways (with no solid behavioral sequences identified).

We were also able to distinguish levels of “predictability” for each individual in the group. Predictability scores reflect how predictable the behavior of each individual is, taking the group as a comparison-norm. We also calculated, separately from overall predictability, each individual's predictability with respect to sequences initiated by 1) non-social behaviors, 2) social behaviors initiated by the focal individual, and 3) social behaviors received by the focal individual.

It was also possible to determine which individuals were most unusual, relative to group norms, in their behavioral transitions. We also calculated separate “unusual transition index” (UTI) scores for sequences initiated by 1) non-social behaviors, 2) social behaviors initiated by the focal individual, and 3) social behaviors received by the focal individual.

Taken together, these various complexity indexes facilitate a deep and rich understanding of the characteristic behavioral patterns and norms for each individual in the group. Various interpretations can be made about the different personality characteristics and how adaptive, accepted and common an individual is within a given group.



In sum, individuals may diverge in the use/expression of the complete behavioral patterns, and such differences may have adaptive functions (Dall, Houston, & McNamara, 2004; Réale & Dingemanse, 2010). When we join the three aspects studied here, diversity, flexibility and complexity, we can construct a quite complex understanding of how individuals differ in their styles and in their potentially adaptive capacities. We can also achieve a better understanding of each member's role in the dynamics of the group, as illustrated with the examples of Ba, El, Pr, Br, and Az in the results section). The deeper information that is possible to obtain about each member of a given group can be helpful for zoos when making management and husbandry decisions. These decisions might have an impact on the group or might imply benefitting one individual at the expense of harming another. Our methods can also help in better understanding differences among groups managed in diverse captive conditions and in comparing captive and wild populations, not only at the individual but also at the group level.

A further advantage of the methods we used is that they provide a model for using observational data for personality research that other researchers of primates can follow. If those researchers also start with data from direct behavior observation, regardless of the initial purposes for which the data collection has occurred, they can afterwards subject their data to analysis using our data-analytic approach as a way of contributing to primate personality research. Our methods are transferrable across species studied (although each species would require its own ethogram), allowing for comparisons among groups and species, while at the same time respecting the behavioral specificities of the groups and species studied. Based on these two ideas, we can envision the extensive behavioral observation data that is often available to researchers studying nonhuman primates being joined to build an understanding of primate personality based on the study of many primates from many different species.

## *Limitations*

By studying only one group of capuchin monkeys, it is difficult to make any generalizations on the degree of personality difference among groups, in general and among individuals, in particular. However, several features showed in our group are not very different from those found in wild populations. For example, the size of our group was relatively small (14 members) as it occurs in the wild where groups range from ten to twenty individuals (Izawa, 1980; Defler, 1982) and tend to fission when the size becomes bigger (Janson, Baldovino, & Di Bitetti, 2012). A further similarity is the sex ratio of our group; indeed, also in the wild only 1-3 males are usually present in the group (Izawa, 1980; Defler, 1982). Previous studies in natural habitats, found one to three adult males per group to be typical (Izawa, 1980; Defler, 1982). In our group, it is noticeable who is the dominant male (Bruce) and who is the highest-ranking female (Priscilla), because none of them ever exhibits effective submissive behaviors (which happens with all other members in the group); this follows what is expected in groups living in the wild (Izawa, 1980). So the major limitation when thinking about the application of these results to other groups is that this researched group is living in and adapting to a captive setting disrupted by human presence (although this disruption is minimized by the fact that humans, except handlers, cannot access the islands).

In terms of possible directions for future research, it could be especially interesting to compare our group with other groups in different zoos, and to verify if some individual characteristics tend to be similar. Also interesting would be a long-term study in order to evaluate the possible changes in individual personalities and group dynamics. One way to do this would be to conduct one or more follow-up rounds of data collection with the same group of capuchins.

Because we do not have any data regarding the prior lives of the capuchin's we studied, we are limited in our interpretation of our data. Prior experiences influence all individuals in general though this is a factor not usually considered in most studies of primate personality. In our group, the older individuals came to Lagos from a different zoo while the younger individuals were born and raised in Lagos. Early experiences may have triggered some differences in personality that we could neither control for nor

fully interpret in this study. However, this only highlights the importance of including historical information (e.g., individuals' child-rearing background), when possible as we try to standardize personality research methods and to clarify the relationship of such methods to their theoretical contexts.

We should also mention that personality change is expectable during maturation (McGuire, Raleigh, & Pollack, 1994) and hierarchical transitions (de Waal, 2002). Hence it would be interesting but not surprising if a follow-up study detected changes. In chimpanzees scores on personality traits of boldness and exploration-persistence tended to decline with age (Massen et al., 2013). From a meta-analysis of studies of personality changes in humans over the life-span Roberts, Walton, & Viechtbauer (2006) found increases with maturity in social dominance (a facet of extraversion), conscientiousness, and emotional stability, with largest increases occurring between ages of 20 and 40. In contrast, they found that social vitality (a 2<sup>nd</sup> facet of extraversion) and openness increases in adolescence but then decreases in old age. These personality changes in relation to age show similarity with chimpanzees (King, Weiss, & Sisco, 2008). In this view, it would be interesting to investigate if age can affect personality changes also in capuchin monkeys in order to delineate a possible personality ontogenetic trajectory in this species.

In this research, our main goal was to demonstrate that we can effectively describe idiosyncratic individual differences that may be present in any observed group. The structures found in this research depend on the behaviors pre-selected for observation, based on the ethogram for capuchins. Further research relying on behavioral observation will be required to ascertain how generalizable these results are and to provide a better foundation for an in-depth understanding of personality in capuchin monkeys.

Nonetheless, we should underline that one of the major advantages of our methodology is that the dependence on direct observation allows having very detailed information about each individual regardless of the number of individuals from the group studied. Plus, not depending only on statistical analysis ensures greater freedom, since one of the major advantages of EthoSeq program is being a mathematical tool capable of extracting patterns even in small samples. Also, this methodology makes possible to compare our findings with those obtained for other species relying on direct behavioral observations, which we recommend.

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**Chapter 3 - The Application of the  
New Methodology to Study  
Personality in *Mandrillus sphinx*: A  
Not-Previously-Studied Species.**

**Personality in Mandrills (*Mandrillus sphinx*): Insights regarding developmental plasticity and social challenges.**<sup>12</sup>

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**Abstract**

Mandrills (*Mandrillus sphinx*) live in dense forests, in large groups, and are sexually dimorphic in an extreme way. Social environment plays a crucial role in the species' maturation process, particularly in males, whom show gender-specific somatic and behavioral variations. Developmental plasticity is of particular importance for this species since it can be a source of phenotypic novelty and is potentially responsible for diversification and speciation processes. Until now, personality in mandrills was extrapolated from studies in baboons. We observed a group of 11 captive mandrills in the Badoca Safari Park, Portugal. We used statistical and non-statistical analyses to expose significant differences amongst the 11 animals concerning: 1) Diversity (frequencies of behaviors observed), 2) Flexibility (behavioral variance), and 3)

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<sup>12</sup> After delivering the thesis a previous published article incorporating this species among others came to my attention. The citation is as follows: Uher, J. (2015). Comparing individuals within and across situations, groups and species: Metatheoretical and methodological foundations demonstrated in primate behaviour. In D. Emmans & A. Laihinen (Eds.). *Comparative Neuropsychology and Brain Imaging* (Vol. 2), Series Neuropsychology: An interdisciplinary Approach. (chapter 14, pp. 223-284). Berlin: Lit Verlag. ISBN 978-3-643-90653-3

Complexity (behavioral sequences observed). In summary, our results indicate that mandrills have very complex and diverse personalities. These results could be explained by the social challenges individuals face living in the mandrill society.

Keywords: *mandrills; personality; developmental plasticity; behavioral sequences; complexity index; predictability index; unusual transitions index.*

## **Introduction**

In any given environment, individuals need to adjust their behavior to ecological and internal environments. Simultaneously, individual behavior can vary from individual to individual (Dall et al., 2004). These individual differences in behavior, which vary minimally across time and conditions, are defined as personality (Gosling, 2001). Such differences may offer some hints on how populations adapted and evolved (Roche et al., 2016). Consequently, personality is a topic transversal to species evolution and development. Personality has been increasingly studied in Primatology (Freeman et al. 2011), but some species have not yet been studied.

Mandrills (*Mandrillus sphinx*) live in large groups based on female matriline with young males leaving the group when they mature (Harrison, 1988). Social organization varies from solitary males to female-male groups that may reach hordes up to 800 individuals (Abernethy et al., 2002; Wickings and Dixson, 1992). The complex social environment plays a key role in the species' maturation process, evidencing somatic and behavioral variation (Singleton, 2012).

In the wild, no long-term social bonds between breeding partners exist (Abernethy, White, & Wickings, 2002). Therefore, the evolution of the strong sexual dimorphism in mandrills was possibly driven by intrasexual competition (Abernethy et al., 2002). Indeed, most of the work conducted on mandrills has focused on their sociality and, consequently, on features of their sexual dimorphism (Setchell 2005). Although our understanding of mandrills' cognitive abilities is limited, there are a few studies conducted in captivity that demonstrate cognitive skills, such as developing emotional bookkeeping systems (Schino and Pellegrini, 2009) and generating new communication

gestures in very specific environments (Laidre, 2008). The limited information we have on mandrills is a consequence of the small number of studies regarding cognition in this species, rather than an indication of limited cognitive abilities among these primates (Perry & Manson, 2003).

Due to the phylogenetic proximity with baboons, some mandrill abilities and behaviors are often extrapolated from those of baboons. Since there is no published work on personality in mandrills, we consider studies of personality in baboons relevant as context to our work. Nevertheless, extrapolations should be done with caution, given that differences within their social organization can dictate different evolutionary paths.

In baboons, several authors studied personality traits using the Emotions Profile Index – the Baboon Form used by familiar and unfamiliar observers’ raters (Buirski et al., 1973; Martau, Caine, & Candland, 1985). The authors observed that submissive individuals were rated as more social and affectionate, while the dominant individuals were rated as more aggressive and less social (Buirski et al., 1973). More recent studies used a bottom-up approach in alternative to the top-down approaches previously used (e.g. Silk et al., 2010, 2012). These studies revealed that females chose to form social-bonds with close kin, especially mothers, daughters, and peer females of similar age (likely paternal half-sisters). Furthermore, these studies also found consistent individual differences in social-behavioral patterns (see also Pereira et al., 2019). In an exploratory Principal Component Analysis applied to behavioral observations of female baboons, three personality dimensions were extracted: “Nice,” “Aloof” and “Loner” (Seyfarth, Silk, & Cheney, 2012). The females considered high on the “Nice” dimension had consistent preferences and were friendly to other females; females high on the “Aloof” dimension had low sociality scores but had stable partner preferences; females high on the “Loner” dimension had low sociality scores and less stable partner preferences. Nevertheless, personality traits observed in female baboons were entrenched within kin and rank networks, not described in isolation from these factors (Seyfarth, Silk, & Cheney, 2014).

In low-ranking male baboons, different behavioral styles appear to modulate endocrine activity, which is not solely dependent on rank and social stressor associated (Virgin & Sapolsky, 1997). Moreover, glucocorticoid production levels were shown to directly impact both physiological and behavioral responses during periods of social instability

(see Cavigelli & Caruso, 2015 for a review). Therefore, different personality styles modulate endocrine activity which has an impact in behavior and in the individuals' ability to cope with challenges.

Additionally, mandrills' reactions to novelty can also help researchers in the study of personality. The mirror and the novel object tests were applied to 578 baboons from the Southwest National Primate Research Center, in an attempt to analyze the variability in response to novel objects and novel social partners (Johnson et al., 2015). After applying an Exploratory Factor Analysis, the authors identified two personality dimensions: "boldness" and "anxiety." They concluded that these two dimensions were significantly heritable, suggesting a sequence variation associated with SNAP25 (single nucleotide polymorphism) responsible for behavioral and neurochemistry differences among these baboons. However, caution is needed when interpreting this type of data. Carter et al. (2012) demonstrated that behavioral tests used to measure boldness might not always reflect individual boldness and could sometimes be incorrectly identifying the anxious dimension as boldness. Later, the same authors (Carter et al. 2014) assessed baboons' personality using a field experiment. The authors provided evidence for boldness and anxiety dimensions being correlated with differences found in individuals' performance of social learning tasks. The baboons who were considered bold and the ones considered more anxious, had a better performance in task solving after watching a conspecific demonstrator (contrary to baboons considered shy and calmer who did not presented a significant change in the task performance). However, Carter et al. (2014) underlined two important factors that might have influenced these results: 1) the demonstrators were considered bold individuals and the experiment could not control how this factor might have influenced audience attentiveness and social learning in observer baboons; 2) some individuals were very difficult to test in the presence of a demonstrator, and this difficulty could have been related to the personality of the demonstrator.

In summary, studies on baboons reveal how important personality is for understanding the social aspects of baboons' lives as well as the species' evolution. Since social environment plays an extreme role in mandrills' somatic and behavioral maturation process, it is expected that personality will also play a key role in this species' developmental and phenotypic plasticities, and ultimately in its

survival. Consequently, the goal of this article is to study personality in mandrills using a bottom-up approach, by analyzing behaviors and identifying personality-related behavioral differences, in a group of captive mandrills. This study uses the “three dimensions of personality” identified in Brandão et al. (2019) : 1) *diversity*, as the individual differences in their average behavioral display (i.e., different individuals presented distinct repertoires of behavior), 2) *flexibility*, as variability across observations of the behavioral responses (i.e., different individuals presented different capacities for variation over time with respect to one or more particular behaviors), and 3) *complexity*, as variability in the specific sequences of behavior (i.e., more complex individuals present more similarly strong consistent combinations of sequences of behavioral responses than do less complex individuals)”. Therefore, we expect to find a large number of differences in behaviors and behavioral patterns among individuals, which may lead us to understand how diverse, flexible and complex personalities can be in these primates.

## **Material and Methods**

### Study site and subjects

We studied a group of 11 mandrills (*Mandrillus sphinx*), 4 males and 7 females from Badoca Park in Alentejo, Portugal. During this period of data collection, one of the females (Ne) had a nursing infant and another one (Lo) was pregnant (Lo delivered a baby in the following October). Despite this fact, it is important to notice that for husbandry reasons, the animals had hormonal control (except for the dominant male). Data collection took place between February and March of 2016. The sample size included all adults and juveniles from the group (following Charpentier et al., 2007 age classification system: infants, 0-1 years; juveniles, 1-3 years; adolescent females, 4-5 years; adolescent males, 5-8 years; adult females, older than 5 years; adult males, older than 9 years). The decision to exclude infants from the sample was based on our goal of studying personality in a more stable phase of its ontogeny.

Our sample group was the only colony of captive mandrills living in Portugal during the observation period for this study. All animals were originally transferred from other European zoos to Badoca, and their relatedness is known (see Pereira et al., 2019 for details on the group's genealogical tree). During the day time, the animals lived in an island-style enclosure with both natural vegetation and enriching artificial structures. The available space measured approximately 1,674 m<sup>2</sup>. The water surrounding the island kept visitors a minimum of 3 m from the animals (at the closest point). Visual contact with tourists occurred only during day hours. The animals spent the night hours in an indoor enclosure of approximately 75 m<sup>2</sup>, with no vegetation but with artificial enriching structures. Provision of food (fruits and vegetables) occurred three times per day – morning, afternoon and evening.

#### Study design and data collection

Focal sampling was used to record the individuals' behavior (Marting and Batson, 2010). The mandrills were observed in sessions of 10 minutes each, with the total number of sessions ranging from 50 to 54 per individual. Prior to the observations, we constructed a complete ethogram for the species (based on literature review: Abernethy, White, & Wickings, 2002; Setchell & Jean Wickings, 2006; Astaras, Mühlenberg, & Waltert, 2008; Schino & Pellegrini, 2009; among other authors), and a data sheet organized with 19 behavioral categories (e.g., scent-marking, affiliation) derived from the complete ethogram. We excluded some behavioral categories that literature review suggested to be more a function of other variables than personality differences (e.g., sleeping). More information about the behaviors included in each category can be found in the supplementary data (Supplementary material B, Table S10).

The behaviors selected were distinguished between events (i.e., behaviors which lasted 1 second or less) and states (i.e., behaviors that lasted longer than 1 second). Events were measured in terms of the number of occurrences. States were measured by the number of seconds.

The 19 categories observed were divided into social and non-social behaviors, and to “abnormal behaviours” and “other behaviours” (to include species non typical and



stereotypic behaviour, and to include behaviours which are not defined in this ethogram, respectively). Within the category of agonistic social behaviors, two subcategories were distinguished: ritualized non-physically aggressive behaviors (e.g., showing teeth) and effective physically aggressive behaviors (e.g., biting). Similarly, submission behaviors category was subdivided into ritualized and effective types (see Table 3.1).

Table 3.1 Table depicting the organization of the 19 behavioral categories derived from the ethogram for mandrills. Each row of the table corresponds to one of the behavioral categories derived from the ethogram.

<b>Behavioral Categories</b>	<b>State</b>	<b>Event</b>	<b>State</b>	<b>Event</b>
	<b>initiated by the focal individual</b>	<b>initiated by the focal individual</b>	<b>received by the focal individual</b>	<b>received by the focal individual</b>
<b>Non-social Behaviors</b>	Self-grooming			
	Scent Marking			
	Solitary Play	Solitary event	play	
	Vocalizations Scratch			
<b>Social Behaviors</b>	Affiliation Initiator	Affiliation Initiator Event	Affiliative Receiver	Affiliative Receiver Event
	Infant Affiliation	Infant Affiliation Event	Infant Affiliation	Infant Affiliation Event
	Sex Initiator		Sex Receiver	
	Play Initiator	Play Initiator Event	Play Receiver	Play Receiver Event
	Parental Behavior			
	Hierarchy Mounting			
	Ritual Agonism Initiator	Ritual Agonism Initiator Event	Ritual Agonism Receiver	Ritual Agonism Receiver Event
	Aggression Initiator	Aggression Initiator Event	Aggression Receiver	Aggression Receiver Event
	Ritual Submission Initiator	Ritual Submission Initiator Event	Ritual Submission Received	Ritual Submission Received Event
	Effective Submission Initiator	Effective Submission Initiator Event	Effective Submission Received	Effective Submission Received Event
<b>Other Behaviors</b>	Fear-Related			
	Wound Grooming			
<b>Abnormal Behaviors Arm Reach</b>	Abnormal Behavior	Abnormal Behavior Event		
	Arm Reach			

Beyond coding the behavioral categories, we recorded all the moments in which an individual was observed in the proximity of conspecifics (proximity was defined as a distance closer than the measure of a fully stretched arm, and the behaviors were coded in a category named (Arm Reach). For the analyses, we further classified these Arm Reach observations with an additional variable indicating the number of conspecifics within arms reach (e.g., “arms reach 1” — the focal animal is within arm reach of one conspecific, “arms reach 3” — the focal animal is within arm reach of three conspecifics). No individual was observed within arm reach of more than three other conspecifics.

All observations were videotaped using cameras attached to the observers’ heads. The observers recorded events by making line strokes on an observation sheet and measured states using a stop-watch and writing the length of time on the observation sheet. When there was any uncertainty about what behavior occurred or how long it lasted, the videotape was reviewed and discussed by the entire research team and decisions were made by consensus. Two observers participated in data collection. A prior test of the Inter-observer reliability of these two observers resulted in a correlation above 90%. Data obtained was analyzed using the IBM computer program SPSS, Version 24 (2016) and the EthoSeq program (Japyassú et al., 2006).

In total, 43 variables were analyzed, combining the behavioral categories (and their subdivisions: initiator, receiver and event or state for each category) and the arm reach categories. We explored the following three aspects of personality: diversity, flexibility, and complexity. Statistical and non-statistical analysis followed the methods used in a previous article from Brandão et al. (2019), where personality was described using the same three aspects.

## Diversity

As defined by Brandão et al. (2019) “*Diversity* refers to differences among all individuals’ average behavioral display (i.e., different individuals presented distinct

repertoires of behavior).” We applied the Random Effect Model (REM)<sup>13</sup> to each behavioral category. The time spent on all the constituent behaviors was treated as a dependent variable. Event- and state-behaviors were treated equally (each event-behavior was assumed to last 1 second). The independent variables were 1) individual engaging in the behavior, and 2) observation session number, (i.e., whether it was the first, second, third, etc. session).

### *Flexibility*

*Flexibility* was defined by Brandão et al. (2019) as “the variability across observations of the behavioral responses (i.e., different individuals presented different capacities for variation over time concerning one or more particular behaviors).” The statistical variance is used to calculate flexibility. The individual variance for each behavioral category represents the flexibility each individual has for that behavioral category.

### *Complexity*

“*Complexity* refers to variability in the specific sequences of behavior (i.e., more complex individuals present more similarly strong consistent combinations of sequences of behavioral responses than less complex individuals)” following Brandao et al. (2019) definition. The specific sequences of behaviors or behavioral patterns were identified and analyzed using the EthoSeq program (Japyassú et al., 2006). For further information about the usage of EthoSeq program for the method of calculating this sequences, please see Brandao et al. (2019) and Japyassu et al., 2006.

EthoSeq found sequences of behaviors for each mandrill in our data set. The complexities of the sequences ranged from 2 to 15 behavioral transitions. Each transition can be from the one pre-transition behavior to one of 25 post-transition behavior possibilities, with different probabilities associated with each of the 25 possible sequences. For EthoSeq analysis, we considered only 26 distinct behavioral categories – the categories were not split into state and event, but the distinction between initiated and received was maintained. The detailed analysis of these

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<sup>13</sup> For more details about REM analysis and methodological implications please see Brandão et al. (2019), Dingemanse et al. (2010), Dingemanse & Doehtermann (2013) and Dingemanse & Wolf (2013).

transitions, given their complexities, is beyond the scope of this paper (for more details, *EthoSeq Outputs and Behavioral Sequences* can be consulted in supplementary materials B, Table S14 and S15, and outputs from SE16 to SE27).

### *The Nine Indices*

We calculated nine indices based on EthoSeq outputs for each of the individuals in the mandrills' group, following the method from previous work with capuchin monkeys (Brandão et al., 2019). For computing the nine indices, we worked exclusively with the data regarding the first transitions of each sequence. We considered the following indices: *Complexity Index (CI)*, *Predictability Index (PI)*, *Predictability Non-Social Index (PIns)*, *Predictability Social Initiating Index (PISI)*, *Predictability Social Receiving Index (PISR)*, *Unusual Transition Index (UTI)*, *Unusual Non-Social Transition Index (UTIns)*, *Unusual Social Initiating Transition Index (UTISI)*, *Unusual Social Receiving Transition Index (UTISR)*. For computing the nine indices, we focused on the first transitions of each sequence. The *Predictability Index (PI)* was calculated using the probability of the second most likely behavior of an individual, considering the categories with consistent subsequent behaviors. Some behaviors were rare as a subsequent behavior to the first behavior, across the group as a whole. These transitions were considered unusual when the associated probability of occurrence across all observations of the group was less than or equal to 15%. The *Unusual Transition Index (UTI)* measures how often a particular individual transitioned from a first behavior to an unusual second behavior.

### **Ethical note**

The research complied with guidelines provided by the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes (ETS n. 123). The research also adhered to the ASAB “guidelines for the treatment of animals in behavioral research and teaching.”

## Results

### Diversity

The REM analysis showed significant individual differences for 32 variables. In this REM analysis, we looked for individual differences in a large number of behavioral categories. When the number of categories is high, some significant differences could be expected to occur due to chance (Type I errors). Hence, we performed a Benjamini-Hochberg correction, which reduced the significant individual differences to 24 variables (Table 3.2).

Table 3.2 The table presents a summary of the results of the REM analysis. The columns represent sequentially: 1) the variables analyzed, 2) the population variance, 3 and 4) the results of the REM, and 5) the critical p-values after the Benjamini-Hochberg correction. P values less than 0.01 are marked with \* and values less than 0.001 are marked with \*\* (Continued on the next page).

Behavioral Categories	variance pop.	Random Effect Model		REM control
		F	Sig.	critical value (Benjamini-Hochberg)
Self-grooming	0.005	17.66	0.001**	0.001*
Scratch	0.002	29.896	0.000**	0.001*
Sent Marking	0.000	0.597	0.442	0.010
Solitary Play	0.000	6.014	0.014*	0.005
Solitary Play Event	0.000	9.908	0.005**	0.003
Vocalizations	0.000	29.610		
Affiliation initiator	0.015	28.720	0.000**	0.001*
Affiliation initiator Event	0.000	38.030	0.000**	0.001*
Sex Initiator	0.000	7.270	0.007**	0.004
Play Initiator	0.000	23.413	0.000**	0.001*
Play Initiator Event	0.000	33.536	0.000**	0.001*
Ritual Agonism Initiator	0.000	0.017	0.897	0.011
Ritual Agonism Initiator Event	0.000	21.742		
Aggression Initiator	0.000	15.374	0.000**	0.001*
Aggression Initiator Event	0.000	47.450	0.000**	0.001*
Ritual Submission Initiator	0.000	6.495	0.013*	0.004
Ritual Submission Initiator Event	0.000	50.634	0.000**	0.001*
Effective Submission Initiator	0.000	46.084	0.000**	0.001*

<b>Behavioral Categories</b>	<b>Random Effect Model</b>			<b>REM control</b>
	<b>variance pop.</b>	<b>F</b>	<b>Sig.</b>	<b>critical value (Benjamini-Hochberg)</b>
Effective Submission Initiator Event	0.000	137.406	0.000**	0.001*
Hierarchy Mounting	0.000	2.685	0.102	0.009
Parental Behavior Initiator	0.024	16.766	0.000**	0.001*
Affiliative Receiver	0.015	28.395	0.000**	0.001*
Affiliative Receiver Event	0.000	26.673	0.000**	0.001*
Infant Affiliation	0.004	3.539	0.061	0.007
Infant Affiliation Event	0.000	1.639	0.201	0.010
Sex Receiver	0.000	2.412	0.135	0.009
Play Receiver	0.000	15.366	0.000**	0.001*
Play Receiver Event	0.000	24.495	0.000**	0.001*
Ritual Agonism Receiver	0.000	9.178	0.004**	0.002
Ritual Agonism Receiver Event	0.000	11.802	0.001**	0.001*
Aggression Receiver	0.000	5.419	0.030*	0.006
Aggression Receiver Event	0.000	38.585		
Ritual Submission Receiver	0.000	4.305	0.040*	0.007
Ritual Submission Receiver Event	0.000	34.948	0.000**	0.001*
Effective Submission Receiver	0.000	24.758	0.000**	0.001*
Effective Submission Receiver Event	0.000	72.484	0.000**	0.001*
Other Behaviors Fear Related	0.000	20.048	0.000**	0.001*
Other Behaviors Wound	0.004	10.054	0.003**	0.002
Abnormal Behavior	0.001	3.365	0.067	0.008
Arm Reach	0.000	151.418	0.000**	0.001*
Arm Reach 1	0.000	195.471	0.000**	0.001*
Arm Reach 2	0.000	16.791	0.000**	0.001*
Arm Reach 3	0.000	2.736		

The behavioral-categories for each individual represent a personality profile. These profiles are represented in Figure 3.1, where each colored line represents one of the individuals of the group. The figure illustrates the diversity of personalities in the group (for more details on descriptive statistics consult supplementary materials B, Table S11).

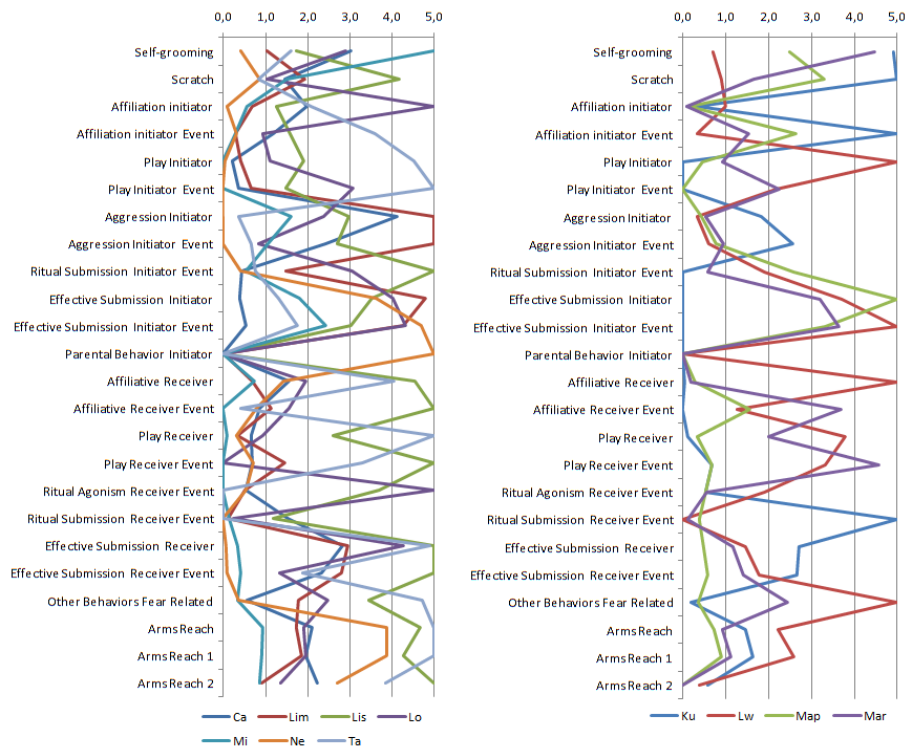


Figure 3.1 For convenience, we divided the results for the 11 individuals in our group into 2 graphics. The graphic on the left represents the profiles of the 7 females. The graphic on the right represents the profiles of the 4 males of the group. The results for each behavioral category were transformed into a 0-5 ratio scale, to facilitate comparison, in which 5 represents the highest mean value obtained in the group and 0 represents a complete absence of instances of that behavioral category.

Examining Figure 3.1, we can see that the different individuals in the group have very different profiles. For example, Ca and Lim, both adult females, are the two most aggressive individuals in the group (4.118 points in a 0-5 ratio scale and 5.000 points respectively in aggression initiator), but they have different profiles. Ca shows very low levels of submission (0.433 points for ritual submission, 0.397 points for effective submission, and 0.536 points for events of effective submission), while Lim generally shows high levels of submission (1.473, 4.782 and 4.277 points respectively). Furthermore, Ca self-grooms more than Lim (3.022 vs. 1.042 points respectively).

Ku, which is the dominant male of the group, has as a unique profile. As expected, he scored zero points for all submissive behavior categories, and he is the individual receiving the most ritual submissive events (5.000 points). He has the highest levels of aggression compared to the other males (1.840 points for aggression initiator and 2.559 points for aggression initiator event), but relatively low compared to the rest of the group. He presented low scores for initiating affiliation (0.343 points) but had the

highest levels for initiating instances of affiliation (5.000 points). Compared with the other adult males of the group (Map and Mar), he has a higher frequency of proximity with conspecifics (see arms reach values). He had the highest score of scratching behavior (5.000 points) and the second highest of self-grooming (4.923 points).

The obtained information about mandrills' behavior can be further processed for understanding better how the group individuals distribute themselves according to some characteristics. A series of dispersion graphics relating information of different pairs of behavioral categories were performed. In most cases the individuals get distributed along the behavioral continuum for each behavioral category, ranging from 0 to 5 (for more details see supplementary material Figure FS1). However, there are a few exceptions especially related to self-grooming, scratching, aggression initiated and submission received. Indeed, increase aggressive behavior was never associated with decrease in receiving submission. Also, high levels of self-grooming was also never associated with high levels of play, scratch and fear related behavior (with exception of Ku, the dominant male). And finally, increase in scratching is also not associated with increased play or fear related behaviors (with the exception of Lis, a subadult female).

### Flexibility

In our study, some individuals presented similar behavior across sessions (measured by intra-individual variance) -- these individuals do not show much flexibility, see Figure 3.2. Others present variations in their behavior according to the situation. Also, the group (inter-individual) variance is different across the behavioral categories. Some behavioral categories showed significant inter-individual variance and others presented no significant inter-individual variance (see group variance in Table 3.2 and S4 in the supplementary material). When analyzing the results obtained on flexibility in general, we can conclude that some individuals have a more flexible behavioral repertoire than others.



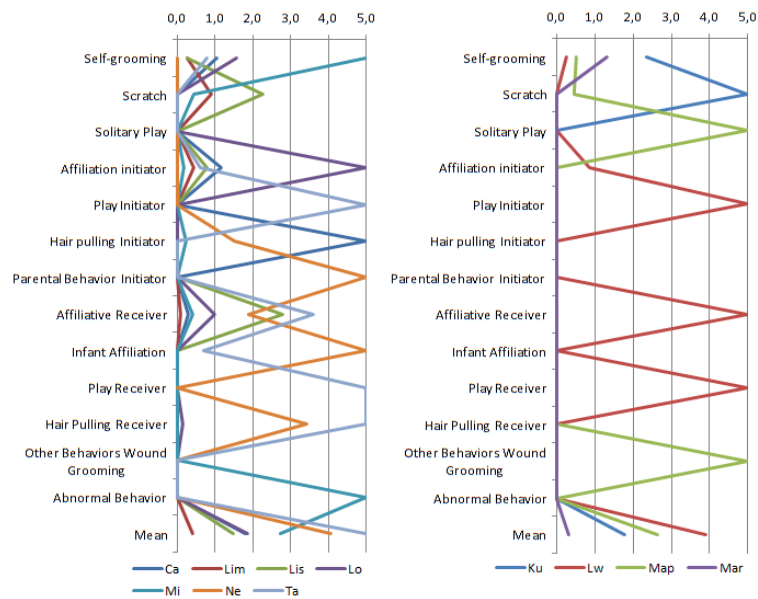


Figure 3.2 For convenience, we divided the results for the 11 individuals in our group into 2 graphics. The graphic on the left represents the flexibility profiles of the 7 females. The graphic on the right represents the flexibility profiles of the 4 males of the group. For each behavioral category, flexibility reflects the extent to which the frequency of that behavior varied for an individual across observation sessions. The results for variance in each behavioral category were transformed into a 0-5 ratio scale, to facilitate comparison, in which 5 represents the highest variance value obtained by any individual for that behavioral category, and 0 represents no variance across all the observation sessions. An individual's Mean Flexibility Score corresponds to the mean-variance for that individual across all behavioral categories, after each variance score was transformed in the 0-5 ratio scale.

In terms of Mean Flexibility Scores (MFS), the most flexible individuals of the group are Ta (5.000 points in a 0-5 ratio scale) and Ne (4.062 points), and the least flexible individuals are Mar (0.318 points) and Lim (0.410 points). Thirteen behavior categories showed flexibility in some individuals of the group, but all the other categories did not show flexibility in any individuals within the group. Thus in those categories, the individuals do not show changes across days and situations. In four behavioral categories, parental behavior, solitary play, wound grooming and abnormal behavior, only one individual of the group shows some degree of flexibility. In the remaining categories, there were always two or more individuals scoring in flexibility. The behavioral categories with some degree of flexibility for almost all individuals of the group were: 1) self-grooming and scratching and 2) affiliative behaviors (initiated and received). For further information see supplementary materials B, Table S13.

For illustrating our results regarding flexibility, we selected the same individuals previously chosen to illustrate diversity. As explained above, Ca and Lim are aggressive adult females. Aggressive behavioral categories initiated by the individual being

observed did not show flexibility in any individuals within the group. This means that Ca and Lim, like most, usually behave aggressively independently of the time and situation. Ca initiates affiliation more than Lim, and also shows more flexibility in her behavior than Lim (1.159 points and 0.427 points respectively), although both have low levels of flexibility. Therefore, Ca shows more capacity to adapt to situations. Ca not only self-grooms more but she is more flexible in her behavior (1.053 points) than Lim (0.263 points). The opposite occurs with scratching - not only did Ca scratch less, she also did not show any flexibility in her scratching behavior (0.000 points), whereas Lim showed some flexibility in her scratching behavior (0.909 points). However, the most important difference between these two females relates to the initiating hair pulling behavior. Although the individuals in the group did not show significant differences in the frequency of initiating hair pulling behavior, Lim never exhibits that behavior, while Ca is the individual with highest flexibility (5.000 points), which implies her behavior varies greatly with time and with different situations.

Ku, the dominant adult male, only showed flexibility for two behavioral categories: 1) scratching with 5.000 points, being the most flexible individual (and also with high frequencies of scratching), and 2) self-grooming with 2.368 points (he had the second highest frequency) and received stable levels of behaviors from others in general (MFS 1.779).

In summary, flexibility information complements diversity information allowing a more detailed picture of the individual personality patterns. Calculating MFS helps to identify how flexible each individual is in comparison to the group. In the dispersion graphics obtained with MFS information and diversity, we verify that no individual was found to have high scores on flexibility along with high frequency scores on: 1) aggression initiation, 2) self-grooming, 3) scratching, 4) ritual submission initiation, 5) ritual agonism receiver, or 6) fear related behavior. In addition, no individual was found having low scores on flexibility and high frequency scores on: 1) play initiation, 2) play receiver, 3) arms reach, 4) effective submission receiver, 5) affiliation receiver, or 6) arms reach (only one individual, Lis female sub-adult, presented low scores on flexibility and high scores in the two last categories; for more information see supplementary material B, Figure S22,S29,S32).

## Complexity

The complexity of individuals' behavior also presented individual differences. We can highlight that for most behavioral categories observed, there are transitions to one, two or three other categories of behaviors which are distinctly characteristic for each individual of the group (except some behavioral categories for which EthoSeq found more common behavioral transitions across individuals).

Considering the sequences of behavior calculated for the group, for some behavioral categories, EthoSeq calculated transitions from one initial behavioral category to only one other subsequent behavioral category (with >15% associated probability) in 6 out of 26 categories; transitions to two other behavioral categories were more frequent, for 9 out of 26; transitions to three other behavioral categories for 6 out of 17; and in the remaining 4 out of 26 behavioral categories there were transitions to 4 or more behavioral categories of behaviors. Consequently, 21 of the 24 behavioral categories computed in EthoSeq, presented up to three similarly characteristic transition choices for most individuals (see supplementary materials B for more details, Figure S1).

The differences among individuals concerning the nine calculated indices can be observed in Figures 3.3 and 3.4. All individuals show moderate to high complexity. Predictability is also moderate to high (see Fig. 3.3). However, regarding predictability, if we look separately at the indices for sequences in which a) the first behaviors are non-social behaviors, b) the first behaviors are "initiation of social behaviors" by the focal individual and c) the first behaviors are "receiving of social behaviors" by the focal individual, we observe that some individuals, show only small differences among the three indices (less than 1 point). In contrast, other individuals show large differences among the three indices (around 2 points), with the largest differences occurring between non-social behaviors and "initiation of social behaviors."

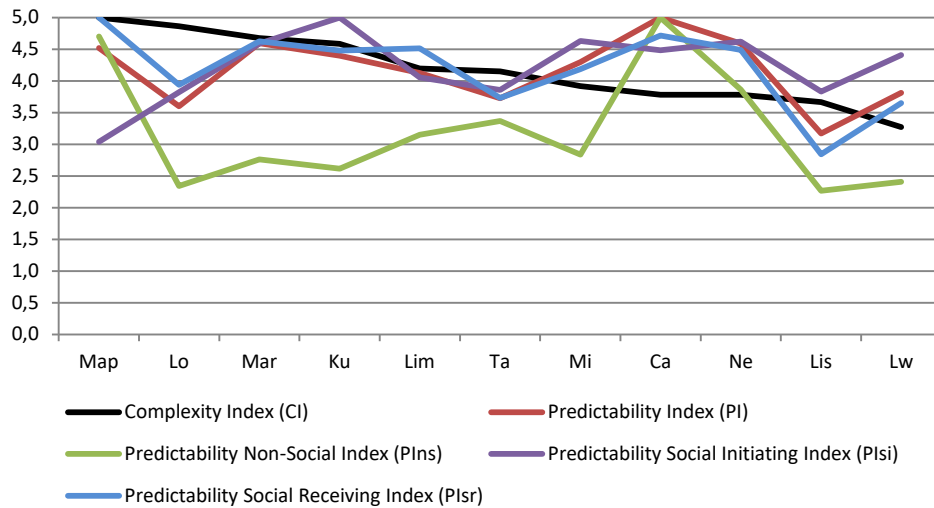


Figure 3.3 The graphic represents the results for the complexity index and the four predictability indices calculated. The results were transformed into a 0-5 ratio scale, for comparison purpose, in which 5 was the highest value obtained in the group for each index.

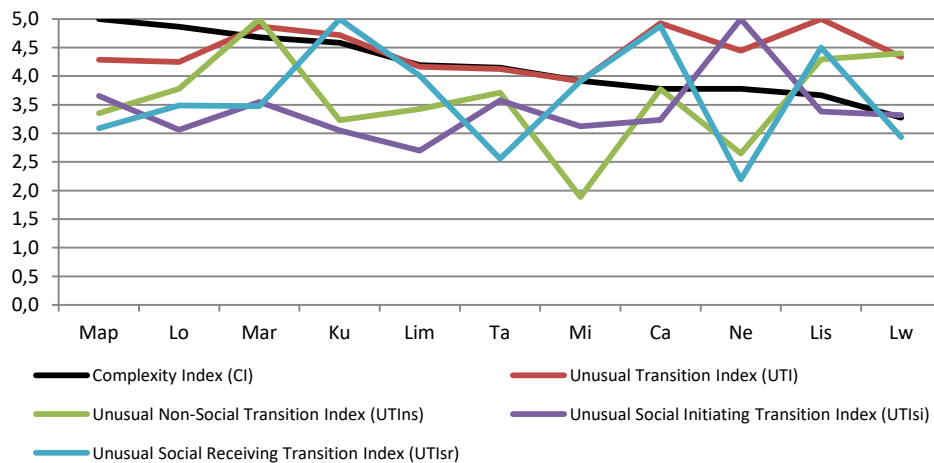


Figure 3.4 The graphic represents the results of the complexity index and the four “unusual” indices calculated. The results were transformed into a 0-5 ratio scale, for comparison purpose, in which 5 was the highest value obtained in the group for each index.

Concerning the Unusual Transitions Index, all individuals show high scores that range from 3.912 (corresponding to Mi) to 5.000 (corresponding to Ne). For some individuals, the three unusual transition indices differ by more than 2 points, whereas in other individuals the three indices tend to be relatively similar (differing only around 1 point). For further information consult Table S14 and S15 in supplementary materials B.

Following the examples of diversity and flexibility, we will examine the results of the generated complexity indices with the same individuals chosen for previous examples.

Ca and Lim, adult females, are the two most aggressive individuals of the group, but Ca is more flexible than Lim overall, as we explained previously. Regarding complexity, Ca is less complex than Lim ( $CI = 3.779$  and  $CI = 4.194$  points respectively). Moreover, Ca is the most predictable individual of the group (predictability index  $PI = 5.000$  points) while Lim is an individual within an intermediate range of predictability ( $PI = 4.125$  points) relative to the other members of the group. The results imply that Ca tends to be a very reliable member of the group -- she is the most predictable member of the group regarding non-social behaviors ( $PI_{ns} = 5.000$  points). Ca behaves very reliably in response to a sequence started by another member of the group ( $PI_{sr} = 4.714$  points), and the group tends to react in consistent ways to her behavior ( $PI_{si} = 4.484$  points). Lim is less predictable, being less reliable towards others and facing a less predictable environment ( $PI_{ns} = 3.151$ ;  $PI_{si} = 4.052$ ; and  $PI_{sr} = 4.511$  points).

In situations when individuals' personalities appear to resemble one another, EthoSeq provides a more in-depth detailed picture (for more details on behavioral trees from EthoSeq output, consult supplementary data from SE16 to SE27). For example, when Ca is aggressive, she receives an effective submission as a response in 75% of instances. In the remaining instances, either she receives a variety of alternative responses from others (none of which occur more than 25% of the time), or she follows her direct aggression with a variety of other behaviors (again none of which occurring more than 25% of the time). When she performs ritualized agonism, she receives affiliation from others in 33.33% of instances (all the other alternative behaviors, either received or initiated by her, occurred in less than 25% of instances). When Lim is aggressive, similarly to Ca, she receives an effective submission as a response in 71.43% of instances. However, when Lim performs ritualized agonism, she receives an effective submission from others in 60% of instances. When Ca receives an aggressive behavior, she always reacts by scratching (100% of the times); when she receives a ritual agonism behavior, this behavior is always (100%) followed by receiving affiliation. These patterns are completely different from Lim. When Lim receives aggression, she reacts by initiating behaviors of effective submission in 87.71% of instances; when she receives a ritual agonism behavior, she always (100%) reacts by initiating effective submission behaviors. We can see by this example how EthoSeq can reveal extremely different patterns about aggressive and agonistic behaviors, in two very similarly aggressive individuals.

The patterns found for these two individuals also differ greatly regarding other behaviors. For Ca, all behaviors following initiating affiliation occur in less than 25% of instances. On the other hand, she initiates affiliation in 44% of instances after receiving affiliation herself. Conversely, when Lim initiates affiliation, she receives affiliation back in 30.77% of instances; when the pattern starts by her receiving affiliation, she initiates effective submissive behaviors in 28.57% of instances. Another example of the great differences in behavioral patterns is seen regarding play behaviors. When Ca starts playing with another individual, she always (100%) receives affiliation in response. Lim on the other hand never receives affiliation in response to initiating play. Instead, Lim starts scratching in half of instances, she receives back play behaviors in 25% of instances, and in the other 25% of instances, she initiates submissive behaviors after initiating play. These individuals differ regarding other behaviors as well, but it becomes clear by the previous few examples, that those differences are exposed by the EthoSeq analysis but not by statistical analysis.

Regarding the Unusual Transition Indices, Ca had higher scores than Lim ( $UTI = 4.928$ ,  $UTIns = 3.773$ ,  $UTIsi = 3.234$ ,  $UTIsr = 4.878$ , and  $UTI = 4.167$ ,  $UTIns = 3.427$ ,  $UTIsi = 2.697$ ,  $UTIsr = 4.009$  respectively).

Taking together all the elements of diversity, flexibility, and complexity, we can make a rich interpretation of these Ca and Lim's personalities and adaptation. Ca is very predictable individual although highly unusual in her behavior. Although Ca is tolerated by other or even closer to others, she shows aggressive, abnormal and anxious behaviors (scratching). Lim is a less predictable individual, but more complex than Ca; her behavioral transitions were more typical when compared with those of the group. Lim's aggressive and submissive reactions appear to be responses to aggression and fear related reactions from others, possibly as an attempt by Lim to be accepted by the other members of the group. Lim is a less tolerated individual compared with Ca, but Lim also appears to be less anxious than Ca and does not present abnormal behaviors.

Ku is the dominant and most aggressive male. As expected, when he initiates aggressive behaviors he receives submissive behaviors in most instances (effective submission in 50% instances and ritual submission in 33.33% of instances), and in the remaining instances he self-grooms after initiating aggression (16.67%).

Map is the least aggressive adult male and, after initiating aggressive behaviors, he receives submissive behaviors in 50% of instances, or he either self-grooms (25% of instances) or scratches (25% of instances). Mar is a more aggressive and less dominant male than Map. When Mar initiates aggression, he receives submissive behaviors in only 33.33% of instances, he receives back aggression in 33.33% of instances, and receives hierarchic mounting in 16.67% of instances. Lw is a sub-adult male and presents the least aggression initiation rates. Notably, after initiating aggression he receives submissive behaviors in 66.67% of instances or he initiates play behavior (33.33%), which represents high tolerance from the group.

Ku is the least complex of the adult males (CI = 4.585 points). He also is the least predictable in his non-social behavior (PIns = 2.615), but has the highest PIsi (5.000 points) of the entire group, meaning that the members of the group tend to behave in a very consistent way towards him. Map is the individual with the highest PIsr (5.000 points), which means that when he receives a given behavior, the subsequent response to that behavior is highly predictable.

There is a large amount of data obtained beyond what we describe above, but analyzing all the data falls beyond the scope of this article. Supporting information (Supplementary Material B, Figure 1 and SE16-27), including the schematic view sequences of the behavioral transitions for each individual, are available online.

In the dispersion graphics of the behavioral data obtained in the diversity section, combined with the data obtained with CI, we verified that no individual presented both high scores in CI and 1) high scores in initiating aggressive behaviors, 2) high scores in arms reach, and 3) high scores in initiating playing behavior. In the dispersion graphics obtained with the behavioral data obtained in the diversity section, combined with the data obtain with PI, we verified: 1) only one individual, Lo (a sub-adult female), presented high scores in self-groom and high scores in PI, and 2) only one individual, Lis (a sub-adult female), presented high scores in scratching and low scores in PI. In the dispersion graphics obtained with the behavioral data of diversity section, combined with the data obtain with UTI, we verified that only one individual, Lis once more, presented high scores in arms reach and high scores in UTI. We present these exceptional cases, because due to their age (sub-adult individuals), it is not certain that

their behavior will not change due to development, and we stress that these exceptions should be pinpointed and monitored in future studies.

The last important information is derived from the dispersion graphics obtained with MFS information combined with CI. We verified that no individual presented high scores in MFS and CI, and no individual presented high scores in MFS and UTI. When we look at the dispersion graphics of UTI and Predictability, we see that all possible combinations between the two indices are observed (supplementary material B). For more details about these analyses see supplementary materials B, Figures S46-S56.

## **Discussion**

Until now, personality in mandrills was extrapolated from studies in baboons. However, these extrapolations from studies on baboons can be somewhat inappropriate because *Mandrillus sphinx* shows extraordinary developmental plasticity regarding somatic and behavioral aspects. Considering this exceptional plasticity, it was expected that personalities, considered to be animal-specific patterns of behavior, would tend to show high variability in mandrills. As predicted, we observed unique combinations of behaviors, with each animal demonstrating distinctive preferred reactions to similar situations. Our results suggest the existence of great diversity, varying flexibility among individuals and high complexity of behavioral patterns in mandrills.

### Diversity

Our results demonstrate a high diversity in this mandrill group. Specifically, we found that 24 behavioral categories varied significantly due to personality-related differences between the individuals. Those categories included non-social behaviors (self-grooming and scratching) and social behaviors (affiliation, playing, aggression, ritualized and effective submission, parental, and fear behaviors), with differences in both the initiation and the receiving of those behaviors from others. Additionally, significant individual differences could be found regarding the number of conspecifics usually found in the proximity of the focal individual. Clear differences in preferences were



detected, with some individuals preferring to be near to one conspecific, whereas others had a preference for being near two other conspecifics. In the dispersion graphics regarding aggression and arms reach as a measure of sociality, we can identify three groups of females: 1) the most isolated females, Mi and Lo, who exhibit low levels of aggression (it is notable that although Lo, a sub-adult, initiates affiliation extremely often, receives very low levels of affiliation from others), 2) the females that are typically close to others and exhibit low levels of aggression, Ne and Ta, and 3) the females that can have varying ranges of proximity with the others but are often aggressive, Ca, Lim and Lis. These three groups appear to have similar features with the groups found by Seyfarth and colleagues (2012, 2014) in female baboons: 1) the “Loners” baboons resemble our first group, 2) the “Nice” baboons resemble our second group, and 3) the “Aloof” baboons resemble our third group.

All males of our group had relatively low levels of aggressive behaviors, all showed low levels of sociality (measured by arms reach), and all except Ku (the dominant male) showed high levels of submissive behaviors. However, it is important to remember that all the animals had hormonal control. In the group of females, we did not see the same pattern of sociality. They were distributed in different ranges of aggression and submission as well as different ranges of affiliation and submission (also spread in different combinations). These results do not support the pattern of the individuals scoring high in submission also scoring high in sociality and in affectionate behavior observed in baboons by Buirski and colleagues in 1973. Nevertheless, the pattern of more aggressive animals being less social, mentioned in Buirski’s work, generally fits with the results of the present study, since there was no individual in this study with the combination of high scores in aggressive behavior and high scores in social behavior (measured by arms reach) or high scores in events of affiliation. Also, all of the most aggressive individuals in our study had medium scores of submission received, while the highest scores in submission received did not correspond to the most aggressive individuals. Nevertheless, we did not observe any clear pattern between initiating aggression and initiating affiliation (as a state).

We found that less sociable individuals (measured by arms reach) could have high and low scores in self-groom and scratching behaviors. The same pattern was found for individuals with low levels of affiliation. Also, more sociable individuals (measured by

arms reach) did not have high scores in self-groom and scratching behaviors. The same pattern was found for individuals with high levels of affiliation. The only exception to this pattern was Lis, a sub-adult female, with high scores in scratching and sociability. However, we have to consider that by being in a transitional phase in her development, this behavioral pattern may represent her unstable hierarchical position in the group or even her changing internal condition. Also, more playful individuals did not have high scores in self-groom or scratching behaviors. The interpretation of our results relating play behavior with medium or low scores of self-groom and scratch seems to agree with studies suggesting that play behavior may be a buffer for stress (i.e., Palagi, Antonacci, & Cordoni, 2007).

Previous research suggested that social stress increases self-directed behaviors as displacement activities (Maestriperi et al., 1992), and physiologically increases glucocorticoids levels in baboons (Bergman et al., 2005; but see Cavigelli & Caruso, 2015 for a review). However, our results do not exhibit this pattern, as the group was quite stable during the studied period. In this group of mandrills, high sociality relates to low self-directed behaviors, but the reverse is not necessarily true. Neither high scores in self-grooming or scratching appear related to fear or stress behaviors. And only one individual, Ku, the dominant male (the only male without hormonal control), had high scores in self-grooming and scratching. His behavior may be due to the lack of natural stress in captivity (i.e., void of competition, predation, etc.), which led Ku to increase his performance of self-directed behaviors to cope with the apathy characteristic of captive settings (Costa et al., 2018). Our results suggest that low levels of self-groom and scratching behaviors may indicate well-being since it was quite a stable group during the studied period.

The results we obtained with mandrills tend to cluster the individuals in three groups for many combinations of the behavioral categories (for more details see supplementary materials FS1). However, the three groups show great variability among the included individuals. These findings support a clear diversity of personalities, with idiosyncratic combinations of behaviors.

The large personality diversity found in mandrills could be related to the extreme group sizes in which this species lives in the natural environment. The number of mandrills that can be found grouped in a horde can be upwards of 800 individuals (Abernethy et

al., 2002). These large groups fission into subunits, but how this organization occurs remains unclear (Astaras et al., 2008). In general, highly social species exhibit a larger diversity of personalities (Von Merten et al., 2017). Hence, the complex social organization presented in mandrills could be responsible for the diversity of personality suggested by this study.

## Flexibility

Flexible individuals adapt their behavior to external conditions, while other individuals do not show such adaptating and are classified as rigid. A given animal does not necessarily show flexibility in every behavior from its repertoire. Therefore, flexibility can be observed for some behaviors and not for others. Likewise, there are behaviors that might not exhibit any individual variation across the members of the observed group. Consequently, all members of a given group might be rigid when considering such behaviors. In this mandrill group, 13 behavioral categories show flexibility in at least one of its members. Some individuals from this group are very flexible in several behavioral categories, like Ta, while others show to be quite rigid in most of the categories and do not show a substantial variance in behavior, like Mar.

In the dispersion graphics of the results regarding flexibility, combined with the ones regarding diversity (see supplementary material for more details, FS2), we find that three groups tend to be formed: 1) the most extreme in flexibility, 2) the most extreme in rigidity, and 3) the one with intermediate degrees. The most flexible individuals, Ta (sub-adult), Ne (adult female) and Lw (sub-adult male), tend to be less aggressive, exhibit less self-grooming, scratching and fear-related behaviors, initiate less ritualized submissive behaviors, and receive more ritualized agonistic behaviors. The most rigid individuals, Mar (adult male) and Lim (adult female), tend to be less social (measured by arms reach) and less playful, receiving little affiliation and little effective submissive behaviors from others. It is known that the existence of socially flexible animals in a group ends up favoring the less flexible individuals, by former social adaptation (Dingemanse and Wolf, 2013). This phenomenon could be underlying this group's behavior variability. Indeed, studying the same group of mandrills on two separate occasions, Pereira and colleagues (2019) found differences in the females' levels of

centrality comparing both observation periods. In combination with Pereira et al.'s claim of the species' variable social network, our present results regarding individual behavioral flexibility demonstrate how in mandrills, flexibility is related to phenotypic plasticity when a diversity of responses is possible. The existence of phenotypic plasticity might enable some individuals of the group to quickly adapt to a novel social environment, thereby diminishing the negative impact of rapid changes (Pfennig et al., 2010; Moczek et al., 2011); Wolf and Weissing, 2012). Differences in personality can be essential to ecological adaptation and an important evolutionary intra-specific variation (Wolf and Weissing, 2012). In the case of mandrills, their developmental plasticity can evolutionarily create phenotypic novelty, which might be a potential engine of diversification and speciation (Singleton, 2012). If some of this behavioral plasticity can be seen as a function of past experience, in a gene-environment correlation, genetic constraints in adaptation might be lessened (Dingemanse and Wolf, 2013). Given the close phylogenetic relationship, non-human primate research efforts are important to human research itself (Itoh, 2002). Such developmental plasticity observed in mandrills may present important clues for human evolution study, since early hominini evolution may also be partly explained by phenotypic plasticity.

## Complexity

Behavioral complexity can be defined as the unique combination or sequence of behavioral responses, characteristic to an individual (i.e., more complex individuals present several equally consistent combinations of sequences of behavioral responses, whereas less complex individuals present fewer combinations). In other words, in this paper we considered the possibility that each animal has its distinct style of transitioning from one behavior to another, displaying its behavioral sequence.

We observed that all the individuals have high or very high degrees of complexity, i.e., they present similarly consistent combinations of behavioral response sequences. Moreover, all the individuals present a medium to a high degree of predictability in their behavior, especially related to sequences initiated by social behaviors. It is important to note that the degree of predictability for sequences initiated by non-social behaviors is much lower. The individuals observed also presented high degrees of unusual

behavioral sequences, i.e., sequences comprised of rarely occurring behaviors as subsequent behaviors to the first behavior. In general, we suggest that each individual has a unique repertoire of behavioral combinations. Some individuals are more unique in their non-social behavior, while others are more unique in their social interactions.

The information about complexity enriches the understanding of the individuals' personalities and the group's distinct reaction towards each individual. In our work with this species, we can notice how this aspect plays a crucial role in understanding the individual in his/her context.

High complexity does not appear associated with high sociality (measured by arms reach), high levels of aggression, or play. In the dispersion graphics about flexibility and complexity, we can see that the individuals in both the extremes of flexibility (the most and the least flexible) are not the most complex. Moreover, the most flexible individuals tend to have the most common behavioral transitions. Flexibility did not show any correlation with predictability, meaning we have predictable and unpredictable individuals both with high and low flexibilities.

Here again, mandrills' capacities for developing this behavioral complexity possibly relates to their need to adapt to larger groups, with posterior fission to smaller subunits. Perhaps individuals are subjected to high pressure, with influence coming from inside and outside of their units. This social pressure might push individuals to differentiate one conspecific from another and learn specific responses for each of the individuals to avoid conflict. We know that mandrills are capable of emotional bookkeeping over long time frames (Schino and Pellegrini, 2009), so the explanatory hypothesis above is a strong possibility. We also know that social information obtained through experience is used to decrease environmental uncertainty (Mathot et al., 2012). Moreover, the environmental uncertainty contributes to generating consistent individual differences in behavior, i.e., in personality (McElreath & Strimling, 2006; Chapman, Morrell, & Krause, 2010; Mathot et al., 2012). Consequently, the more extreme personality differences observed in this mandrill group could have its origin in the previously described mechanisms.

## Limitations

The major limitation of our research was having studied only a single captive group of mandrills. We are not aware of the extent to which our findings are generalizable to other mandrill groups, especially in the wild. Nevertheless, we observed the species-specific behaviors of organizing in subunits, with individuals not being in close contact with more than two other conspecifics. But we cannot be certain that our group's subunits function in a similar way to the subunits within hordes in their natural environment.

However, our aim is not to generalize our findings to mandrills as a species. Our main goal is to demonstrate that we can describe in detail three aspects of personality - diversity, flexibility, and complexity - and how these aspects contribute to rich descriptions of personality that can be used for understanding this species' characteristics. The results of the current study might have implications in our understanding of evolution and the speciation process. We highly recommend efforts to replicate this study with mandrills under different conditions and environments.

An additional remark is that we did not take into consideration the past life history of the individuals in the group studied. Some of the animals came from other zoos and might have suffered traumatic experiences. We could not control early experiences that might have triggered some differences in personality. Although prior experiences influence all individuals in general, and given that this is a factor not usually considered in most studies in this area, we strongly suggest that this information be taken into account in future research. Changes during maturation as well as hierarchical transitions might lead to personality changes (de Waal, 2002; McGuire et al., 1994). Consequently, some of our results might be subject to variations in a couple of years. Given the particularly high developmental plasticity of this species, it would be of particular interest to replicate the current research and compare ontogenetic changes in the individuals observed.

Mandrills' diverse personality patterns, flexibility, and social complexity are evidenced in this paper. Our methodology allows: 1) understanding of individual personality in a detailed manner; 2) statistical and non-statistical analysis for comparison of personality amongst individuals; and 3) the assessment of behavioral patterns both for the group

and for each specific individual, uncovering unique characteristics in their behavior.

#### CONFLICT OF INTERESTS

The authors declare no conflict of interests.

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# **Chapter 4 – Exploring the Usefulness of the Methodology for Species Comparison**

**Lemurs' personalities: A comparative analysis between ring-tailed lemurs (*Lemur catta*) and red-ruffed lemurs (*Varecia rubra*).**

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**Abstract**

Personality has been linked to cognitive capacities within different species. Recently, connections between the range of personalities found in a species, and that species' brain neocortex size and associated cognitive capacities, have been suggested. We compared two species of lemurs, *Lemur catta* and *Varecia rubra*. Among lemurs, these two species share characteristics like diurnality and frugivory, which brain evolution research has associated with increased brain capacities compared to nocturnal and folivorous lemurs. The two species which we compared, *L. catta* and *V. rubra*, have been found to differ in overall cognitive capacities, with the former being more cognitively evolved than the latter. We expected that *Lemur catta* would have more differentiated (i.e., more diverse, more flexible, and more complex) personalities, than *Varecia rubra*. Our results confirmed this hypothesis. The phylogenetic implications

regarding the relationship of neocortex size evolution and cognitive capacities, to personality will be discussed.

**Keywords:** personality; strepsirrhines; red-ruffed lemurs; ring-tailed lemurs; diversity; flexibility; complexity; behavioral transitions; species diversity index; species flexibility index; species complexity index.

## **Introduction**

Comparative studies in personality are important for the phylogenetic implications that can be derived from them. Increasingly more research has been linking individual differences in cognition with personality in different species (Carere & Locurto, 2011; Giudice & Giudice, 2017; Sih & Del Giudice, 2012). Recently, it has been proposed that a relationship exists between, a) brain evolution and cognitive capacities, and b) changes in personality diversity, flexibility and complexity (Brandão, Basseches, and Vicente, in prep). Toscano, Gownaris, & Heerhartz (2016) have also proposed that a relationship exists between personality and specialization, thereby linking ecological and evolutionary consequences of personality to the individual fitness.

For a phylogenetic perspective on personality and brain evolution, the studies with strepsirrhines are essential. Nevertheless, the knowledge about strepsirrhines is scarce, especially related to brain evolution, cognitive abilities and personality. Several of the theories related to brain evolution in haplorhines primates do not seem to apply to strepsirrhines. One of the theories is Dunbar's (Dunbar, 2009) social brain hypothesis which relates group size and brain size as a proxy for social complexity in haplorhine primates (Dunbar & Shultz, 2007b, 2007a). Most of the lemur species do not have the same social complexity (Jolly, 1966) nor socio-cognitive abilities as haplorhines (Genty & Roeder, 2006), and lemurs have smaller social groups with more incidents of pairbonding (Jolly, 1998). Nonetheless, in some non-primate species, pairbonding social organization explains the patterns of encephalization, with species that pairbond having relatively bigger brains than species that do not (Dunbar & Shultz, 2007a). In lemurs, a

relationship between pairbonding and brain size was not found (MacLean, Barrickman, Johnson, & Wall, 2009).

Recent research has supported the ecological, and evolutionary-developmental hypotheses, which claim that increase of brain size is predicted mainly by diet, especially a change from folivory to frugivory (e.g. DeCasien, Williams, & Higham, 2017). MacLean, Barrickman, Johnson, & Wall (2009) found significant differences among lemurs: frugivorous species have larger brains than folivorous species. Moreover, cathemeral lemur species (the species with more flexible activity patterns) have larger brains than diurnal species (MacLean et al., 2009), and diurnal species have larger neocortices when compared to nocturnal strepsirrhines (MacLean et al., 2009; Striedter, 2005).

In the present study, we take two model lemur species, red-ruffed lemurs (*Varecia rubra*) and ring-tailed lemurs (*Lemur catta*), to study intra- and inter- species differences in personality. Both species are diurnal and frugivorous (MacLean et al., 2009), so the two major factors that have been related to relative brain size are present in both species. However, ring-tailed lemurs feed on more than fruit in their terrestrial habitats, which provide a wide array of leaves, fruits or flowers of heliophile terrestrial vines, of ornamental plants, or of herbaceous species (Simmen, Hladik, & Ramasiarisoa, 2003). On the contrary, red-ruffed lemurs have a homogeneous diet of fruit because they spend most of their time in tree-crowns (Vasey, 2002). Group size and social organization differ in some ways between these two species. Ring-tailed lemurs are predominantly matrilineal with multi-male/multi-female groups, no pairbonding, and female philopatry (Hood & Jolly, 1995; Sussman, 1991). Ring-tailed lemurs' groups range from 3-27 individuals (mean group size varies between 11.5 and 16), they have an interbirth interval (IBI) of 15 months, litter size is one baby, and they exhibit allomaternal care with babies carried on their mother's fur (MacLean et al., 2009 Tecot et al. 2013). Red-ruffed lemurs tend to be organized in multi-male/multi-female communities, in which females tend to be dominant, with a fission-fusion type of social organization in which smaller subgroups emerge in communal areas during mating and gestation periods (Morland, 1993; M. E. Pereira, Seeligson, & Macedonia, 1988; Michael E. Pereira, Kaufman, Kappeler, & Overdorff, 1990). Red-ruffed lemurs' groups can be small (ranging from 2-6 individuals) or large (ranging from 18-31 individuals);

they have an IBI of 12 months and an average litter size of 2.1; and they exhibit allomaternal care with babies carried orally, then parked in nests and other locations (Vasey, 2002; Tecot et al. 2013).

Red-ruffed lemurs are the largest members of lemuridae family in terms of body size. Their overall brain volume is larger compared to that of other lemurs (e.g., sportive lemur, mouse lemur) and even to that of some new world primates (e.g., common marmoset, squirrel monkey) (Striedter, 2005). Nevertheless, if we focus on the relative brain-to-body size ratio, ring-tailed lemurs have a higher relative brain size (ratio value is 0.011) than red-ruffed lemurs (0.009) (MacLean et al., 2009). Also a recent study about the evolution of neocortical folding through primate phylogeny shows a non-linear relationship between wavelength and fold depth (Heuer et al., 2019). Namely, with an increasing number of sulci, the wavelength tends to decrease in number and later stabilize. It was found that black-and-white ruffed lemurs (*Varecia variegata*) had a higher fold wavelength and a lower fold depth than those of ring-tailed lemurs. These differences are expected to have some implications related to cognitive abilities.

Rosati, Rodriguez, & Hare (2014) compared spatial memory between several lemurs, including the red-ruffed lemurs and ring-tailed lemurs. In this study, the authors found support for the ecological hypothesis: the most frugivorous species (ruffed lemurs) have the most accurate spatial memory. Red-ruffed lemurs used a *spatial strategy* to encode food location; this strategy is a hippocampal-based strategy, which is most typical for heterogeneous environments (Rosati, Rodriguez, & Hare, 2014). The olfactory and hippocampal cortices are especially important in processing social and ecological information (Stephan & Andy, 1970). In contrast, ring-tailed lemurs used a mixed strategy including *habitat-based strategies*; these strategies are basal-ganglia-based strategies, which are more common in homogeneous environments (Rosati et al., 2014). Spatial and habitat-based strategies are used in parallel by rodents and humans, and the importance of each strategy depends on the context (Burgess, 2008; Packard & Goodman, 2013). Red-ruffed lemurs use spatial memory for which they have greater capacity, while ring-tailed lemurs use strategies similar to those used by rodents, humans and the other lemurs studied (Rosatti et al., 2014). Also, in the same study, ring-tailed lemurs performed better than red-ruffed lemurs in trial-by-trial learning.



It is important for social animals to learn information about intra-group relationships and dominance hierarchy. Transitive inference is a form of deductive reasoning that has been suggested as one cognitive mechanism by which animals could learn this type of social information (MacLean, Merritt, & Brannon, 2008). MacLean's et al. (2008) research revealed that ring-tailed lemurs have a predisposition to organize information along a common underlying dimension (i.e. symbolic distance between the stimuli in a pair). This result supports the hypothesis that social complexity acts as a selective pressure driving the evolution of capacities for transitive inferences. Individuals living in large social groups with linear dominance hierarchies have a survival advantage if they are capable of inferring the rank order of their conspecifics (MacLean et al., 2008). There is evidence of ring-tailed lemurs' social learning capacities (Kendal et al., 2010), whereas for red-ruffed lemurs, more data is needed to discard alternative explanations such as intuitive resolution of problems instead of social learning (Dean, Hoppitt, Laland, & Kendal, 2011; Stoinski, Drayton, & Price, 2011).

Laterality is another area of interest in brain and behavioral evolution of primates. Ring-tailed lemurs seem to differ from red-ruffed lemurs in laterality and hand preference. Most of the research with lemurs has studied spontaneous behavior performed in a natural context. In such studies, there is no clear pattern of lateralization at group level, but there is some bias to the left preference at the individual level (Regaiolli, Spiezio, & Hopkins, 2016). For example, studies in red-ruffed lemurs point towards left preference (Forsythe, Milliken, Stafford, & Ward, 1988; Nelson, O'Karma, Ruperti, & Novak, 2009). In contrast, a recent study with ring-tailed lemurs performing unimanual and bimanual experimental tasks showed that these lemurs demonstrate a right hand preference (Regaiolli et al., 2016). The authors note that this preference is similar to other terrestrial primates, and that ring-tailed lemurs can be considered the most terrestrial lemurs.

A few studies exist that show ring-tailed lemurs being more similar than other lemurs to terrestrial haplorhine primates -- with higher cognitive abilities. Nevertheless, we found no comparison studies between ring-tailed lemurs and red-ruffed lemurs regarding personality. In our current work, we studied three variables related to personality: 1) diversity; 2) flexibility, and 3) complexity. The study of these aspects follows the model from Brandão's et al. (2019) work with capuchin monkeys. *Diversity* refers to the

number of behaviors that can be seen as being different among individuals within their group. *Flexibility* refers to the variability that can be found in a given behavior when performed by each individual over time. *Complexity* refers to the specific way in which any given individual sequences its behavior, especially in the case of forming regular behavioral patterns. Our hypothesis is that ring-tailed lemurs will demonstrate higher levels of diversity, flexibility and complexity (as defined in our study) compared to red-ruffed lemurs, due to ring-tailed lemurs' higher cognitive capacities and the larger relative brain size. In ring-tailed lemurs, we expected to find: 1) more differences between individuals that reflect different roles in the complex social environment (measured by a "diversity index"); 2) a higher capacity for adaptation to different social and non-social environments (measured by a "flexibility index"); and, 3) a richer repertoire of specific behavior patterns for each individual (measured by a "complexity index").

## **Material and Methods**

We observed a group of 10 ring-tailed lemurs composed of 3 females and 7 males from Badoca Park in Alentejo, and a group of 8 red-ruffed lemurs composed of 3 females and 5 males from the Lagos' Zoo in Algarve, both in Portugal.

The ring-tailed lemurs lived in a mixed-species outdoor enclosure, with trees surrounded by water, but with frequent human disturbance (people could enter the enclosure by paying an extra fee to be in closer contact with the lemurs, which could happen twice a day on weekends). Their enclosure was shared with 3 members of another lemur species, red-bellied lemurs (*Eulemur rubriventer*). The ring-tailed lemurs usually spent most of their time on the ground or in the lower levels of trees, whereas the red-bellied lemurs preferred the canopies. The lemurs were fed twice a day (morning and afternoon); the keepers delivered the food near the walls of the cement enclosure. At night, the lemurs were locked in a cement house-like structure and released the next day.

The red-ruffed lemurs group lived as a single species on two artificial islands connected by a bridge and a rope, with artificial structures (such as stairs, swings and little houses) and some arboreal vegetation. Other species lived on isolated neighboring islands in the

same lake. The small houses could be used by the red-ruffed lemurs as night shelters since they did not sleep in an indoor facility. The animals can have direct views of visitors who could stand at a minimum of 3 meters from the islands' shores. The lemurs were fed twice a day (morning and afternoon); the keepers delivered the food to the island shores by wading across the moat.

The both lemur species were observed in sessions of 10 minutes each. Observations of red-ruffed lemurs occurred between December 2014 and February 2015. Observations of ring-tailed lemurs occurred between March and April 2016. The number of sessions per individual ranged from 17 to 35 for ring-tailed lemurs, and 16 to 51 for red-ruffed lemurs, with the exception of an individual named Ma that only had 12 sessions because he was removed from the group in the middle of the observation period. The differences in number of observation sessions across individuals were due to factors external to the study design (e.g., zoo management procedures not initially predicted). This study was designed to compare personalities during a relatively stable ontogenetic period. Therefore, for ring-tailed lemurs, we observed subadults (2 years old), young adults (3-4 years old) and adults (4 years old or older) (age classifications from Gould, Sussman & Sauther 2003); because red-ruffed lemurs mature earlier a (female adult maturity between 18-20 months – Foerg, 1982; and male adult maturity at 36-48 month – Vasey, 2007) we only observed adults. We built an identification sheet with characteristics of each individual. Prior to the observations, we constructed a complete ethogram for the species (based on literature review e.g.: Vick & Conley, 1976; Pereira, Seeligson, & Macedonia, 1988; Morland, 1990; Britt, 2000; Gould, Sussman, & Sauther, 2003; Pomerantz, Meiri, & Terkel, 2013; Farmer-Dougan, 2014).

We excluded from the complete ethogram certain behaviors that our literature review suggested were more a function of variables other than personality differences (e.g., eating behavior was excluded because access to food is closely related to hierarchical position). Then, the remaining behaviors were organized into categories (Supplementary materials, Tables S1 and S2). We categorized the selected behaviors as either events or states, and as either non-social or social behaviors. Within the agonistic social behaviors, we distinguished two subcategories: ritualized non-physically aggressive behaviors (e.g., showing teeth) and effective physically aggressive behaviors (e.g., biting). Similarly, we distinguished submission behaviors into either ritualized or

effective types. We coded the proximity of conspecifics as Arms Reach (proximity was defined as a distance closer than the measure of a fully stretched arm). For analytic purpose, we divided these observations into 5 extra variables ranging from arms reach 1 -- being within arm reach of one conspecific, to arms reach 5 -- being within arm reach of five or more conspecifics). For more details about the categories we used, see Tables 4.1 and 4.2.

Table 4.1 Table depicting our organization of the 14 behavioral categories derived from the ethogram for ring-tailed lemurs (*Lemur catta*), plus abnormal behavior and arm reach. Each row of the table corresponds to one of the behavioral categories derived from the ethogram.

<b>Behavioral categories</b>	<b>State initiated by the focal individual</b>	<b>Event initiated by the focal individual</b>	<b>State received by the focal individual</b>	<b>Event received by the focal individual</b>	
<b>Non-social behaviors</b>	Huddling				
	Vocalizations	Vocalizations Event			
	Selfgrooming				
	Scratching				
	Sent Marking				
	Solitary Play	Solitary event      Play			
<b>Social behaviors</b>	Affiliation Initiator	Affiliation Initiator Event	Affiliation Receiver	Affiliation Receiver Event	
	Sex Initiator		Sex Receiver		
	Play Initiator	Play Initiator Event	Play Receiver	Play Receiver Event	
	Ritual Agonism Initiator	Ritual Agonism Initiator Event	Ritual Agonism Receiver	Ritual Agonism Receiver Event	
	Aggression Initiator	Aggression Initiator Event	Aggression Receiver	Aggression Receiver Event	
	Ritual Submission Initiator	Ritual Submission Initiator Event	Ritual Submission Received	Ritual Submission Received Event	
	Effective Submission Initiator	Effective Submission Initiator Event	Effective Submission Receiver	Effective Submission Receiver Event	
	Parental Behavior				
	<b>Abnormal Behaviors</b>	Abnormal Behavior	Abnormal Behavior Event		
	<b>Arms Reach</b>	Arms Reach			

Table 4.2 Table depicting our organization of the 12 behavioral categories derived from the ethogram for red-ruffed lemurs (*Varecia rubra*), plus abnormal behavior and arm reach. Each row of the table corresponds to one of the behavioral categories derived from the ethogram.

<b>Behavioral categories</b>	<b>State initiated by the focal individual</b>	<b>Event initiated by the focal individual</b>	<b>State received by the focal individual</b>	<b>Event received by the focal individual</b>	
<b>Non-social behaviors</b>	Vocalizations	Vocalizations Event			
	Selfgrooming				
	Sent Marking				
	Solitary Play	Solitary Play event			
<b>Social behaviors</b>	Affiliation Initiator	Affiliation Initiator Event	Affiliation Receiver	Affiliation Receiver Event	
	Sex Initiator		Sex Receiver		
	Play Initiator	Play Initiator Event	Play Receiver	Play Receiver Event	
	Ritual Agonism Initiator	Ritual Agonism Initiator Event	Ritual Agonism Receiver	Ritual Agonism Receiver Event	
	Aggression Initiator	Aggression Initiator Event	Aggression Receiver	Aggression Receiver Event	
	Ritual	Ritual	Ritual	Ritual	
	Submission Initiator	Submission Initiator Event	Submission Received	Submission Received Event	
	Effective	Effective	Effective	Effective	
	Submission Initiator	Submission Initiator Event	Submission Receiver	Submission Receiver Event	
	Parental Behavior				
	<b>Abnormal Behaviors</b>	Abnormal Behavior	Abnormal Behavior Event		
		Arms Reach			

All observations were video-taped, and recorded in the observation sheet. Two observers participated in data collection. A prior test of the Inter-observer reliability of these two observers resulted in a correlation above 90%. Data obtained was analyzed using IBM computer program SPSS, Version 24 (2016) and the EthoSeq program (Japyassú, Alberts, Izar, & Sato, 2006). In accord with their species' ethogram, 43 variables were analyzed for ring-tailed lemurs and 41 variables were analyzed for red-ruffed lemurs (see supplementary materials S21 and S22 for descriptive statistics). For more methodological details, please consult Brandão's et al. (2019) paper. We explored three dimensions of personality: diversity, flexibility and complexity.

## *Diversity*

"Diversity" refers to differences among all individuals' average behavioral display (i.e., different individuals presented distinct repertoires of behavior) (Brandão et al., 2019). The Random Effect Model (REM) was applied to each behavioral category, following the methodology presented in previous papers (Brandão et al., 2019; Brandão et al. in prep.).

### 1.1 *Species Diversity Index (SDI)*.

To compare results between both lemur species, we created a *Species Diversity Index (SDI)*. The formula for calculating each group's SDIsp is:

$$\mathbf{SDI} = \mathbf{Cat.} / \mathbf{Cat.}_{\mathbf{REM}}$$

where **Cat.**, the value of which differs from one group to another, is the total number of categories considered for REM analysis, and **Cat.<sub>REM</sub>** is the total number of categories for which the REM analysis found significant individual differences.

### 1.2 *The Species Diversity Indices derived from SDI*

Using the same formula, we also created four other indices: 1) a *Species Diversity Index for Non-social behaviors (SDIns)* using the mean variance of only individual non-social behavioral categories; 2) *Species Diversity Index for Social Initiated Behaviors (SDIsi)*, using the mean variance of only social initiating behavioral categories; 3) *Species Diversity Index for Social Received Behaviors (SFIsr)* using the mean variance of only social receiving behavioral categories; and 4) *Species Diversity Index for Social Proximity (SFIsp)* using the mean variance of social proximity measured by arm reach.

## *Flexibility*

As described in Brandão et al., (2019) “*Flexibility*” refers to variability across observations of individuals’ behavioral responses (i.e., different individuals presented different capacities for behavioral variation over time in response to one or more particular behaviors). The group variance for each behavioral category represents the variability observed in the group. The individual variance for each behavioral category represents the flexibility each individual has for any behavioral category.

### *2.1 Species Flexibility Index*

We created a *Species Flexibility Index (SFI)* to compare both groups. Formula for calculating each group’s SFI:

$$\text{SFI} = \frac{\sum (\text{MF}_1 * 5) / \text{MF}_h + (\text{MF}_2 * 5) / \text{MF}_h + (\text{MF}_3 * 5) / \text{MF}_h + \dots + (\text{MF}_i * 5) / \text{MF}_h}{n}$$

Where **n**, whose value differs from one group to another, is the total number of individuals in the group (target species); **MF** is the mean variance calculated for each individual of that group; **MF<sub>h</sub>** is the highest value of MF obtained across all individuals of all groups being compared (in this case 2 groups, *Red-ruffed lemurs* and *Ring-tailed lemurs*).

### *2.2 The Species Flexibility Indices derived from SFI*

Using the same formula, we also created three other indices: 1) a *Species Flexibility Index for Non-social behaviors (SFI<sub>ns</sub>)* using the mean variance of only individual non social behavioral categories; 2) *Species Flexibility Index for Social Initiated Behaviors (SFI<sub>si</sub>)*, using the mean variance of only social initiating behavioral categories; and 3) *Species Flexibility Index for Social Received Behaviors (SFI<sub>sr</sub>)* using the mean variance of only social receiving behavioral categories.

## *Complexity*

As described by Brandão et al., (2019), “*Complexity*” refers to variability in the specific sequences of behavior (i.e., more complex individuals present more similarly strong consistent combinations of behavioral response sequences than less complex individuals). Using the EthoSeq program (Japyassú et al., 2006), we analyzed the behavioral patterns that we found for each individual observed, in each lemurs’ group. EthoSeq uses mathematical Graph Theory in its analysis of behavior sequences (it is not an inferential statistical method).<sup>14</sup>

For the purpose of EthoSeq analysis, in the case of ring-tailed lemurs, we considered only 22 distinct behavioral categories -- we did not distinguish the state categories from their identically-named event categories. In the case of red-ruffed lemurs, we considered only 20 distinct behavioral categories -- we did not distinguish the state categories from their identically-named event categories. Following Brandão’s et al. (2019) methodological approach for the analysis of each individual, we considered those sequelae which occur 25% or more of the time. However, when calculating the behavioral transitions for the whole group, we considered all sequelae that occur 15% or more of the time. The detailed analysis of these transitions, given their complexities, is beyond the scope of this paper (for more details *EthoSeq Outputs and Behavioral Sequences* can be consulted in supplementary materials, Tables S8 and 9, and outputs form SE1 to SE20).

### *3.1 The Nine Indices*

We calculated nine indices based on EthoSeq outputs for each of the individuals in the lemur groups, following the method from previous work with capuchin monkeys (Brandão et al., 2019). For computing the nine indices, we worked exclusively with the data corresponding to the first transition of each sequence. We calculated the following indices: *Complexity Index (CI)*, *Predictability Index (PI)*, *Predictability Non-Social Index (PIns)*, *Predictability Social Initiating Index (PISI)*, *Predictability Social Receiving Index (PISR)*, *Unusual Transition Index (UTI)*, *Unusual Non-Social Transition Index (UTIns)*, *Unusual Social Initiating Transition Index (UTIsi)*, and *Unusual Social*

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<sup>14</sup> Please read Brandão et al. (2019) for more details about the methodology used for identify behavioral sequences.



*Receiving Transition Index (UTIsr)*. The *Predictability Index (PI)* was calculated using the probability of the second-most likely behavior of an individual, for the categories with consistent subsequent behaviors. Some behaviors were rare as a subsequent behavior to the first behavior, across the group as a whole. These transitions were considered unusual when the associated probability of occurrence across all observations of the group was less than or equal to 15%. The *Unusual Transition Index (UTI)* measures how often a particular individual transitioned from a first behavior to an unusual second behavior.

### 3.2 *Species Complexity Index*

We created a *Species Complexity Index* to compare both groups. To construct this index, we used the CI values before transforming them into a 0-5 scale for all the individuals of both groups. We then proceeded to transform the results into a 0-5 scale, in which 5 was the highest value obtained by one individual across all groups (in the present research the 2 lemurs' groups). Finally, we used the individual complexity indices to calculate the mean SCI for each species.

Formula for calculating each species' SCI:

$$SCI = \frac{\sum((x_{1CI} * 5) / y_{CI}) + ((x_{2CI} * 5) / y_{CI}) + ((x_{3CI} * 5) / y_{CI}) + \dots + ((x_{nCI} * 5) / y_{CI})}{n}$$

Where **n** is the group's total number of individuals (8 for *V. rubra* and 10 for *L. catta*), **x<sub>CI</sub>** is the CI for each individual, and **y<sub>CI</sub>** is the highest individual CI across both groups.

#### 3.2.1 *The species indices derived from complexity index*

Following the same formula used to calculate the Species Complex Index, we calculated the other 8 indices: *Species Predictability Index (SPI)*, *SPI Non-social (SPI<sub>ns</sub>)*, *SPI*

*Initiating Social behaviors (SPIsi), SPI Receiving Social behaviors (SPIsr), Species Unusual Transition Index (SUTI), SUTI Non-social behaviors (SUTIns), SUTI Initiating Social behaviors (SUTIsi) and SUTI Receiving Social behaviors (SUTIsr).*

## **Results**

We found intra- and inter-group personality differences regarding the diversity, flexibility and complexity of actions. We analyzed the results for each aspect of personality in detail.

### *Diversity*

The REM analysis showed significant individual differences in 18 behavioral categories for ring-tailed lemurs and 20 variables for red-ruffed lemurs. In this REM analysis, we looked for individual differences in a large number of behavioral categories. Given the high number of categories, some significant differences could be expected to occur due to chance (Type I errors). Hence, we performed a Benjamini-Hochberg correction, which reduced the significant individual differences to 15 variables for ring-tailed lemurs and 9 variables for red-ruffed lemurs (see table 4.3).

Table 4.3 The table presents a summary of the results of the Random Effect Model applied for ring-tailed lemur (*Lemur catta*) and red-ruffed lemur (*Varecia rubra*) groups. Columns are hereby presented in the following order: 1) the variables analyzed, 2) the population variance, 3) freedom degrees, 4) the Random Effect Model p-values (Note: p-values less than 0.05 are marked with \* and p-values less than 0.01 are marked with \*\*) and 5) Benjamini-Hochberg correction for the critical p-value for each analysis, marked only for the categories that remain significant (Continued on the next page)

Behavioral Categories	<i>Varecia rubra</i> Random Effect Model				<i>Lemur catta</i> Random Effect Model			
	variance pop.	F	Sig.	REM B-H control	variance pop.	F	Sig.	REM B-H control
Huddling					0.169	118.249	0.000*	0.001*
Vocalizations	0.000	6.992	0.011*	0.003	0.000	0.713	0.406	0.013
Vocalizations Event	0.000	1.453	0.263	0.016	0.000	12.643	0.001*	0.002*
Selfgrooming	0.005	84.801	0.000*	*	0.004	54.833	0.000*	0.001*
Self-grooming Event	0.000	4.532	0.036*	0.007				
Scratching					0.001	16.938	0.000*	0.001*
Sent Marking	0.000	16.238	0.000*	*	0.000	2.057	0.157	0.007
Sent Marking Event	0.000	4.334	0.038*	0.008				
Solitary Play	0.004	4.006	0.049*	0.010				
Solitary Play event	0.000	0.722	0.398	0.017				
Affiliation Initiator	0.008	19.123	0.000*	*	0.013	80.423	0.000*	0.001*
Affiliation Initiator Event	0.000	4.104	0.047*	0.009	0.000			
Sex Initiator	0.000	3.751	0.054	0.011				
Play Initiator	0.001	9.266	0.005*	0.002	0.000	1.706	0.193	0.009
Play Initiator Event	0.000	5.972	0.017*	0.005	0.000	1.000	0.318	0.010
Ritual Agonism Initiator	0.000	6.181	0.014*	0.004	0.000	0.770	0.381	0.012
Ritual Agonism Initiator Event	0.000	3.844	0.053	0.010	0.000	2.131	0.145	0.006
Aggression Initiator								
Aggression Initiator Event	0.000	22.267	0.000*	*	0.000	8.822	0.004*	0.003
Ritual Submission Initiator	0.000	0.631	0.432	0.018				
Ritual Submission Initiator Event	0.000	0.106	0.745	0.019				
Effective Submission Initiator								
Effective Submission Initiator Event	0.000	2.434	0.120	0.013	0.000	14.630	0.000*	0.001*
Parental Behavior					0.127	45.605	0.000*	0.001*
Affiliation Receiver	0.007	13.864	0.000*	*	0.020	15.755	0.000*	0.001*
Affiliation Receiver Event	0.000	8.029	0.005*	0.002	0.000	4.814	0.029*	0.004
Sex Receiver					0.000			
Play Receiver					0.000	1.765	0.185	0.008

Behavioral Categories	<i>Varecia rubra</i>				<i>Lemur catta</i>			
	variance pop.	F	Sig.	REM B-H control	variance pop.	F	Sig.	REM B-H control
Play Receiver Event					0.000	0.974	0.328	0.011
Ritual Agonism Receiver	0.000	1.352	0.246	0.015	0.000	2.700	0.101	0.005
Ritual Agonism Receiver Event	0.000	5.315	0.029*	0.006	0.000	0.069	0.793	0.013
Aggression Receiver								
Aggression Receiver Event*	0.000	19.435	0.000*	0.001*	0.000	16.463	0.000*	0.001*
Ritual Submission Received								
Ritual Submission Received Event								
Effective Submission Receiver								
Effective Submission Receiver Event	0.000	2.372	0.126	0.014	0.000	6.062	0.015*	0.004
Abnormal Behavior								
Abnormal Behavior Event								
Arms Reach*	0.000	71.154	0.000*	0.001*	0.000	163.807	0.000*	0.001*
Arms Reach 1*	0.000	92.892	0.000*	0.001*	0.000	83.019	0.000*	0.001*
Arms Reach 2*	0.000	10.650	0.001*	0.002*	0.000	62.356	0.000*	0.001*
Arms Reach 3*	0.000	6.013	0.020*	0.006	0.000	70.461	0.000*	0.001*
Arms Reach 4*	0.000	2.287	0.132	0.015	0.000	34.596	0.000*	0.001*
Arms Reach 5*	0.000	3.905	0.055	0.012	0.000	113.995	0.000*	0.001*

The behavioral-category results for each individual represent a personality profile. These profiles are represented in Figure 4.1, where each colored line represents one of the individuals of the group. The figure illustrates the diversity of personalities in both groups (for more details on descriptive statistics consult supplementary materials C, Table S20 and S21).

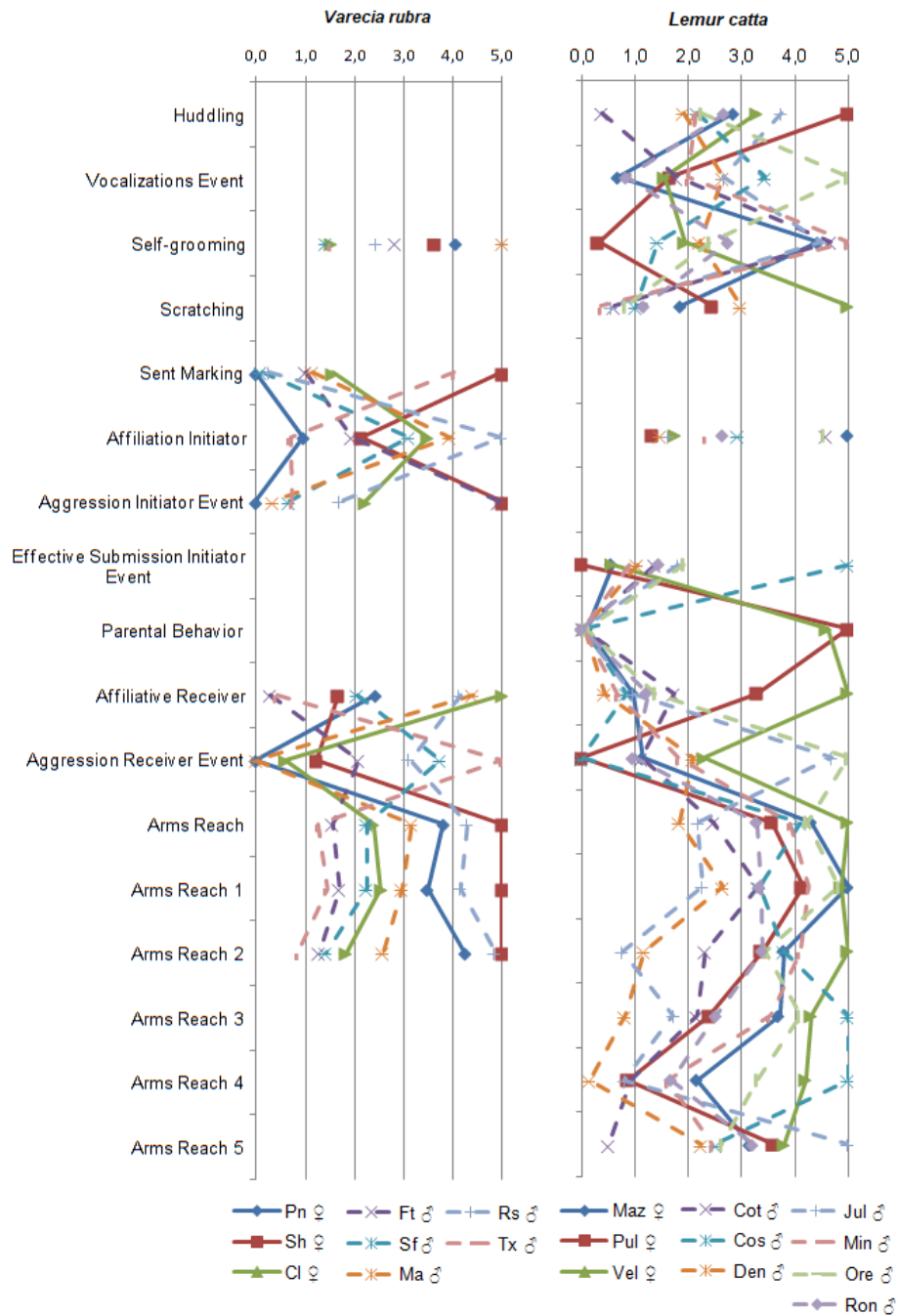


Figure 4.1 The left graphic represents the profiles of the 8 red-ruffed lemurs (*Varecia rubra*). The right graphic represents the profiles of the 10 ring-tailed lemurs (*Lemur catta*). To facilitate comparison, the results for each behavioral category were transformed into a 0-5 scale, in which 5 represents the value obtained for each group and 0 represents a complete absence of instances of that behavioral category.

We found significant individual differences in behavioral categories specific to each species as well as those common to both species (figure 4.1). For the behaviors presenting a significant difference in both species, we also found inter-group

differences. For example, several male red-ruffed lemurs received medium to high degrees of affiliation (“Affiliation receiver” with 2.00 or more points), whereas the male ring-tailed lemurs only received very low affiliation efforts from their conspecifics (lower than 2.00 points).

The dispersion graphics indicate that red-ruffed lemurs exhibited no relationship between initiating behaviors of aggression and self-grooming. No individuals presented high levels of receiving aggression and high levels of self-grooming. In contrast, there was a positive relationship between self-grooming and arm reach. Individuals tended to form two groups: 1) individuals with high conspecific closeness (i.e., high frequency of arm reach events) tended to show high levels of self-grooming behaviors (Sh, Pn, females, and Rs, Ma, males) and 2) individuals with low conspecific closeness tended to show low levels of self-grooming behaviors (Cl, female, and Sf, Tx, and Ft, males). With respect to scent marking, no individuals exhibited high levels of scent marking and high levels of affiliation, neither initiating nor receiving. For more details consult supplementary data Figures S57 to S78.

The dispersion graphics indicate that ring-tailed lemurs differ from red-ruffed lemurs. In contrast to red-ruffed lemurs, there was a tendency for a positive relationship between self-grooming and receiving aggression, although this tendency is weak. The two individuals that self-groomed less were the ones that receive less aggressive behaviors from others; a paradigmatic case is Pul (female) and Cos (male) who were not observed receiving aggression from others and were the ring-tailed lemurs that self-groomed the least. Huddling, a behavior very common in the group, showed a curious relationship with self-grooming: 1) Pul who had one of the lowest values of self-grooming was the female with the highest value of huddling, 2) individuals with intermediate values of self-grooming presented intermediate values of huddling, and 3) high values of self-grooming did not present a relationship with huddling. There was no clear relationship between initiating affiliation and self-grooming, but there was a relationship between receiving affiliation and self-grooming: no individuals had simultaneously high values of receiving affiliation and high values of self-grooming. Dispersion graphics indicate that, similarly to red-ruffed lemurs, ring-tailed lemurs did not present a relationship between initiating behaviors of aggression and self-grooming. However, there was no ring-tailed lemur with high levels of receiving aggression and low levels of self-

grooming. In contrast with red-ruffed lemurs, there was no clear relationship between self-grooming and arm reach in ring-tailed lemurs. Moreover, no individuals with high levels of self-grooming presented high levels of vocalizations, and all the females presented low levels of vocalizations. There was a tendency for a negative relationship between self-grooming and scratching; the three individuals that self-groomed most (Jul, Cot and Min, all males) are the ones that scratched least. Females scratched more than males (with the exception of Den) and also tended to receive more affiliation. There is no linear relation between scratching and receiving aggression. Also, no individuals presented high levels of scratching and high levels of submission. For more details consult supplementary material C, Figure S67 to Figure 78.

Species Diversity Index is low for red-ruffed lemurs when compared to ring-tailed lemurs. The individuals in the group all presented similar values for initiating social behaviors (SDIsi 0.182) and non-social behavior (SDIns 0.250). In contrast, ring-tailed lemurs' main personality differences were particularly related to non-social behaviors (SDIns 0.667). Different red-ruffed lemurs tended to receive more differentiated behaviors from conspecifics (SDIsr 0.333) than ring-tailed lemurs (SDIsr 0.250). However, red-ruffed lemurs tended to differentiate less with respect to the number of conspecifics they spent time near (SDIsp 0.600), whereas ring-tailed lemurs were more diverse with respect to the numbers of conspecifics they spent time near (SDIsp 1.000). Consequently, the ring-tailed lemur group exhibited more personality diversity (SDI 0.536) than the red-ruffed lemur group (SDI 0.240) (see figure 4.2).

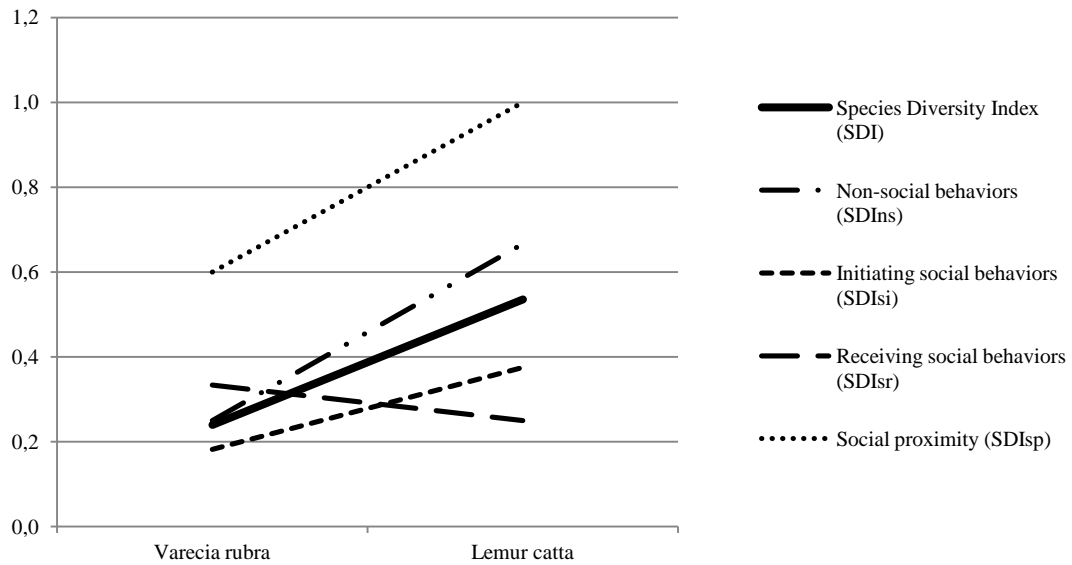


Figure 4.2 The graphic represents the species diversity index and the four other indices: one relating to non-social behaviors, two relating to social behaviors and one relating to social proximity.

### *Flexibility*

The population variability differed across the behavioral categories considered above. Some behavioral categories did not show significant variability across individuals while other categories did (see groups' variance for both species in Table 3). The individual variance for each behavioral category represents the flexibility each individual has for that behavioral category (see supplementary material C, Figure S86 to Figure S90). When we consider the variability of the different individuals across behaviors, some individuals exhibited a more flexible behavioral repertoire than others (figure 4.3).



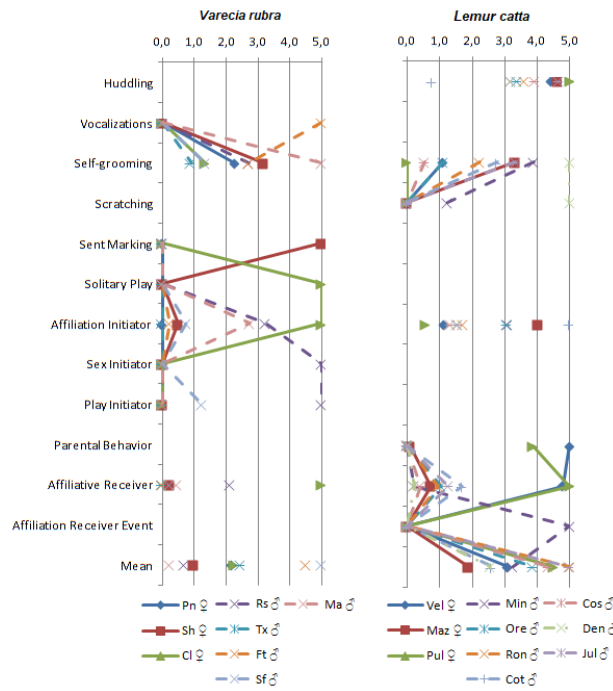


Figure 4.3 The left graphic represents the flexibility profiles of the 8 red-ruffed lemurs (*Varecia rubra*). The right graphic represents the flexibility profiles of the 10 ring-tailed lemurs (*Lemur catta*). For each behavioral category, flexibility reflects the extent to which the frequency of that behavior varied for an individual across observation sessions. To facilitate comparison, the results for variance in each behavioral category were transformed into a 0-5 ratio scale, in which 5 represents the highest variance value obtained by any individual for that behavioral category in each group, and 0 represents no variance across all the observation sessions. An individual's Mean Flexibility Score corresponds to the mean variance for that individual across all behavioral categories, after each variance score was transformed in the 0-5 ratio scale.

Comparing individuals' Mean Flexibility Scores it becomes clear that the range of scores for ring-tailed lemurs (1.885-5.000 points) shows a higher distribution than for red-ruffed lemurs (0.251-5.000). With regard to the total number of categories for which individual flexibility was found red-ruffed lemurs present one more category than ring-tailed lemurs.

The dispersion graphics show a tendency for a negative relationship between flexibility (MFS) and self-grooming for red-ruffed lemurs. There were no individuals with high values for both flexibility and scent marking. The most flexible individuals did not receive high levels of affiliation. There tended to be a negative relationship between flexibility and closeness to other conspecifics (measured by arm reach 2). Specifically, the individuals with high levels of closeness to conspecifics were the most inflexible,

and the individuals with the lowest values of closeness were the most flexible. For more details, please consult supplementary materials Figures S3.

In contrast, ring-tailed lemurs showed no relationship between flexibility (MFS) and self-grooming. Regarding scratching, the most inflexible individuals were the ones that scratched least, and females had high values of both flexibility and scratching. There was a strong negative relationship between flexibility and initiating effective submissive behaviors. Specifically, the most flexible individuals tended to have low levels of submissive behaviors. Similar to red-ruffed lemurs, ring-tailed lemurs also tended to present a negative relationship between flexibility and high levels of closeness to conspecifics (arm reach 4). However this tendency is weak. For more details please consult supplementary materials Figures S4.

The species flexibility index (SFI) was higher for ring-tailed lemurs. All the derivate indices (SFIns, SFIsi, SFIsr) were also higher, which indicates that *Ring-tailed lemurs* are more flexible than *Red-ruffed lemurs*.

In figure 4.4, it is clearly shown that ring-tailed lemurs are more flexible than red-ruffed lemurs. Ring-tailed lemurs presented very flexible non-social behaviors and social behaviors initiated by the focal individual compared to red-ruffed lemurs. The two species exhibited closer values for flexibility regarding receiving social behaviors.

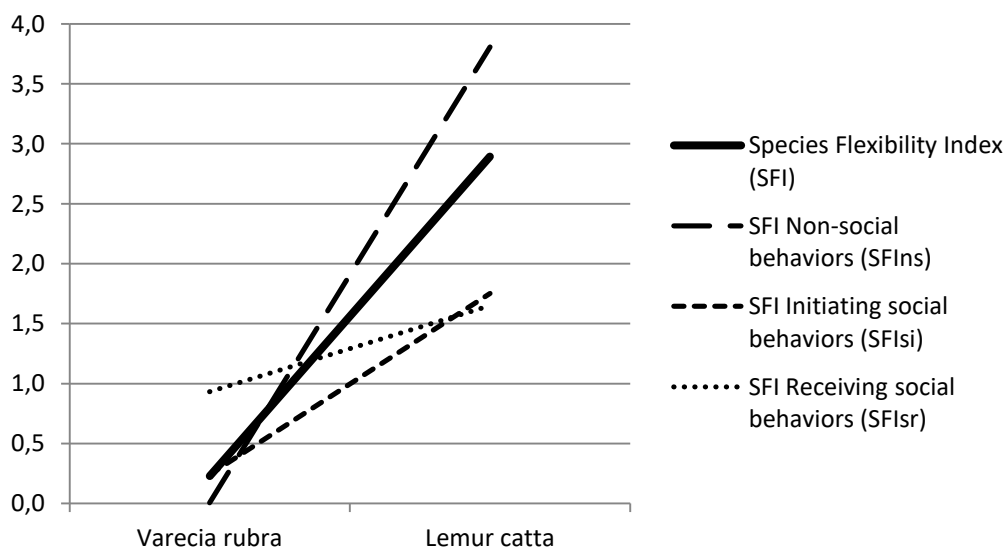


Figure 4.4 Graphic representation of Species Flexibility Index and 3 other derived indices calculated for ring-tailed lemurs (*Lemur catta*) and red-ruffed lemurs (*Varecia rubra*).

## Complexity

Using the EthoSeq program (Japyassú et al., 2006), we analyzed the behavioral patterns for each individual we observed. The complexities of the behavioral sequences ranged from 2 to 5 behavioral transitions for ring-tailed lemurs and 2 to 4 for red-ruffed lemurs. Each transition could be from the pre-transition behavior to one of 16 post-transition behaviors for ring-tailed lemurs and one of 14 post-transition behaviors for red-ruffed lemurs, with different probabilities associated with each of the 16 or 14 possible sequences. The detailed analysis of these transitions, given their complexities, is beyond the scope of this paper (for more detail, *EthoSeq Schematic Matrices* can be consulted in supplementary materials C, Table S27 and S28). However, we can generally state that for most behavioral categories there is a transition to another category of behaviors that is typical among most individuals (see supplementary materials S8 and S9). For example, when a red-ruffed lemur starts to self-groom, he/she transitions to some affiliation-related behavior (either receiving or emitting affiliation) on 42.95% or more of the occasions (also based on the group analysis). In the case of ring-tailed lemurs, when a ring-tail lemur starts to self-groom, he/she transitions to some affiliation-related behavior (either receiving or emitting affiliation) on 54.11% or more of the occasions (based on the group analysis). (supplementary materials C, Figure S91 and Figure S94).

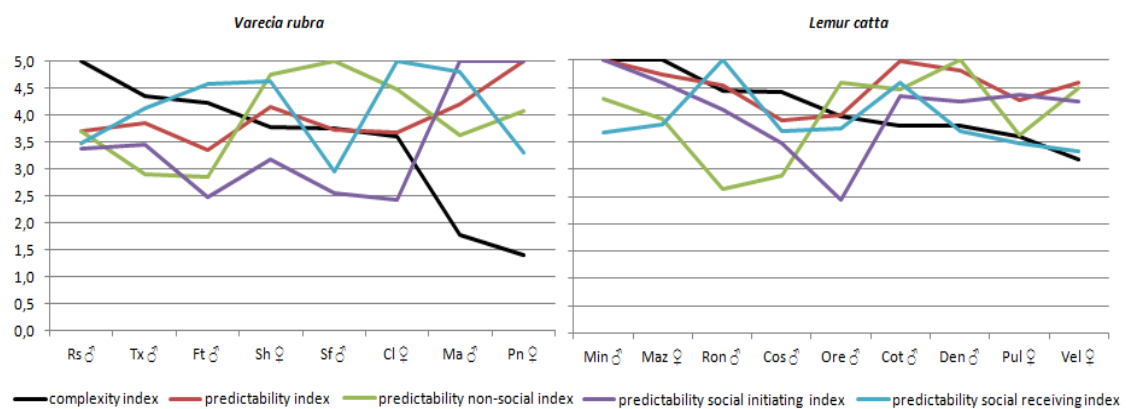


Figure 4.5 The graphics represent the complexity index results for the four predictability indices calculated for each group of lemurs. The results were transformed into a 0-5 ratio scale, for comparison purposes, in which 5 was the highest value obtained in the group for each index. This transformation was computed independently for each group

When comparing the results of both groups, we found that ring-tailed lemur individuals had more complex personalities (they tended to have more alternative responses to similar situations; see figure 4.5). In both groups, the most complex individuals tended to be the males of the group. Regarding the relationship between complexity and predictability, dispersion graphics indicate that, in red-ruffed lemurs, the least complex individuals tended to be the most predictable, and the most complex individuals tended to be the least predictable (see supplementary materials C, Figures 86-89). In contrast, some ring-tailed lemurs could be both very complex and very predictable. Further, dispersion graphics confirm no relationship between complexity and predictability for ring-tailed lemurs (see supplementary materials C Figure 90).

Regarding predictability subscales, the highest levels of predictability of non-social behavior subscale (PI<sub>ns</sub>) scores as well as the lowest levels of predictability in initiation of social behavior scores (PI<sub>si</sub>), in red-ruffed lemurs, tended to be found in individuals with intermediate levels of complexity. In ring-tailed lemurs, we cannot observe such a clear pattern.

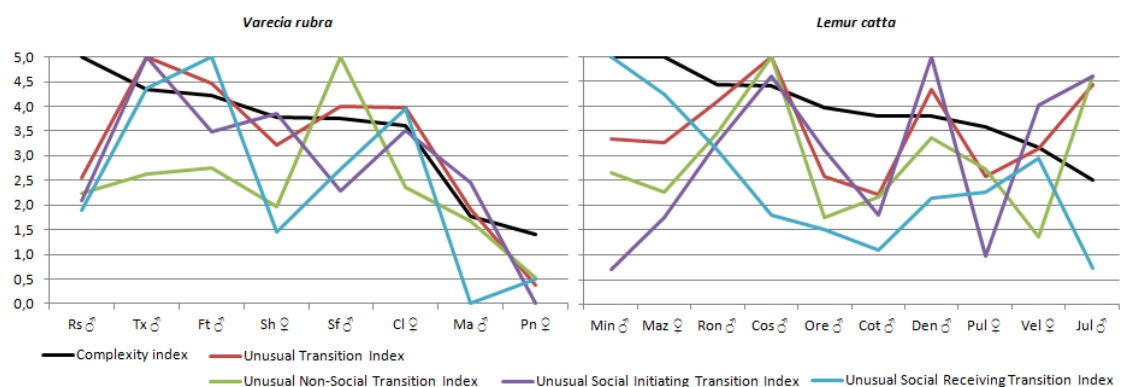


Figure 4.6 The graphic represents the complexity index results and the four “unusual” indices calculated for both groups of lemurs. The results were transformed into a 0-5 ratio scale, for comparison purposes, in which 5 was the highest value obtained in the group for each index. This transformation was computed independently for each group.

Observing figure 4.6, we see that for red-ruffed lemurs individual variation curves are quite similar for complexity and unusual transition index (UTI) scores. Dispersion graphics confirm a tendency for the least complex individuals to have the least unusual behavioral transitions, and the most complex individuals to have the most unusual

behavioral transitions, with the exception of Rs, who showed high complexity but relatively low unusual behavioral transitions index scores (see supplementary material figure S7). With respect to the subcategories of the UTI, for initiation of non-social behaviors (UTIns) there is not much variation across individuals (Sf and Pn are the exceptions). As to the more social subcategories of UTI (UTIsi and UTIsr) the tendency for individuals with more complex personalities to have more unusual behavior patterns was also found (Sh and Ma are the exceptions, presenting relatively lower values for the unusual social receiving transitions when compared to the other indices). In general, dispersion graphics indicate that the correspondence between personality complexity and unusual patterns of behavior is due to unusual social behavior and not to unusual non social behavior.

In ring-tailed lemurs, complexity and unusual transition indices did not show a clear relationship (see fig. 4.6 and dispersion graphic S8). The two least complex individuals had high UTIsi scores (meaning they were more likely to initiate unusual social sequences) and the two most complex individuals had low UTIsi scores though overall, no relationship between these two variables could be identified. With respect to being recipients of unusual social behavior (UTIsr) the least complex individual was least likely to receive such behavior and the two most complex individuals were most likely to receive such behavior, but again no overall relationship between these two variables could be identified.

In what follows we will examine the results of the indices that directly compared species to further understand personality differences between the species studied. The Species Complexity Index (SCI) calculation reveals that ring-tailed lemurs had more complex personalities than red-ruffed lemurs (see figure 4.7). Moreover, the calculations of all Species Predictability Indices (SPI) (except the SPIsi, for social behaviors initiated by the focal individual) indicated that ring-tailed lemurs were also more predictable. For the Species Unusual Transition Indices (SUTI) that related to social behavior indicated that ring-tailed lemurs were less unusual in their behavioral transitions than red-ruffed lemurs. But the SUTIns scores indicated that ring-tailed lemurs tend to exhibit more unusual non-social behaviors.

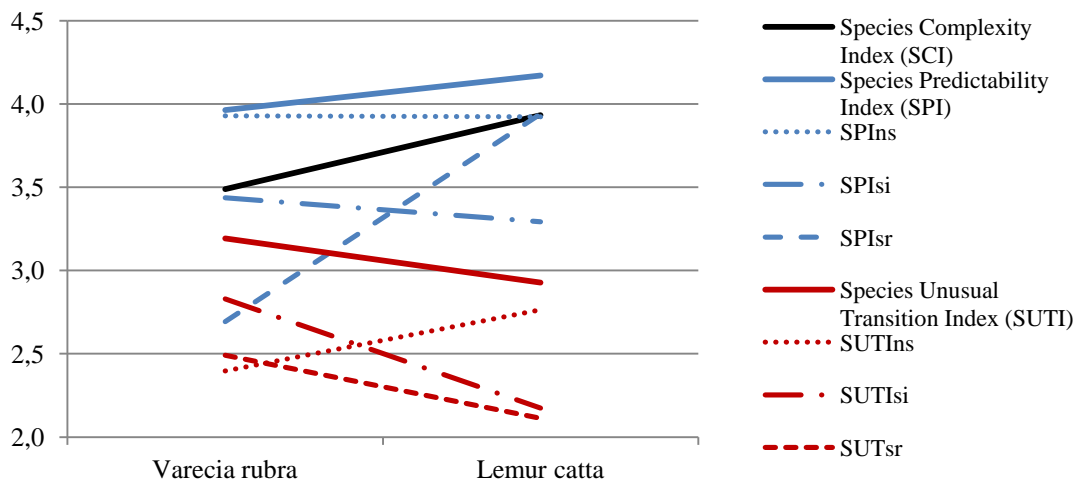


Figure 4.7 Graphic representation of Species Complexity Index, Species Predictability Index and its 3 derived indices, along with Species Unusual Transition Index and its 3 derived indices, calculated for ring-tailed lemurs (*Lemur catta*) and red-ruffed lemurs (*Varecia rubra*).

## Discussion

In support of our hypothesis, we found differences in personality in the three aspects explored in this study, which confirm that ring-tailed lemurs are more diverse, more flexible and more complex than the red-ruffed lemurs. The results suggest a positive relationship between the personality sophistication and cognitive capacities. The results also indicate that the species have different group dynamics. In general, red-ruffed lemurs had simpler and more linear inter-individual dynamics than did ring-tailed lemurs.

### Diversity

The ring-tailed lemurs exhibited more diverse personality, presenting more variables that differentiate the individuals from one another. Ring-tailed lemurs showed differentiation in several non-social behaviors, whereas red-ruffed lemurs showed differentiation in fewer non-social behaviors. These findings suggest that the diversity in non-social behaviors is higher for ring-tailed lemurs.

With regards to initiating social behaviors, both species presented differences related to affiliation. However, ring-tailed lemur individuals showed differentiation in submissive behaviors, whereas red-ruffed lemurs showed differentiation in aggressive behaviors. Elsewhere, higher cognitive skills were correlated with more social submission behavior in mice (Matzel, Kolata, Light, & Sauce, 2016). Although the referenced research was intended to compare behavior between individuals, we can hypothesize that these findings might also be observed when comparing species with different cognitive capacities. In fact, ring-tailed lemurs have larger relative brain sizes (MacLean et al., 2009) and demonstrate higher cognitive abilities compared to those of red-ruffed lemurs (Kendal et al., 2010; MacLean et al., 2008).

In addition, ring-tailed lemurs' tendency to be in proximity to other conspecifics varied substantially. We observed inter-individual differences ranging from proximity to one conspecific up to 6 or more conspecifics. In contrast, red-ruffed lemurs seemed to prefer having only one or two close conspecifics. These differences might reflect the differences in the social organization of each species. Red-ruffed lemurs live in a fission-fusion type of social organization, where smaller subunits emerge at reproductive times (Morland, 1993; M. E. Pereira et al., 1988; Michael E. Pereira et al., 1990), in contrast to ring-tailed lemurs that live in multi-male/multi-female groups with dominant matriline (Hood & Jolly, 1995; Sussman, 1991). The need for organizing in smaller subunits at reproductive and breeding periods could explain personality preference varying between preferring to be near to one conspecific or two, in red-ruffed lemurs. In contrast, the bigger and more hierarchical type of group organization of ring-tailed lemurs may fit better with the variability of having individuals who prefer to be close to either one, a few or a big group of conspecifics.

Self-grooming does not appear to be related to anxiety in red-ruffed lemurs. There was no relationship between aggressiveness (emitting or receiving) and self-grooming. The most social red-ruffed lemurs (sociality measured by arm reach) tended to self-groom more, perhaps as a relaxation behavior, and the least social individuals self-groomed less. In contrast to there being no relationship between aggression and self-grooming in red-ruffed lemurs, the two ring-tailed lemurs that never received aggression were the ones that self-groomed the least. Our interpretation of this finding is that the two individuals receiving no aggression were the dominant female and male in the

hierarchy, and perhaps had less need for self-grooming. No relationship between sociality (measured by arm reach or huddling) and self-grooming appeared in ring-tailed lemurs. It has been claimed regarding ring-tailed lemurs that self-grooming could represent a leisure behavior that is more common in enclosures than in the wild (Kerridge, 2005; Sauther et al. 2006). We conceptualize individual differences in self-grooming frequencies as personality differences.

Scratching appeared to be related to social structure for ring-tailed lemurs. Scratching could be considered an anxious behavior in ring-tailed lemurs and grooming behaviors could play a role in reducing anxiety (Sclafani, Norscia, Antonacci, & Palagi, 2012). Contrary to what was found by Sclafani et al. (2012), our females scratched more than males. This finding could be related to the fact that our observations did not focus only on mating season. Nevertheless, some of the differences found between individuals can be attributed to personality in ring-tailed lemurs. In contrast, scratching behavior did not demonstrate personality differences in red-ruffed lemurs.

Scent-marking behavior demonstrated personality differences in red-ruffed lemurs. These differences did not appear to have a relationship with other factors. In contrast to red-ruffed lemurs, ring-tailed lemurs did not show personality differences regarding scent-marking behavior.

As a more general conclusion about diversity, we can mention that the Species Diversity Index (SDI) indicated that red-ruffed lemurs are less diverse than ring-tailed lemurs, as predicted. Ring-tailed lemurs demonstrated more differentiation in both non-social and social behaviors. In other words, ring-tailed lemurs tended to respond in more individualized ways to the various members of their group. These findings are in agreement with research that demonstrated high social capacities for ring-tailed lemurs (Kendal et al., 2010; MacLean et al., 2008).

### *Flexibility*

Individuals in both lemur groups exhibited flexibility in some behaviors, but when the groups were compared to one another, ring-tailed lemurs were clearly more flexible



than red-ruffed lemurs. The major difference in flexibility appeared in non-social behaviors, with ring-tailed lemurs being much more flexible than red-ruffed lemurs. These major differences in non-social behavior could be related to the species' foraging capacities. As previous studies have demonstrated, ring-tailed lemurs use both habitat-based and spatial-based strategies to encode food location, alternating between the strategies according to the environment (Rosati et al., 2014). This behavior requires a higher degree of flexibility, which we observed in our data.

In past research right hand preference that is typical of terrestrial primates was found in ring-tailed lemurs (Regaiolli et al., 2016), whereas left hand preference was found in red-ruffed lemurs (Forsythe et al., 1988; Nelson et al., 2009). Might there be a relationship between hand preference and flexibility? We know that right hand preference at the species level is associated with the development of the left hemisphere, and such development provides for increased cognitive capacities such as the capacity for language. Such capacities might also provide a basis for personality flexibility. If future research on various primate species were to indicate a consistent relationship between personality flexibility and the existence and degree of right hand preference, it would support this hypothesis. This in turn would allow the measurement of personality flexibility to provide a window into the brain-lateralization-related cognitive capacities of primates.

### *Complexity*

Our analysis of personality complexity revealed slightly longer possible sequences, and more alternative responses, for ring-tailed lemurs in comparison with red-ruffed lemurs. For ring-tailed lemurs, all individuals but one scored a complexity index (CI) of 3.5 or greater, whereas red-ruffed lemurs did not consistently score as high. This result supports the hypothesis that in a more cognitively developed species like ring-tailed lemurs individuals with greater personality complexity would be more likely to develop in comparison with a less cognitively developed species like red-ruffed lemurs.

Red-ruffed lemurs appeared to have a simpler behavioral organization. The most complex individuals tended to be the least predictable, and the most predictable

individuals tended to be the least complex. The fluctuations reflected in personality complexity appeared in red-ruffed lemurs to be related to responses to particular unusual experiences, rather than being the results of development of complex repertoires that are expectable for the species due to adaptation to variations in situations that are common to members of the species (as appears to be the case for ring-tailed lemurs).

Among ring-tailed lemurs, on the other hand, we observed individuals that were both complex and predictable; complexity was related to multiple stable alternative patterns of behavior. In addition, individuals with low complexity and low predictability (i.e., more erratic) were observed. These differences between the species could be seen as another example of ring-tailed lemurs having higher social capacities than red-ruffed lemurs (Kendal et al., 2010; MacLean et al., 2008). Species predictability index regarding social behaviors initiated by the focal animal (SPI<sub>si</sub>) were slightly lower for ring-tailed lemurs than for red-ruffed lemurs. This difference possibly relates to the highly complex social structure of ring-tailed lemurs (Jolly et al., 2006). Among ring-tailed lemurs, the response an individual initiates possibly does not depend solely on his/her hierarchical position, but also on personality differences of conspecifics.

Scores calculated for the species unusual transitions index for non-social behaviors (SUT<sub>Ins</sub>) were higher for Ring-tailed lemurs than for red-ruffed lemurs. This higher number of unique behavior sequences initiated by a non-social behavior in ring-tailed lemurs can be understood as a result of their greater personality complexity.

In both groups, males' personalities tended to be more complex than those of females. This difference in behavioral complexity could be explained by female dominance in lemurs. In this form of social organization, females just establish their own hierarchy and males have to defer to them, while males need to establish their own hierarchy and, in parallel, establish close relationships with high-ranking females (Sclafani et al., 2012; Sussman, 1992). In both groups, the alpha females scored low in complexity and high in predictability (and had low levels of unusual behaviors), especially for sequences initiated by social behaviors. These findings could also be explained by the form of social organization in which females develop dominance strategies and males develop deference strategies (Dean, Hoppitt, Laland, & Kendal, 2011b). Stability and predictability in females' behavior facilitate males' development of deference strategies.

These differences in complexity indices between sexes should be further explored because these two groups were male-biased (there were more males than females in each group). Sex-ratio has been demonstrated to have an effect on innovation and learning processes (Dean et al., 2011b), so it could also have an effect on the complexity index. This possibility should be further explored.

In summary, our data confirms our hypothesis that ring-tailed lemurs have more diverse, flexible and complex personalities than red-ruffed lemurs. These differences could be predicted due to the higher cognitive capacities of this species. It will be important for future research to compare the results obtained from lemurs with other primate species, especially haplorhine species, to see if cognitive capacity also presents a relationship with personality differences, and to determine if brain differences could be underlying the findings.

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**Chapter 5 – Preliminary Results**  
**Corroborate the Neurodevelopmental**  
**Approach to the Phylogeny and Ontogeny**  
**of Primate Personality**

**How diverse, flexible and complex are primate personalities? A comparative analysis.**

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**Abstract**

In recent primate research there has been increasing interest in the relationships among personality, cognition and brain evolution. The increasing cognitive capacities for learning and solving problems occurring during primate-brain evolution could be expected to have the evolutionary consequence of more differentiated personalities. In this research we compared six species: two strepsirrhines species (*Varecia rubra*, red-ruffed lemurs, and *Lemur catta*, ring-tailed lemurs) and four haplorrhines species – two platyrrhines (*Saimiri boliviensis*, bolivian-squirrel monkeys, and *Sapajus appella*, tufted-capuchin monkeys) and two catarrhines (*Hylobates lar*, white-handed gibbons and

*Mandrillus sphinx*, mandrills). We explored the personality dimensions of diversity, flexibility and complexity. We expected *Sapajus apella* to be the species with the most differentiated range of personalities – high levels of diversity, flexibility and complexity. These expectations were based on their high cognitive abilities and brain development (i.e., high neocortex ratio). We found that *Sapajus apella* were the most diverse and complex, but *Lemur catta* was the most flexible. Our results are discussed here in the light of brain evolution theories, cognitive abilities and the survival value of personality.

**Keywords:** personality, primates' phylogeny, brain development, diversity, flexibility, complexity.

## **Introduction**

In recent research there has been increasing interest in the relationships between individual differences in cognition and personality in different species (Giudice & Giudice, 2017). At the species level, the increasing complexity of cognitive processes such as general intelligence, domain-specific abilities, abstract reasoning, and executive functions, during primate evolution, has been seen in two ways: 1) as a product of a brain enlargement occurring in response to increasingly complex social environments (Dunbar, 1992, 2009; Dunbar & Shultz, 2007; Flinn, Nepomnaschy, Muehlenbein, & Ponzi, 2011), and/or 2) as a response to increasingly challenging non-social ecological pressures (DeCasien, Williams, & Higham, 2017; MacLean, Barrickman, Johnson, & Wall, 2009; Toscano, Gownaris, & Heerhartz, 2016).

Passingham and Wise (2012) proposed that brain evolution of prefrontal cortex areas – areas responsible for the executive functions (such as planning and solving problems in complex and ambiguous situations) – is a response both to social and non-social ecological pressures. Recently, Brandão, Basseches and Vicente (in prep.<sup>a</sup>) proposed a relationship (across species) between specific features of personality and size/complexity of the prefrontal cortex. The increasing cognitive capacities for learning and solving problems occurring during primate-brain evolution could be expected to

have the evolutionary consequence of more differentiated personalities. The authors proposed that personality should be seen as a dynamic structure. The more complex a prefrontal cortex a species has, the more complex personality structure will be in that species.

This article reports on a study testing whether a recently articulated methodological approach to the study of personality (Brandão, Costa, Rodrigues, & Vicente, 2019) could be used to explore the link between brain evolution, cognitive abilities and personality dynamic structure. For this research we compared six species: two strepsirrhines species (*Varecia rubra* and *Lemur catta*) and four haplorrhines species – two platirrhines (*Saimiri boliviensis* and *Sapajus appella*) and two catarrhines (*Hylobates lar* and *Mandrillus sphinx*). The choice of the species for this initial exploration represented an attempt to include the main branches of the primate family tree, although the choices were restricted to the species available for observation.

The two lemur species *Varecia rubra* (red ruffed lemurs) and *Lemur catta* (ring-tailed lemurs) are both diurnal and frugivorous (MacLean et al., 2009). *Varecia rubra* is considered to have some primitive features like anestrus vaginal closure, three nipples, giving birth to litters, and behaviors including building nests for the care of their young, transporting infants in their mouths, parking them in the nests or other places in the trees, and nursing young “on schedule” (Boskoff, 1977; Foerg, 1982; M. E. Pereira, Seeligson, & Macedonia, 1988). *Lemur catta* feed not only on fruits but also on leaves and flowers from terrestrial habitats (Simmen, Hladik, & Ramasiarisoa, 2003). They typically have one baby at a time, with babies carried on fur and nursed “on demand” (MacLean et al., 2009; Tecot et al. 2013).

*Lemur catta* is considered to be a species with more complex cognitive abilities when compared to *Varecia rubra*. *Lemur catta* present more sophisticated social learning capacities (Kendal et al., 2010; MacLean, Merritt, & Brannon, 2008), mixed strategies for spatial and habitat based memory which increases their adaptability to both homogeneous and heterogeneous environments (Rosati, Rodriguez, & Hare, 2014), and right hand preference like other terrestrial primates (Regaiolli, Spiezio, & Hopkins, 2016). In contrast *Varecia rubra* present left hand preference (Forsythe, Milliken, Stafford, & Ward, 1988; Nelson, O’Karma, Ruperti, & Novak, 2009) and the use of spatial strategies to encode food location (Rosati et al., 2014).

*Varecia rubra* has a larger overall brain volume when compared to other lemurs (e.g., sportive lemur, mouse lemur) and even to some new world primates (e.g., common marmoset, squirrel monkey) (Striedter, 2005). Nevertheless, *Lemur catta* has a larger brain size relative to body size with a ratio value of 0.011 while *Varecia rubra* presents a ratio value of 0.009 (MacLean et al., 2009). Bush & Allman (2004) supplementary material contains data allows calculating a ratio of frontal neocortical gray matter to total neocortical gray matter value of 0.306 for *Lemur catta*. There is no value available for *Varecia rubra*. A recent study of the evolution of folds in neocortical tissue through primate phylogeny shows a non-linear relation between lengths and depths of folds (Heuer et al., 2019). Over the course of evolution the number of folds increases while their length tends to decrease until a point of stabilization is reached. It was discovered that *Varecia variegata* (black-and-white ruffed lemur) had a higher fold length and a lower fold depth than *Lemur catta*.

Based on these differences our theory would predict that *Lemur catta* would have more complex personality structures than *Varecia rubra*. These predictions were confirmed in a previous study using the same methodological approach of this current study (Brandão, Rodrigues, Costa and Vicente, in prep.<sup>b</sup>). The current study builds on data from the previous study by comparing the data with data from four species of haplorrhines.

The two platyrrhine species studied, *Saimiri boliviensis* (squirrel monkeys) and *Sapajus appella* (capuchin monkeys) are sympatric species of neotropical monkeys (Klein & Klein, 1973). There is considerable overlap in these two platyrrhine species' diets of fruits and insects (Galetti & Pedroni, 1994; Klein & Klein, 1973; Lima & Ferrari, 2003) although *Sapajus appella* also eats small invertebrates (Izawa, 1978; Milano & Monteiro-Filho, 2009). Social organization is different in these two species. *Saimiri boliviensis* live in groups ranging from 45 to 75 individuals (Boinski & Cropp, 1999), with a strict dominance hierarchy in which females dominate over males and males are peripheral members of groups, except in breeding season (Wilson, 2011). In *Sapajus appella*, groups range from 10 to 20 individuals including 1-3 males (Defler, 1982; Izawa, 1980), usually with one dominant male in a weak dominance hierarchy (Visalberghi, Valenzano, & Preuschoft, 2006).

*Sapajus appella* have short fingers with opposable thumbs which makes them the most

dexterous of the platyrrhines (Fleagle, 2013). Also, they have long lactation periods, long inter-birth intervals, and long life spans (MacKinnon, 2013). Capuchin species, including the *Sapajus appella* in our study, present exceptional cognitive capacities (demonstrated by the capacity for complex tool use and some evidence of culture), great behavioural flexibility and complex social structure (e.g., Byrne & Suomi, 1996; Fragaszy et al., 2017; Ottoni, 2015; Perry, 2011). *Saimiri boliviensis* have comparatively less developed cognitive capacities.

*Sapajus appella*, , have relatively larger brains than other platyrrhines primates, and like genus *Pan* (chimpanzees and bonobos) have high brain size to body size ratios (Edwards, Lonsdorf, & Pontzer, 2017). The ratio of neocortex size to rest of brain size is higher for *Sapajus appella* with a value of 2.36, compared to *Saimiri boliviensis* with a value of 2.21 (Dunbar, 1992). It was found that *Saimiri boliviensis* and *Sapajus appella* have similar brain fold lengths but *Saimiri boliviensis* have lower fold depth than *Sapajus appella* (Heuer et al., 2019). We do not have information about the prefrontal cortex volume of these two platyrrhine species. However, Bush & Allman's (2004) data allow for calculation of a ratio of frontal neocortical gray matter to total neocortical gray matter value of 0.243 for *Saimiri sciureus*.

Research on personality trait-structure suggests that that of *Sapajus appella* partially overlaps with that of great apes (Morton et al., 2013; Robinson et al., 2016; Uher, Addressi, & Visalberghi, 2013; Uher & Visalberghi, 2016). Research using the same methodological approach as the current article demonstrated diverse, flexible and complex personalities in *Sapajus appella* (Brandão et al., 2019). Based on the cognitive and brain differences between *Saimiri boliviensis* and *Sapajus appella*, our theory led us to expect that *Saimiri boliviensis* would have less diverse, flexible and complex personalities than we found in *Sapajus appella*. Wilson's (2011) research provided some support for this expectation because it found that in the less cognitively complex *Saimiri sciureus* (phylogenetically close to *Saimiri boliviensis*), individuals presented with less complex personalities than in *Cebus appella* (phylogenetically close to *Sapajus appella*).

The two catarrhines species observed, *Mandrillus sphinx* (mandrills) and *Hylobates lar* (white-handed gibbon), have extremely different forms of social organization and habitat distribution. *Mandrillus sphinx*, belong to the family Cercopithecidae and live in

Africa in tropical rain forests. *Mandrillus sphinx* are omnivorous but consume mainly fruit (Hoshino, 1985). They live in large groups based on female matrilineal groups with young males leaving the group when they mature (Harrison, 1988). Social organization varies from solitary males to female-male groups to hordes that contain multiple groups which may be as large as 800 individuals (K. a Abernethy, White, & Wickings, 2002; Wickings & Dixson, 1992). In the wild, no long-term social bonds between breeding partners exist (Abernethy, White, & Wickings, 2002). Therefore, the evolution of strong sexual dimorphism, somatic and behavioral variation in *Mandrillus sphinx* was possibly driven by intra-sexual competition (K. a Abernethy et al., 2002; Singleton, 2012).

*Hylobates lar* (white-handed gibbon) belong to the superfamily Hominoidea and family Hylobatidae, living in Asian rain forests. *Hylobates lar* use mainly arboreal locomotion and are usually found high in the canopy (Ungar, 1996; Vereecke, D'Août, & Aerts, 2006). They eat a large variety of foods, especially fruit and leaves (Fleagle, 2013). *Hylobates lar* are sexually monomorphic (Smith & Jungers, 1997). *Hylobates lar* usually live in serial monogamous pairs. At some sites there are also multi-male groups as well as groups with multiple adult females, but most females are polyandrous, including females living in single-male groups (Barelli, Boesch, Heistermann, & Reichard, 2008; Barelli, Heistermann, Boesch, & Reichard, 2008; Reichard & Barelli, 2008). Within-group aggression is rare but most between-group interactions are agonistic. The latter often involve chasing but also can be purely vocal (Bartlett, 2003). Adult females lead group movements most often (Barelli, Boesch, et al., 2008).

Cognition research with *Mandrillus sphinx* is very scarce. The capacity for object permanence, defined as the ability to mentally follow a hidden object, was not found in *Mandrillus sphinx* (Gabel et al., 2009). There are only two case-reports of spontaneous tool-use for self-care by *Mandrillus sphinx* (Pansini & de Ruiter, 2011; Vincent, 1973). *Mandrillus sphinx* tend to have faster reaction times than humans; they can solve tasks demanding color and shape discrimination, although they have error biases towards some colors and shapes with biological relevance (Leighty et al., 2011). Individuals' differences in performance in these tasks were observed and found to be influenced both by social hierarchy position and test circumstances. For a community of *Mandrillus sphinx* in captivity, the creation and social transmission over ten years of a social meaningful gesture was reported (Laidre, 2011). Social reciprocity was found in

*Mandrillus sphinx* but there is evidence that they do not plan their social interactions with the expectation of reciprocity (Schino & Pellegrini, 2009, 2011). Overall, the cognitive capacities of *Mandrillus sphinx* seem to be closer to those of other monkeys than to those of apes.

Some researchers have conducted studies of cognition in various species of gibbons (Hylobatidae), including *Hylobates lar*. Problem solving and tool-use studies show gibbons can learn of simple rules associating tools with goals when the relationship between tool and goal is easily perceived (Cunningham, Anderson, & Mootnick, 2006; Geissmann, 2009; Pereira, Peixoto, & Brandão, 2018). When the relationship had to be produced or the tool and goal object were not physically situated in the same location their performance was very poor and there was no evidence of gibbons being able to use previously acquired knowledge to solve a novel task (Cunningham & Anderson, 2006; Cunningham et al., 2006; D'Agostino & Cunningham, 2015). Performance in comprehension of object permanence was similar to great apes for some individuals, but there were great individual differences with others performing much more poorly (Fedor, Skollár, Szerencsy, & Ujhelyi, 2008). The capacity for using visual cues, very important for human communication, is present in gibbons (Caspar, Mader, Pallasdies, Lindenmeier, & Begall, 2018). Moreover there is evidence of a strong lateralization of hand preference at the individual level for very specific tasks. However, there is no consistent lateralization at the population level (Caspar et al., 2018; Fan et al., 2017). Cognition research results show great heterogeneity of capacities among individuals not allowing for general conclusions.

Bush & Allman's (2004) data allow calculating a ratio of frontal neocortical gray matter to total neocortical gray matter value of 0.269 for *Mandrillus sphinx* and 0.347 for *Hylobates lar*. One study of *Mandrillus sphinx* personality, using the same methodological approach as that of the current study, demonstrated the existence of significant personality diversity among individuals, with flexible and complex personality structures (Brandão et al., in prep.<sup>5</sup>). In the same research some similarities with personality of baboons was found. No other research on *Mandrillus sphinx* personality or on *Hylobates lar* has been published up to this date.

In the current study we compared the chosen six species using the methodology proposed by Brandão et al. (2019) as well as the indices developed and explored in a



comparative study of two lemur species by Brandão et al. (in prep.<sup>b</sup>) We hoped to be able to explore the differences among these species with respect to diversity, flexibility and complexity. Of the six species compared, we expected *Sapajus apella* to be the species with the most differentiated range of personalities, (i.e., with high levels of diversity, flexibility and complexity). These expectations were based on their high cognitive abilities and brain development (i.e., high neocortex ratio). We also expected to find quite differentiated personalities in *Lemur catta* due to their high cognitive abilities. Brain information is scarce for lemurs, as well as for the other species in the study, although we know there has been a parallel evolution since strepsirrhines and haplorrhines divided from their common ancestor.

## Material and Methods

For this study we observed groups of 2 strepsirrhines species (*Varecia rubra* and *Lemur catta*) and 4 of haplorhine species – 2 platirrhines species (*Saimiri boliviensis* and *Sapajus apella*) and 2 catarrhines species (*Mandrillus sphinx* and *Hylobates lar*). All the groups are located in Portugal (see table 5.1).

Table 5.1 Species observed. Total number of female and males for each group. Location of the groups.

Species	Females	Males	Location
<i>Varecia rubra</i>	3	5	Lagos' Zoo, Algarve
<i>Lemur catta</i>	3	7	Badoca Park, Alentejo
<i>Saimiri boliviensis</i>	3	3	Lagos' Zoo, Algarve
<i>Sapajus apella</i>	11	3	Lagos' Zoo, Algarve
<i>Mandrillus sphinx</i>	7	4	Badoca Park, Alentejo
<i>Hylobates lar</i>	1	1	Maia's Zoo, Porto
	2	2	Lagos' Zoo, Algarve

For information about living conditions of *Varecia rubra* and *Lemur catta* please see Brandão<sup>a</sup> et al. (in prep.<sup>b</sup>), for *Sapajus apella* please see Brandão et al. (2019), and for *Mandrillus sphinx* please see Brandão, et al. (in prep.<sup>c</sup>). *Hylobates lar* in Lagos' Zoo, was one family comprising the father and mother, 2 sub-adults (the older one was a male near to adulthood, with about 8 years of age, and the younger was a female, with about 6 years of age), and one baby (who was not formally observed). They lived on an

island with ropes, wood structures and arboreal vegetation. For *Hylobates lar* in Maia's Zoo, only one male and one female living on the same island were observed. They did not form a sexual couple. The *Saimiri boliviensis*'s group lived on two artificial islands connected by a bridge and a rope, with artificial structures (such as stairs, swings and little houses) connected by ropes, and some arboreal vegetation. *Saimiri boliviensis* spent nights in shelters in an indoor facility. As a final note it is important to acknowledge that while the enclosure at Lagos' Zoo provided excellent living conditions for the animals, its structure impaired our observations by limiting observation points and sight lines. Additionally, females of the group spent the majority of the observation time, inside their tree houses.

Individuals' of all species were observed in sessions of 10 minutes each. The differences across individuals in number of observation sessions were due to factors external to the study design (see table 5.2 for more details).

Table 5.2 Number of observation sessions per individual and dates of observation for each species.

<b>Species</b>	<b># sessions per individual</b>	<b>Dates of observation</b>
<i>Varecia rubra</i>	16-51	December 2014 to February 2015
<i>Lemur catta</i>	17-35	March and April 2016
<i>Saimiri boliviensis</i>	50	April and May 2015
<i>Sapajus apella</i>	59-83	February to May 2015
<i>Mandrillus sphinx</i>	50-54	February and March of 2016
<i>Hylobates lar</i>	51-52	March to June 2015

Only adults and sub-adults were observed. The study was designed to compare adult personalities and not as a developmental study in which age would be considered an important variable. Decisions about who were adults and sub-adults were based on the literature for each species. We built an identification sheet with characteristics of each individual we observed.

Prior to the observations, we constructed a complete ethogram for each species based on species-specific research literature. We excluded some behaviors that we viewed as less relevant to personality differences (e.g., eating behavior). The remaining behaviors were organized into categories. For the species not studied elsewhere more information about the behaviors included in each category can be found in the supplementary data

(Supplementary materials, Tables S1 and S2). The construction and organization of the categories followed the methodology explained at Brandão et al. (2019). As explained in the article for the selected behaviors we made distinctions between events and states, non-social or social behaviors, ritualized non-physically aggressive behaviors and effective physically aggressive behaviors. We also recorded all the moments in which an individual was observed in the proximity of conspecifics. All observations were video-taped and we used observation sheets and a stop-watch to measure time, as extensively explained in the cited work. Data obtained was analyzed using the IBM computer program SPSS, Version 24 (2016) and the EthoSeq program (Japyassú, Alberts, Izar, & Sato, 2006). The total number of variables analyzed for each group can be found in the first line of table 4. We will now discuss the three dimensions of personality proposed by Brandão's et al. (2019) work with capuchin monkeys that we explored — diversity, flexibility and complexity.

### *Diversity*

"Diversity" refers to the number of behavioral categories for which significant differences were found across individuals' within a group (i.e., the extent to which different individuals presented distinct repertoires of behavior) (Brandão et al., 2019). The Random Effect Model (REM) was applied to each behavioral category, following the methodology presented in previous papers (Brandão et al., 2019; Brandão<sup>b</sup> et al. sub.)

<sup>15</sup>. In the present work we focused on the *Species Diversity Index (SDI)* to compare groups and on the derived indices: *Species Diversity Index non-social (SDIns)* specific for non-social behaviors, *Species Diversity Index social initiating (SDIsi)* specific for behaviors initiated by the focal individual, and *Species Diversity Index social receiving (SDIsr)* specific for behaviors received by the focal individual. We followed the formulas presented in the previous work with *Varecia rubra* and *Lemur catta* (Brandão<sup>b</sup> et al. sub.).

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<sup>15</sup> For more details about REM applications to this type of data analysis please refer to Brandão et al. (2019).

### *Flexibility*

As discussed in Brandão et al., (2019) “*Flexibility*” refers to variability across observations of individuals’ behavioral responses. The individual variance across observations for each behavioral category represents the flexibility each individual has for any behavioral category. In the present work we focused first on the *Species Flexibility Index (SFI)* – a measure of flexibility of all individuals across all behavioral categories -- to compare groups. Then we focused on the derived indices: *Species Flexibility Index non-social (SFIns)* specific for non-social behaviors, *Species Flexibility Index social initiating (SFIsi)* specific for behaviors initiated by the focal individual, and *Species Flexibility Index social receiving (SFIsr)* specific for behaviors received by the focal individual. We used the formulas presented in the previous work with *Varecia rubra* and *Lemur catta* (Brandão et al. prep.<sup>b</sup>).

### *Complexity*

“*Complexity*” as defined by Brandão et al., (2019) refers to inter-individual variability in the number of specific sequences of behavior exhibited (more complex individuals present a greater number of strong consistent combinations of sequences of behavioral responses than less complex individuals). Using the EthoSeq program (Japyassú et al., 2006), we analyzed the behavioral patterns that were found for each individual observed, in all six species. EthoSeq uses mathematical Graph Theory in its analysis of behavior sequences (it is not an inferential statistical method).<sup>16</sup>

Using our observational data, the program found sequences of behaviors for each individual. The total number of behavioral categories for which patterns were found by EthoSeq in each species appears on the first line of table 6. Included in these totals are sequences found in many individuals as well as “unusual transitions”—sequences found often in an individual that did not follow a common pattern for the species. The number of categories for which one or more individuals presented unusual transitions can be found in table 6, Line 2. We calculated nine indices based on EthoSeq outputs, following the method from previous work (Brandão et al., 2019; Brandão<sup>b</sup> et al. prep.). For computing the nine indices, we worked exclusively with the data regarding the first transition in each sequence. We considered the following indices: *Species Complexity*

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<sup>16</sup> Please read Brandão et al. (2019) for more details about the methodology used for identifying behavioral sequences.

*Index (SCI), Species Predictability Index (SPI), Species Predictability Non-Social Index (SPIns), Species Predictability Social Initiating Index (SPIsi), Species Predictability Social Receiving Index (SPIsr), Species Unusual Transition Index (SUTI), Species Unusual Non-Social Transition Index (SUTIns), Species Unusual Social Initiating Transition Index (SUTIsi), Species Unusual Social Receiving Transition Index (SUTIsr)*. See Brandão<sup>b</sup> et al. prep. for formulas for all Species Indices.

The *Species Predictability Indices* were calculated using the probabilities of the most likely second behavior in a sequence for an individual, given a first behavior, for categories with consistent subsequent behaviors. Some behaviors were rare as a subsequent behavior to the first behavior across the group as a whole. These transitions were considered unusual when the associated probability of occurrence across all observations of group members was less than or equal to 15%. The individual's *Unusual Transition indices* measure how often a particular individual transitioned from a first behavior to an unusual second behavior. The *Species Unusual Transition indices* represent the average score for the members of each species studied.

### **Ethical note**

This research complied with guidelines provided by the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes (ETS n. 123). This research also adhered to the Association for the Study of Animal Behaviour “guidelines for the treatment of animals in behavioral research and teaching.”

### **Results**

We found personality differences regarding diversity, flexibility and complexity both across individuals of each species group and among species groups. We analyzed in detail the results for each aspect of personality variation.

### *Diversity*

The REM analysis showed significant individual differences for the group/species analyzed. Some significant differences could be expected to occur due to chance (Type I errors). Therefore, we performed a Benjamini-Hochberg correction. Table 5.3 summarizes the list of behavioral categories for which significant differences across individuals were found.

Table 5.3 List of behavioral categories for which significant differences across individuals were found, after Benjamini-Hochberg correction (Continued on the next page).

<i>Varecia rubra</i>	<i>Lemur catta</i>	<i>Saimiri boliviensis</i>	<i>Sapajus apella</i>	<i>Mandrillus sphinx</i>	<i>Hylobates lar</i>
Selfgrooming	Huddling	Arms Reach	Self-grooming	Self-grooming	Self-grooming
Sent Marking	Vocalizations Event	Arms Reach 1	Solitary Play	Scratch	Parental Behavior
Affiliation Initiator	Selfgrooming		Urine Wash	Affiliation initiator	Solitary Play
Aggression Initiator Event	Scratching		Affiliation Initiator	Affiliation initiator Event	Play Initiator
Affiliation Receiver	Affiliation Initiator		Affiliation Initiator Event	Play Initiator	Affiliation Receiver
Aggression Receiver Event	Effective Submission Initiator Event		Play Initiator	Play Initiator Event	Arms Reach
Arms Reach	Parental Behavior		Play Initiator Event	Aggression Initiator	Arms Reach 1
Arms Reach 1	Affiliation Receiver		Ritual Agonism Initiator Event	Aggression Initiator Event	Arms Reach 2
Arms Reach 2	Aggression Receiver Event		Aggression Initiator	Ritual Submission Initiator Event	Arms Reach 3
	Arms Reach		Effective Agonism Initiator Event	Effective Submission Initiator	
	Arms Reach 1		Ritual Submission Initiator Event	Effective Submission Initiator Event	
	Arms Reach 2		Effective Submission Initiator	Parental Behavior Initiator	
	Arms Reach 3		Effective Submission Initiator Event	Affiliation Receiver	
	Arms Reach 4		Affiliation Receiver	Affiliation Receiver Event	
	Arms Reach 5		Affiliation Receiver Event	Play Receiver	
			Play Receiver Event	Play Receiver Event	
			Aggression Receiver Event	Ritual Agonism Receiver Event	
			Ritual Submission Received Event	Ritual Submission Receiver Event	
			Effective Submission Receiver Event	Effective Submission Receiver	
			Arms Reach	Effective Submission Receiver Event	
			Arms Reach 1	Other Behaviors Fear Related	
			Arms Reach 2	Arms Reach	
			Arms Reach 3	Arms Reach 1	
			Arms Reach 4	Arms Reach 2	
<b>Total 9</b>	<b>Total 15</b>	<b>Total 2</b>	<b>Total 24</b>	<b>Total 24</b>	<b>Total 9</b>

The frequencies of the behavioral categories found for each individual in the study can be understood as a personality profile. Qualitative and quantitative analyses of the profiles for some of the researched groups can be found elsewhere (Brandão et al., 2019; Brandão et al. in prep<sup>a</sup>; Brandão et al. in prep<sup>b</sup>). At the species level, we used the ratio of the number of behavioral categories with significant inter-individual differences after the REM B-H analysis to the number of behavioral categories observed to calculate Species Diversity indices (see table 5.4).

Table 5.4 Species Diversity Index and subindices: Species Diversity Index non-social (SDIns) specific for non-social behaviors; Species Diversity Index social initiating (SDIsi) specific for behaviors initiated by the focal individual; and Species Diversity Index social receiving (SDIsr) specific for behaviors received by the focal individual.

	<i>Varecia rubra</i>	<i>Lemur catta</i>	<i>Saimiri boliviensis</i>	<i>Sapajus apella</i>	<i>Hylobate s lar</i>	<i>Mandrillus sphinx</i>
Variables for analysis	25	28	18	40	21	41
REM B-H Variables	9	15	2	24	9	24
<b>SDI</b>	0.360	0.536	0.111	0.600	0.429	0.585
Total non-social variables	8	6	3	5	4	5
Total REM B-H non-social	2	4	0	3	2	2
<b>SDIns</b>	0.250	0.667	0.000	0.600	0.500	0.400
Total social initiating var.	11	8	6	14	7	15
Total REM B-H social ini.	2	3	0	10	2	10
<b>SDIsi</b>	0.182	0.375	0.000	0.714	0.286	0.667
Total social receiving var.	6	8	4	13	6	15
Total REM B-H social rec.	2	2	0	6	1	8
<b>SDIsr</b>	0.333	0.250	0.000	0.462	0.167	0.533



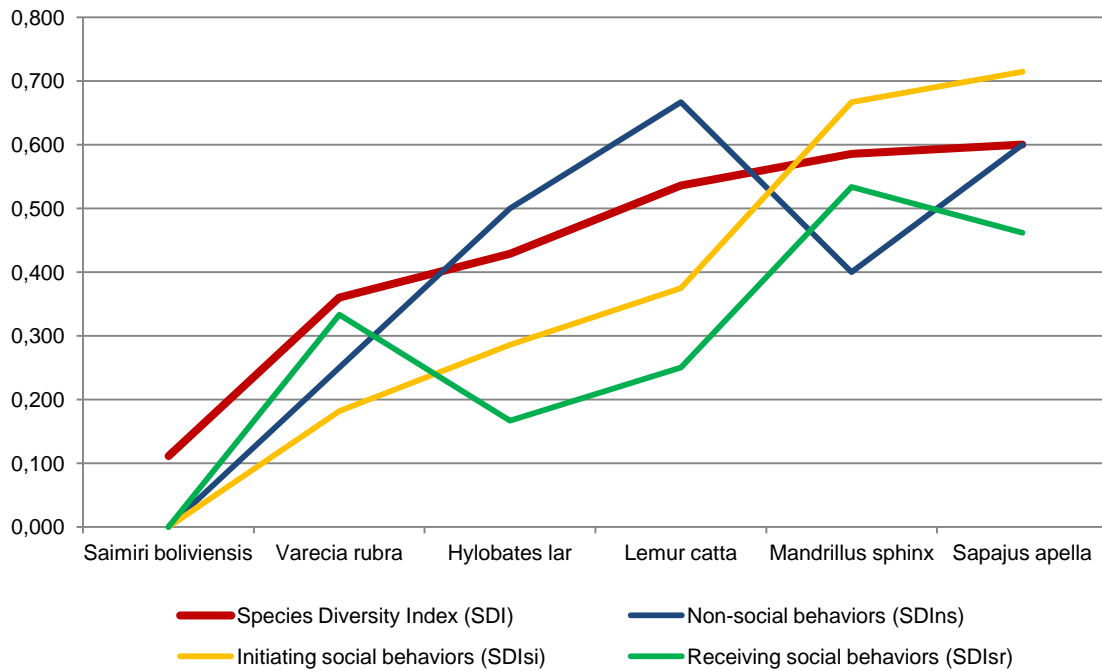


Figure 5.1 The graph represents the species diversity index and the three other indices, one relating to non-social behaviors, and two relating to social behaviors.

The two species with the highest Species Diversity Index (SDI) are *Sapajus apella* and *Mandrillus sphinx*; in contrast the two species with the lowest SDI are *Saimiri boliviensis* and *Varecia rubra* (see figure 5.1). Regarding non-social behaviors – SDIns, the results indicate that *Lemur catta* has the highest score. This means that individuals of this species are most diverse in their non-social behaviors; *Sapajus apella* has the second highest SDIns. Regarding social behaviors initiated by the focal individual – SDIsi, the results indicate that *Sapajus apella* is the species with most diversity, followed by *Mandrillus sphinx*. This mean that the individuals of these two species are the most socially different from each other. Regarding social behaviors received by the focal individual – SDIsr, the results indicate that *Mandrillus sphinx* is most diverse followed by *Sapajus apella*, indicating that the individuals of these species tend to be treated in more differentiated ways by others. The two species with highest diversity in social behaviors received by the focal individual – SDIsr are *Sapajus apella* and *Varecia rubra*, indicating that the individuals of these species tend to be treated in more differentiated ways by the others.

### *Flexibility*

Some behavioral categories did not show significant variability across individuals of the different species represented in our groups, while other categories did. The individual variance for each behavioral category represents the flexibility each animal has for any behavioral category. When we consider the variability of the different individual animals across behaviors, some animals exhibit a more flexible behavioral repertoire than others. The number of categories with individuals exhibiting flexibility in their behaviors varies from one species to the other. Table 5.5 shows which categories showed variability over time.

Table 5.5 Behavioral categories that exhibit individual flexibility for each species studied.

<i>Varecia rubra</i>	<i>Lemur catta</i>	<i>Saimiri boliviensis</i>	<i>Sapajus apella</i>	<i>Mandrillus sphinx</i>	<i>Hylobates lar</i>
Self-grooming	Huddling	Ritual Agonism Initiator	Self-grooming	Self-grooming	Self-grooming
Solitary Play	Selfgrooming	Effective Agonism Initiator	Solitary Play	Scratch	Solitary Play
Sent Marking	Scratching	Affiliative Receiver	Affiliation Initiator	Solitary Play	Simple Vocalization
Vocalizations	Affiliation Initiator		Play Initiator	Affiliation initiator	Complex Vocalization
Play Initiator	Parental Behavior		Ritual Agonism Initiator Event	Play Initiator	Play Initiator
Sex Initiator	Affiliation Receiver		Ritual Submission Initiator	Hair pulling Initiator	Affiliation Initiator
Affiliation Initiator	Affiliation Receiver Event		Parental Behavior	Parental Behavior Initiator	Parental Behavior
Affiliative Receiver			Affiliative Receiver	Affiliative Receiver	Social Vocalization Initiator
			Play Receiver	Infant Affiliation	Ritual Agonism Initiator
			Ritual Agonism Receiver	Play Receiver	Affiliative Receiver
			Abnormal Behavior	Hair Pulling Receiver	Social Vocalization Receiver
			Arms Reach	Other Behaviors Wound Grooming	Ritual Agoism Receiver
			Arms Reach 2	Abnormal Behavior	
<b>Total 8</b>	<b>Total 7</b>	<b>Total 3</b>	<b>Total 13</b>	<b>Total 13</b>	<b>Total 12</b>

The Species Flexibility Index (SFI) is higher in the lemur species (*Varecia rubra* and *Lemur catta*; see figure 5.2) than in the other four species. Of the four haplorhines species, *Sapajus apella* is the most flexible. Flexibility for non-social behaviors – SFIns, is by far the highest for *Lemur catta*. Of the other species exhibiting a *Hylobates lar* has a somewhat higher score than the other four species. The species with highest variability for social behaviors (SFI<sub>si</sub> and SFI<sub>sr</sub>) is *Sapajus apella*, followed by *Lemur catta*.

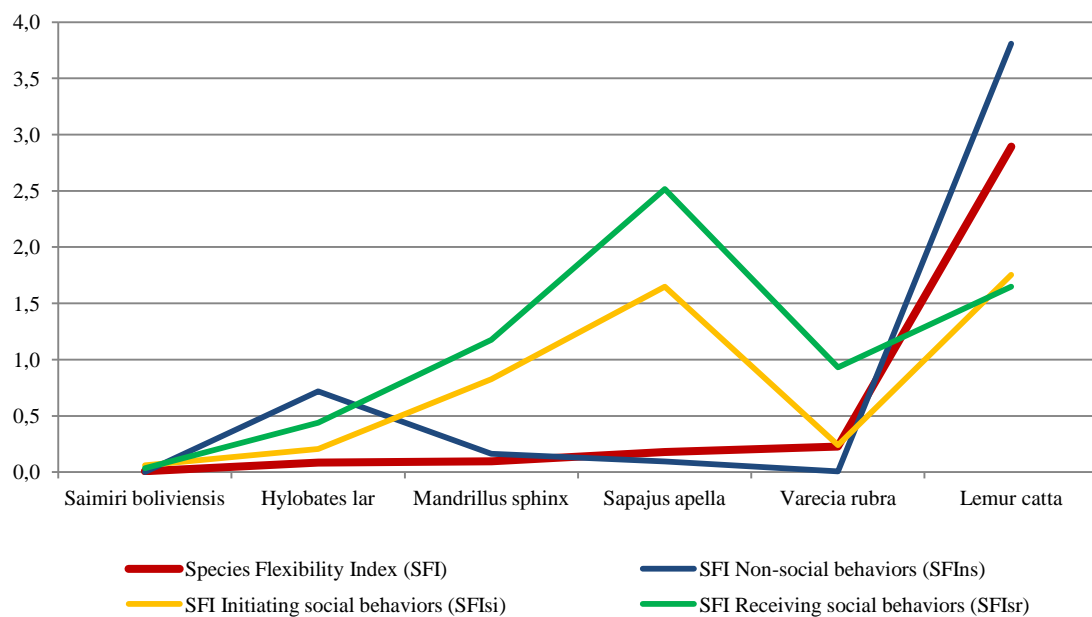


Figure 5.2 The graph represents the species flexibility index and the three other indices, one relating to non-social behaviors, and two relating to social behaviors.

### Complexity

We used the EthoSeq program (Japyassú et al., 2006) to identify behavioral patterns for each animal observed and to calculate the probabilities of each behavioral pattern occurring. The complexity and the probabilities of the behavioral sequences discovered varied. In general terms, for most behavioral categories there is a transition to another category of behaviors which is typical for most individuals. For each individual and for each group, we counted the number of behavioral categories for which a pattern of

subsequent behaviors was identified by EthoSeq, following Brandão et al's. (2019) proposal. In table 6 a summary of the results for each species can be found. Moreover, for each species we counted the number of categories that had unusual behavioral transitions (for which the associated probability of occurrence across all observations of group members was less than or equal to 15%; see table 5.6). It was not possible to use EthoSeq to calculate numbers of transitions for *Saimiri boliviensis*, because an insufficient number of patterns of behavioral sequences were found for members of that species.

Table 5.6 Summary of number of categories with transitions for each species, and the number of categories for which at least one individual made an unusual transition.

	<i>Varecia rubra</i>	<i>Lemur catta</i>	<i>Sapajus apella</i>	<i>Mandrillus sphinx</i>	<i>Hylobates lar</i>
Total of categories with patterns	15	17	19	26	18
Categories with unusual transitions	12	12	19	21	12
Ratio cat. unusual /total cat. pattr.	0.800	0.706	1.000	0.808	0.667

The results obtained allowed the calculation of several indices (see figures 5.3 and 5.4). The calculation of the Species Complexity Index (SCI) reveals that *Sapajus apella* followed by *Lemur catta* are the species in which the most complex personalities are found

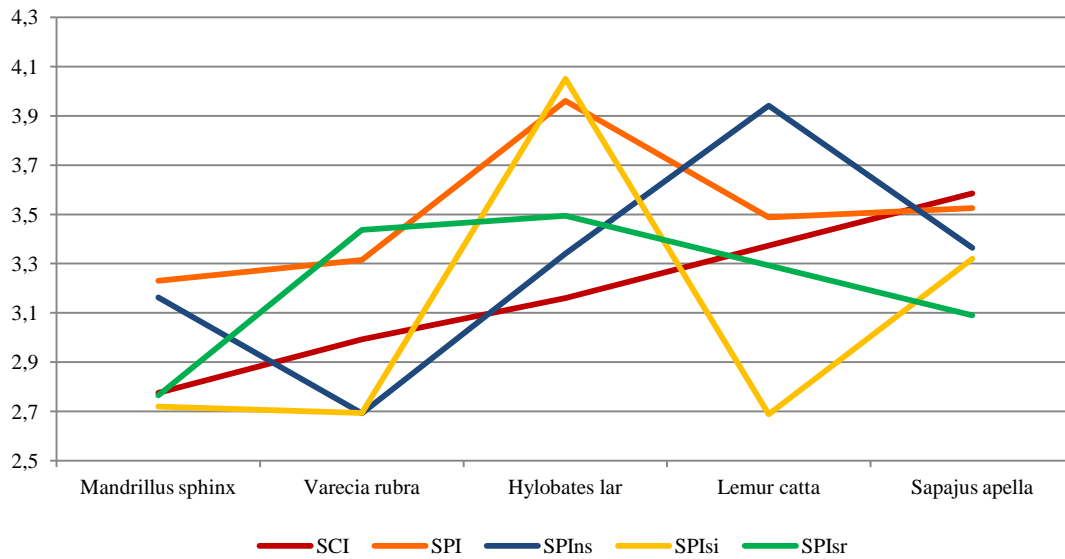


Figure 5.3 The graph represents the species complexity index, the species predictability index, and the other three indices, one relating to non-social behaviors, and two relating to social behaviors.

The degree of behavior predictability (SPI) also varied across the species that we studied. *Hylobates lar* had the highest SPI. With the exception of that species, the figure suggests some co-variance between SPI and SCI. Perhaps if a larger range of species were studied using the proposed methodology, a correlation across species between the two indices would be found. Regarding predictability of non-social behaviors (SPIns) *Lemur catta* is the most predictable species and *Varecia rubra* is the least predictable one. The most predictable species regarding social behaviors initiated by the focal animal (SPISI) is *Hylobates lar* followed by *Sapajus apella*. All the other species have comparatively lower values of SPISI. Regarding social behaviors received by the focal animal (SPISr), *Hylobates lar* and *Varecia rubra* are the most predictable species.

The Species Unusual Transition Index (SUTI) has an opposite tendency from the SCI. The number of unusual transitions tends to be higher in the less complex species (figure 4). All the other SUTI indices have a similar tendency to the SCI. Our understandings of these tendencies and their exceptions will be articulated in the next section.

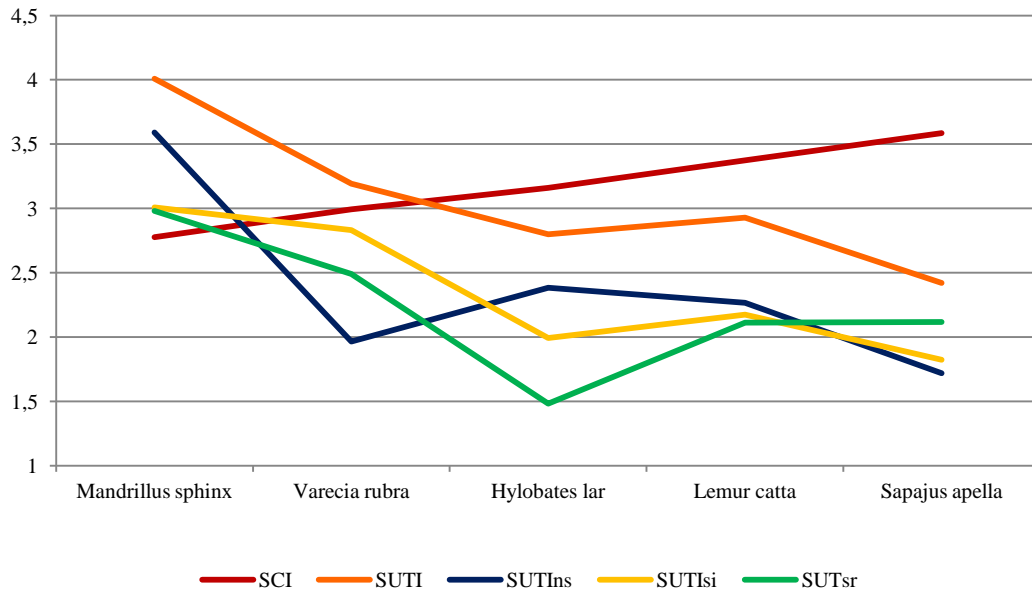


Figure 5.4 The graph represents the species complexity index, the species unusual transition index, and the other three indices, one relating to non-social behaviors, and two relating to social behaviors.

For non-social unusual transitions (SUTIns) *Varecia rubra* appears to be an exception presenting lower scores than might be expected from the species' relatively low SCI. For social unusual transitions (SUTIsi and SUTIsr) *Hylobates lar* appears to be an exception presenting lower results than might be expected from the species intermediate SCI.

## Discussion

This research demonstrates the richness of information that can be obtained by studying personality using the methods described above. These methods can also be used to study the relationships between personality diversity, flexibility and complexity on the one hand and cognitive, social and ecological differences within and across species on the other hand. The evolutionary implications of these relationships will be discussed.

## Diversity

Our results demonstrated that, as we expected, the most cognitively developed species, *Sapajus apella*, had the most diverse personalities. The individuals of the studied group had high diversity in both social and non social behaviors. *Mandrillus sphinx* also had high overall diversity scores, but this was attributable to very high diversity in ways of receiving social behaviors and much lower diversity in non-social behaviors. *Mandrillus sphinx* individuals appeared to be primarily concerned with adapting their behavior towards others. This concern may be explained by the hierarchical structure of their society, with large groups and high intra-sexual competition (K. A. Abernethy, White, & Wickings, 2002; Harrison, 1988; Singleton, 2012). *Lemur catta* is the species in which we found the highest level of diversity in non-social behaviors. This result might be explainable by the fact that, for lemurs in general, increased cognitive capacity does not seem to be a result of social factors, but rather a result of ecological factors such as the complexity of foraging challenges (MacLean et al., 2009) for which flexibility in non-social behavior might provide an evolutionary advantage.

Of the two strepsirrhines species, *Lemur catta* had more diverse personalities than *Varecia rubra* as was expected due to their differences in cognitive capacities (Brandão et al., in prep<sup>b</sup>). But these two lemurs' species both had more diverse personalities than *Saimiri bolivienses*. This result would need to be replicated in the future with a different *Saimiri boliviensis* group, since observations of this particular group were highly constrained by poor sightlines. Since the social organization of this species entails females staying in the center of the group's space, and the artificial houses functioned as the center of the physical context for our observations, females' behavior was especially difficult to observe. Nevertheless, the difference between *Saimiri boliviensis* and *Lemur catta* is understandable since *Lemur catta* have been found to have highly developed cognitive abilities. Moreover *Lemur catta* has a higher measured ratio (0.306) of frontal neocortical gray matter to total neocortical gray matter in comparison to what we could infer about *Saimiri boliviensis* from other research (a ratio of approximately 0.243) (Bush & Allman, 2004). Regarding *Varecia rubra* our results highlight the need for a better understanding of their cognitive abilities in comparison with *Saimiri boliviensis*, and of what this suggests regarding brain evolution. In general, our results indicate the need for more information about brain differences, especially



with regard to frontal neocortical brain areas.

Of the two catarrhines species, *Mandrillus sphinx* presented more diverse personalities than did *Hylobates lar*, reflected in all the diversity indices except the one related to non-social behaviors. This exception might be explained by social organization. *Hylobates lar* groups normally have female leadership in which females are polyandrous and present low levels of intra-group and inter-group physical aggression (Barelli, Boesch, et al., 2008; Bartlett, 2003). Consequently individuals might tend to be similar in social behavior while being more different in ways of interacting with the ecological environment. This explanation could also be applied to the result that in comparison with *Hylobates lar*, *Varecia rubra* scored higher in diversity regarding socially received behaviors. The latter species has female dominance but intra-group aggressive interactions are more frequent than in the former species (Kaufman, 1991; Michael E. Pereira, Kaufman, Kappeler, & Overdorff, 1990; Raps & White, 1995; White, Burton, Buchholz, & Glander, 1992). Consequently it is plausible to consider that *Varecia rubra* individuals may be more concerned about adapting their behavior responses to others' behavior.

### *Flexibility*

The two lemur species were found to have the most flexible personalities of the species studied. Since flexibility increases capacity to respond to environmental changes, this result might reflect an evolutionary response to the foraging complexities that lemurs faced in responding to ecological pressures (MacLean et al., 2009). Considering the four haplorrhines species studied, *Sapajus apella*'s scores indicate that they are the most flexible species regarding individuals' personalities. This flexibility is mainly related with social behaviors. Capuchins in general have complex and tolerant societies that allow for learning complex skills to develop over the course of years (Visalberghi and Faagaszy, 2012; Visalberghi, Valenzano, & Preuschoft, 2006). High personality flexibility gives individuals the opportunity to adapt their social behavioral in response to different social conditions. Similarly *Mandrills sphinx* has some degree of personality flexibility with respect to social behaviors, possibly a response to a complex environment in which hundreds of individuals, organized into smaller social units,

nevertheless have to co-exist. In contrast, *Hylobates lar* are especially flexible regarding non-social behaviors. This flexibility may be related to the great heterogeneity of results found in cognitive research with this genus.

### *Complexity*

Personality complexity refers to patterns of behavior specific to an individual. More complex personalities have more alternative subsequent behaviors for the same initial behavior. It is not surprising that the most complex personalities were observed in *Sapajus apella*, since according to prior research, this species is among the most cognitively evolved primate species. Prior research has also indicated that *Lemur catta* species has highly developed cognitive capacities relative to other strepsirrhines species. *Lemur catta* scored second highest on complexity measures of the species in our study.

Of our two species of catarrhines *Hylobates lar* demonstrated more complex personalities than *Mandrillus sphinx*. Although it is not clear if *Hylobates lar* is more cognitive developed than *Mandrillus sphinx*, the former species has a higher ratio (0.347) of frontal neocortical gray matter to total neocortical gray matter than does *Mandrillus sphinx* (0.269) (Bush & Allman, 2004). Even though they show less personality diversity than *Mandrillus sphinx*, it may make sense that *Hylobates lar*, as apes and members of the Hominoidea superfamily, showed more complex sets of stable alternative behavioral patterns. Even though the cognitive superiority of great apes and humans to monkeys is generally accepted, research has shown more variability in the cognitive abilities of the lesser apes (including *Hylobates lar*) in comparison to monkeys. While more research is clearly needed to explore and explained this variability, our research on personality suggests that *Hylobates lar*'s complexity of personality, may be indicative of an evolutionarily prior stage of complex brain-structural foundations needed for the higher cognitive capacities of great apes. Regarding the degree of predictability the different species have in their behavior, *Hylobates lar* is the species with the most predictable personalities, followed by *Sapajus apella* and then *Lemur catta*. This means that although complex, *Hylobates lar*'s behavior follows relatively stable patterns. With respect to sub-indices, *Hylobates lar* the species with most predictable social behavior, while *Lemur catta* is is the species

with most predictable non-social behavior, and *Sapajus apella* is a more balanced in its predictability, having high values for non-social and social initiating behaviors. We can hypothesize that these results derive from a difference in evolutionary pressures. *Lemur catta* may have been more responsive to ecological pressures, *Hylobates lar* may have been more responsive to social pressures, and *Sapajus apella* the most cognitively evolved species in our study may have been responding to both ecological and social pressures in combination. In *Sapajus apella* the high degree of personality stability and predictability regarding social behavior presumably decreases tensions in the group by using predictability to prevent conflicts. The high degree of personality stability and predictability regarding non-social behavior presumably decreases competition by establishing stable intra-group differences in behaviors for accessing resources, thus preventing conflicts.

Finally, although unusual transitions (those unexpected sequences of responses that do not follow common patterns for the group) were present in all species, the quantity of them showed an inverse relationship with complexity: species with more complex personalities have the fewest instances of unusual behavioral patterns. In an attempt to understand this inverse relationship, we considered that a lower likelihood of particular combinations might be the result of a natural selection process. We hypothesized that having lower levels of unusual behavior and lower levels of complexity make the individuals very similar to each other. Consequently, if significant environmental changes occur, then the species' probability of survival would be decreased. On the other hand, too high levels of unusual behaviors combined with too high levels of complexity, would make it too cognitively demanding for individuals to effectively manage the large variety of possible reactions of others. This would result in higher levels of conflict, which in turn would decrease the probability of survival either for the most unusual individuals or for the group as a whole. Consequently, the combinations of low complexity but high unusualness, and high complexity but low unusualness can be considered to have better survival probabilities, which would explain the inverse relationship found in our results.

### *Final Remarks on Personality Phylogeny*

The present research provides a rich perspective on personality. We have argued that the brain structure that allows the development of differentiated personalities, along with cognitive capacities, has evolved in response to both ecological and social pressures (Brandão et al. in prep<sup>a</sup>). While we expected that *Sapajus apella*, the most cognitively developed species that we studied, would demonstrate the most diverse, flexible and complex personalities, we found that their scores were the highest only in diversity and complexity. We also found that their predictability index was relatively high. We understand these results as follows: the relatively low FSI that we found for *Sapajus apella* is based on analyzing the variability of behavioral categories without considering behavioral sequences. In contrast the SCI and the SPI are both based on behavioral sequences. We see the high scores on the latter two indices as compensating for the relatively low SFI scores, in providing both flexibility (through more ways of combining behaviors) and predictability. Our data suggest the phylogenetic possibility of personality increasing flexibility through complex combinations of behavior while maintaining consistency of behavior across time.

To further explore implications of these findings for primate brain and personality phylogeny, it is important to first replicate our study with other groups of the same species we studied. Beyond that, studying additional species using the same methods also will be very important. For example, it would be important to see whether we find results consistent with what we found for *Sapajus apella* in the most cognitively developed non-human primate species. Such results would suggest that similar adaptive strategies may have played similar important roles in these other species' evolutionary responses. It would be equally important to explore personality in less cognitively developed species in order to understand the earlier stages of the process of personality phylogeny.

Furthermore, assessing personality using direct behavior observation and the present methodology will allow discrimination 1) of the species for whom brain evolution appears to be more driven by ecological factors – the “ecological” hypothesis (DeCasien et al., 2017) from 2) species for whom brain evolution appears to be more driven by social factors – the social brain hypothesis (Dunbar, 2009; Dunbar & Shultz, 2007), as well as from 3) species for whom both social and ecological pressures contributed to

brain evolution in more balanced ways. More data from more species researched using the methodology illustrated here will also allow us to confirm whether this approach is as promising as it seems to us now.

The species available for observation and the periods of time available constrained our choices of species for this study. Nevertheless, in the light of our efforts to consider the main branches of the primate family tree, we are currently very hopeful regarding the promise of the results we obtained, and we hope to have demonstrated the usefulness of this methodological approach for the study of primate personality.

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## **Chapter 6 - Epilogue-Prologue**

At the core of the work presented in this thesis is an exercise in deductive thinking. This exercise, explained in chapter 1, starts from three premises about the personality of primates. The first premise: Personality is a dynamic structure, changing through the individual's ontogeny; the second premise: Personality organizes interactions with the external world into a complex internal model; and the third premise: Personality evolved through primates' phylogeny along with the brain structures that sustain it. The author reviews a set of researches through the lenses of these premises, selecting the ones most relevant to demonstrating that personality can be studied ontogenetically, considering the first two premises, and phylogenetically, considering the last premise. These researches regarding brain function, development and evolution provide a basis for deducing a neurodevelopmental theory of personality that integrates those research results and the three premises into coherent explanation of personality ontology and phylogeny in primates. This theory proposes that every primate has a continually changing, neurologically based, internal model of self in relation with environment that dynamically integrates environmental information (physical and social). Personality is seen as an emergent property of this neurological functioning.

The neurodevelopmental theory of personality proposed in this thesis allows us to answer Niko Tinbergen's (1963) four questions, normally raised by the study of behavior:

“How does it work? (Proximate causation or control) - The personality as a dynamic structure works as a model of the external world. Based on this model, the organism makes decisions that translate into behaviors. The consequences of these behaviors, both internal and external, are incorporated into the model as new information, in order to fine-tune its predictions.

"How did it develop?" (Development or ontogeny) - This model is based on a neurological structure. This structure will initially develop depending on the genetic information that determines the formation of the neurological structure. Later the learning process will determine the cognitive-emotional structure of the model – the model represents the world in relation to the individual. This model can be seen as the set of neural networks that will dynamically organize and use the information that is acquired. The model gains stability over the individual's ontogeny (therefore

individuals' behavior become more stable), as it becomes progressively more capable of making correct predictions.

"What is it for?" (Function) – The main function of the personality is the organization of environmental information, especially social information, in order to make decisions (which trigger behaviors) based on the predictions that the model produces. In this way, the model allows quick decisions, especially in complex social environments and in ambiguous situations, making the individual more effective in his/her response to environmental challenges. This in turns increases chances of survival and reproductive success.

"How did it evolve?" (Evolution or phylogeny) – Because the personality is based on a neurological structure it is possible to study its evolution by studying the evolution of this neurological structure. The neuronal areas involved evolved in response to the increasing complexity challenges of the physical and social environment. The neuropsychological functions associated with these areas developed throughout evolution, corresponding to an increase in the capacities for prediction and managing progressively larger amounts of information, especially of an ambiguous type. Animals with these more developed neuronal areas have greater prediction and management skills (that is, they have more developed executive functions).

Approaching the personality from this neurodevelopmental theoretical point of view allows resolving the nature vs. nurture tension, as gives a theoretical foundation to the idea of continuity among primate species.

This summary of the theoretical aspect of this thesis could be considered as an "Epilogue," from the Greek *epílogos* (ἐπίλογος), "conclusion" derived from *epi* (ἐπί), "in addition" and *logos* (λόγος), "word" or "reason." However, the author would like the proposed theory to be a prologue for the study of personality in the future. "Prologue" (from the Greek *prólogos* - προλογος), is a term that began to be used in the Greek tragedy, and that enunciated the theme of the play. Etymologically *pro* (πρό) means "before" and *logos* (λογος) "word" or "reason." Since Heraclitus (535 – 475 BC), the word *logos* begin to be used to mean knowledge. Accordingly, the author would like the proposed theory to be considered as opening the way to knowledge. In other words, to be considered as an initiator of a dynamic process of reflection and investigation of



knowledge about the personality which is integrative and above all transdisciplinary. A theory that would evolve, integrating reflections in several areas from paleontology and archeology to artificial intelligence and medical bionics.

This theoretical work of marked transdisciplinary character assumes that understanding the phenomenon of personality cannot be accomplished within a single discipline. Although research within this theoretical framework can be interdisciplinary, understanding the meaning of the results of that research requires a transdisciplinary approach. Therefore, the author's hope is that other researchers in the future will be interested in building on this theoretical approach. The author believes that the theoretical proposal made can be refined as new scientific data emerge.

The author also hopes this theory may be of interest to researchers within the broad context of philosophy of science. Although the theoretical proposal allows understanding the ontogeny and phylogeny of personality in primates, a more in-depth reading of it may reveal that it will probably never be possible to fully understand all the variables involved in personality ontogeny and phylogeny and the mechanisms of interaction between them. For example, personality is idiosyncratic, so each individual is unique, especially in more cognitively developed species like humans. The proposed theory explains how this idiosyncrasy arises. Still, it also highlights that one will probably never be able to fully understand and predict how personality will develop throughout an individual's life. There are limitations to possible explanations at the phylogenetic level, as well, as there are important information gaps regarding knowledge about behavior and neurophysiology in extinct species.

This theory of personality poses important philosophical questions with social implications. For example: Are we really so different from other species, especially primate species? How much does the recognition of individuality in other species, pose a question of to what extent humans have guardianship responsibility to other primates? If they do, what would be the legal implications? How responsible are we, as a society, for human individuals' personality ontogeny? Shouldn't we assume a more active role in creating the most adequate child-rearing conditions? How much will our different decisions in facing global environmental threats ultimately impact the development of more "humane" vs. more cruel human beings? Will a robot with capacity to learn through interaction with the environment develop a personality? If it is possible for

robots to develop personalities, what should be the legal framework for regulating robot behavior? Could personality disorders develop in these non-living objects and if so, how should humans deal with them? All of the previous questions and others that could be posed challenge the commonly assumed borders between humans and non-humans as well as the assumed scope of our social responsibility. In times of huge social, environmental and physical change, the neurodevelopmental theoretical perspective of personality provides a lens through which to reflect on much broader range of issue than personality psychology of earlier eras typically considered.

The neurodevelopmental personality theory at the center of this thesis also led, at the empirical level, to a novel approach to the collection and processing of data about personality. This approach was used in a series of studies reported in chapters 2, 3 and 4. In this research, direct behavioral observation was used as a means of reducing bias in data collection that was characteristic of much prior research. Data collection no longer depended on subjective assessments of the individuals' behavior and implicit comparisons of them with other members of the species or even others' species. After data collection, the data were treated in such a way that each individual was compared with the members of his/her own group. Thus, the relative aspect of each individual's personality description is interpreted according in relation to other members of the group to which s/he belongs. This methodological simplicity in data collection allows the use of databases containing information that were not initially collected based on an a priori model of personality assessment. This possibility is a great advantage and confirms that it is possible to make assessments regarding the personality of the observed individuals independently of theoretical personality models, i.e., observers may be blind to any pre-conceived objectives of the observation.

The author defined three general personality indices: diversity, flexibility, and complexity. The use of these three indices is a novelty in the study of personality in primates. "Diversity" consists of the number of behaviors distinguishing individuals. "Flexibility" assesses the behavior variability for each individual. Finally, "Complexity" represents the range of alternative behavior patterns that are found in each individual (as well as the degrees of the individual's predictability and uniqueness). These novel methods make it possible to analyze individuals in relation to group without losing the richness of analysis at the level of the individuals' unique personalities.

Based on the three mentioned indices, it was possible to develop other indices that allow inter-species comparison: the Species Diversity Index, the Species Flexibility Index, and the Species Complexity Index, reported in chapters 4 and 5. This comparison respects species-specific characteristics, as the observations are guided by each species' ethogram separate from the data analysis of the distribution and patterns of behaviors within each species and each individual assessed. To repeat, it is possible to use this methodology as a blind assessment of personality using behavioral observations. This degree of control of the assessment bias in areas where there may be a subjective interpretation of the behavior is generally associated with laboratory tests in a controlled environment. This methodological proposal allows the same degree of control for personality assessment with observations made both within and outside of laboratory environments.

Within the overall context of the goals of this thesis, the use of this methodology allowed the collection and analysis of data from several species. These included mandrills, gibbons, red-ruffed lemurs, and ring-tailed lemurs, for which there was little or no prior research on personality. The comparison among species provided initial support to a phylogenetic claim of the thesis' theoretical proposal: The more cognitively developed species will present more differentiated personalities.

It is hoped that this research approach will be progressively more used in studies of personality as well as studies whose central foci is not personality. This methodology has the advantage of not represent an additional effort to behavioral data collection. This methodology allows researching personality in its interactions with other variables. The method was published in the article "Using behavior observations to study personality in a group of capuchin monkeys (*Cebus apella*) in captivity," and has been used by other researchers, to explore the relationships between personality and social network construction in capuchin monkeys (article in prep.). The author hopes that this will be the beginning of a research effort to include "personality" as one of the variables to consider in studies of primate behavior.

Finally, this methodology allows studies on personality ontogeny to be carried out with less data-collection effort and less vulnerability to effects of subjectivity. Since it does not depend on subjective assessments, it does not require the training of observers, and data collection does not need to be done by the same researchers. It is enough to have

data regarding the same variables at various points in time for longitudinal studies to be carried out. As the observed variables are considered as independent, even if the data collection does not include from the beginning all the variables observed at other points in time, those variables that are comparable can be studied independently of the remaining variables that are not. Longitudinal personality studies are thus made more accessible. Currently, there is already data collected that will allow us to complete a longitudinal study concerning capuchin monkeys building on the data in chapter 2. It is possible that several research groups already have observation data over the years from groups of various species. Within the framework articulated in this thesis, these data can be used to assess personality and its ontogenetic changes.

In sum, the author hopes that this empirical work will also be a prologue for the future approach to empirical personality research in primates and perhaps even non-primates! It will be up to future researchers to assess the relevance and usefulness of the methodology for the goals of their investigations.

# **Supplementary Materials**

## Supplementary Material

### A. Using behavior observations to study personality in a group of capuchin monkeys (*Cebus apella*) in captivity

Table S1. Ethogram of the behaviors reported in this study. Although Affiliation category is very broad and certainly some behaviors included might show differences due to personality, we decided to maintain all into the same category group to prevent the increase of total number of variables to be observed, under the assumption that the differences in some of the behaviors included would not obscure potential differences in the broad category (Continued on the next page).

	<b>Class behaviour</b>	<b>Definition</b>
<b>Individual</b>	<b>Self-grooming</b>	Picking his own dirt and ticks and/or brushes his hair or skin with the mouth and/or hand(s). Self-groom of injuries is not included in this category. The subject picks up a substance (e.g. fruits, insects, leaves) and rub it over its own fur with its hands and feet.
	<b>Scent marking</b>	Blotting a certain spot through odour, with urine, faeces or with the discharge of glandular secretions, anogenital rasping, foot rasping and chest rasping.
	<b>Solitary play</b>	Running unusually, flipping, spinning, including acrobatic moves. May include an alimentary item. May manipulate enrichment and other artificial devices as well as branches and wood.
	<b>Affiliation</b>	Sitting together with touching body, foraging together, food solicitation/providing, chasing/moving together, lip smack, eyebrow raising, head tilt, chest rubbing, back into lap, genital display, reunion display. Includes also social grooming (an individual request or provides cleaning of the hair or skin with mouth and/or hands by another individual).
	<b>Courtship/ sex act</b>	Genital display, turning head and reaching back, genital inspection, touching and running, extended arms, nuzzling, body touching, frontal/back posture, backing into lap/mounting solicitation, chest rubbing, head tilt, eyebrow raising/scalp lift, with grin and vocalization, submissive grin/silent bared-teeth display, mutual gaze, mounting attempt, mounting, ejaculation, masturbation.
	<b>Play</b>	Relaxed open mouth, open mouth silent bared-teeth, mutual gazing, head cocking, back posture, genital display, mounting, fighting, tug-of-war, pulling the tail, grabbing, slipping down in a spiral.
	<b>Ritualized Agonism</b>	Vocal exchange, threat display, open-mouth threat face.
<b>Social</b>	<b>Aggression</b>	Aggression with contact, coalition.
	<b>Ritualized Submission</b>	Submissive grin/silent bared-teeth display, open mouth grin/ open-mouth silent bared-teeth, eyebrow raising/scalp lift, head tilt.
	<b>Effective Submission</b>	Submissive retreat/fleet.
	<b>Parenting</b>	Brest feeding, parental grooming, infant transport, restrain. Head cocking, frontal posture.

	<b>Class behaviour</b>	<b>Definition</b>
<b>Rare</b>	<b>Abnormal behaviour</b>	Stereotypic (head twirl, pacing, rocking), self-injurious (hair pulling, mutilation, head banging, stereotypic scratching, sucking fingers or hand), excessive self-grooming, coprophagy.
	<b>Others</b>	Any behaviour (social or individual) not described by this catalogue.
	<b>Not visible</b>	Out of the observer's sight – observer can't disclose the behaviour that the individual is performing.

Table S2. Descriptive statistics for categories for which significant relationships were found. Includes group means and group maximums, and each individual has its own mean and maximum per category. In bold are the highest means and the highest maximums, in grey are the lowest means (Continued on the next page).

<b>Behavioral Categories</b>	Group		Pr		Ch		Br		El		Mg		In	
	mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.
Self-grooming	0.003	0.567	0.002	0.104	0.001	0.030	0.000	0.005	0.001	0.020	0.001	0.069	0.003	0.048
Solitary Play	0.007	0.682	0.001	0.079	0.000	0.025	0.012	0.577			0.015	0.582		
Urine Wash	0.001	0.009	0.000	0.003	0.000	0.003	0.001	0.005	0.001	0.004	0.000	0.003	0.001	0.005
Affiliation Initiator	0.136	1.000	0.217	0.985	0.221	0.857	0.205	0.985	0.053	0.604	0.085	0.807	0.036	0.297
Affiliation Initiator Event	0.000	0.017	<b>0.000</b>	0.003	0.001	0.007	0.000	0.010			0.001	0.009	<b>0.001</b>	0.017
Play Initiator	0.008	0.672	0.001	0.057	0.003	0.200					0.016	<b>0.672</b>	0.018	0.628
Play Initiator Event	0.000	0.004									0.000	0.002		
Ritual Agonism Initiator Event	0.000	0.010	0.000	0.002	<b>0.000</b>	0.002	0.000	0.002			<b>0.000</b>	<b>0.010</b>	0.000	0.003
Aggression Initiator	0.000	0.039	0.000	0.014	0.000	0.014	0.000	0.004	<b>0.001</b>	<b>0.039</b>	0.000	0.002	0.000	0.005
Aggression Initiator Event	0.000	0.014	0.000	0.002	0.000	<b>0.014</b>	0.000	0.004	0.000	0.002	0.000	0.002	0.000	0.005
Ritual Submission Initiator Event	0.000	0.007			0.000	0.003	0.000	0.002	0.000	0.003	<b>0.000</b>	0.002	0.000	0.002
Effective Submission Initiator	0.001	0.060			0.000	0.003			0.001	0.007	0.000	0.002	0.001	0.032
Effective Submission Initiator Event	0.000	0.010			0.000	0.003			<b>0.001</b>	0.007	0.000	0.002	0.001	0.007
Affiliative Receiver	0.122	1.000	0.120	<b>1.000</b>	0.094	0.767	<b>0.228</b>	0.886	0.078	0.752	0.112	0.990	0.069	0.545
Affiliative Receiver Event	0.000	0.012	0.000	0.009	0.000	0.002	0.000	0.007	0.000	0.002	0.000	0.003	0.000	0.003
Play Receiver Event	0.000	0.000			<b>0.000</b>	0.000			0.000	0.000	0.000	0.000	0.000	0.000
Aggression Receiver Event	0.000	0.005			0.000	0.002			<b>0.000</b>	0.002	0.000	0.002	0.000	<b>0.005</b>
Ritual Submission Received Event	0.000	0.018	0.000	0.002	0.000	0.004	0.000	0.003			0.000	0.005	0.000	0.003

Behavioral Categories	Group		Pr		Ch		Br		El		Mg		In	
	mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.
Effective Submission Receiver Event	0.000	0.008	0.000	0.005	0.000	0.005	0.000	0.008	0.000	0.003	0.000	0.002	0.000	0.002
Arms Reach	0.015	0.389	0.018	0.081	0.019	0.038	<b>0.026</b>	<b>0.389</b>	<b>0.007</b>	0.018	0.011	0.029	0.008	0.053
Arms Reach 1	0.009	0.111	0.010	0.048	0.012	0.037	0.013	<b>0.111</b>	<b>0.005</b>	0.015	0.006	0.017	0.006	0.025
Arms Reach 2	0.004	0.222	0.006	0.032	0.004	0.017	<b>0.009</b>	<b>0.222</b>	<b>0.001</b>	0.008	0.003	0.012	0.001	0.023
Arms Reach 3	0.001	0.056	0.002	0.015	0.001	0.010	<b>0.003</b>	<b>0.056</b>	0.000	0.005	0.001	0.008	0.000	0.005
Arms Reach 4	0.000	0.036	0.000	0.005	0.000	0.007	0.001	0.011			0.000	0.002	<b>0.000</b>	0.002

Table S3. Continuation of S2. Descriptive statistics for categories for which significant relationships were found. Includes group means and group maximums, and each individual has its own mean and maximum per category. In bold are the highest means and the highest maximums, in grey are the lowest means (Continued on the next page).

Behavioral Categories	Na		Az		Ba		Bu		Kr		Ga		Pe		Bo	
	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.
Self-grooming	0.000	0.015	0.001	0.029	<b>0.013</b>	0.350	0.012	<b>0.567</b>	<b>0.000</b>	0.007			0.004	0.140	0.006	0.208
Solitary Play	0.001	0.077	<b>0.064</b>	<b>0.682</b>	0.002	0.110			0.002	0.049	0.000	0.025	<b>0.000</b>	0.008	0.015	0.323
Urine Wash	0.000	0.004	0.001	0.005	<b>0.000</b>	0.004	0.001	<b>0.009</b>	0.001	0.005	0.000	0.004	<b>0.001</b>	0.009	0.000	0.004
Affiliation Initiator	0.060	0.573	<b>0.014</b>	0.153	0.037	0.380	0.202	<b>1.000</b>	<b>0.315</b>	0.890	0.092	<b>1.000</b>	0.148	0.945	0.217	<b>1.000</b>
Affiliation Initiator Event	0.000	0.012	0.001	<b>0.017</b>	0.000	0.010	0.000	0.005	0.000	0.005	0.000	0.007	0.000	0.013	0.000	0.005
Play Initiator			<b>0.046</b>	0.621					0.030	0.290			<b>0.001</b>	0.030	0.014	0.313
Play Initiator Event			<b>0.000</b>	<b>0.004</b>					0.000	0.002			<b>0.000</b>	0.002	0.000	0.002
Ritual Agonism Initiator Event					0.000	0.002	0.000	0.002	0.000	0.003			0.000	0.002	0.000	0.003
Aggression Initiator	<b>0.000</b>	0.002	0.000	0.003	0.001	0.007	0.000	0.010	0.000	0.003	0.000	0.005	0.000	0.008	0.000	0.005
Aggression Initiator Event	0.000	0.002	0.000	0.003	<b>0.001</b>	0.007	0.000	0.002	0.000	0.003	0.000	0.005	<b>0.000</b>	0.002	0.000	0.005
Ritual Submission Initiator Event			<b>0.000</b>	0.002	0.000		0.000	0.002	0.000	<b>0.007</b>	0.000	0.002	0.000	0.003		
Effective Submission Initiator	0.001	0.005	<b>0.002</b>	<b>0.060</b>	0.000	0.002	0.000	0.003	<b>0.000</b>	0.003	0.001	0.005	0.001	0.010		
Effective Submission Initiator Event	0.001	0.005	0.001	0.005	0.000	0.002	0.000	0.003	<b>0.000</b>	0.003	0.001	0.005	0.001	<b>0.010</b>	0.000	0.002
Affiliative Receiver	0.128	<b>1.000</b>	<b>0.054</b>	0.590	0.141	0.828	0.120	<b>1.000</b>	0.134	0.827	0.225	<b>1.000</b>	0.075	0.820	0.078	0.608



Behavioral Categories	Na		Az		Ba		Bu		Kr		Ga		Pe		Bo	
	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.	Mean	max.
Affiliative Receiver Event	<b>0.000</b>	0.002	0.000	0.005	0.000	0.003	<b>0.000</b>	<b>0.012</b>			0.000	0.002	0.000	0.003	0.000	0.003
Play Receiver Event	0.000	0.000	<b>0.000</b>	0.000			0.000	0.000	0.000	0.000			<b>0.000</b>	0.000	0.000	0.000
Aggression Receiver Event	0.000	0.003	0.000	0.003	0.000	0.002	0.000	0.002	0.000	0.004	<b>0.000</b>	0.002	0.000	0.002	0.000	0.002
Ritual Submission Received Event			<b>0.000</b>	0.002			0.000	0.005	0.000	0.003	<b>0.000</b>	<b>0.018</b>	0.000	0.005	<b>0.000</b>	0.002
Effective Submission Receiver Event	<b>0.000</b>	0.003	0.000	<b>0.008</b>	0.000	0.003	<b>0.001</b>	0.007	0.000	0.003	0.000	0.007	0.000	0.005	0.000	0.007
Arms Reach	0.008	0.034	0.011	0.053	0.009	0.038	0.016	0.120	0.025	0.055	0.015	0.054	0.008	0.035	0.023	0.092
Arms Reach 1	0.006	0.026	0.009	0.029	0.008	0.026	0.010	0.048	<b>0.014</b>	0.034	0.009	0.030	0.005	0.013	0.014	0.044
Arms Reach 2	0.001	0.012	0.002	0.021	0.002	0.012	0.005	0.080	0.007	0.022	0.005	0.043	0.002	0.015	0.006	0.039
Arms Reach 3	0.000	0.006	0.000	0.006	<b>0.000</b>	0.005	0.000	0.003	0.002	0.009	0.001	0.015	0.000	0.005	0.003	0.027
Arms Reach 4					0.000	0.003			0.001	0.011	0.000	0.003	0.000	0.018	<b>0.001</b>	<b>0.036</b>

Table S4. The table presents the group variance and individual variability for the categories with variance different from zero in at least one of the animals in the group (Continued on the next page).

Behavioral Categories	Group Variande	Pr	Ch	Br	El	Mg	In	Na	Az	Ba
		Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Self-grooming	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
Sent Marking	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Solitary Play	0.002	0.000	0.000	0.006	0.000	0.006	0.000	0.000	0.014	0.000
Solitary Play event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Urine Wash	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Affiliation Initiator	0.046	0.079	0.042	0.079	0.015	0.018	0.004	0.014	0.001	0.006
Affiliation Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sex Initiator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Play Initiator	0.003	0.000	0.001	0.000	0.000	0.009	0.008	0.000	0.011	0.000
Play Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Initiator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

		Pr	Ch	Br	El	Mg	In	Na	Az	Ba
<b>Behavioral Categories</b>	<b>Group Variande</b>	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Ritual Agonism Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aggression Initiator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aggression Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Submission Initiator	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000
Ritual Submission Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Effective Submission Initiator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Effective Submission Initiator Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Parental Behavior	0.056	0.078	0.033	0.000	0.000	0.000	0.010	0.098	0.000	0.002
Affiliative Receiver	0.038	0.039	0.026	0.045	0.020	0.050	0.018	0.036	0.016	0.034
Affiliative Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sex Receiver	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Play Receiver	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.000
Play Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Receiver	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aggression Receiver	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aggression Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Submission Received	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ritual Submission Received Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Effective Submission Receiver	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Effective Submission Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Abnormal Behavior	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.001	0.000
Abnormal Behavior Event	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 2	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S5. Continuation of table S4. The table presents the group variance and individual variability for the categories with variance different from zero in at least one of the animals in the group (Continued on the next page).

	Bu	Kr	Ga	Pe	Bo
<b>Behavioral Categories</b>	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Self-grooming	0.005	0.000	0.000	0.000	0.001
Sent Marking	0.000	0.000	0.000	0.000	0.000
Solitary Play	0.000	0.000	0.000	0.000	0.002
Solitary Play event	0.000	0.000	0.000	0.000	0.000
Urine Wash	0.000	0.000	0.000	0.000	0.000
Affiliation Initiator	0.084	0.064	0.029	0.063	0.042
Affiliation Initiator Event	0.000	0.000	0.000	0.000	0.000
Sex Initiator	0.000	0.000	0.000	0.000	0.000
Play Initiator	0.000	0.005	0.000	0.000	0.003
Play Initiator Event	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Initiator	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Initiator Event	0.000	0.000	0.000	0.000	0.001
Aggression Initiator	0.000	0.000	0.000	0.000	0.000
Aggression Initiator Event	0.000	0.000	0.000	0.000	0.000
Ritual Submission Initiator	0.000	0.000	0.000	0.000	0.000
Ritual Submission Initiator Event	0.000	0.000	0.000	0.000	0.000
Effective Submission Initiator	0.000	0.000	0.000	0.000	0.000
Effective Submission Initiator Event	0.000	0.000	0.000	0.000	0.000
Parental Behavior	0.043	0.032	0.211	0.000	0.034
Affiliative Receiver	0.026	0.045	0.071	0.029	0.021
Affiliative Receiver Event	0.000	0.000	0.000	0.000	0.000
Sex Receiver	0.000	0.000	0.000	0.000	0.000
Play Receiver	0.000	0.000	0.000	0.000	0.000
Play Receiver Event	0.000	0.000	0.000	0.000	0.000
Ritual Agonism Receiver	0.000	0.000	0.000	0.000	0.001
Ritual Agonism Receiver Event	0.000	0.000	0.000	0.000	0.000
Aggression Receiver	0.000	0.000	0.000	0.000	0.000

	Bu	Kr	Ga	Pe	Bo
<b>Behavioral Categories</b>	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Aggression Receiver Event	0.000	0.000	0.000	0.000	0.000
Ritual Submission Received	0.000	0.000	0.000	0.000	0.000
Ritual Submission Received Event	0.000	0.000	0.000	0.000	0.000
Effective Submission Receiver	0.000	0.000	0.000	0.000	0.000
Effective Submission Receiver Event	0.000	0.000	0.000	0.000	0.000
Abnormal Behavior	0.000	0.000	0.000	0.000	0.000
Abnormal Behavior Event	0.000	0.000	0.000	0.000	0.000
Arms Reach	0.000	0.000	0.000	0.000	0.000
Arms Reach 1	0.000	0.000	0.000	0.000	0.000
Arms Reach 2	0.000	0.000	0.000	0.000	0.000
Arms Reach 3	0.000	0.000	0.000	0.000	0.000
Arms Reach 4	0.000	0.000	0.000	0.000	0.000
Arms Reach 5	0.000	0.000	0.000	0.000	0.000
Arms Reach 6	0.000	0.000	0.000	0.000	0.000

Table S6. The table presents the abbreviations of the behavioural categories analyzed using the EthoSeq Software to analyze the behavioral transitions and sequences.

<b>BEHAVIOR CATEGORY</b>	<b>BEHAVIOR</b>	<b>ABBREVIATION</b>
<b>NON SOCIAL BEHAVIORS</b>	Self-grooming	Selfg
	Scent Marking	Scent
	Solitary Play	Solplay
	Urine Wash	UW
<b>SOCIAL BEHAVIOR</b>	Affiliation Initiator	Affi
	Sex Initiator	Sexi
	Play Initiator	Playi
	Parental Behaviour	Parent
	Ritual Agonism Initiator	Ritagi
	Aggression Initiator	Effagi
	Ritual Submission Initiator	Ritsubi
	Effective Submission Initiator	Effsubi
	Affiliative Receiver	Affir
	Infant Affiliation Receiver	Affrinfant
	Sex Receiver	Sexr
	Play Receiver	Playr
	Ritual Agonism Receiver	Ritagr
	Aggression Receiver	Effagr
	Ritual Submission Received	Ritsubr
	Effective Submission Received	Effsubr
<b>RARE</b>	Abnormal Behavior	Abnorm

Table S7. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S1). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group (Continued on the following pages).

	<b>Group</b> 1st trans.		<b>Pr</b> 1st trans.		<b>Ch</b> 1st trans.		<b>Br</b> 1st trans.		<b>El</b> 1st trans.		<b>Mg</b> 1st trans.	
<b>Selfgrooming</b> (sg)	affi rec	31.37%	affi ini	50.00%	affi ini	100.00%	affi ini	50.00%	uw	50.00%	uw	100.00%
	affi ini	27.45%	rit ag ini	25.00%			affi rec	50.00%	rit sub ini	50.00%		
<b>Solitary Play</b> (soli play)	affi ini	29.11%	parent	25.00%	effe sub ini	50.00%	affi rec	100.00%			affi ini	83.33%
	affi rec	24.05%	affi rec	100.00%	parent	50.00%						
	play ini	18.99%										
<b>Urine Wash</b> (uw)	affi ini	40.86%	affi rec	37.50%	affi ini	61.54%	affi rec	55.56%	affi rec	42.86%	affi ini	41.67%
	affi rec	26.88%	parent	37.50%					effe sub ini	28.57%		
<b>Scent Marking</b> (sm)	affi ini	50.00%					affi rec	33.33%			affi ini	100.00%
	affi rec	25.00%					affi ini	33.33%				
	uw	25.00%					uw	33.33%				
<b>Affiliation Initiator</b> (affi ini)	affi rec	45.58%	parent	39.24%	affi rec	62.96%	affi rec	72.00%	affi rec	38.10%	affi rec	37.74%
<b>Sex Initiator</b> (sex ini)	affi ini	33.33%			sex rec	100.00%	affi ini	100.00%			rit ag ini	100.00%
	affi rec	22.22%										
	sex rec	22.22%										
<b>Play Initiator</b> (play ini)	affi ini	38.20%	affi ini	41.67%	affi ini	50.00%					affi ini	40.00%
	affi rec	17.98%	affi rec	33.33%	affi rec	50.00%					affi rec	40.00%
<b>Ritual Initiator</b> (rit ag ini)	<b>Agonism</b>											
	affi ini	29.09%	affi ini	50.00%	affi rec	100.00%	rit sub rec	57.14%			affi ini	25.00%
	affi rec	20.00%	affi rec	25.00%							rit sub rec	33.33%
	effe sub rec	14.55%	effe sub rec	25.00%								
	rit sub rec	14.55%										

	<b>Group</b> 1st trans.		<b>Pr</b> 1st trans.		<b>Ch</b> 1st trans.		<b>Br</b> 1st trans.		<b>El</b> 1st trans.		<b>Mg</b> 1st trans.	
<b>Aggression Initiator</b> (effe ag ini)	effe sub rec	38.89%	rit sub rec	50.00%	affi ini	33.33%	effe sub rec	50.00%	affi rec	50.00%		< 25%
	affi rec	19.44%	rit ag rec	25.00%	affi rec	33.33%	affi rec	33.33%	effec sub ini	50.00%		
	affi ini	16.67%	effe ag rec	25.00%	effe sub rec	33.33%						
<b>Ritual Submission Initiator</b> (rit sub ini)	affi rec	41.38%			affi ini	100.00%			affi rec	100.00%	abnorm	60.00%
<b>Effective Submission Initiator</b> (effe sub ini)	affi rec	42.48%			affi ini	50.00%			affi rec	62.96%	affi ini	57.14%
	affi ini	24.84%			uw	25.00%					abnorm	42.86%
<b>Parental Behavior</b> (parent)	affi rec	50.00%	affi ini	61.11%	affi rec	50.00%						
	affi ini	37.18%	affi rec	31.48%	solu play	33.33%						
<b>Affiliative Receiver</b> (affi rec)	affi ini	47.08%	affi ini	56.60%	affi ini	62.96%	affi ini	60.32%		< 25%	affi ini	54.84%
<b>Sex Receiver</b> (sex rec)	affi ini	50.00%	abnorm	100.00%	sex ini	50.00%						
	affi rec	25.00%			affi ini	50.00%						
	sex ini	25.00%										
<b>Play Receiver</b> (play rec)	affi rec	32.65%			affi rec	66.67%			affi rec	50.00%	affi ini	50.00%
	play ini	20.41%							effe sub ini	50.00%	play ini	50.00%
	solu play	18.37%										
<b>Ritual Agonism Receiver</b> (rit ag rec)	rit sub ini	27.27%	affi rec	50.00%	affi ini	100.00%	sex ini	100.00%	uw	100.00%	rit sub ini	50.00%
	affi rec	18.18%	parent	50.00%							effe ag rec	50.00%
<b>Aggression Receiver</b> (effe ag rec)	effe sub ini	55.56%	rit ag ini	100.00%	effe sub ini	50.00%			effe sub ini	54.55%	uw	50.00%
	affi ini	17.78%			affi rec	50.00%					rit ag ini	50.00%

	<b>Group</b> 1st trans.		<b>Pr</b> 1st trans.		<b>Ch</b> 1st trans.		<b>Br</b> 1st trans.		<b>El</b> 1st trans.		<b>Mg</b> 1st trans.		
<b>Ritual Submission Received</b> (rit sub rec)	affi ini 37.78%	affi ini 31.11%	affi ini 40.00%	parent 40.00%	affi ini 100.00%	affi ini 37.50%	affi rec 37.50%				affi ini 50.00%	rit ag ini 50.00%	
			affi rec 20.00%										
<b>Effective Submission Receiver</b> (effe sub rec)	affi rec 42.48%	affi ini 24.84%	affi ini 41.67%	affi rec 33.33%	affi rec 57.14%	affi ini 33.33%	affi rec 33.33%	affi ini 33.33%	affi ini 33.33%	affi rec 33.33%	effe sub ini 33.33%	affi ini 33.33%	rit ag ini 33.33%
<b>Abnormal Behavior</b> (abnorm)	affi ini 40.00%		effe ag ini 100.00%									affi ini 50.00%	



Table S8. Continuation of table S7. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S1). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group (Continued on the following pages).

	<b>In</b> 1st trans.		<b>Na</b> 1st trans.		<b>Az</b> 1st trans.		<b>Ba</b> 1st trans.		<b>Bu</b> 1st trans.		<b>Kr</b> 1st trans.	
<b>Selfgrooming</b> (sg)	affi rec	40.00%	affi rec	100.00%	affi rec	33.33%	affi rec	57.14%	affi rec	42.86%	affi ini	100.00%
					play ini	33.33%	affi ini	28.57%	uw	28.57%		
<b>Solitary Play</b> (soli play)			affi rec	100.00%	play ini	31.11%	affi ini	100.00%			affi ini	75.00%
<b>Urine Wash</b> (uw)	affi rec	38.46%	affi rec	63.34%	soli play	35.00%	affi rec	60.00%	affi ini	60.00%	affi ini	83.33%
			affi ini	27.27%	play ini	25.00%						
<b>Scent Marking</b> (sm)												
<b>Affiliation Initiator</b> (affi ini)	affi rec	35.71%	affi rec	72.73%	soli play	30.30%	affi rec	58.33%	affi rec	56.82%	affi rec	38.71%
<b>Sex Initiator</b> (sex ini)	affi rec	50.00%	affi rec	100.00%							sex rec	100.00%
	effe ag ini	50.00%										
<b>Play Initiator</b> (play ini)	affi ini	50.00%			soli play	25.64%					affi ini	62.50%
	affi rec	25.00%									affi rec	25.00%
	parent	25.00%										
<b>Ritual Agonism Initiator</b> (rit ag ini)	effe ag ini	33.33%					affi rec	50.00%	affi ini	50.00%	affi ini	80.00%
	rit sub ini	33.33%							affi rec	50.00%		
	rit ag rec	33.33%										

	<b>In</b> 1st trans.		<b>Na</b> 1st trans.		<b>Az</b> 1st trans.		<b>Ba</b> 1st trans.		<b>Bu</b> 1st trans.		<b>Kr</b> 1st trans.	
<b>Aggression Initiator</b> (effe ag ini)	affi rec	33.33%	affi ini	50.00%	effe sub rec	100.00%	effe sub rec	46.15%	effe sub rec	100.00%	affi ini	75.00%
			rit sub rec	50.00%							effe sub rec	25.00%
<b>Ritual Submission Initiator</b> (rit sub ini)	affi rec	25.00%			effe ag rec	50.00%	affi rec	66.67%	effe sub ini	100.00%	affi rec	60.00%
	effe sub ini	25.00%			soli play	50.00%	rit ag ini	33.33%			affi ini	40.00%
	rit sub rec	25.00%										
	self groom	25.00%										
<b>Effective Submission Initiator</b> (effe sub ini)	affi rec	35.29%	affi rec	63.64%	affi ini	26.32%	affi rec	60.00%	affi rec	100.00%	affi ini	33.33%
	affi ini	29.41%					affi ini	40.00%			affi rec	33.33%
											play ini	33.33%
<b>Parental Behavior</b> (parent)	affi ini	45.45%	affi rec	55.56%			affi rec	100.00%	affi rec	55.56%	affi rec	75.00%
	affi rec	36.36%	affi ini	44.44%								
<b>Affiliative Receiver</b> (affi rec)	affi ini	38.46%	affi ini	42.00%		< 25%	affi ini	33.33%	affi ini	46.94%	affi ini	63.27%
			effe sub ini	34.00%								
<b>Sex Receiver</b> (sex rec)											affi ini	100.00%
<b>Play Receiver</b> (play rec)					affi rec	29.63%					affi ini	28.57%
					soli play	29.63%					affi rec	28.57%
					play ini	25.93%						
<b>Ritual Agonism Receiver</b> (rit ag rec)	affi rec	33.33%			rit sub ini	33.33%	effe ag ini	50.00%			uw	50.00%
					effe sub ini	33.33%	rit sub ini	50.00%			rit sub ini	50.00%

	<b>In</b> 1st trans.		<b>Na</b> 1st trans.		<b>Az</b> 1st trans.		<b>Ba</b> 1st trans.		<b>Bu</b> 1st trans.		<b>Kr</b> 1st trans.	
					affi rec	33.33%						
<b>Aggression Receiver</b> (effe ag rec)	effe sub ini	80.00%	effe sub ini	83.33%	effe sub ini	100.00%	affi ini	100.00%	affi ini	100.00%	affi ini	100.00%
<b>Ritual Submission Received</b> (rit sub rec)	effe ag ini	50.00%	affi rec	100.00%	rit ag rec	100.00%			affi ini	100.00%	affi ini	50.00%
	rit ag ini	50.00%									affi rec	50.00%
<b>Effective Submission Receiver</b> (effe sub rec)	affi ini	50.00%	affi ini	50.00%	solu play	33.33%	affi rec	80.00%	affi rec	54.55%	affi ini	50.00%
	effe sub ini	50.00%	effe sub ini	50.00%							affi rec	25.00%
											rit ag ini	25.00%
<b>Abnormal Behavior</b> (abnorm)					solu play	37.50%						
					uw	25.00%						
					affi rec	25.00%						

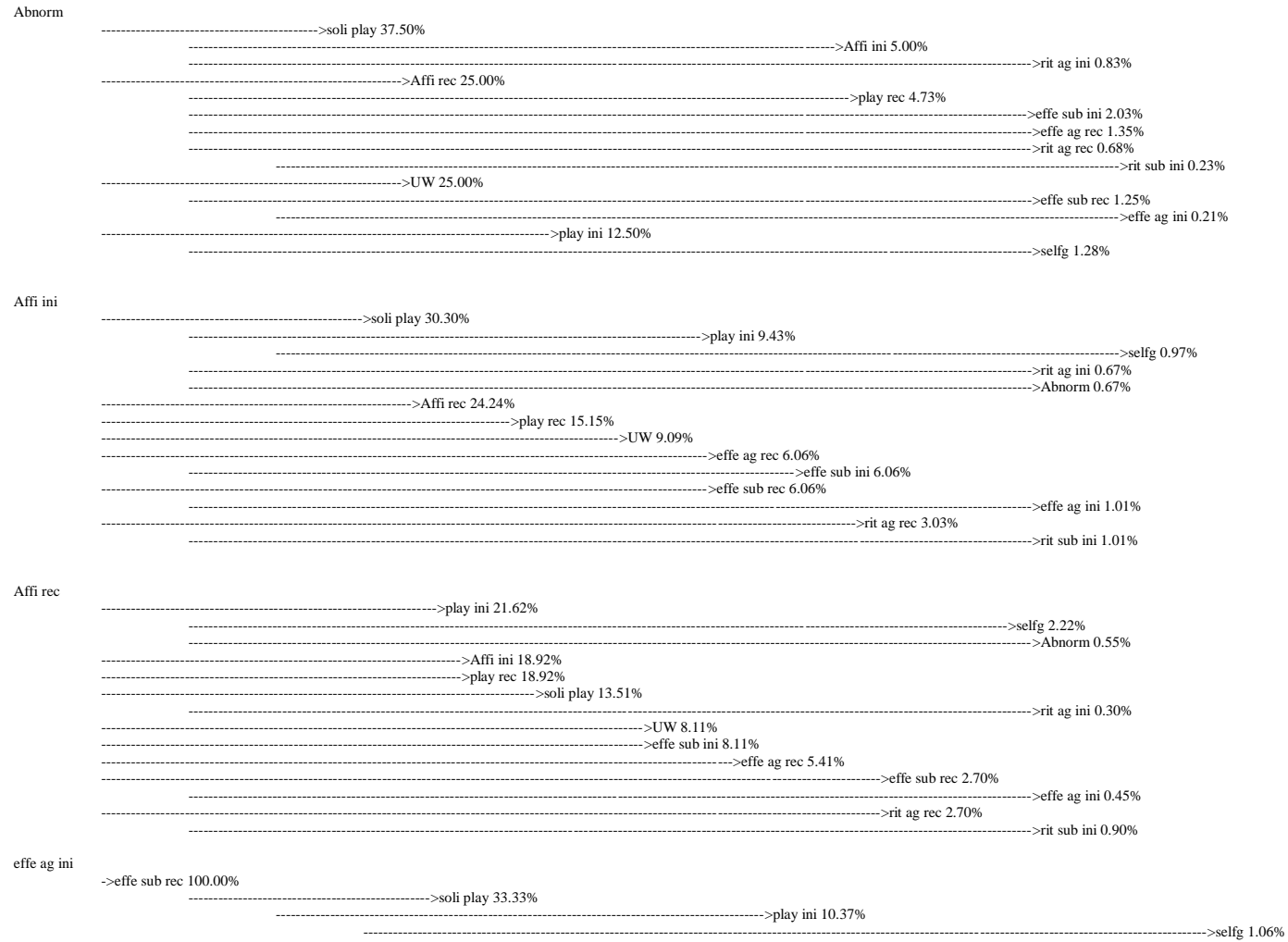
Table S9. Continuation of table S7 and S8. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S1). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group.

	<b>Ga</b> 1st trans.		<b>Pe</b> 1st trans.		<b>Bo</b> 1st trans.	
<b>Selfgrooming</b> (sg)			affi ini effe ag ini	75.00% 25.00%	affi ini	66.67%
<b>Solitary Play</b> (soli play)	affi rec uw	50.00% 50.00%	abnorm	100.00%	affi ini	61.54%
<b>Urine Wash</b> (uw)	affi ini play rec	41.67% 41.67%	affi ini	50.00%	affi ini	50.00%
<b>Scent Marking</b> (sm)						
<b>Affiliation Initiator</b> (affi ini)	affi rec parent	53.19% 25.53%	affi rec	35.71%	affi rec	38.03%
<b>Sex Initiator</b> (sex ini)						
<b>Play Initiator</b> (play ini)			affi ini	100.00%	affi ini	50.00%
<b>Ritual Agonism Initiator</b> (rit ag ini)			affi ini effe sub rec	50.00% 50.00%	affi rec effe sub rec	28.57% 28.57%

	<b>Ga</b> 1st trans.		<b>Pe</b> 1st trans.		<b>Bo</b> 1st trans.	
<b>Aggression Initiator</b> (effe ag ini)	rit sub rec	41.67%	rit ag ini	50.00%	effe sub rec	55.56%
	effe sub rec	33.33%	effe sub ini	50.00%		
<b>Ritual Submission Initiator</b> (rit sub ini)	affi rec	66.67%	affi rec	100.00%		
	affi ini	33.33%				
<b>Effective Submission Initiator</b> (effe sub ini)	affi ini	66.67%	affi rec	40.00%	solu play	50.00%
					affi rec	25.00%
<b>Parental Behavior</b> (parent)	affi rec	67.27%			affi rec	60.00%
<b>Affiliative Receiver</b> (affi rec)	affi ini	34.94%	affi ini	47.62%	affi ini	68.09%
<b>Sex Receiver</b> (sex rec)						
<b>Play Receiver</b> (play rec)			affi rec	50.00%	affi ini	50.00%
			uw	25.00%	affi rec	25.00%
			effe sub ini	25.00%	play ini	25.00%
<b>Ritual Agonism Receiver</b> (rit ag rec)						
<b>Aggression Receiver</b> (effe ag rec)			uw	25.00%	affi ini	50.00%
			affi ini	25.00%	affi rec	50.00%

	<b>Ga</b> 1st trans.		<b>Pe</b> 1st trans.		<b>Bo</b> 1st trans.	
			effe sub ini	25.00%		
			rit sub rec	25.00%		
<b>Ritual Submission Received</b> (rit sub rec)	affi rec	50.00%	affi ini	100.00%	affi ini	100.00%
<b>Effective Submission Receiver</b> (effe sub rec)	affi rec	72.73%	affi rec	80.00%	affi ini	83.33%
	affi ini	27.27%				
<b>Abnormal Behavior</b> (abnorm)			affi ini	66.67%		

# SE1. View of probability behavioral sequences of the behavioral transitions of Az.



```

----->UW 4.44%
----->rit ag ini 0.74%
----->Affi rec 16.67%
----->play rec 3.15%
----->effe sub ini 16.67%
----->rit ag rec 0.88%
----->rit sub ini 0.88%
----->Abnorm 0.88%
----->Affi ini 16.67%
----->effe ag rec 1.01%

```

effe ag rec

```

->effe sub ini 100.00%
----->Affi ini 26.32%
----->Affi rec 6.38%
----->soli play 21.05%
----->play ini 6.55%
----->selfg 0.67%
----->rit ag ini 0.47%
----->UW 10.53%
----->rit ag rec 5.26%
----->Abnorm 5.26%
----->rit sub ini 5.26%
----->play rec 5.26%
----->effe sub rec 5.26%
----->effe ag ini 0.88%

```

effe sub ini

```

----->Affi ini 26.32%
----->Affi rec 6.38%
----->soli play 21.05%
----->play ini 6.55%
----->selfg 0.67%
----->rit ag ini 0.47%
----->UW 10.53%
----->effe ag rec 5.26%
----->rit sub ini 5.26%
----->Abnorm 5.26%
----->play rec 5.26%
----->effe sub rec 5.26%
----->effe ag ini 0.88%
----->rit ag rec 5.26%

```

effe sub rec

```

----->soli play 33.33%
----->play ini 10.37%
----->selfg 1.06%
----->UW 4.44%
----->rit ag ini 0.74%
----->effe ag rec 1.01%
----->Abnorm 0.88%
----->rit sub ini 0.88%
----->rit ag rec 0.88%
----->Affi rec 16.67%
----->play rec 3.15%
----->effe ag ini 16.67%

```



play ini

```

----->soli play 25.64%
----->rit ag ini 0.57%
----->play rec 23.08%
----->Affi ini 12.82%
----->effe sub rec 0.78%
----->effe ag ini 0.13%
----->Affi rec 10.26%
----->selfg 10.26%
----->effe sub ini 7.69%
----->rit ag rec 0.40%
----->rit sub ini 0.40%
----->UW 5.13%
----->Abnorm 2.56%
----->effe ag rec 2.56%

```

play rec

```

----->Affi rec 29.63%
----->Affi ini 5.61%
----->effe sub ini 2.40%
----->effe ag rec 1.60%
----->rit ag rec 0.80%
----->rit sub ini 0.27%
----->effe sub rec 0.80%
----->effe ag ini 0.13%
----->soli play 29.63%
----->rit ag ini 0.66%
----->play ini 25.93%
----->Abnorm 0.66%
----->UW 11.11%
----->selfg 3.70%

```

rit ag rec

```

----->Affi rec 33.33%
----->play ini 7.21%
----->selfg 0.74%
----->play rec 6.31%
----->rit sub ini 33.33%
----->effe ag rec 16.67%
----->soli play 16.67%
----->rit ag ini 0.37%
----->effe sub ini 33.33%
----->Affi ini 8.77%
----->UW 3.51%
----->Abnorm 1.75%
----->effe sub rec 1.75%
----->effe ag ini 0.29%

```

rit sub ini

```

----->soli play 50.00%
----->play ini 15.56%
----->selfg 1.60%
----->Affi rec 10.00%
----->UW 6.67%
----->play rec 4.44%

```

```

----->rit ag ini 1.11%
----->effe ag rec 50.00%
----->effe sub ini 50.00%
----->Affi ini 13.16%
----->effe sub rec 2.63%
----->effe ag ini 0.44%
----->Abnorm 2.63%
----->rit ag rec 2.63%

```

rit sub rec

```

->rit ag rec 100.00%
----->rit sub ini 33.33%
----->effe ag rec 16.67%
----->soli play 16.67%
----->rit ag ini 0.37%
----->Affi rec 33.33%
----->play ini 7.21%
----->selfg 0.74%
----->play rec 6.31%
----->effe sub ini 33.33%
----->Affi ini 8.77%
----->UW 3.51%
----->Abnorm 1.75%
----->effe sub rec 1.75%
----->effe ag ini 0.29%

```

selfg

```

----->Affi rec 33.33%
----->Affi ini 6.31%
----->UW 2.70%
----->effe sub ini 2.70%
----->effe ag rec 1.80%
----->rit ag rec 0.90%
----->rit sub ini 0.30%
----->effe sub rec 0.90%
----->effe ag ini 0.15%
----->play ini 33.33%
----->Abnorm 0.85%
----->play rec 16.67%
----->soli play 16.67%
----->rit ag ini 0.37%

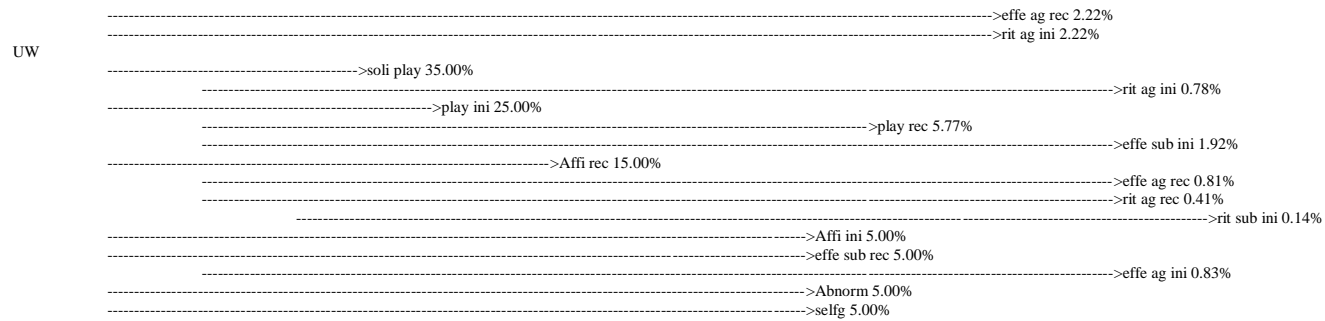
```

soli play

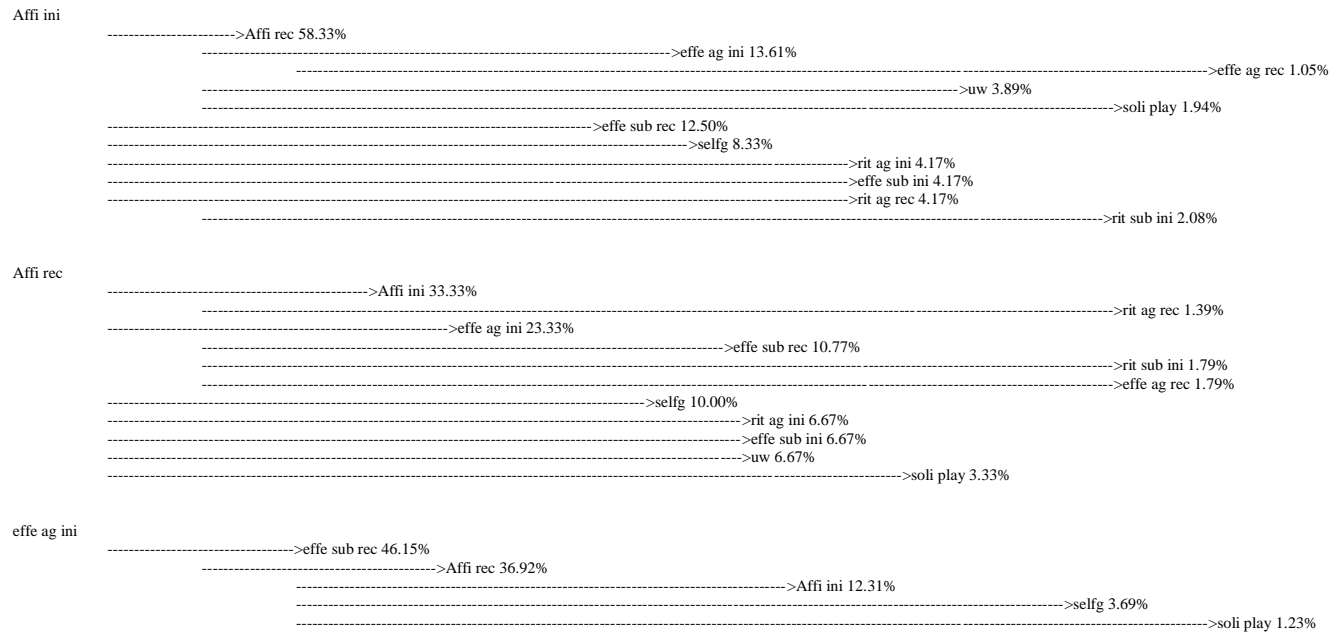
```

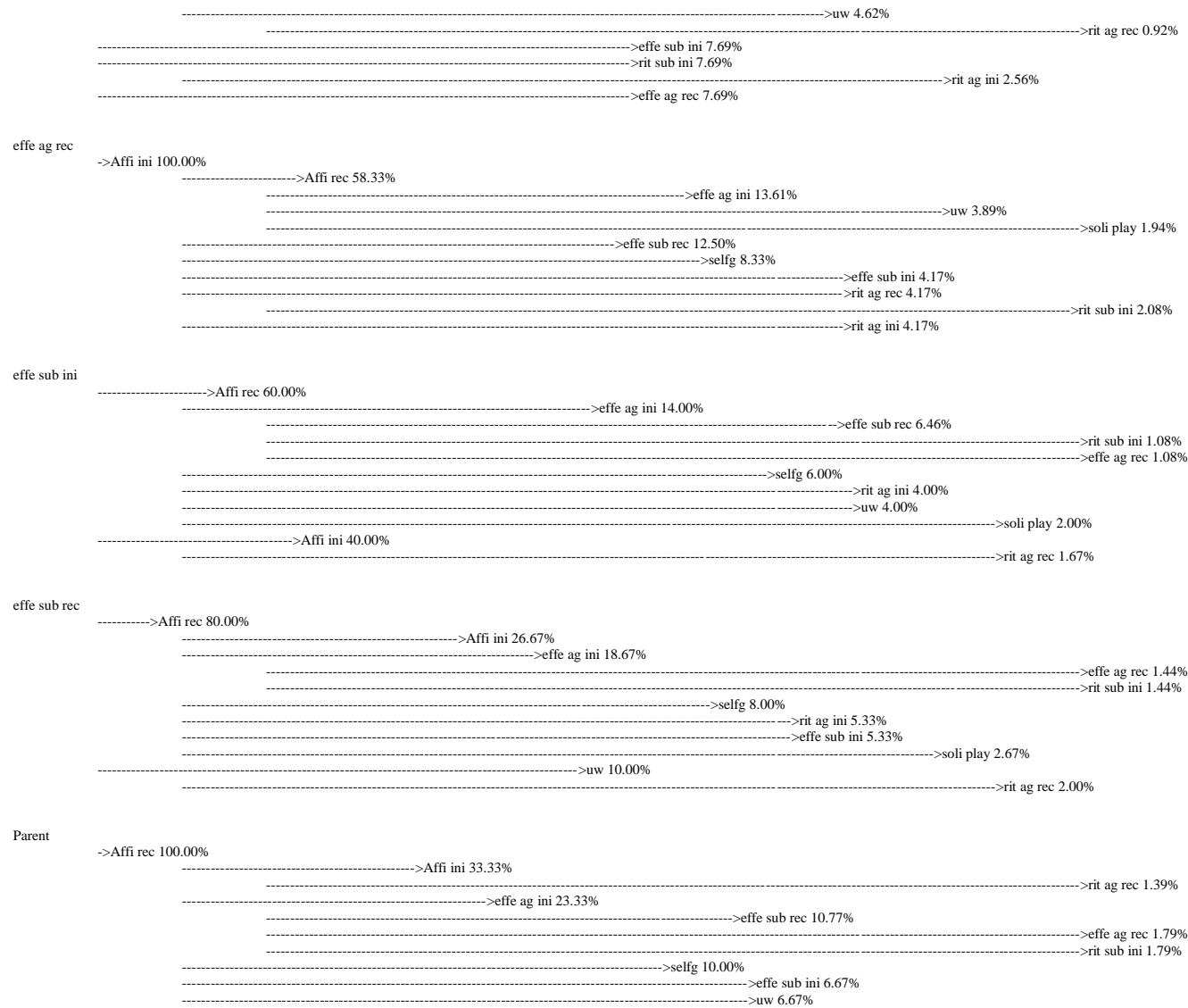
----->play ini 31.11%
----->selfg 3.19%
----->Affi rec 20.00%
----->rit ag rec 0.54%
----->UW 13.33%
----->Affi ini 13.33%
----->play rec 8.89%
----->effe sub ini 4.44%
----->rit sub ini 0.23%
----->effe sub rec 2.22%
----->effe ag ini 0.37%
----->Abnorm 2.22%

```



SE2. View of probability behavioral sequences of the behavioral transitions of Ba.





```

----->rit ag ini 6.67%
----->solu play 3.33%

rit ag ini
----->Affi rec 50.00%
----->selfg 5.00%
----->uw 3.33%
----->effe sub ini 3.33%
----->solu play 1.67%
----->Affi ini 16.67%
----->rit ag rec 0.69%
----->rit sub ini 16.67%
----->effe ag ini 16.67%
----->effe sub rec 7.69%
----->effe ag rec 1.28%

rit ag rec
----->effe ag ini 50.00%
----->effe sub rec 23.08%
----->uw 2.31%
----->effe sub ini 3.85%
----->effe ag rec 3.85%
----->rit sub ini 50.00%
----->Affi rec 33.33%
----->Affi ini 11.11%
----->selfg 3.33%
----->solu play 1.11%
----->rit ag ini 16.67%

rit sub ini
----->Affi rec 66.67%
----->Affi ini 22.22%
----->rit ag rec 0.93%
----->effe ag ini 15.56%
----->effe sub rec 7.18%
----->effe ag rec 1.20%
----->selfg 6.67%
----->uw 4.44%
----->effe sub ini 4.44%
----->solu play 2.22%
----->rit ag ini 33.33%

selfg
----->Affi rec 57.14%
----->effe ag ini 13.33%
----->effe sub rec 6.15%
----->effe ag rec 1.03%
----->rit sub ini 1.03%
----->effe sub ini 3.81%
----->uw 3.81%
----->rit ag ini 3.81%
----->Affi ini 28.57%
----->rit ag rec 1.19%
----->solu play 14.29%

solu play

```

```

->Affi ini 100.00%
----->Affi rec 58.33%
----->effe ag ini 13.61%
----->effe ag rec 1.05%
----->uw 3.89%
----->effe sub rec 12.50%
----->selfg 8.33%
----->effe sub ini 4.17%
----->rit ag ini 4.17%
----->rit ag rec 4.17%
----->rit sub ini 2.08%

```

```

uw
----->Affi rec 60.00%
----->effe ag ini 14.00%
----->effe sub rec 6.46%
----->effe ag rec 1.08%
----->selfg 6.00%
----->effe sub ini 4.00%
----->rit ag ini 4.00%
----->rit ag rec 2.00%
----->rit sub ini 10.00%
----->Affi ini 20.00%
----->rit ag rec 20.00%
----->rit sub ini 10.00%

```

### SE3. View of probability behavioral sequences of the behavioral transitions of Bo.

```

Affi ini
----->Affi rec 38.03%
----->solu play 11.27%
----->play ini 8.45%
----->effe ag ini 8.45%
----->uw 8.45%
----->effe sub rec 5.63%
----->play rec 5.63%
----->rit ag ini 4.23%
----->Parent 2.82%
----->effe sub ini 1.41%
----->effe ag rec 1.41%
----->selfg 1.41%
----->Abnorm 1.41%
----->rit sub rec 1.41%

```

```

Affi rec
----->Affi ini 68.09%
----->solu play 7.67%
----->uw 5.75%
----->effe ag ini 5.75%
----->play rec 3.84%
----->effe sub rec 3.84%
----->rit sub rec 0.96%
----->effe ag rec 0.96%
----->Abnorm 0.96%

```

```

----->rit ag ini 6.38%
----->play ini 6.38%
----->effe sub ini 2.13%
----->selfg 2.13%
----->Parent 2.13%

effe ag ini
----->effe sub rec 55.56%
----->Affi ini 46.30%
----->Affi rec 17.61%
----->soli play 5.22%
----->play ini 3.91%
----->uw 3.91%
----->play rec 2.61%
----->Parent 1.30%
----->Abnorm 0.65%
----->rit sub rec 0.65%
----->effe ag rec 0.65%
----->effe sub ini 0.65%
----->rit ag ini 4.63%
----->selfg 0.66%

effe ag rec
----->Affi rec 50.00%
----->rit ag ini 3.19%
----->selfg 1.06%
----->effe sub ini 1.06%
----->Affi ini 50.00%
----->soli play 5.63%
----->play ini 4.23%
----->effe ag ini 4.23%
----->uw 4.23%
----->effe sub rec 2.82%
----->play rec 2.82%
----->Parent 1.41%
----->Abnorm 0.70%
----->rit sub rec 0.70%

effe sub ini
----->soli play 50.00%
----->Affi ini 30.77%
----->effe ag ini 2.60%
----->play rec 1.73%
----->effe sub rec 1.73%
----->Parent 0.87%
----->rit sub rec 0.43%
----->effe ag rec 0.43%
----->Abnorm 0.43%
----->play ini 3.85%
----->uw 3.85%
----->Affi rec 25.00%
----->rit ag ini 1.60%
----->selfg 0.53%

effe sub rec
----->Affi ini 83.33%
----->Affi rec 31.69%

```

```

----->soli play 9.39%
----->uw 7.04%
----->play ini 7.04%
----->effe ag ini 7.04%
----->play rec 4.69%
----->Parent 2.35%
----->effe ag rec 1.17%
----->Abnorm 1.17%
----->rit sub rec 1.17%
----->effe sub ini 1.17%
----->rit ag ini 8.33%
----->selfg 1.19%

```

Parent

```

----->Affi rec 60.00%
----->Affi ini 40.85%
----->soli play 4.60%
----->effe ag ini 3.45%
----->uw 3.45%
----->effe sub rec 2.30%
----->play rec 2.30%
----->rit sub rec 0.58%
----->Abnorm 0.58%
----->effe ag rec 0.58%
----->play ini 3.83%
----->rit ag ini 3.83%
----->selfg 1.28%
----->effe sub ini 1.28%

```

play ini

```

----->Affi ini 50.00%
----->Affi rec 19.01%
----->soli play 5.63%
----->uw 4.23%
----->effe ag ini 4.23%
----->rit ag ini 2.11%
----->Parent 1.41%
----->effe ag rec 0.70%
----->Abnorm 0.70%
----->rit sub rec 0.70%
----->effe sub ini 10.00%
----->effe sub rec 10.00%
----->selfg 10.00%
----->play rec 10.00%

```

play rec

```

----->Affi ini 50.00%
----->soli play 5.63%
----->uw 4.23%
----->effe ag ini 4.23%
----->effe sub rec 2.82%
----->rit ag ini 2.11%
----->Parent 1.41%
----->rit sub rec 0.70%
----->effe ag rec 0.70%
----->Abnorm 0.70%
----->play ini 25.00%
----->selfg 2.50%

```



```

----->Affi rec 25.00%----->effe sub ini 2.50%
rit ag ini
----->Affi rec 28.57%----->effe sub ini 0.61%
----->effe sub rec 28.57%----->Affi ini 23.81%
----->uw 14.29%----->solu play 2.68%
----->selfg 14.29%----->effe ag ini 2.01%
----->play ini 2.38%----->play rec 1.34%
----->rit sub rec 0.34%----->Parent 0.67%
----->Abnorm 0.34%
rit sub rec
->Affi ini 100.00%
----->Affi rec 38.03%----->solu play 11.27%
----->effe ag ini 8.45%
----->play ini 8.45%
----->uw 8.45%----->effe sub rec 5.63%
----->play rec 5.63%
----->rit ag ini 4.23%----->Parent 2.82%
----->Abnorm 1.41%
----->effe ag rec 1.41%
----->selfg 1.41%
----->effe sub ini 1.41%
selfg
----->Affi ini 66.67%----->Affi rec 25.35%----->solu play 7.51%
----->effe ag ini 5.63%
----->uw 5.63%----->play rec 3.76%
----->Parent 1.88%
----->effe ag rec 0.94%
----->rit sub rec 0.94%
----->Abnorm 0.94%
----->rit ag ini 16.67%----->effe sub rec 4.76%
----->play ini 16.67%----->effe sub ini 1.67%
solu play
----->Affi ini 61.54%----->Affi rec 23.40%----->effe ag ini 5.20%
----->play rec 3.47%

```

```

----->effe sub rec 3.47%
----->rit ag ini 2.60%
----->Parent 1.73%
----->rit sub rec 0.87%
----->selfg 0.87%
----->Abnorm 0.87%
----->effe ag rec 0.87%
----->effe sub ini 7.69%
----->uw 7.69%
----->play ini 7.69%

```

```

uw
----->Affi ini 50.00%
----->solu play 5.63%
----->play ini 4.23%
----->play rec 2.82%
----->rit ag ini 2.11%
----->Parent 1.41%
----->rit sub rec 0.70%
----->Abnorm 0.70%
----->effe sub ini 0.70%
----->Affi rec 20.00%
----->effe ag rec 10.00%
----->effe ag ini 10.00%
----->effe sub rec 5.56%
----->selfg 10.00%

```

#### SE4. View of probability behavioral sequences of the behavioral transitions of Br.

```

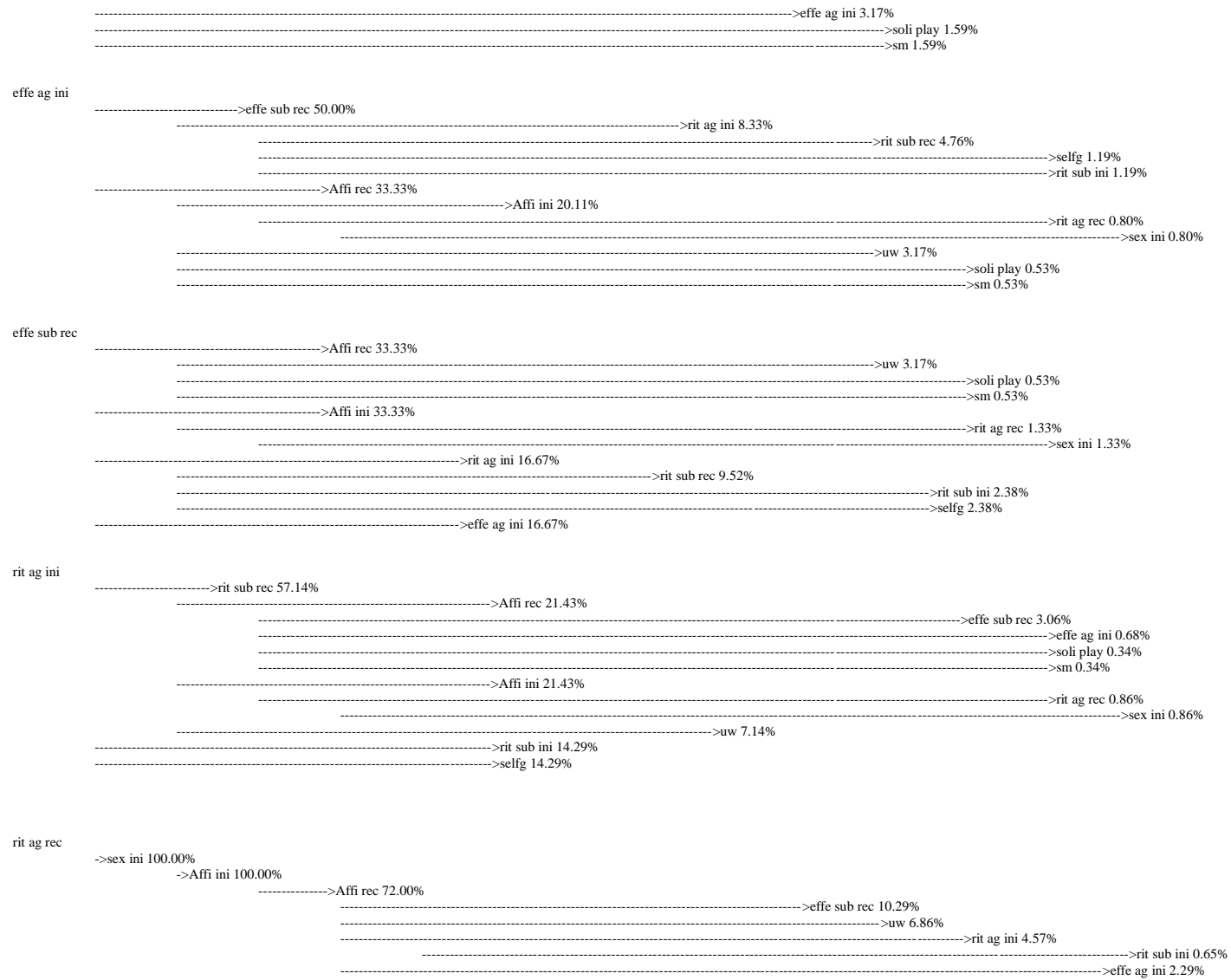
Affi ini
----->Affi rec 72.00%
----->effe sub rec 10.29%
----->uw 6.86%
----->rit ag ini 4.57%
----->rit sub ini 0.65%
----->effe ag ini 2.29%
----->solu play 1.14%
----->sm 1.14%
----->rit sub rec 8.00%
----->selfg 1.00%
----->rit ag rec 4.00%
----->sex ini 4.00%

```

```

Affi rec
----->Affi ini 60.32%
----->rit sub rec 4.83%
----->rit ag rec 2.41%
----->sex ini 2.41%
----->effe sub rec 14.29%
----->uw 9.52%
----->rit ag ini 6.35%
----->rit sub ini 0.91%
----->selfg 0.91%

```



```

----->sm 1.14%
----->soli play 1.14%
----->rit sub rec 8.00%
----->selfg 1.00%

rit sub rec
----->Affi rec 37.50%
----->effe sub rec 5.36%
----->rit ag ini 2.38%
----->rit sub ini 0.34%
----->effe ag ini 1.19%
----->soli play 0.60%
----->sm 0.60%
----->Affi ini 37.50%
----->rit ag rec 1.50%
----->sex ini 1.50%
----->selfg 12.50%
----->uw 12.50%

selfg
----->Affi rec 50.00%
----->effe sub rec 7.14%
----->uw 4.76%
----->rit ag ini 3.17%
----->rit sub ini 0.45%
----->effe ag ini 1.59%
----->sm 0.79%
----->soli play 0.79%
----->Affi ini 50.00%
----->rit sub rec 4.00%
----->rit ag rec 2.00%
----->sex ini 2.00%

sex ini
->Affi ini 100.00%
----->Affi rec 72.00%
----->effe sub rec 10.29%
----->uw 6.86%
----->rit ag ini 4.57%
----->rit sub ini 0.65%
----->effe ag ini 2.29%
----->soli play 1.14%
----->sm 1.14%
----->rit sub rec 8.00%
----->selfg 1.00%
----->rit ag rec 4.00%

sm
----->uw 33.33%
----->rit ag ini 3.70%
----->selfg 0.53%
----->rit sub ini 0.53%
----->Affi ini 33.33%
----->rit sub rec 2.67%
----->rit ag rec 1.33%

```

```

----->sex ini 1.33%
----->Affi rec 33.33%
----->effe sub rec 4.76%
----->effe ag ini 1.06%
----->solu play 0.53%

```

soli play

```

->Affi rec 100.00%
----->Affi ini 60.32%
----->rit sub rec 4.83%
----->rit ag rec 2.41%
----->sex ini 2.41%
----->effe sub rec 14.29%
----->uw 9.52%
----->rit ag ini 6.35%
----->rit sub ini 0.91%
----->selfg 0.91%
----->effe ag ini 3.17%
----->sm 1.59%

```

uw

```

----->Affi rec 55.56%
----->Affi ini 33.51%
----->rit ag rec 1.34%
----->sex ini 1.34%
----->effe sub rec 7.94%
----->effe ag ini 1.76%
----->solu play 0.88%
----->sm 0.88%
----->rit ag ini 11.11%
----->rit sub rec 6.35%
----->rit sub ini 1.59%
----->selfg 1.59%

```

## SE5. View of probability behavioral sequences of the behavioral transitions of Bu.

Affi ini

```

----->Affi rec 56.82%
----->effe sub rec 10.44%
----->selfg 6.96%
----->effe ag rec 1.16%
----->effe ag ini 1.16%
----->uw 18.18%
----->rit ag ini 4.55%
----->effe sub ini 4.55%
----->Parent 4.55%
----->rit sub ini 2.27%

```

```

----->rit sub rec 2.27%

Affi rec
----->Affi ini 46.94%
----->uw 8.53%
----->effe sub ini 2.13%
----->rit ag ini 2.13%
----->effe sub rec 18.37%
----->selfg 12.24%
----->Parent 4.08%
----->rit sub ini 2.04%
----->effe ag ini 2.04%
----->rit sub rec 2.04%
----->effe ag rec 2.04%

effe ag ini
->effe sub rec 100.00%
----->Affi rec 54.55%
----->selfg 6.68%
----->rit sub ini 1.11%
----->effe ag rec 1.11%
----->rit sub rec 1.11%
----->Affi ini 36.36%
----->uw 6.61%
----->rit ag ini 1.65%
----->effe sub ini 1.65%
----->Parent 9.09%

effe ag rec
->Affi ini 100.00%
----->Affi rec 56.82%
----->effe sub rec 10.44%
----->selfg 6.96%
----->effe ag ini 1.16%
----->uw 18.18%
----->effe sub ini 4.55%
----->rit ag ini 4.55%
----->Parent 4.55%
----->rit sub rec 2.27%
----->rit sub ini 2.27%

effe sub ini
->Affi rec 100.00%
----->Affi ini 46.94%
----->uw 8.53%
----->rit ag ini 2.13%
----->effe sub rec 18.37%
----->selfg 12.24%
----->Parent 4.08%
----->effe ag rec 2.04%
----->rit sub rec 2.04%
----->rit sub ini 2.04%
----->effe ag ini 2.04%

effe sub rec
----->Affi rec 54.55%

```

```

----->selfg 6.68%
----->effe ag rec 1.11%
----->rit sub ini 1.11%
----->effe ag ini 1.11%
----->rit sub rec 1.11%
----->Affi ini 36.36%
----->uw 6.61%
----->rit ag ini 1.65%
----->effe sub ini 1.65%
----->Parent 9.09%

```

Parent

```

----->Affi rec 55.56%
----->Affi ini 26.08%
----->rit ag ini 1.19%
----->effe sub rec 10.20%
----->selfg 6.80%
----->effe ag ini 1.13%
----->rit sub ini 1.13%
----->effe ag rec 1.13%
----->rit sub rec 1.13%
----->effe sub ini 11.11%
----->uw 11.11%

```

rit ag ini

```

----->Affi rec 50.00%
----->effe sub rec 9.18%
----->selfg 6.12%
----->effe ag ini 1.02%
----->effe ag rec 1.02%
----->Affi ini 50.00%
----->uw 9.09%
----->Parent 2.27%
----->effe sub ini 2.27%
----->rit sub rec 1.14%
----->rit sub ini 1.14%

```

rit sub ini

```

->effe sub ini 100.00%
->Affi rec 100.00%
----->Affi ini 46.94%
----->uw 8.53%
----->rit ag ini 2.13%
----->effe sub rec 18.37%
----->selfg 12.24%
----->Parent 4.08%
----->effe ag ini 2.04%
----->effe ag rec 2.04%
----->rit sub rec 2.04%

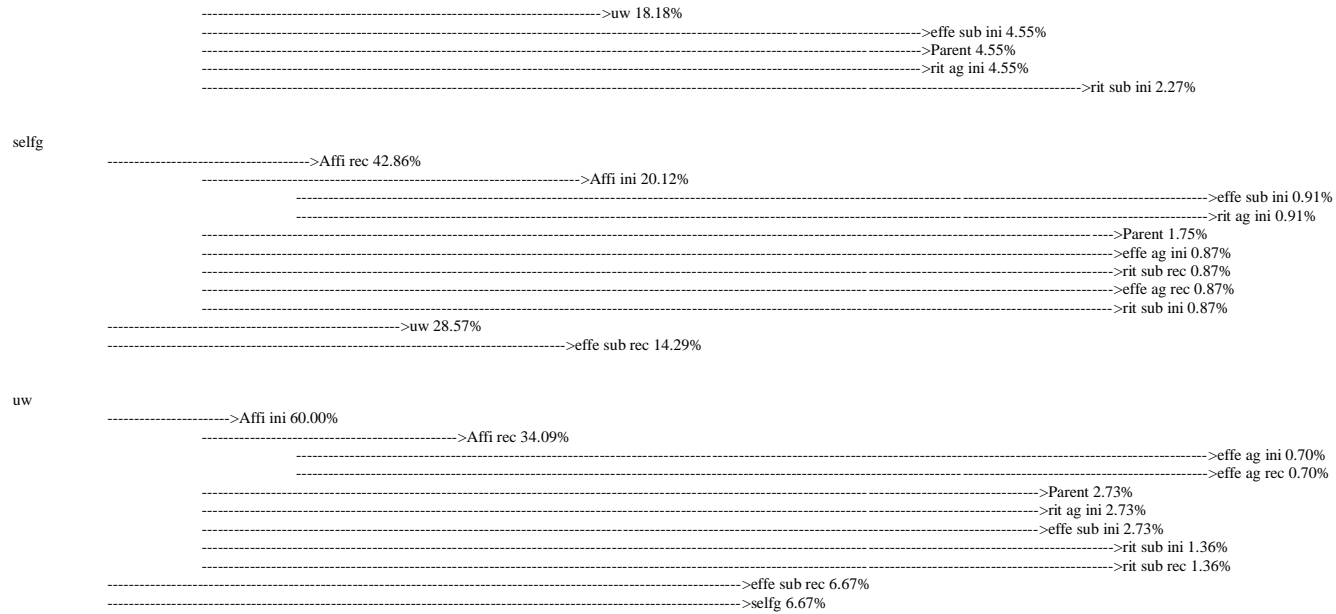
```

rit sub rec

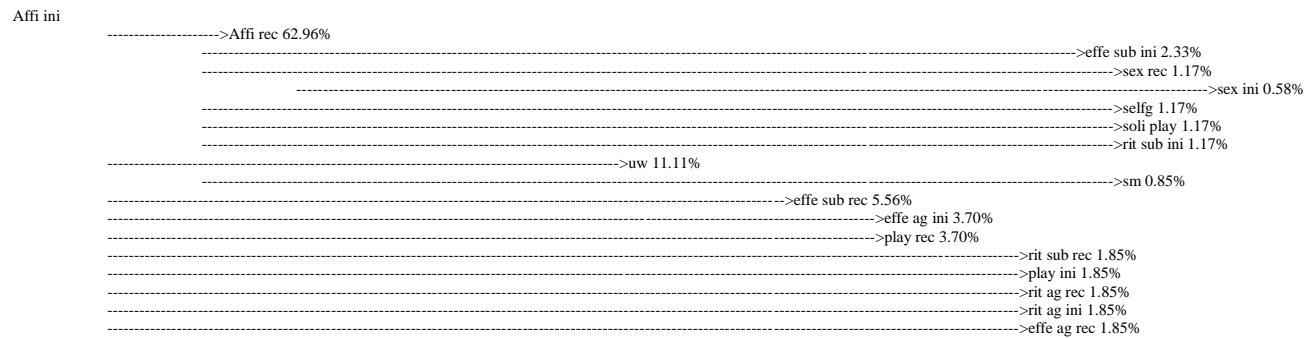
```

->Affi ini 100.00%
----->Affi rec 56.82%
----->effe sub rec 10.44%
----->selfg 6.96%
----->effe ag rec 1.16%
----->effe ag ini 1.16%

```



SE6. View of probability behavioral sequences of the behavioral transitions of Ch.





```

----->parent 1.85%

Affi rec
----->Affi ini 62.96%
----->play rec 2.33%
----->rit ag ini 1.17%
----->rit sub rec 1.17%
----->rit ag rec 1.17%
----->uw 9.26%
----->sm 0.71%
----->effe sub rec 5.56%
----->effe sub ini 3.70%
----->effe ag ini 3.70%
----->soli play 1.85%
----->effe ag rec 1.85%
----->sex rec 1.85%
----->sex ini 0.93%
----->parent 1.85%
----->selfg 1.85%
----->play ini 1.85%
----->rit sub ini 1.85%

effe ag ini
----->effe sub rec 33.33%
----->Affi ini 33.33%
----->uw 3.70%
----->sm 0.28%
----->play rec 1.23%
----->rit sub rec 0.62%
----->rit ag rec 0.62%
----->rit ag ini 0.62%
----->Affi rec 33.33%
----->effe sub ini 1.23%
----->selfg 0.62%
----->soli play 0.62%
----->sex rec 0.62%
----->sex ini 0.31%
----->effe ag rec 0.62%
----->play ini 0.62%
----->parent 0.62%
----->rit sub ini 0.62%

effe ag rec
----->effe sub ini 50.00%
----->uw 12.50%
----->sm 0.96%
----->parent 0.96%
----->effe sub rec 6.25%
----->sex ini 6.25%
----->sex rec 6.25%
----->Affi rec 50.00%
----->Affi ini 31.48%
----->play rec 1.17%
----->rit ag ini 0.58%
----->rit sub rec 0.58%
----->rit ag rec 0.58%
----->effe ag ini 1.85%
----->soli play 0.93%

```

----->selfg 0.93%  
----->play ini 0.93%  
----->rit sub ini 0.93%

**Chifres**

effe sub ini  
----->Affi ini 50.00%  
----->Affi rec 31.48%  
----->selfg 0.58%  
----->rit sub ini 0.58%  
----->effe ag ini 1.85%  
----->play rec 1.85%  
----->rit ag ini 0.93%  
----->effe ag rec 0.93%  
----->play ini 0.93%  
----->rit sub rec 0.93%  
----->rit ag rec 0.93%  
----->uw 25.00%  
----->parent 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sm 1.92%  
----->sex ini 12.50%  
----->sex rec 12.50%  
----->effe sub rec 12.50%

effe sub rec  
----->Affi rec 57.14%  
----->uw 5.29%  
----->sm 0.41%  
----->effe sub ini 2.12%  
----->effe ag ini 2.12%  
----->rit sub ini 1.06%  
----->sex rec 1.06%  
----->sex ini 0.53%  
----->selfg 1.06%  
----->play ini 1.06%  
----->sm 1.06%  
----->parent 1.06%  
----->effe ag rec 1.06%  
----->Affi ini 42.86%  
----->play rec 1.59%  
----->rit ag rec 0.79%  
----->rit sub rec 0.79%  
----->rit ag ini 0.79%

parent  
----->Affi rec 50.00%  
----->Affi ini 31.48%  
----->play rec 1.17%  
----->rit ag rec 0.58%  
----->rit ag ini 0.58%  
----->uw 4.63%  
----->sm 0.36%  
----->effe sub rec 2.78%  
----->effe ag ini 1.85%  
----->selfg 0.93%  
----->play ini 0.93%  
----->effe ag rec 0.93%  
----->rit sub ini 0.93%

```

----->soli play 33.33%
----->effe sub ini 16.67%
----->sex ini 2.08%
----->sex rec 2.08%
----->rit sub rec 16.67%

```

play ini

```

----->Affi rec 50.00%
----->effe sub ini 1.85%
----->sex rec 0.93%
----->sex ini 0.46%
----->soli play 0.93%
----->rit sub ini 0.93%
----->selfg 0.93%
----->Affi ini 50.00%
----->uw 5.56%
----->sm 0.43%
----->effe sub rec 2.78%
----->play rec 1.85%
----->effe ag ini 1.85%
----->effe ag rec 0.93%
----->rit ag rec 0.93%
----->rit sub rec 0.93%
----->rit ag ini 0.93%
----->parent 0.93%

```

play rec

```

----->Affi rec 66.67%
----->Affi ini 41.98%
----->rit ag rec 0.78%
----->rit sub rec 0.78%
----->rit ag ini 0.78%
----->uw 6.17%
----->sm 0.47%
----->effe sub rec 3.70%
----->effe ag ini 2.47%
----->effe sub ini 2.47%
----->play ini 1.23%
----->sex rec 1.23%
----->sex ini 0.62%
----->soli play 1.23%
----->effe ag rec 1.23%
----->selfg 1.23%
----->parent 1.23%
----->rit sub ini 1.23%

```

rit ag ini

```

->Affi rec 100.00%
----->Affi ini 62.96%
----->play rec 2.33%
----->rit ag rec 1.17%
----->rit sub rec 1.17%
----->uw 9.26%
----->sm 0.71%
----->effe sub rec 5.56%
----->effe sub ini 3.70%

```

```

----->effe ag ini 3.70%
----->play ini 1.85%
----->rit sub ini 1.85%
----->parent 1.85%
----->soli play 1.85%
----->effe ag rec 1.85%
----->sex rec 1.85%
----->sex ini 0.93%
----->selfg 1.85%

```

rit ag rec

```

->Affi ini 100.00%
----->Affi rec 62.96%
----->effe sub ini 2.33%
----->sex rec 1.17%
----->sex ini 0.58%
----->rit sub ini 1.17%
----->soli play 1.17%
----->selfg 1.17%
----->uw 11.11%
----->sm 0.85%
----->effe sub rec 5.56%
----->play rec 3.70%
----->effe ag ini 3.70%
----->effe ag rec 1.85%
----->rit sub rec 1.85%
----->parent 1.85%
----->rit ag ini 1.85%
----->play ini 1.85%

```

rit sub ini

```

->Affi ini 100.00%
----->Affi rec 62.96%
----->effe sub ini 2.33%
----->selfg 1.17%
----->sex rec 1.17%
----->sex ini 0.58%
----->soli play 1.17%
----->uw 11.11%
----->sm 0.85%
----->effe sub rec 5.56%
----->play rec 3.70%
----->effe ag ini 3.70%
----->effe ag rec 1.85%
----->rit sub rec 1.85%
----->play ini 1.85%
----->rit ag rec 1.85%
----->parent 1.85%
----->rit ag ini 1.85%

```

rit sub rec

```

----->Affi rec 50.00%
----->effe sub ini 1.85%
----->soli play 0.93%
----->sex rec 0.93%
----->sex ini 0.46%
----->selfg 0.93%
----->rit sub ini 0.93%

```

```

----->Affi ini 50.00%
----->uw 5.56%
----->sm 0.43%
----->effe sub rec 2.78%
----->play rec 1.85%
----->effe ag ini 1.85%
----->effe ag rec 0.93%
----->parent 0.93%
----->rit ag rec 0.93%
----->play ini 0.93%
----->rit ag ini 0.93%

```

```

selfg
->Affi ini 100.00%
----->Affi rec 62.96%
----->effe sub ini 2.33%
----->solu play 1.17%
----->sex rec 1.17%
----->sex ini 0.58%
----->rit sub ini 1.17%
----->uw 11.11%
----->sm 0.85%
----->effe sub rec 5.56%
----->play rec 3.70%
----->effe ag ini 3.70%
----->effe ag rec 1.85%
----->rit sub rec 1.85%
----->play ini 1.85%
----->rit ag rec 1.85%
----->parent 1.85%
----->rit ag ini 1.85%

```

```

sex ini
->sex rec 100.00%
----->Affi ini 50.00%
----->Affi rec 31.48%
----->effe sub ini 1.17%
----->solu play 0.58%
----->rit sub ini 0.58%
----->selfg 0.58%
----->uw 5.56%
----->sm 0.43%
----->effe sub rec 2.78%
----->effe ag ini 1.85%
----->play rec 1.85%
----->rit ag rec 0.93%
----->effe ag rec 0.93%
----->rit sub rec 0.93%
----->play ini 0.93%
----->rit ag ini 0.93%
----->parent 0.93%

```

```

sex rec
----->sex ini 50.00%
----->Affi ini 50.00%
----->Affi rec 31.48%
----->effe sub ini 1.17%

```

```

----->rit sub ini 0.58%
----->selfg 0.58%
----->soli play 0.58%
----->uw 5.56%
----->sm 0.43%
----->effe sub rec 2.78%
----->effe ag ini 1.85%
----->play rec 1.85%
----->rit ag rec 0.93%
----->effe ag rec 0.93%
----->rit sub rec 0.93%
----->play ini 0.93%
----->rit ag ini 0.93%
----->parent 0.93%

```

soli play

```

----->effe sub ini 50.00%
----->Affi ini 25.00%
----->play rec 0.93%
----->effe ag ini 0.93%
----->play ini 0.46%
----->rit ag ini 0.46%
----->effe ag rec 0.46%
----->rit ag rec 0.46%
----->uw 12.50%
----->sm 0.96%
----->sex ini 6.25%
----->sex rec 6.25%
----->effe sub rec 6.25%
----->parent 50.00%
----->Affi rec 25.00%
----->selfg 0.46%
----->rit sub ini 0.46%
----->rit sub rec 8.33%

```

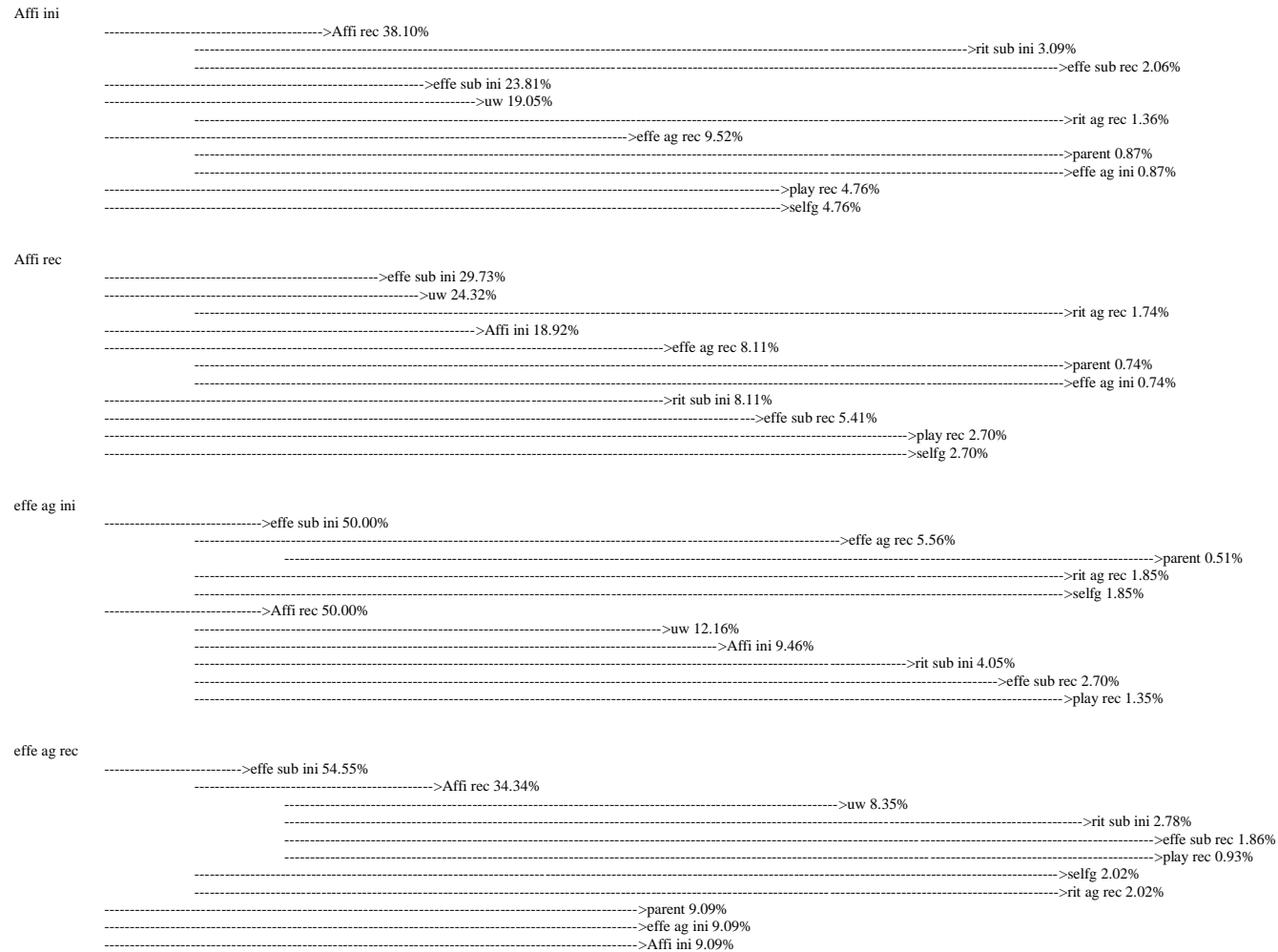
uw

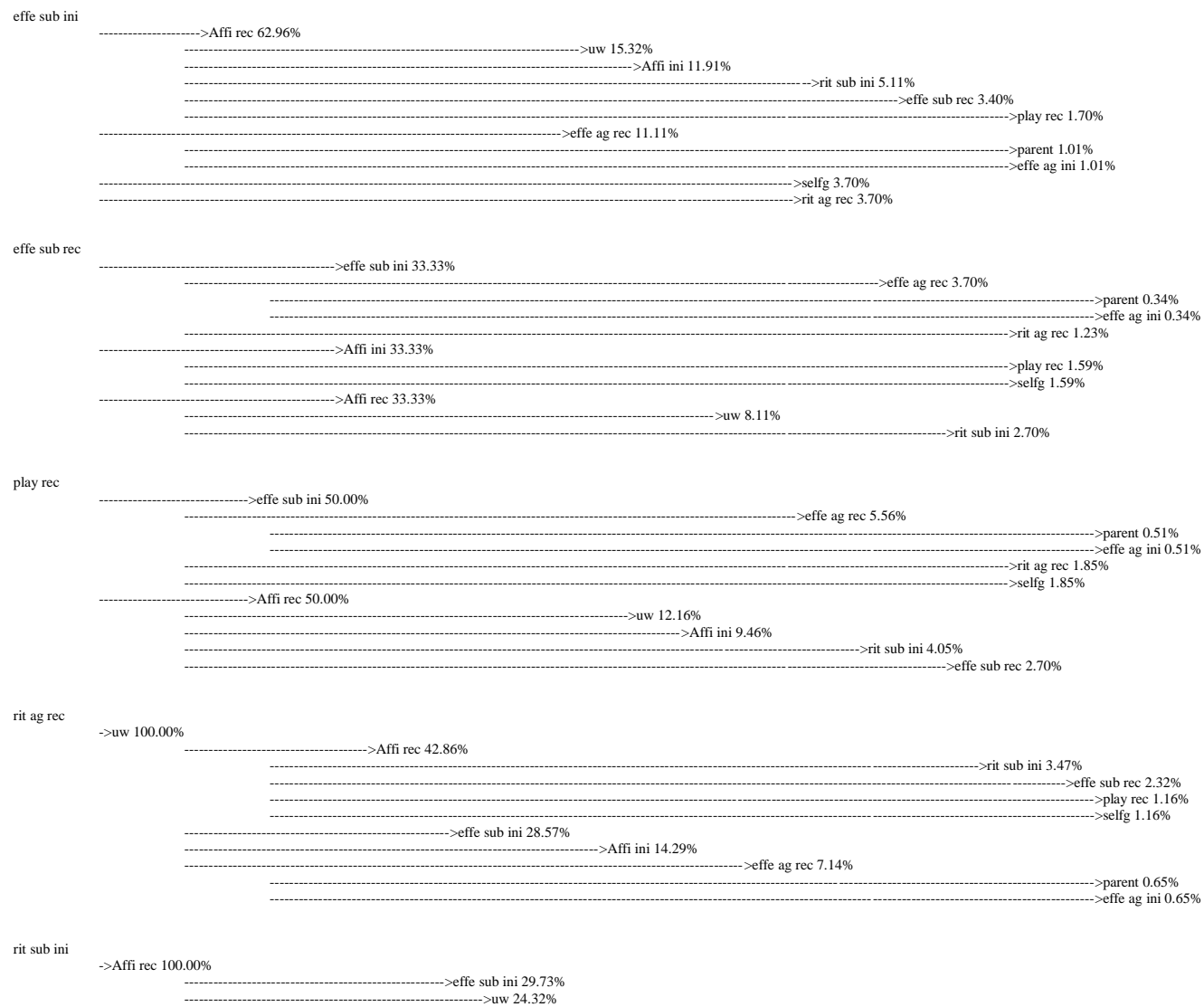
```

----->Affi ini 61.54%
----->Affi rec 38.75%
----->selfg 0.72%
----->rit sub ini 0.72%
----->effe sub rec 3.42%
----->effe ag ini 2.28%
----->play rec 2.28%
----->rit ag rec 1.14%
----->effe ag rec 1.14%
----->rit ag ini 1.14%
----->play ini 1.14%
----->effe sub ini 7.69%
----->sex ini 0.96%
----->sex rec 0.96%
----->sm 7.69%
----->parent 7.69%
----->soli play 2.56%
----->rit sub rec 1.28%

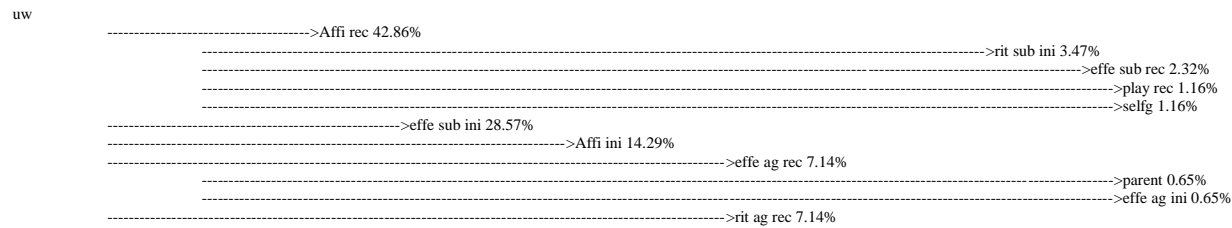
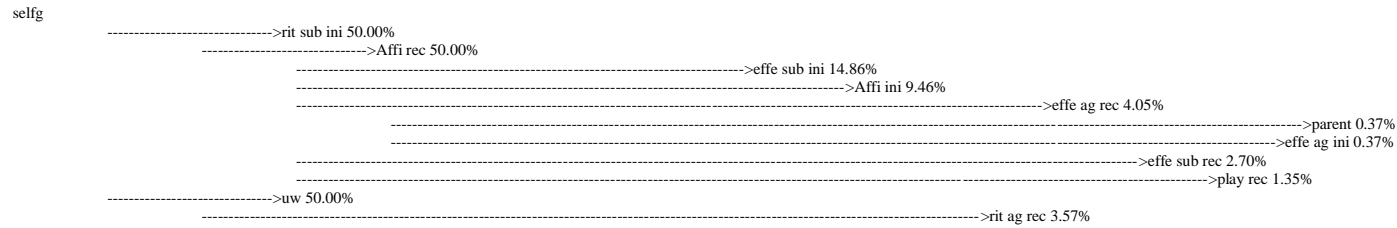
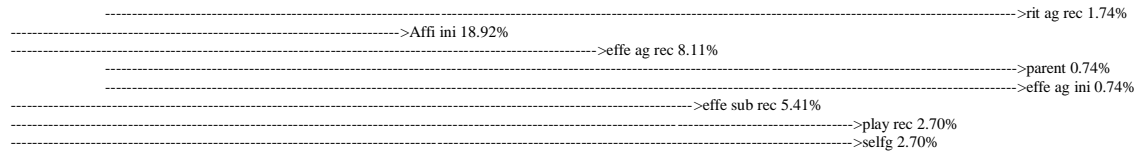
```

SE7. View of probability behavioral sequences of the behavioral transitions of El.

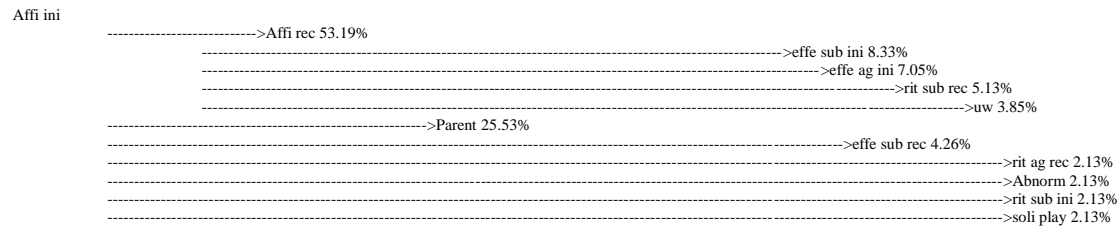








SE8. View of probability behavioral sequences of the behavioral transitions of Ga.



Affi rec

```

----->Affi ini 34.94%
----->rit ag rec 0.74%
----->Abnorm 0.74%
----->effe sub ini 15.66%
----->Parent 14.46%
----->effe ag ini 13.25%
----->effe sub rec 4.42%
----->rit sub rec 9.64%
----->uw 7.23%
----->soli play 1.20%
----->rit sub ini 1.20%

effe ag ini
----->rit sub rec 41.67%
----->Parent 6.94%
----->uw 3.47%
----->effe sub rec 33.33%
----->Affi rec 24.24%
----->effe sub ini 3.80%
----->rit sub ini 0.29%
----->soli play 0.29%
----->Affi ini 9.09%
----->rit ag rec 0.19%
----->Abnorm 0.19%

effe sub ini
----->Affi rec 66.67%
----->Affi ini 23.29%
----->rit ag rec 0.50%
----->Abnorm 0.50%
----->Parent 9.64%
----->effe ag ini 8.84%
----->effe sub rec 2.95%
----->rit sub rec 6.43%
----->rit sub ini 0.80%
----->soli play 0.80%
----->uw 6.67%

effe sub rec
----->Affi rec 72.73%
----->effe sub ini 11.39%
----->Parent 10.51%
----->effe ag ini 9.64%
----->rit sub rec 7.01%
----->uw 5.26%
----->soli play 0.88%
----->rit sub ini 0.88%
----->Affi ini 27.27%
----->rit ag rec 0.58%
----->Abnorm 0.58%

Parent
----->Affi rec 67.27%
----->Affi ini 23.50%
----->rit ag rec 0.50%
----->Abnorm 0.50%
----->effe sub ini 10.54%

```

```

----->effe ag ini 8.92%
----->effe sub rec 2.97%
----->rit sub rec 6.48%
----->uw 4.86%
----->rit sub ini 0.81%
----->soli play 0.81%

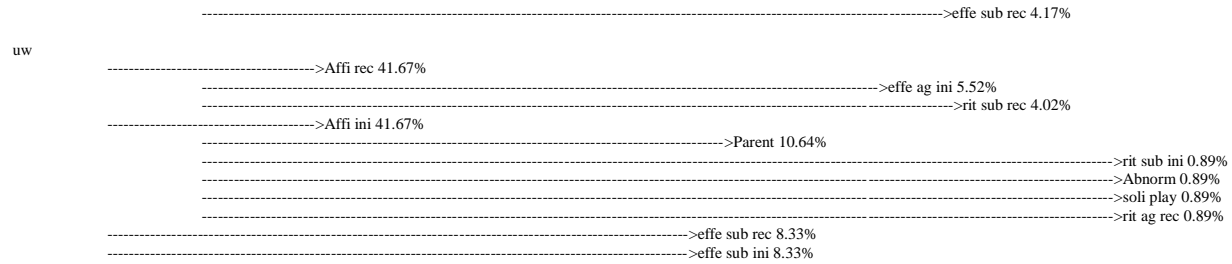
rit ag rec
->rit sub ini 100.00%
----->Affi rec 66.67%
----->effe sub ini 10.44%
----->Parent 9.64%
----->effe ag ini 8.84%
----->effe sub rec 2.95%
----->rit sub rec 6.43%
----->uw 4.82%
----->soli play 0.80%
----->Affi ini 33.33%
----->Abnorm 0.71%

rit sub ini
----->Affi rec 66.67%
----->effe sub ini 10.44%
----->Parent 9.64%
----->effe ag ini 8.84%
----->effe sub rec 2.95%
----->rit sub rec 6.43%
----->uw 4.82%
----->soli play 0.80%
----->Affi ini 33.33%
----->rit ag rec 0.71%
----->Abnorm 0.71%

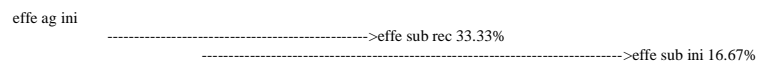
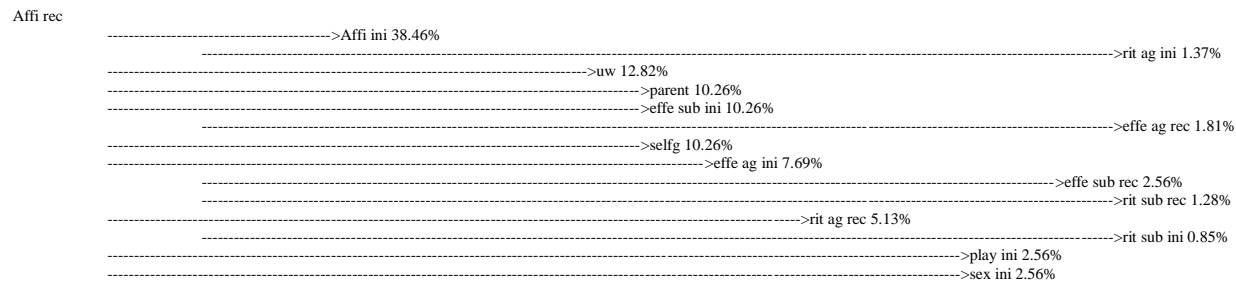
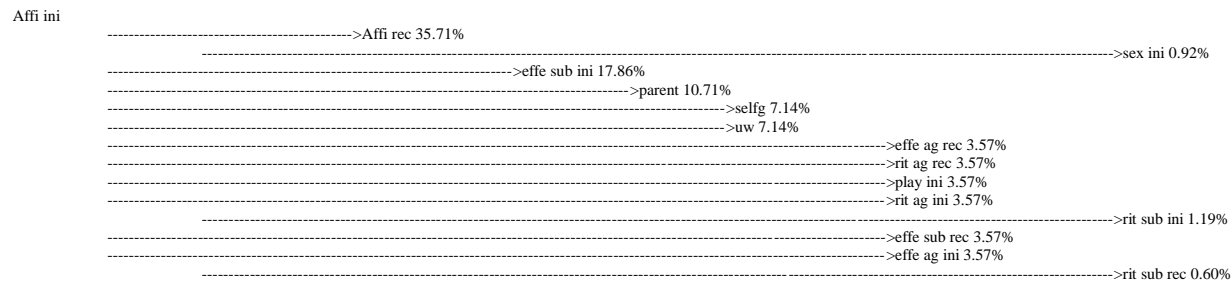
rit sub rec
----->Affi rec 50.00%
----->Affi ini 17.47%
----->rit ag rec 0.37%
----->Abnorm 0.37%
----->effe sub ini 7.83%
----->soli play 0.60%
----->rit sub ini 0.60%
----->effe ag ini 16.67%
----->effe sub rec 5.56%
----->Parent 16.67%
----->uw 8.33%

soli play
----->Affi rec 50.00%
----->effe sub ini 7.83%
----->Parent 7.23%
----->effe ag ini 6.63%
----->rit sub rec 4.82%
----->rit sub ini 0.60%
----->uw 50.00%
----->Affi ini 20.83%
----->rit ag rec 0.44%
----->Abnorm 0.44%

```



### SE9. View of probability behavioral sequences of the behavioral transitions of In.



```

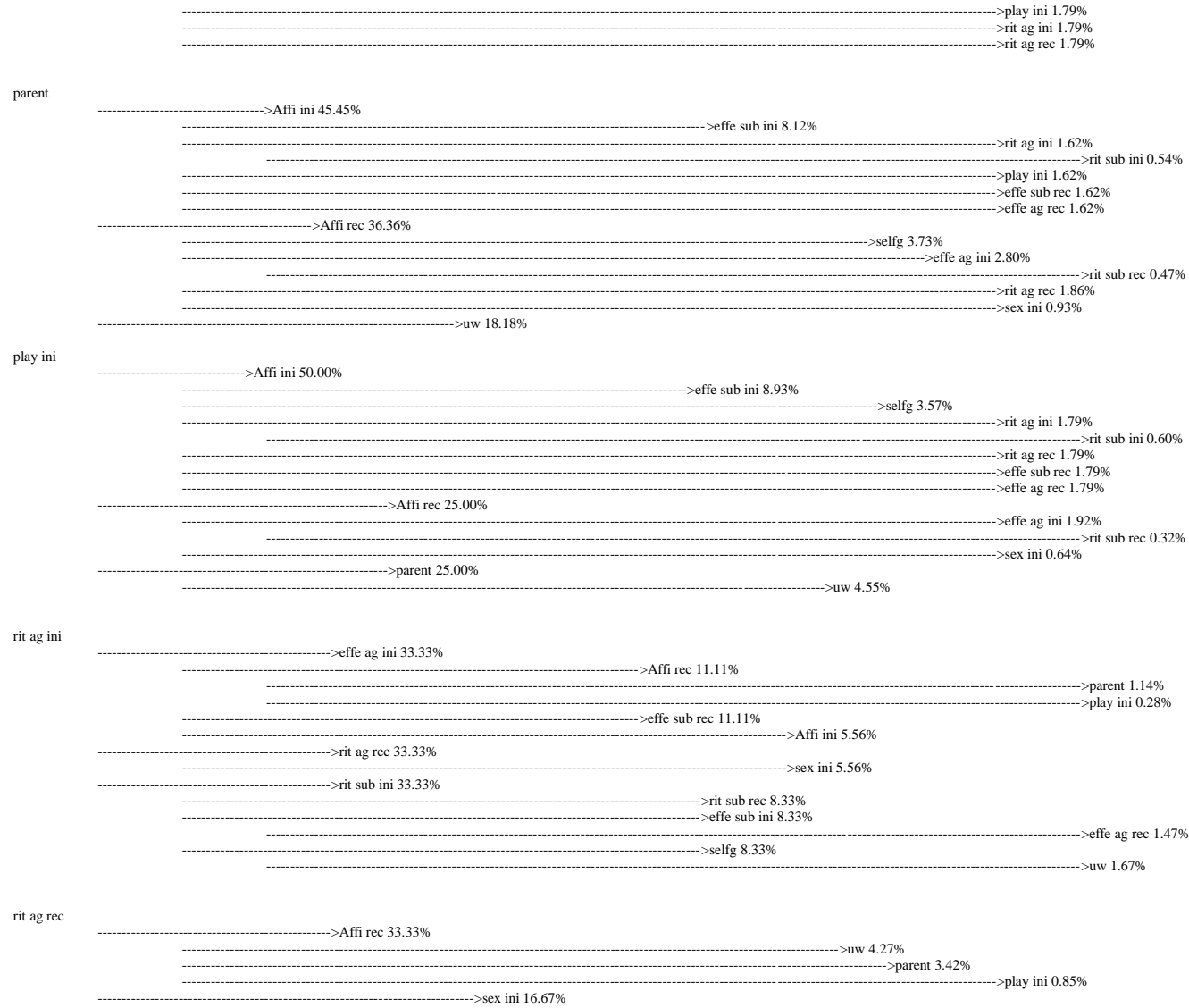
----->effe ag rec 2.94%
----->Affi rec 33.33%
----->uw 4.27%
----->selfg 3.42%
----->parent 3.42%
----->rit ag rec 1.71%
----->play ini 0.85%
----->sex ini 0.85%
----->rit sub rec 16.67%
----->rit sub ini 8.33%
----->Affi ini 16.67%
----->rit ag ini 0.60%

effe ag rec
----->effe sub ini 80.00%
----->Affi rec 28.24%
----->uw 3.62%
----->parent 2.90%
----->effe ag ini 2.17%
----->rit ag rec 1.45%
----->sex ini 0.72%
----->Affi ini 23.53%
----->rit ag ini 0.84%
----->play ini 0.84%
----->selfg 4.71%
----->rit sub ini 4.71%
----->rit sub rec 1.18%
----->effe sub rec 4.71%

effe sub ini
----->Affi rec 35.29%
----->uw 4.52%
----->parent 3.62%
----->effe ag ini 2.71%
----->rit ag rec 1.81%
----->sex ini 0.90%
----->Affi ini 29.41%
----->play ini 1.05%
----->rit ag ini 1.05%
----->effe ag rec 17.65%
----->effe sub rec 5.88%
----->selfg 5.88%
----->rit sub ini 5.88%
----->rit sub rec 1.47%

effe sub rec
----->effe sub ini 50.00%
----->effe ag rec 8.82%
----->rit sub ini 2.94%
----->rit sub rec 0.74%
----->Affi ini 50.00%
----->Affi rec 17.86%
----->sex ini 0.46%
----->parent 5.36%
----->selfg 3.57%
----->uw 3.57%
----->effe ag ini 1.79%

```



```

----->effe ag ini 8.33%
----->effe sub rec 2.78%
----->rit sub ini 16.67%
----->rit sub rec 4.17%
----->selfg 4.17%
----->Affi ini 16.67%
----->rit ag ini 0.60%
----->effe sub ini 16.67%
----->effe ag rec 2.94%

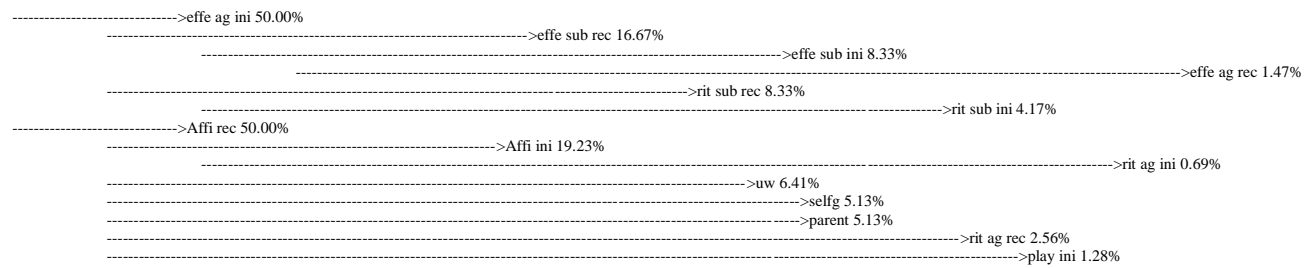
rit sub ini
----->selfg 25.00%
----->effe sub rec 5.00%
----->uw 5.00%
----->rit ag ini 0.38%
----->Affi rec 25.00%
----->Affi ini 9.62%
----->parent 2.56%
----->rit ag rec 1.28%
----->play ini 0.64%
----->sex ini 0.64%
----->effe sub ini 25.00%
----->effe ag rec 4.41%
----->rit sub rec 25.00%
----->effe ag ini 12.50%

rit sub rec
----->effe ag ini 50.00%
----->effe sub rec 16.67%
----->Affi ini 8.33%
----->rit ag ini 0.30%
----->Affi rec 16.67%
----->parent 1.71%
----->rit ag rec 0.85%
----->sex ini 0.43%
----->play ini 0.43%
----->rit sub ini 50.00%
----->effe sub ini 12.50%
----->effe ag rec 2.21%
----->selfg 12.50%
----->uw 2.50%

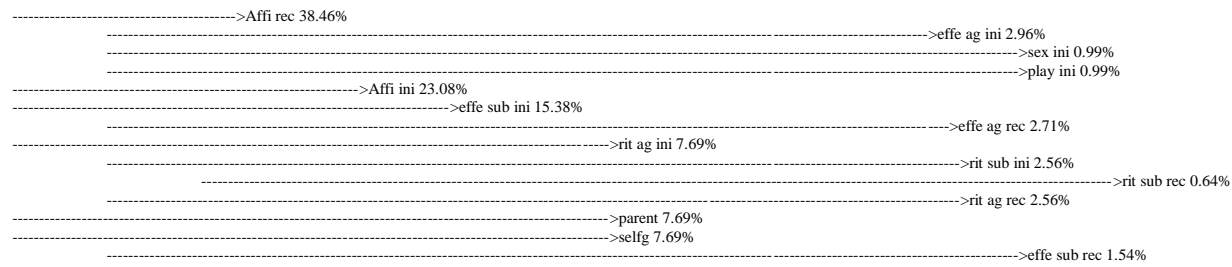
selfg
----->Affi rec 40.00%
----->parent 4.10%
----->effe ag ini 3.08%
----->rit sub rec 0.51%
----->rit ag rec 2.05%
----->play ini 1.03%
----->sex ini 1.03%
----->Affi ini 20.00%
----->effe sub rec 20.00%
----->effe sub ini 10.00%
----->effe ag rec 1.76%
----->rit sub ini 0.59%
----->uw 20.00%
----->rit ag ini 1.54%

```

sex ini

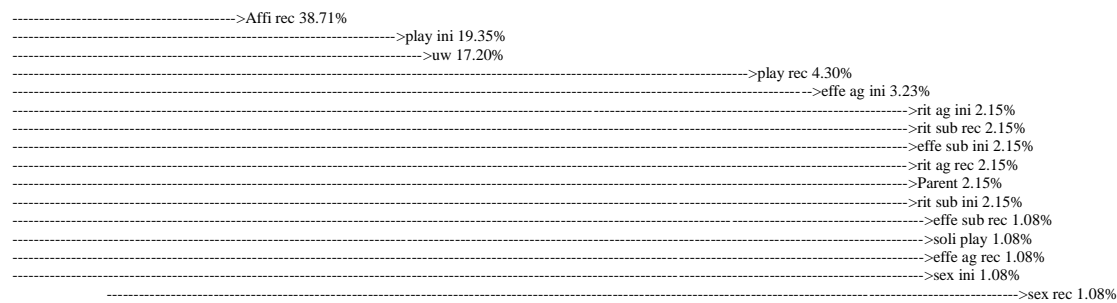


uw



### SE10. View of probability behavioral sequences of the behavioral transitions of Kr.

Affi ini





Affi rec

```

----->Affi ini 63.27%
----->play ini 12.24%
----->play rec 2.72%
----->effe ag ini 2.04%
----->rit ag rec 1.36%
----->rit ag ini 1.36%
----->effe sub ini 1.36%
----->Parent 1.36%
----->effe ag rec 0.68%
----->effe sub rec 0.68%
----->solu play 0.68%
----->sex ini 0.68%
----->sex rec 0.68%
----->uw 18.37%
----->rit sub ini 4.08%
----->rit sub rec 2.04%

```

effe ag ini

```

----->Affi ini 75.00%
----->Affi rec 29.03%
----->play ini 14.52%
----->uw 12.90%
----->play rec 3.23%
----->rit sub rec 1.61%
----->rit sub ini 1.61%
----->Parent 1.61%
----->rit ag rec 1.61%
----->effe sub ini 1.61%
----->effe ag rec 0.81%
----->solu play 0.81%
----->sex ini 0.81%
----->sex rec 0.81%
----->effe sub rec 25.00%
----->rit ag ini 6.25%

```

effe ag rec

```

->Affi ini 100.00%
----->Affi rec 38.71%
----->play ini 19.35%
----->uw 17.20%
----->play rec 4.30%
----->effe ag ini 3.23%
----->rit ag ini 2.15%
----->rit sub rec 2.15%
----->rit ag rec 2.15%
----->effe sub ini 2.15%
----->rit sub ini 2.15%
----->Parent 2.15%
----->effe sub rec 1.08%
----->solu play 1.08%
----->sex ini 1.08%
----->sex rec 1.08%

```

effe sub ini

```

----->rit sub rec 33.33%

```

```

----->Affi ini 33.33%----->Affi rec 16.67%
----->uw 5.73%
----->play rec 1.43%
----->effe ag ini 1.08%
----->Parent 0.72%
----->rit sub ini 0.72%
----->rit ag rec 0.72%
----->sex ini 0.36%
----->sex rec 0.36%
----->effe ag rec 0.36%
----->effe sub rec 0.36%
----->play ini 33.33%
----->soli play 1.39%
----->rit ag ini 1.39%

effe sub rec
----->Affi ini 50.00%
----->play ini 9.68%
----->uw 8.60%
----->play rec 2.15%
----->effe ag ini 1.61%
----->Parent 1.08%
----->rit sub rec 1.08%
----->rit sub ini 1.08%
----->rit ag rec 1.08%
----->effe sub ini 1.08%
----->effe ag rec 0.54%
----->sex ini 0.54%
----->sex rec 0.54%
----->soli play 0.54%
----->Affi rec 25.00%
----->rit ag ini 25.00%

Parent
----->Affi rec 75.00%
----->Affi ini 47.45%
----->play ini 9.18%
----->play rec 2.04%
----->effe sub ini 1.02%
----->rit ag ini 1.02%
----->rit ag rec 1.02%
----->effe sub rec 0.51%
----->sex ini 0.51%
----->sex rec 0.51%
----->effe ag rec 0.51%
----->soli play 0.51%
----->uw 13.78%
----->rit sub ini 3.06%
----->rit sub rec 1.53%
----->effe ag ini 1.53%

play ini
----->Affi ini 62.50%
----->uw 10.75%
----->play rec 2.69%
----->effe ag ini 2.02%
----->rit sub ini 1.34%

```

```

----->rit sub rec 1.34%
----->rit ag rec 1.34%
----->effe sub ini 1.34%
----->Parent 1.34%
----->effe ag rec 0.67%
----->sex ini 0.67%
----->sex rec 0.67%
----->Affi rec 25.00%
----->solu play 4.17%
----->rit ag ini 4.17%
----->effe sub rec 0.83%

play rec
----->Affi rec 28.57%
----->rit sub ini 1.17%
----->Affi ini 28.57%
----->effe ag ini 0.92%
----->rit sub rec 0.61%
----->Parent 0.61%
----->effe sub ini 0.61%
----->rit ag ini 0.61%
----->rit ag rec 0.61%
----->effe ag rec 0.31%
----->sex ini 0.31%
----->sex rec 0.31%
----->effe sub rec 0.31%
----->play ini 14.29%
----->uw 14.29%
----->solu play 14.29%

rit ag ini
----->Affi ini 80.00%
----->Affi rec 30.97%
----->play ini 15.48%
----->uw 13.76%
----->play rec 3.44%
----->effe ag ini 2.58%
----->rit ag rec 1.72%
----->effe sub ini 1.72%
----->rit sub rec 1.72%
----->rit sub ini 1.72%
----->Parent 1.72%
----->effe ag rec 0.86%
----->solu play 0.86%
----->sex ini 0.86%
----->sex rec 0.86%
----->effe sub rec 20.00%

rit ag rec
----->rit sub ini 50.00%
----->Affi rec 30.00%
----->uw 50.00%
----->Affi ini 41.67%

```

```

----->play ini 8.06%
----->effe ag ini 1.34%
----->Parent 0.90%
----->effe sub ini 0.90%
----->rit sub rec 0.90%
----->rit ag ini 0.90%
----->effe sub rec 0.45%
----->sex ini 0.45%
----->sex rec 0.45%
----->effe ag rec 0.45%
----->play rec 4.17%
----->soli play 0.60%

```

rit sub ini

```

----->Affi rec 60.00%
----->uw 11.02%
----->rit sub rec 1.22%
----->Affi ini 40.00%
----->play ini 7.74%
----->play rec 1.72%
----->effe ag ini 1.29%
----->rit ag ini 0.86%
----->rit ag rec 0.86%
----->Parent 0.86%
----->effe sub ini 0.86%
----->effe ag rec 0.43%
----->effe sub rec 0.43%
----->sex ini 0.43%
----->sex rec 0.43%
----->soli play 0.43%

```

rit sub rec

```

----->Affi rec 50.00%
----->uw 9.18%
----->rit sub ini 2.04%
----->Affi ini 50.00%
----->play ini 9.68%
----->play rec 2.15%
----->effe ag ini 1.61%
----->rit ag ini 1.08%
----->rit ag rec 1.08%
----->Parent 1.08%
----->effe sub ini 1.08%
----->effe ag rec 0.54%
----->effe sub rec 0.54%
----->sex ini 0.54%
----->sex rec 0.54%
----->soli play 0.54%

```

selfg

```

->Affi ini 100.00%
----->Affi rec 38.71%
----->play ini 19.35%

```

```

----->uw 17.20%
----->play rec 4.30%
----->effe ag ini 3.23%
----->rit sub rec 2.15%
----->effe sub ini 2.15%
----->rit sub ini 2.15%
----->Parent 2.15%
----->rit ag rec 2.15%
----->rit ag ini 2.15%
----->solu play 1.08%
----->effe sub rec 1.08%
----->effe ag rec 1.08%
----->sex ini 1.08%
----->sex rec 1.08%

```

sex ini

```

->sex rec 100.00%
->Affi ini 100.00%
----->Affi rec 38.71%
----->play ini 19.35%
----->uw 17.20%
----->play rec 4.30%
----->effe ag ini 3.23%
----->effe sub ini 2.15%
----->rit ag ini 2.15%
----->Parent 2.15%
----->rit sub rec 2.15%
----->rit ag rec 2.15%
----->rit sub ini 2.15%
----->solu play 1.08%
----->effe ag rec 1.08%
----->effe sub rec 1.08%

```

sex rec

```

->Affi ini 100.00%
----->Affi rec 38.71%
----->play ini 19.35%
----->uw 17.20%
----->play rec 4.30%
----->effe ag ini 3.23%
----->rit ag ini 2.15%
----->effe sub ini 2.15%
----->Parent 2.15%
----->rit sub rec 2.15%
----->rit ag rec 2.15%
----->rit sub ini 2.15%
----->sex ini 1.08%
----->solu play 1.08%
----->effe ag rec 1.08%
----->effe sub rec 1.08%

```

solu play

```

----->Affi ini 75.00%
----->Affi rec 29.03%

```

```

----->play ini 14.52%
----->uw 12.90%
----->play rec 3.23%
----->effe ag ini 2.42%
----->Parent 1.61%
----->effe sub ini 1.61%
----->rit sub ini 1.61%
----->rit ag ini 1.61%
----->rit sub rec 1.61%
----->rit ag rec 1.61%
----->effe ag rec 0.81%
----->effe sub rec 0.81%
----->sex ini 0.81%
----->sex rec 0.81%

```

uw

```

----->Affi ini 83.33%
----->Affi rec 32.26%
----->play ini 16.13%
----->effe ag ini 2.69%
----->rit ag ini 1.79%
----->Parent 1.79%
----->effe sub ini 1.79%
----->rit sub ini 1.79%
----->rit sub rec 1.79%
----->rit ag rec 1.79%
----->effe ag rec 0.90%
----->effe sub rec 0.90%
----->sex ini 0.90%
----->sex rec 0.90%
----->play rec 8.33%
----->solu play 1.19%

```

### SE11. View of probability behavioral sequences of the behavioral transitions of Mg.

Abnormal

```

----->Affi ini 50.00%
----->Affi rec 18.87%
----->sex ini 0.61%
----->selfg 0.61%
----->solu play 3.77%
----->effe ag ini 3.77%
----->uw 2.83%
----->play rec 0.94%
----->rit ag rec 0.94%
----->effe sub rec 16.67%
----->play ini 2.78%
----->rit ag ini 8.33%
----->rit sub rec 2.78%
----->effe ag rec 0.69%
----->rit sub ini 8.33%
----->effe sub ini 8.33%

```

Affi ini

----->Affi rec 37.74%  
----->selfg 1.22%  
----->sex ini 1.22%  
----->Abnormal 15.09%  
----->effe sub ini 7.55%  
----->effe ag ini 7.55%  
----->solu play 7.55%  
----->effe sub rec 5.66%  
----->rit ag ini 5.66%  
----->rit sub rec 1.89%  
----->uw 5.66%  
----->play ini 1.89%  
----->rit ag rec 1.89%  
----->effe ag rec 0.94%  
----->play rec 1.89%  
----->rit sub ini 1.89%

Affi rec

----->Affi ini 54.84%  
----->Abnormal 8.28%  
----->effe sub ini 4.14%  
----->effe ag ini 4.14%  
----->rit sub ini 1.03%  
----->play rec 1.03%  
----->rit ag rec 1.03%  
----->effe ag rec 0.52%  
----->play ini 1.03%  
----->uw 9.68%  
----->solu play 9.68%  
----->rit ag ini 3.23%  
----->effe sub rec 3.23%  
----->rit sub rec 3.23%  
----->selfg 3.23%  
----->sex ini 3.23%

effe ag ini

----->play rec 16.67%  
----->play ini 8.33%  
----->Affi rec 16.67%  
----->solu play 1.61%  
----->selfg 0.54%  
----->sex ini 0.54%  
----->effe sub rec 16.67%  
----->rit ag rec 16.67%  
----->rit sub ini 8.33%  
----->Abnormal 5.00%  
----->effe ag rec 8.33%  
----->uw 4.17%  
----->rit sub rec 16.67%  
----->rit ag ini 8.33%  
----->Affi ini 16.67%  
----->effe sub ini 1.26%

effe ag rec  
 ----->rit ag ini 50.00%  
 ----->rit sub rec 16.67%  
 ----->effe sub rec 8.33%  
 ----->play ini 1.39%  
 ----->rit sub ini 4.17%  
 ----->uw 50.00%  
 ----->Affi ini 20.83%  
 ----->soli play 1.57%  
 ----->Affi rec 8.33%  
 ----->selfg 0.27%  
 ----->sex ini 0.27%  
 ----->effe sub ini 8.33%  
 ----->Abnormal 8.33%  
 ----->effe ag ini 4.17%  
 ----->rit ag rec 0.69%  
 ----->play rec 0.69%

effe sub ini  
 ----->Affi ini 57.14%  
 ----->Affi rec 21.56%  
 ----->sex ini 0.70%  
 ----->selfg 0.70%  
 ----->soli play 4.31%  
 ----->effe ag ini 4.31%  
 ----->uw 3.23%  
 ----->play rec 1.08%  
 ----->rit ag rec 1.08%  
 ----->effe ag rec 0.54%  
 ----->Abnormal 42.86%  
 ----->effe sub rec 7.14%  
 ----->play ini 1.19%  
 ----->rit ag ini 3.57%  
 ----->rit sub rec 1.19%  
 ----->rit sub ini 3.57%

effe sub rec  
 ----->rit ag ini 33.33%  
 ----->rit sub rec 11.11%  
 ----->rit sub ini 2.78%  
 ----->uw 2.78%  
 ----->Affi ini 33.33%  
 ----->Abnormal 5.03%  
 ----->effe sub ini 2.52%  
 ----->soli play 2.52%  
 ----->effe ag ini 2.52%  
 ----->rit ag rec 0.63%  
 ----->play rec 0.63%  
 ----->play ini 16.67%  
 ----->effe ag rec 3.33%  
 ----->Affi rec 16.67%  
 ----->selfg 0.54%  
 ----->sex ini 0.54%

play ini  
 ----->Affi rec 40.00%  
 ----->soli play 3.87%  
 ----->sex ini 1.29%



```

----->selfg 1.29%
----->Affi ini 40.00%
----->Abnormal 6.04%
----->effe ag ini 3.02%
----->effe sub ini 3.02%
----->effe sub rec 2.26%
----->play rec 0.75%
----->rit ag rec 0.75%
----->effe ag rec 20.00%
----->rit ag ini 10.00%
----->rit sub rec 3.33%
----->rit sub ini 0.83%
----->uw 10.00%

play rec
----->play ini 50.00%
----->Affi rec 20.00%
----->sex ini 0.65%
----->selfg 0.65%
----->effe ag rec 10.00%
----->uw 5.00%
----->rit ag ini 5.00%
----->rit sub rec 1.67%
----->Affi ini 50.00%
----->Abnormal 7.55%
----->soli play 3.77%
----->effe ag ini 3.77%
----->effe sub ini 3.77%
----->effe sub rec 2.83%
----->rit sub ini 0.94%
----->rit ag rec 0.94%

rit ag ini
----->rit sub rec 33.33%
----->Affi ini 25.00%
----->Affi rec 9.43%
----->selfg 0.30%
----->sex ini 0.30%
----->effe ag ini 1.89%
----->effe sub ini 1.89%
----->soli play 1.89%
----->rit ag rec 0.47%
----->play rec 0.47%
----->effe sub rec 16.67%
----->play ini 2.78%
----->rit sub ini 8.33%
----->Abnormal 5.00%
----->effe ag rec 8.33%
----->uw 8.33%

rit ag rec
----->effe ag rec 50.00%
----->uw 25.00%
----->effe sub ini 4.17%
----->effe ag ini 2.08%
----->play rec 0.35%
----->rit ag ini 25.00%
----->rit sub rec 8.33%

```

```

----->rit sub ini 50.00%
----->Abnormal 30.00%
----->Affi ini 15.00%
----->Affi rec 5.66%
----->selfg 0.18%
----->sex ini 0.18%
----->soli play 1.13%
----->effe sub rec 5.00%
----->play ini 0.83%

rit sub ini
----->Abnormal 60.00%
----->Affi ini 30.00%
----->Affi rec 11.32%
----->selfg 0.37%
----->sex ini 0.37%
----->effe ag ini 2.26%
----->soli play 2.26%
----->play rec 0.57%
----->rit ag rec 0.57%
----->effe sub rec 10.00%
----->play ini 1.67%
----->effe sub ini 5.00%
----->rit ag ini 5.00%
----->rit sub rec 1.67%
----->effe ag rec 0.42%
----->uw 20.00%

rit sub rec
----->Affi ini 50.00%
----->Affi rec 18.87%
----->selfg 0.61%
----->sex ini 0.61%
----->Abnormal 7.55%
----->effe sub ini 3.77%
----->effe ag ini 3.77%
----->soli play 3.77%
----->rit ag rec 0.94%
----->play rec 0.94%
----->rit ag ini 50.00%
----->effe sub rec 8.33%
----->play ini 1.39%
----->rit sub ini 4.17%
----->uw 4.17%
----->effe ag rec 4.17%

selfg
->uw 100.00%
----->Affi ini 41.67%
----->soli play 3.14%
----->rit ag ini 2.36%
----->play ini 0.79%
----->Affi rec 16.67%
----->sex ini 0.54%
----->Abnormal 16.67%
----->effe sub rec 2.78%
----->rit sub ini 1.39%
----->effe sub ini 16.67%

```

```

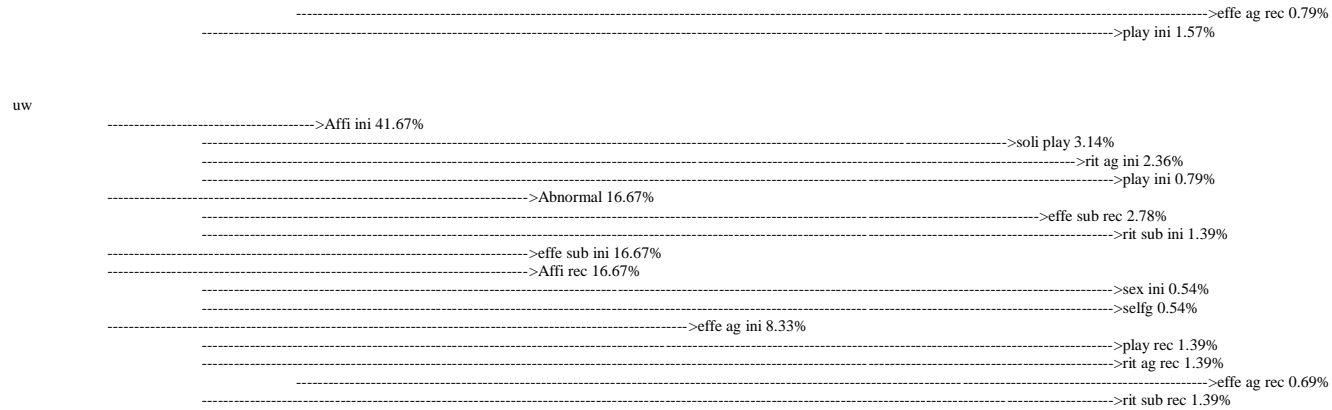
----->effe ag ini 8.33%
----->rit ag rec 1.39%
----->effe ag rec 0.69%
----->rit sub rec 1.39%
----->play rec 1.39%

sex ini
->rit ag ini 100.00%
----->rit sub rec 33.33%
----->Affi ini 25.00%
----->Affi rec 9.43%
----->selfg 0.30%
----->soli play 1.89%
----->effe ag ini 1.89%
----->effe sub ini 1.89%
----->rit ag rec 0.47%
----->play rec 0.47%
----->effe sub rec 16.67%
----->play ini 2.78%
----->effe ag rec 8.33%
----->rit sub ini 8.33%
----->Abnormal 5.00%
----->uw 8.33%

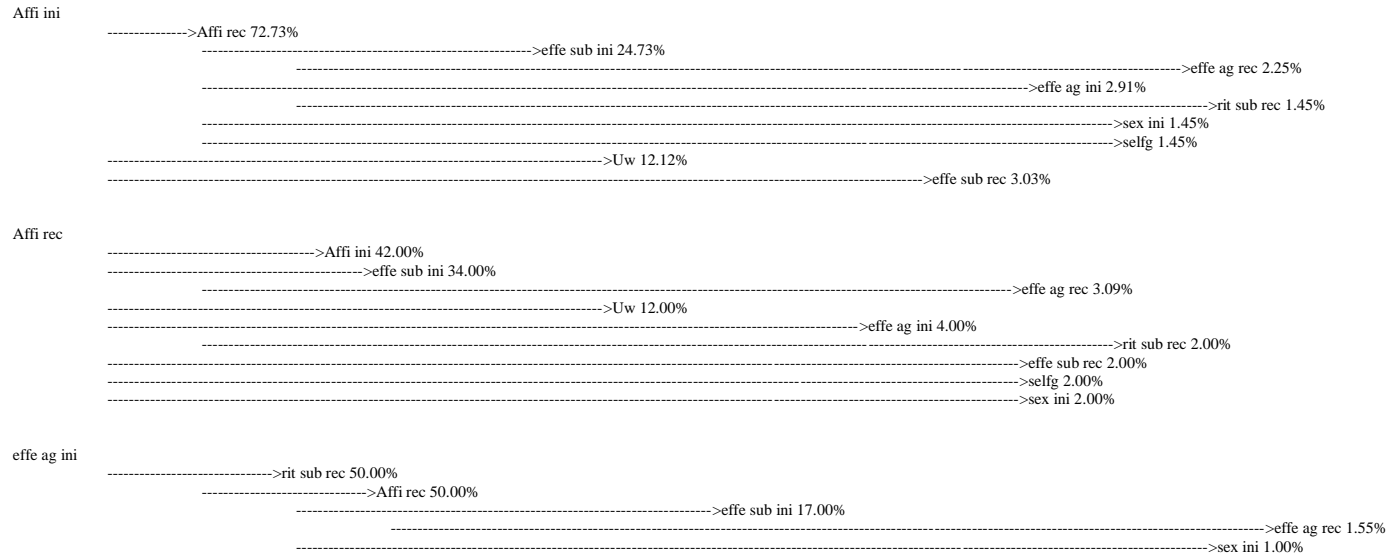
sm
->Affi ini 100.00%
----->Affi rec 37.74%
----->sex ini 1.22%
----->selfg 1.22%
----->Abnormal 15.09%
----->soli play 7.55%
----->effe ag ini 7.55%
----->effe sub ini 7.55%
----->effe sub rec 5.66%
----->uw 5.66%
----->rit ag ini 5.66%
----->rit sub rec 1.89%
----->play rec 1.89%
----->rit ag rec 1.89%
----->effe ag rec 0.94%
----->play ini 1.89%
----->rit sub ini 1.89%

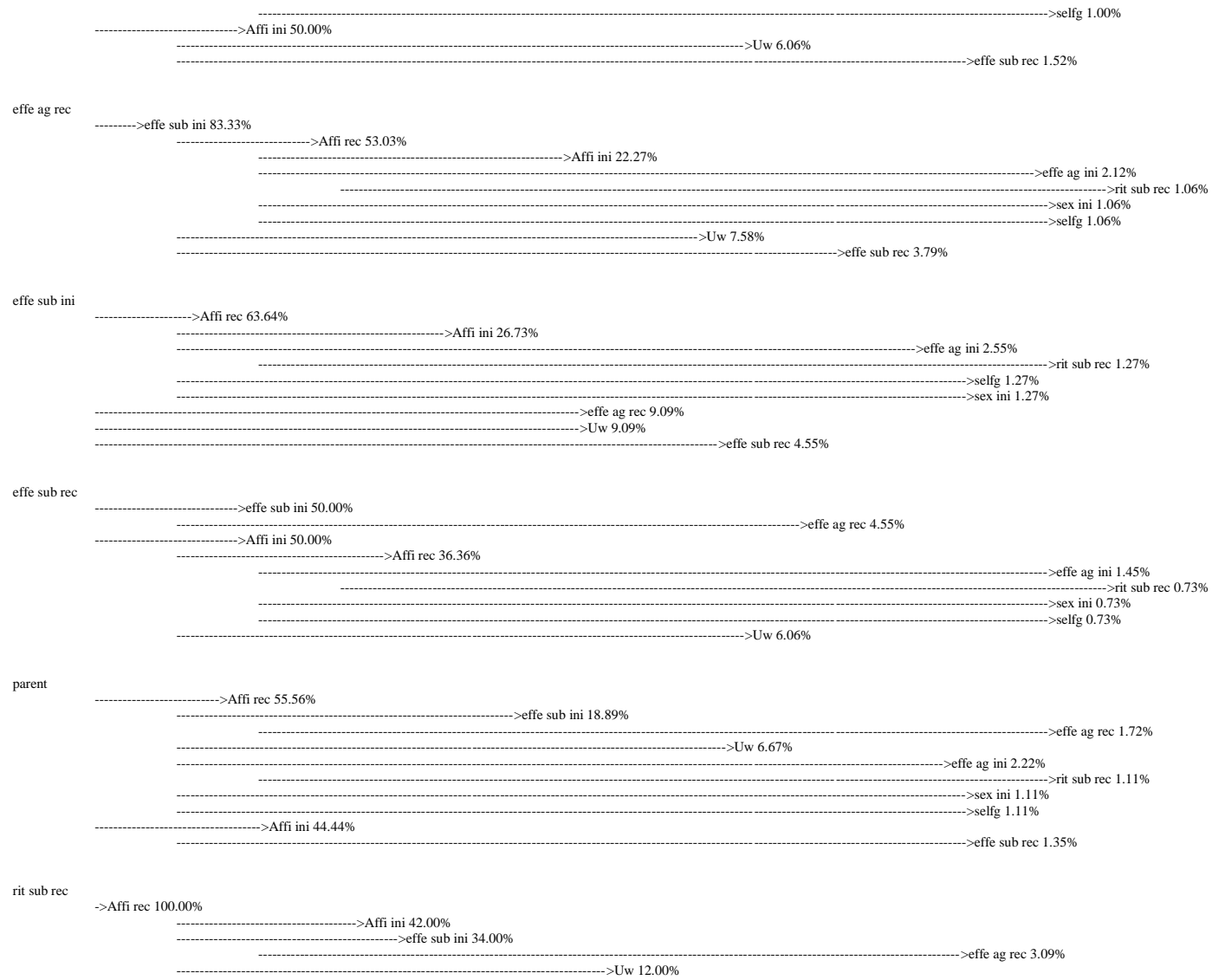
soli play
----->Affi ini 83.33%
----->Affi rec 31.45%
----->selfg 1.01%
----->sex ini 1.01%
----->Abnormal 12.58%
----->effe sub ini 6.29%
----->effe ag ini 6.29%
----->rit ag ini 4.72%
----->rit sub rec 1.57%
----->effe sub rec 4.72%
----->uw 4.72%
----->rit sub ini 1.57%
----->play rec 1.57%
----->rit ag rec 1.57%

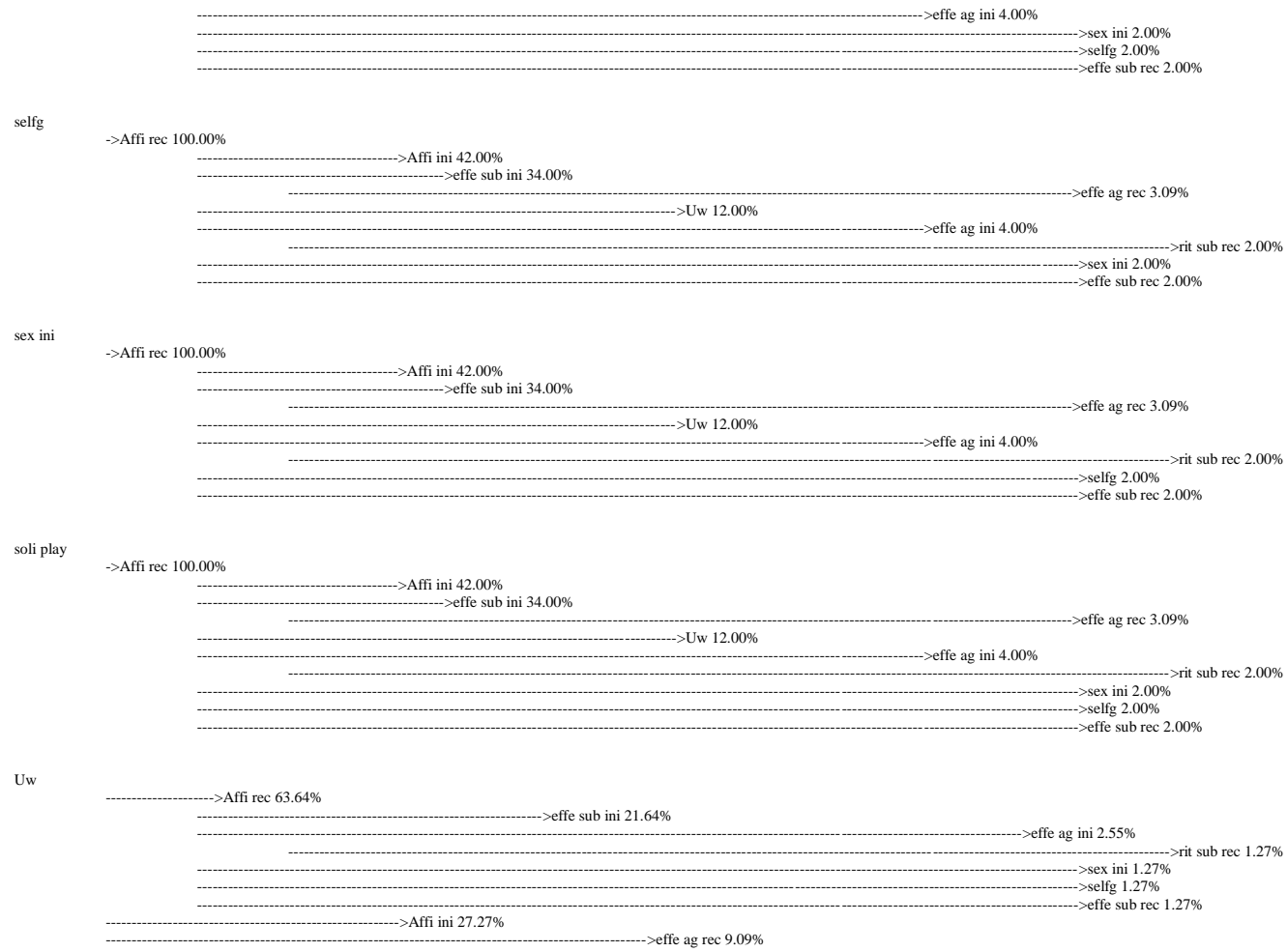
```



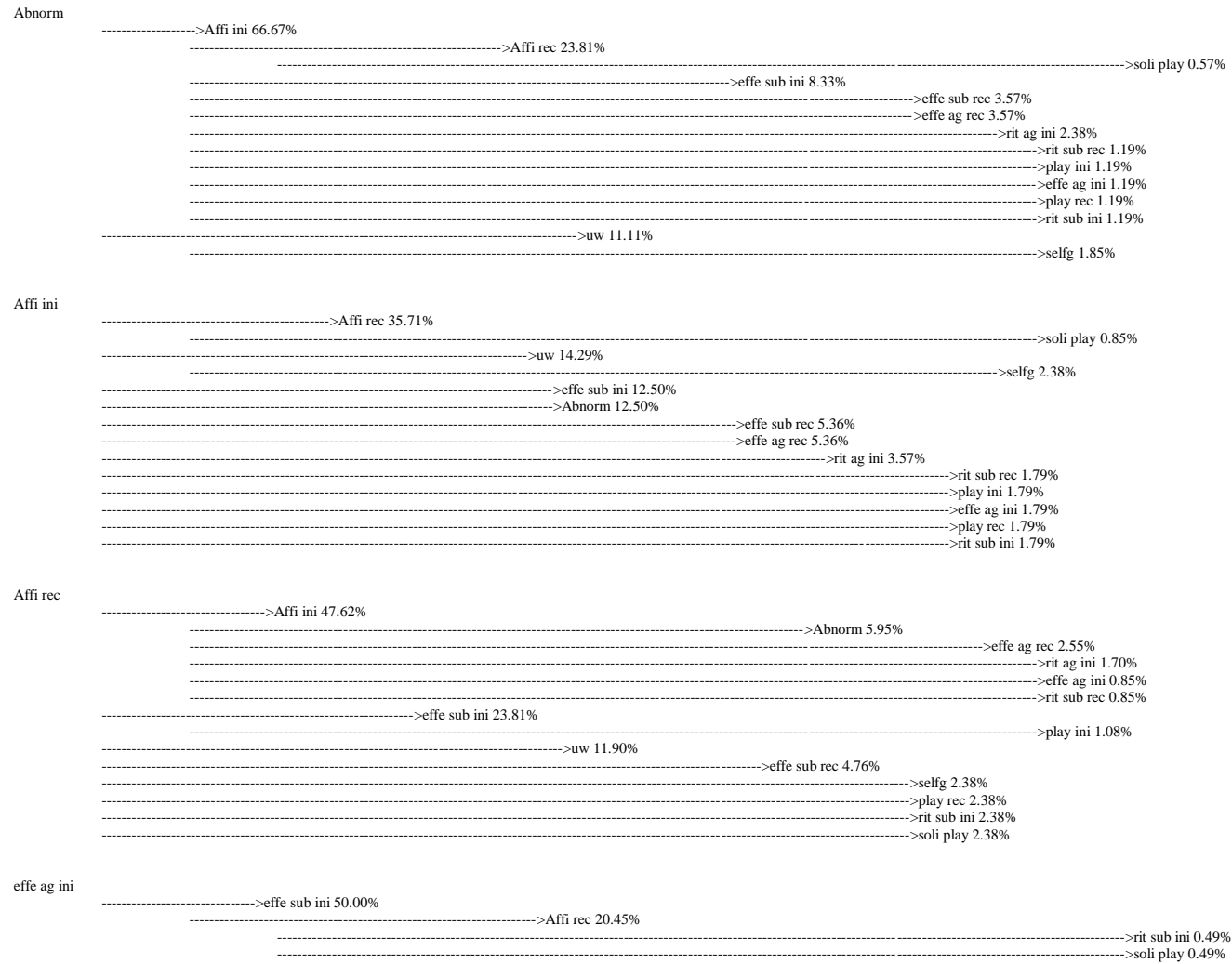
SE12. View of probability behavioral sequences of the behavioral transitions of Na.







SE13. View of probability behavioral sequences of the behavioral transitions of Pe.



```

----->uw 6.82%
----->selfg 1.14%
----->play ini 2.27%
----->play rec 2.27%
----->rit ag ini 50.00%
----->effe sub rec 25.00%
----->Affi ini 25.00%
----->Abnorm 3.13%
----->effe ag rec 1.34%
----->rit sub rec 0.45%

effe ag rec
----->rit sub rec 25.00%
----->Affi ini 25.00%
----->effe sub rec 1.34%
----->rit ag ini 0.89%
----->rit sub ini 0.45%
----->effe sub ini 25.00%
----->Affi rec 10.23%
----->soli play 0.24%
----->play rec 1.14%
----->play ini 1.14%
----->uw 25.00%
----->Abnorm 4.17%
----->selfg 4.17%
----->effe ag ini 1.04%

effe sub ini
----->Affi rec 40.91%
----->soli play 0.97%
----->rit sub ini 0.97%
----->Affi ini 31.82%
----->Abnorm 3.98%
----->effe ag rec 1.70%
----->rit ag ini 1.14%
----->rit sub rec 0.57%
----->uw 13.64%
----->selfg 2.27%
----->effe ag ini 0.57%
----->effe sub rec 4.55%
----->play ini 4.55%
----->play rec 4.55%

effe sub rec
----->Affi rec 80.00%
----->Affi ini 38.10%
----->Abnorm 4.76%
----->effe ag rec 2.04%
----->rit ag ini 1.36%
----->rit sub rec 0.68%
----->effe sub ini 19.05%
----->play ini 0.87%
----->play rec 1.90%
----->rit sub ini 1.90%
----->soli play 1.90%
----->uw 20.00%
----->selfg 3.33%

```



```

----->effe ag ini 0.83%

play ini
->Affi ini 100.00%
----->Affi rec 35.71%
----->solu play 0.85%
----->uw 14.29%
----->selfg 2.38%
----->Abnorm 12.50%
----->effe sub ini 12.50%
----->effe ag rec 5.36%
----->effe sub rec 5.36%
----->rit ag ini 3.57%
----->effe ag ini 1.79%
----->rit sub ini 1.79%
----->rit sub rec 1.79%
----->play rec 1.79%

play rec
----->Affi rec 50.00%
----->Affi ini 23.81%
----->effe ag rec 1.28%
----->rit ag ini 0.85%
----->rit sub rec 0.43%
----->effe sub rec 2.38%
----->solu play 1.19%
----->rit sub ini 1.19%
----->uw 25.00%
----->selfg 4.17%
----->effe ag ini 1.04%
----->Abnorm 4.17%
----->effe sub ini 25.00%
----->play ini 1.14%

rit ag ini
----->effe sub rec 50.00%
----->Affi rec 40.00%
----->effe sub ini 9.52%
----->play rec 0.95%
----->solu play 0.95%
----->rit sub ini 0.95%
----->uw 10.00%
----->selfg 1.67%
----->Affi ini 50.00%
----->Abnorm 6.25%
----->effe ag rec 2.68%
----->rit sub rec 0.89%
----->play ini 0.89%
----->effe ag ini 0.89%

rit sub ini
->Affi rec 100.00%
----->Affi ini 47.62%
----->Abnorm 5.95%
----->effe ag rec 2.55%
----->rit ag ini 1.70%

```

```

----->effe ag ini 0.85%
----->rit sub rec 0.85%
----->effe sub ini 23.81%
----->play ini 1.08%
----->uw 11.90%
----->effe sub rec 4.76%
----->play rec 2.38%
----->soli play 2.38%
----->selfg 2.38%

```

rit sub rec

```

->Affi ini 100.00%
----->Affi rec 35.71%
----->uw 14.29%
----->Abnorm 12.50%
----->effe sub ini 12.50%
----->effe ag rec 5.36%
----->effe sub rec 5.36%
----->rit ag ini 3.57%
----->effe ag ini 1.79%
----->play rec 1.79%
----->rit sub ini 1.79%
----->play ini 1.79%
----->soli play 0.85%
----->selfg 2.38%

```

selfg

```

----->Affi rec 75.00%
----->Affi ini 35.71%
----->Abnorm 4.46%
----->effe ag rec 1.91%
----->rit sub rec 0.64%
----->effe sub ini 17.86%
----->play ini 0.81%
----->uw 8.93%
----->play rec 1.79%
----->rit sub ini 1.79%
----->soli play 1.79%
----->effe ag ini 25.00%
----->rit ag ini 12.50%
----->effe sub rec 6.25%

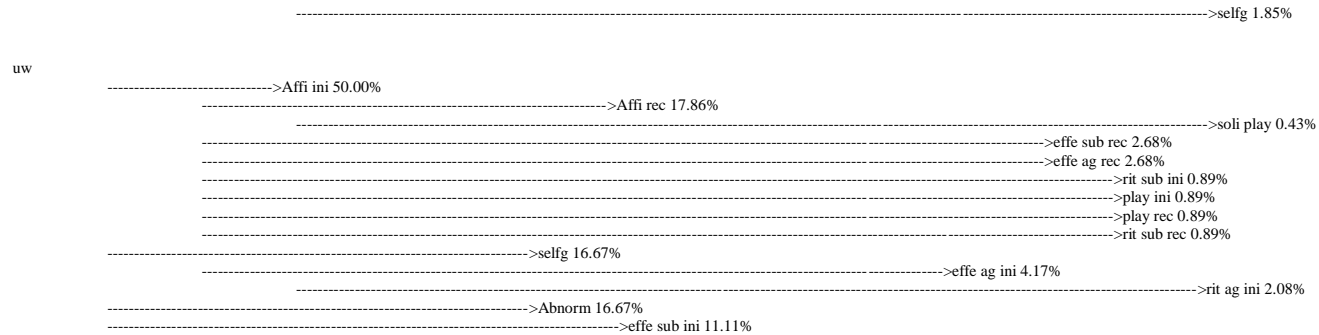
```

soli play

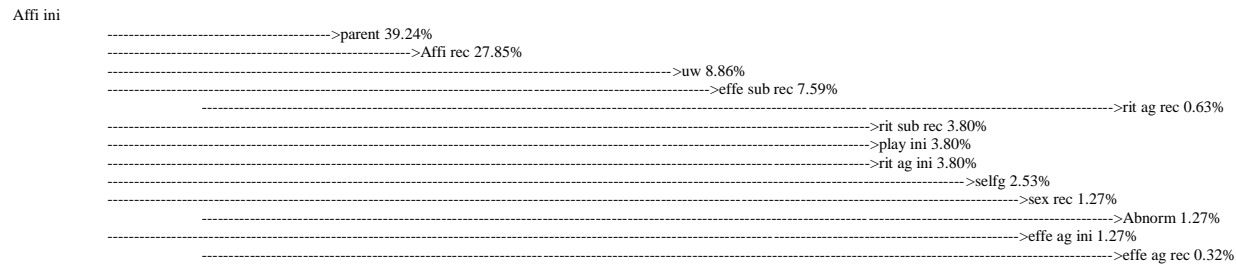
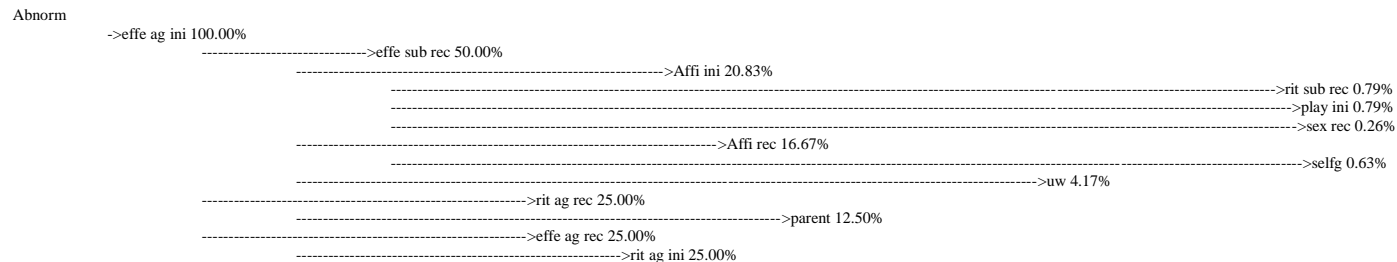
```

->Abnorm 100.00%
----->Affi ini 66.67%
----->Affi rec 23.81%
----->effe sub ini 8.33%
----->effe sub rec 3.57%
----->effe ag rec 3.57%
----->rit ag ini 2.38%
----->effe ag ini 1.19%
----->play ini 1.19%
----->play rec 1.19%
----->rit sub rec 1.19%
----->rit sub ini 1.19%
----->uw 11.11%

```



SE14. View of probability behavioral sequences of the behavioral transitions of Pr.



Affi rec

----->Affi ini 56.60%  
----->parent 22.21%  
----->play ini 2.15%  
----->rit ag ini 2.15%  
----->rit sub rec 2.15%  
----->sex rec 0.72%  
----->Abnorm 0.72%  
----->uw 7.55%  
----->effe sub rec 5.66%  
----->selfg 3.77%  
----->effe ag ini 1.89%  
----->effe ag rec 0.47%  
----->rit ag rec 0.47%

effe ag ini

----->effe sub rec 50.00%  
----->Affi ini 20.83%  
----->rit sub rec 0.79%  
----->play ini 0.79%  
----->sex rec 0.26%  
----->Abnorm 0.26%  
----->Affi rec 16.67%  
----->selfg 0.63%  
----->uw 4.17%  
----->rit ag rec 25.00%  
----->parent 12.50%  
----->effe ag rec 25.00%  
----->rit ag ini 25.00%

effe ag rec

->rit ag ini 100.00%  
----->Affi ini 50.00%  
----->parent 19.62%  
----->uw 4.43%  
----->play ini 1.90%  
----->rit sub rec 1.90%  
----->selfg 1.27%  
----->sex rec 0.63%  
----->Abnorm 0.63%  
----->effe ag ini 0.63%  
----->effe sub rec 25.00%  
----->rit ag rec 2.08%  
----->Affi rec 25.00%

effe sub rec

----->Affi ini 41.67%  
----->parent 16.35%  
----->play ini 1.58%  
----->rit sub rec 1.58%  
----->rit ag ini 1.58%

----->sex rec 0.53%  
 ----->Abnorm 0.53%  
 ----->Affi rec 33.33%  
 ----->selfg 1.26%  
 ----->effe ag ini 0.63%  
 ----->effe ag rec 0.16%  
 ----->uw 8.33%  
 ----->rit ag rec 8.33%

parent

----->Affi ini 61.11%  
 ----->uw 5.41%  
 ----->effe sub rec 4.64%  
 ----->rit sub rec 2.32%  
 ----->rit ag ini 2.32%  
 ----->play ini 2.32%  
 ----->selfg 1.55%  
 ----->sex rec 0.77%  
 ----->Abnorm 0.77%  
 ----->Affi rec 31.48%  
 ----->effe ag ini 1.85%  
 ----->rit ag rec 0.46%  
 ----->effe ag rec 0.46%

play ini

----->Affi ini 66.67%  
 ----->parent 26.16%  
 ----->uw 5.91%  
 ----->effe sub rec 5.06%  
 ----->rit ag rec 0.42%  
 ----->rit ag ini 2.53%  
 ----->rit sub rec 2.53%  
 ----->selfg 1.69%  
 ----->sex rec 0.84%  
 ----->Abnorm 0.84%  
 ----->effe ag ini 0.84%  
 ----->effe ag rec 0.21%  
 ----->Affi rec 33.33%

rit ag ini

----->Affi ini 50.00%  
 ----->parent 19.62%  
 ----->uw 4.43%  
 ----->play ini 1.90%  
 ----->rit sub rec 1.90%  
 ----->selfg 1.27%  
 ----->effe ag ini 0.63%  
 ----->effe ag rec 0.16%  
 ----->sex rec 0.63%  
 ----->Abnorm 0.63%  
 ----->Affi rec 25.00%  
 ----->effe sub rec 25.00%

```

----->rit ag rec 2.08%

rit ag rec
----->Affi rec 50.00%
----->uw 3.77%
----->effe sub rec 2.83%
----->selfg 1.89%
----->effe ag ini 0.94%
----->effe ag rec 0.24%
----->parent 50.00%
----->Affi ini 30.56%
----->rit ag ini 1.16%
----->play ini 1.16%
----->rit sub rec 1.16%
----->sex rec 0.39%
----->Abnorm 0.39%

rit sub rec
----->parent 40.00%
----->effe ag ini 0.74%
----->effe ag rec 0.19%
----->Affi ini 40.00%
----->uw 3.54%
----->effe sub rec 3.04%
----->rit ag rec 0.25%
----->play ini 1.52%
----->rit ag ini 1.52%
----->selfg 1.01%
----->sex rec 0.51%
----->Abnorm 0.51%
----->Affi rec 20.00%

selfg
----->Affi ini 50.00%
----->Affi rec 13.92%
----->uw 4.43%
----->rit sub rec 1.90%
----->play ini 1.90%
----->sex rec 0.63%
----->Abnorm 0.63%
----->effe ag ini 0.63%
----->effe ag rec 0.16%
----->rit ag ini 25.00%
----->effe sub rec 6.25%
----->rit ag rec 0.52%
----->parent 25.00%

sex rec
->Abnorm 100.00%
->effe ag ini 100.00%

```

```

----->effe sub rec 50.00%
----->Afi ini 20.83%
----->rit sub rec 0.79%
----->play ini 0.79%
----->Afi rec 16.67%
----->selfg 0.63%
----->uw 4.17%
----->rit ag rec 25.00%
----->parent 12.50%
----->effe ag rec 25.00%
----->rit ag ini 25.00%

```

soli play

```

->Afi rec 100.00%
----->Afi ini 56.60%
----->parent 22.21%
----->rit ag ini 2.15%
----->rit sub rec 2.15%
----->play ini 2.15%
----->sex rec 0.72%
----->Abnorm 0.72%
----->uw 7.55%
----->effe sub rec 5.66%
----->selfg 3.77%
----->effe ag ini 1.89%
----->effe ag rec 0.47%
----->rit ag rec 0.47%

```

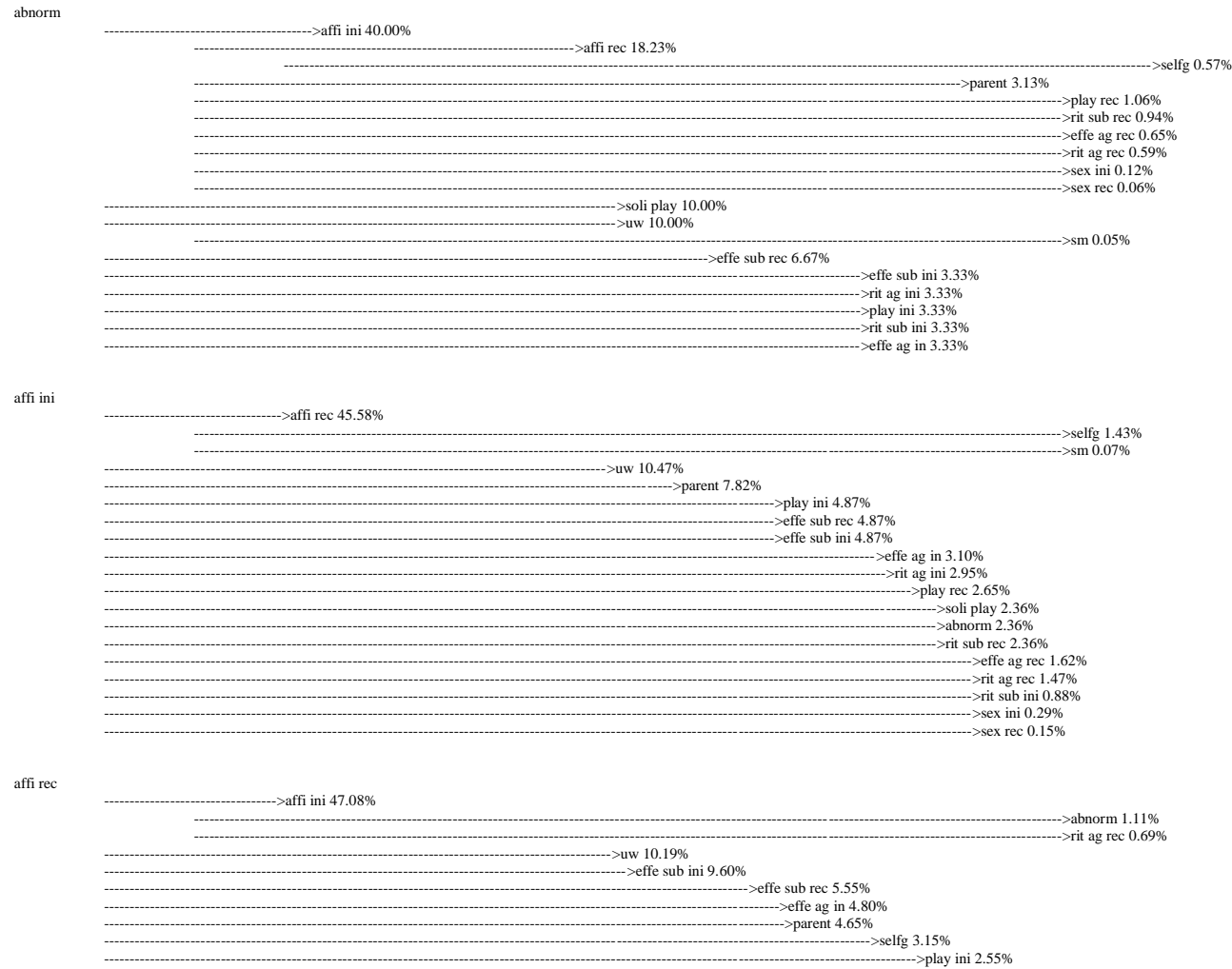
uw

```

----->Afi rec 37.50%
----->effe sub rec 2.12%
----->selfg 1.42%
----->effe ag ini 0.71%
----->effe ag rec 0.18%
----->rit ag rec 0.18%
----->parent 37.50%
----->Afi ini 25.00%
----->rit ag ini 0.95%
----->rit sub rec 0.95%
----->play ini 0.95%
----->sex rec 0.32%
----->Abnorm 0.32%

```

SE15. View of probability behavioral sequences of the capuchin monkeys' group.





----->soli play 2.40%  
 ----->rit sub rec 2.10%  
 ----->rit ag ini 1.65%  
 ----->play rec 1.65%  
 ----->effe ag rec 1.50%  
 ----->rit sub ini 1.50%  
 ----->sex ini 0.45%  
 ----->sm 0.15%  
 ----->sex rec 0.15%

effe ag in

----->effe sub rec 38.89%  
 ----->rit ag ini 2.24%  
 ----->soli play 0.75%  
 ----->affi rec 19.44%  
 ----->uw 1.98%  
 ----->selfg 0.61%  
 ----->sm 0.03%  
 ----->affi ini 16.67%  
 ----->parent 1.30%  
 ----->play ini 0.81%  
 ----->abnorm 0.39%  
 ----->rit sub rec 11.11%  
 ----->effe sub ini 4.17%  
 ----->effe ag rec 2.78%  
 ----->rit ag rec 2.78%  
 ----->sex ini 0.38%  
 ----->sex rec 0.08%  
 ----->rit sub ini 1.39%  
 ----->play rec 1.39%

effe ag rec

----->effe sub ini 55.56%  
 ----->affi rec 23.60%  
 ----->selfg 0.74%  
 ----->sm 0.04%  
 ----->soli play 2.18%  
 ----->effe sub rec 1.82%  
 ----->abnorm 1.45%  
 ----->play ini 1.09%  
 ----->rit ag rec 0.73%  
 ----->play rec 0.73%  
 ----->rit sub ini 0.73%  
 ----->sex ini 0.36%  
 ----->sex rec 0.08%  
 ----->affi ini 17.78%  
 ----->rit ag ini 4.44%  
 ----->uw 4.44%  
 ----->rit sub rec 2.22%  
 ----->effe ag in 2.22%  
 ----->parent 2.22%

effe sub ini

----->affi rec 42.48%  
 ----->effe ag in 2.04%  
 ----->parent 1.97%  
 ----->selfg 1.34%  
 ----->rit sub rec 0.89%

```

----->sm 0.06%
----->affi ini 24.84%
----->rit ag ini 0.73%
----->uw 7.84%
----->effe ag rec 5.88%
----->soli play 3.92%
----->effe sub rec 3.27%
----->abnorm 2.61%
----->play ini 1.96%
----->rit sub ini 1.31%
----->play rec 1.31%
----->rit ag rec 1.31%
----->sex ini 0.65%
----->sex rec 0.15%

```

effe sub rec

```

----->affi rec 41.35%
----->uw 4.22%
----->effe sub ini 3.97%
----->selfg 1.30%
----->rit sub rec 0.87%
----->effe ag rec 0.62%
----->rit sub ini 0.62%
----->sex ini 0.19%
----->sex rec 0.06%
----->sm 0.06%
----->affi ini 36.54%
----->play ini 1.78%
----->play rec 0.97%
----->abnorm 0.86%
----->rit ag ini 5.77%
----->effe ag in 2.88%
----->parent 2.88%
----->soli play 1.92%
----->rit ag rec 0.96%

```

parent

```

----->affi rec 50.00%
----->uw 5.10%
----->effe sub ini 4.80%
----->effe sub rec 2.77%
----->effe ag in 2.40%
----->selfg 1.57%
----->effe ag rec 0.75%
----->rit sub ini 0.75%
----->sex ini 0.22%
----->sm 0.07%
----->sex rec 0.07%
----->affi ini 37.18%
----->play ini 1.81%
----->rit ag ini 1.10%
----->play rec 0.99%
----->abnorm 0.88%
----->rit ag rec 0.55%
----->soli play 1.28%

```

```

----->rit sub rec 1.28%

play ini
----->affi ini 38.20%
----->uw 4.00%
----->parent 2.99%
----->effe sub rec 1.86%
----->effe ag in 1.18%
----->rit ag ini 1.13%
----->rit sub rec 0.90%
----->rit ag rec 0.56%
----->rit sub ini 0.34%
----->sex ini 0.11%
----->sex rec 0.06%
----->affi rec 17.98%
----->sm 0.03%
----->soli play 12.36%
----->play rec 11.24%
----->selfg 5.62%
----->effe sub ini 4.49%
----->effe ag rec 2.25%
----->abnorm 1.12%

play rec
----->affi rec 32.65%
----->affi ini 15.37%
----->rit ag rec 0.23%
----->effe sub rec 1.81%
----->effe ag in 1.57%
----->parent 1.52%
----->rit sub rec 0.69%
----->rit ag ini 0.54%
----->rit sub ini 0.49%
----->effe ag rec 0.49%
----->sex ini 0.15%
----->sex rec 0.05%
----->play ini 20.41%
----->soli play 18.37%
----->abnorm 0.46%
----->uw 10.20%
----->sm 0.05%
----->effe sub ini 4.08%
----->selfg 2.04%

rit ag ini
----->affi ini 29.09%
----->parent 2.27%
----->play ini 1.42%
----->play rec 0.77%
----->soli play 0.69%
----->affi rec 20.00%
----->effe sub ini 1.92%
----->sm 0.03%
----->effe sub rec 14.55%
----->rit sub rec 14.55%
----->rit sub ini 7.27%
----->abnorm 0.75%
----->selfg 3.64%

```

```

----->uw 3.64%
----->effe ag in 3.64%
----->rit ag rec 1.82%
----->sex ini 0.25%
----->sex rec 0.06%
----->effe ag rec 1.82%

rit ag rec
----->rit sub ini 27.27%
----->abnorm 2.82%
----->selfg 0.94%
----->rit sub rec 0.94%
----->solu play 0.94%
----->affi rec 18.18%
----->play ini 0.46%
----->play rec 0.30%
----->sex ini 13.64%
----->sex rec 3.03%
----->rit ag ini 1.52%
----->affi ini 9.09%
----->effe sub ini 9.09%
----->uw 9.09%
----->sm 0.05%
----->parent 4.55%
----->effe ag rec 4.55%
----->effe ag in 4.55%
----->effe sub rec 1.77%

rit sub ini
----->affi rec 41.38%
----->affi ini 19.48%
----->rit ag rec 0.29%
----->uw 4.22%
----->effe sub rec 2.30%
----->effe ag in 1.99%
----->parent 1.92%
----->play ini 1.05%
----->play rec 0.68%
----->sex ini 0.19%
----->sm 0.06%
----->sex rec 0.06%
----->effe sub ini 10.34%
----->abnorm 10.34%
----->effe ag rec 3.45%
----->rit sub rec 3.45%
----->solu play 3.45%
----->selfg 3.45%
----->rit ag ini 3.45%

rit sub rec
----->affi ini 37.78%
----->play ini 1.84%
----->play rec 1.00%
----->abnorm 0.89%
----->solu play 0.89%
----->effe ag rec 0.61%
----->affi rec 31.11%
----->effe sub ini 2.99%

```

----->sm 0.05%

----->parent 8.89%

----->effe ag in 6.67%

----->effe sub rec 2.59%

----->rit ag ini 4.44%

----->uw 4.44%

----->rit sub ini 2.22%

----->rit ag rec 2.22%

----->sex ini 0.30%

----->sex rec 0.07%

----->selfg 2.22%

selfg

----->affi rec 31.37%

----->effe sub ini 3.01%

----->rit sub rec 0.66%

----->effe ag rec 0.47%

----->sex ini 0.14%

----->sex rec 0.05%

----->affi ini 27.45%

----->parent 2.15%

----->abnorm 0.65%

----->rit ag rec 0.40%

----->uw 13.73%

----->sm 0.07%

----->effe sub rec 5.88%

----->play ini 5.88%

----->soli play 3.92%

----->rit ag ini 3.92%

----->effe ag in 1.96%

----->rit sub ini 1.96%

----->play rec 1.96%

sex ini

----->affi ini 33.33%

----->uw 3.49%

----->parent 2.61%

----->play ini 1.62%

----->play rec 0.88%

----->soli play 0.79%

----->abnorm 0.79%

----->effe ag rec 0.54%

----->rit ag rec 0.49%

----->sex rec 22.22%

----->affi rec 22.22%

----->effe sub ini 2.13%

----->selfg 0.70%

----->sm 0.03%

----->rit ag ini 11.11%

----->rit sub rec 1.62%

----->rit sub ini 0.81%

----->effe ag in 11.11%

----->effe sub rec 4.32%

sex rec

----->affi ini 50.00%

----->uw 5.24%

----->parent 3.91%

```

----->play ini 2.43%
----->effe sub ini 2.43%
----->effe sub rec 2.43%
----->play rec 1.33%
----->abnorm 1.18%
----->solu play 1.18%
----->rit sub rec 1.18%
----->effe ag rec 0.81%
----->rit ag rec 0.74%
----->rit sub ini 0.44%
----->affi rec 25.00%
----->selfg 0.79%
----->sm 0.04%
----->sex ini 25.00%
----->effe ag in 2.78%
----->rit ag ini 2.78%

```

sm

```

----->affi ini 50.00%
----->parent 3.91%
----->play ini 2.43%
----->effe sub ini 2.43%
----->effe sub rec 2.43%
----->effe ag in 1.55%
----->rit ag ini 1.47%
----->play rec 1.33%
----->solu play 1.18%
----->abnorm 1.18%
----->rit sub rec 1.18%
----->effe ag rec 0.81%
----->rit ag rec 0.74%
----->rit sub ini 0.44%
----->sex ini 0.15%
----->sex rec 0.07%
----->uw 25.00%
----->selfg 1.08%
----->affi rec 25.00%

```

solu play

```

----->affi ini 29.11%
----->parent 2.28%
----->effe sub rec 1.42%
----->rit sub rec 0.69%
----->rit ag rec 0.43%
----->sex rec 0.04%
----->affi rec 24.05%
----->effe ag in 1.15%
----->rit sub ini 0.36%
----->sex ini 0.11%
----->play ini 18.99%
----->selfg 1.07%
----->uw 10.13%
----->sm 0.05%
----->play rec 5.06%
----->effe sub ini 5.06%
----->abnorm 2.53%
----->effe ag rec 1.27%
----->rit ag ini 1.27%

```

uw

```
----->affi ini 40.86%
----->parent 3.19%
----->rit ag ini 1.21%
----->rit sub rec 0.96%
----->sex rec 0.06%
----->affi rec 26.88%
----->effe ag in 1.29%
----->rit sub ini 0.40%
----->effe sub ini 6.45%
----->selfg 4.30%
----->soli play 3.76%
----->abnorm 3.23%
----->play ini 2.69%
----->effe sub rec 2.15%
----->effe ag rec 1.61%
----->play rec 1.61%
----->rit ag rec 1.08%
----->sex ini 0.15%
```

## B. The Complex Personality of Mandrills (*Mandrillus sphinx*)

Table S10. Ethogram of the behaviors reported in this study.

	<b>Behaviour</b>	<b>Definition</b>
<b>Individual</b>	Self-grooming	Picking own dirt and ticks, brushing hair or skin with the mouth and/or hand(s). Self-groom of injuries are not included. May include fur rubbing and self-scratch.
	Sternal gland marking	Repeated back and forth motion of the animal sternal gland area into a surface, having the neck and jaw lifted up.
	Solitary play	Motion and actions with no clear purpose, such as moving repeatedly in the same structure, somersaulting, back flips and erratic movements. May include an alimentary item or manipulation of enrichment objects or other artificial device.
	Abnormal	Stereotypic (spinning, pacing and rocking), self-injurious (Hair pulling, mutilation/self-biting, head banging, stereotypic scratching, sucking fingers or hand, aggressive impulse), excessive self-grooming, coprophagy or aggressive interaction with objects (rail pulling, fence biting, ball biting).
	Affiliative	Allogrooming, grooming solicitation posture, mounting, physical contact, foraging together, food solicitation, food provisioning, chasing/moving together, play, presenting, notification/greeting, silent bared teeth, crest raise.
	Social play	Interaction between two or more individuals that may include chasing and wrestling in a friendly manner. Individuals present a characteristic facial expression and specific vocalizations which distinguish it from agonistic behaviours.
	Sexual behaviour	Mounting, genital inspection, masturbation, copulation call, over male aggression, initiation copulation, sexual presentation.
	Agonistic ritualized	Threat display, jaw chomping, chase, bouncing.
	Effective agonism	Aggression with contact, rough behaviour.
	Effective submission	Submissive retreat, scream, avoidance.
<b>Social</b>	Submission ritualized	Receptor of hierarchy mounting, silent bared teeth, presenting.
	Hierarchy mounting	An individual puts itself in a position which allows copulation but do not perform back and forth movements. If copulation occurs, then it's scored as a sexual behaviour.
	Parental	Brest feeding, parental grooming, infant transport, restrain, allonursing.
	Hair pulling another	Pulling hair of another individual. May include trichotillophagia.





	<b>Group Variance</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>	<b>Lwiro</b>	<b>Mapendo</b>	<b>Martin</b>	<b>Mirinda</b>	<b>Nefertari</b>	<b>Tania</b>
<b>Self-grooming</b>	0.005	0.004	0.009	0.001	0.001	0.006	0.001	0.002	0.005	0.019	0.000	0.003
<b>Scratch</b>	0.002	0.000	0.011	0.002	0.005	0.000	0.000	0.001	0.000	0.001	0.000	0.000
<b>Solitary Play</b>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	x	x	0.000
<b>Affiliation initiator</b>	0.015	0.019	0.000	0.007	0.013	0.082	0.014	0.000	0.000	0.003	0.000	0.010
<b>Play Initiator</b>	0.000	0.000	x	0.000	0.000	0.000	0.001	0.000	0.000	x	0.000	0.001
<b>Hair pulling Initiator</b>	0.002	0.020	x	x	x	x	x	x	x	0.001	0.006	x
<b>Parental Behavior</b>	0.024	x	x	0.000	x	x	x	x	x	x	0.175	x
<b>Affiliation Receiver</b>	0.015	0.003	0.000	0.001	0.028	0.010	0.050	0.000	0.000	0.004	0.019	0.036
<b>Infant Affiliation</b>	0.004	x	x	x	0.000	x	x	x	x	x	0.028	0.004
<b>Play Receiver</b>	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.001
<b>Hair Pulling Receiver</b>	0.006	x	x	x	0.000	0.001	x	x	x	x	0.024	0.035
<b>Wound Grooming</b>	0.004	x	x	x	0.000	x	x	0.037	x	x	x	x
<b>Abnormal Behavior</b>	0.001	0.000	x	x	x	x	x	x	0.000	0.008	0.000	x

Table S12. Individual means for each significant behavioral category. All the results for each behavioral category were transformed into a 0-5 ratio scale, in which 5 represents the highest mean value obtained in the group and 0 represents a complete absence of instances of that behavioral category (Continued on the next page).

<b>Behavioral Categories</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>	<b>Lwiro</b>	<b>Mapendo</b>	<b>Martin</b>	<b>Mirinda</b>	<b>Nefertari</b>	<b>Tania</b>
<b>Self-grooming</b>	0.018	0.029	0.006	0.010	0.017	0.004	0.015	0.026	0.029	0.002	0.009
(0-5 conversion)	<b>3.022</b>	<b>4.923</b>	<b>1.042</b>	<b>1.731</b>	<b>2.903</b>	<b>0.710</b>	<b>2.501</b>	<b>4.467</b>	<b>5.000</b>	<b>0.404</b>	<b>1.616</b>
<b>Scratch</b>	0.009	0.032	0.012	0.026	0.007	0.006	0.021	0.011	0.010	0.005	0.005
(0-5 conversion)	<b>1.454</b>	<b>5.000</b>	<b>1.939</b>	<b>4.157</b>	<b>1.040</b>	<b>0.891</b>	<b>3.311</b>	<b>1.658</b>	<b>1.511</b>	<b>0.855</b>	<b>0.838</b>
<b>Affiliation initiator</b>	0.061	0.011	0.021	0.039	0.154	0.031	0.004	0.002	0.017	0.003	0.064
(0-5 conversion)	<b>1.986</b>	<b>0.343</b>	<b>0.676</b>	<b>1.267</b>	<b>5.000</b>	<b>0.998</b>	<b>0.129</b>	<b>0.080</b>	<b>0.562</b>	<b>0.083</b>	<b>2.080</b>
<b>Affiliation initiator Event</b>	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(0-5 conversion)	<b>1.175</b>	<b>5.000</b>	<b>0.283</b>	<b>1.590</b>	<b>0.934</b>	<b>0.329</b>	<b>2.627</b>	<b>1.534</b>	<b>0.300</b>	<b>0.311</b>	<b>3.607</b>
<b>Play Initiator</b>	0.001		0.001	0.006	0.003	0.015	0.001	0.003		0.000	0.013
(0-5 conversion)	<b>0.204</b>	<b>0.000</b>	<b>0.406</b>	<b>1.909</b>	<b>1.114</b>	<b>5.000</b>	<b>0.449</b>	<b>0.912</b>	<b>0.000</b>	<b>0.037</b>	<b>4.529</b>
<b>Play Initiator Event</b>	0.000		0.000	0.000	0.000	0.000		0.000			0.000
(0-5 conversion)	<b>0.360</b>	<b>0.000</b>	<b>0.673</b>	<b>1.483</b>	<b>3.067</b>	<b>2.160</b>	<b>0.000</b>	<b>2.246</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>
<b>Aggression Initiator</b>	0.001	0.001	0.002	0.001	0.001	0.000	0.000	0.000	0.001		0.000
(0-5 conversion)	<b>4.118</b>	<b>1.840</b>	<b>5.000</b>	<b>2.967</b>	<b>2.369</b>	<b>0.340</b>	<b>0.431</b>	<b>0.531</b>	<b>1.615</b>	<b>0.000</b>	<b>0.374</b>
<b>Aggression Initiator Event</b>	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(0-5 conversion)	<b>2.432</b>	<b>2.559</b>	<b>5.000</b>	<b>2.709</b>	<b>0.834</b>	<b>0.608</b>	<b>0.770</b>	<b>0.947</b>	<b>1.064</b>	<b>0.000</b>	<b>0.668</b>
<b>Ritual Submission Initiator Event</b>	0.000		0.000	0.001	0.001	0.000	0.001	0.000	0.000	0.000	0.000
(0-5 conversion)	<b>0.433</b>	<b>0.000</b>	<b>1.473</b>	<b>5.000</b>	<b>3.049</b>	<b>1.907</b>	<b>2.578</b>	<b>0.572</b>	<b>0.548</b>	<b>0.417</b>	<b>0.764</b>
<b>Effective Submission Initiator</b>	0.000		0.003	0.002	0.003	0.002	0.003	0.002	0.001	0.002	0.001
(0-5 conversion)	<b>0.397</b>	<b>0.000</b>	<b>4.782</b>	<b>3.521</b>	<b>4.015</b>	<b>3.705</b>	<b>5.000</b>	<b>3.199</b>	<b>1.795</b>	<b>3.621</b>	<b>1.304</b>
<b>Effective Submission Initiator Event</b>	0.000		0.002	0.002	0.002	0.002	0.002	0.002	0.001	0.002	0.001
(0-5 conversion)	<b>0.536</b>	<b>0.000</b>	<b>4.277</b>	<b>3.014</b>	<b>4.328</b>	<b>5.000</b>	<b>3.331</b>	<b>3.645</b>	<b>2.423</b>	<b>4.689</b>	<b>1.760</b>
<b>Parental Behavior Initiator</b>			0.000							0.321	
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>

<b>Behavioral Categories</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>	<b>Lwiro</b>	<b>Mapendo</b>	<b>Martin</b>	<b>Mirinda</b>	<b>Nefertari</b>	<b>Tania</b>
<b>Affiliative Receiver</b>	0.029	0.001	0.013	0.084	0.036	0.093	0.005	0.003	0.014	0.027	0.075
(0-5 conversion)	<b>1.553</b>	<b>0.029</b>	<b>0.697</b>	<b>4.539</b>	<b>1.957</b>	<b>5.000</b>	<b>0.277</b>	<b>0.186</b>	<b>0.743</b>	<b>1.445</b>	<b>4.055</b>
<b>Affiliative Receiver Event</b>	0.000		0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000
(0-5 conversion)	<b>0.852</b>	<b>0.000</b>	<b>1.122</b>	<b>5.000</b>	<b>1.555</b>	<b>1.255</b>	<b>1.561</b>	<b>3.682</b>	<b>0.000</b>	<b>0.784</b>	<b>0.402</b>
<b>Play Receiver</b>	0.001	0.000	0.001	0.004	0.002	0.006	0.001	0.003	0.000	0.000	0.008
(0-5 conversion)	<b>0.671</b>	<b>0.101</b>	<b>0.334</b>	<b>2.592</b>	<b>0.926</b>	<b>3.787</b>	<b>0.336</b>	<b>1.995</b>	<b>0.078</b>	<b>0.302</b>	<b>5.000</b>
<b>Play Receiver Event</b>	0.000	0.000	0.000	0.000		0.000	0.000	0.000		0.000	0.000
(0-5 conversion)	<b>0.679</b>	<b>0.667</b>	<b>1.463</b>	<b>5.000</b>	<b>0.000</b>	<b>3.319</b>	<b>0.667</b>	<b>4.570</b>	<b>0.000</b>	<b>0.720</b>	<b>3.286</b>
<b>Ritual Agonism Receiver Event</b>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	
(0-5 conversion)	<b>0.541</b>	<b>0.531</b>	<b>0.521</b>	<b>3.693</b>	<b>5.000</b>	<b>1.909</b>	<b>0.531</b>	<b>0.552</b>	<b>0.000</b>	<b>0.541</b>	<b>0.000</b>
<b>Ritual Submission Receiver Event</b>	0.000	0.001	0.000	0.000	0.000		0.000	0.000	0.000		
(0-5 conversion)	<b>1.536</b>	<b>5.000</b>	<b>0.122</b>	<b>1.192</b>	<b>0.250</b>	<b>0.000</b>	<b>0.371</b>	<b>0.122</b>	<b>0.128</b>	<b>0.000</b>	<b>0.000</b>
<b>Effective Submission Receiver</b>	0.002	0.002	0.002	0.003	0.002	0.001	0.000	0.001	0.000	0.000	0.003
(0-5 conversion)	<b>2.818</b>	<b>2.700</b>	<b>2.938</b>	<b>5.000</b>	<b>4.261</b>	<b>1.463</b>	<b>0.468</b>	<b>1.157</b>	<b>0.333</b>	<b>0.066</b>	<b>4.889</b>
<b>Effective Submission Receiver Event</b>	0.001	0.001	0.001	0.002	0.001	0.001	0.000	0.001	0.000	0.000	0.001
(0-5 conversion)	<b>2.320</b>	<b>2.653</b>	<b>2.813</b>	<b>5.000</b>	<b>1.345</b>	<b>1.771</b>	<b>0.567</b>	<b>1.401</b>	<b>0.403</b>	<b>0.080</b>	<b>1.886</b>
<b>Other Behaviors Fear Related</b>	0.000	0.000	0.000	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.001
(0-5 conversion)	<b>0.561</b>	<b>0.177</b>	<b>1.774</b>	<b>3.453</b>	<b>2.474</b>	<b>5.000</b>	<b>0.353</b>	<b>2.442</b>	<b>0.347</b>	<b>0.360</b>	<b>4.712</b>
<b>Arms Reach</b>	0.006	0.004	0.005	0.013	0.005	0.006	0.002	0.003	0.003	0.011	0.014
(0-5 conversion)	<b>2.115</b>	<b>1.465</b>	<b>1.725</b>	<b>4.664</b>	<b>1.911</b>	<b>2.217</b>	<b>0.733</b>	<b>0.919</b>	<b>0.931</b>	<b>3.866</b>	<b>5.000</b>
<b>Arms Reach 1</b>	0.005	0.004	0.004	0.010	0.005	0.006	0.002	0.003	0.002	0.009	0.012
(0-5 conversion)	<b>1.965</b>	<b>1.631</b>	<b>1.844</b>	<b>4.259</b>	<b>1.957</b>	<b>2.587</b>	<b>0.899</b>	<b>1.126</b>	<b>0.898</b>	<b>3.881</b>	<b>5.000</b>
<b>Arms Reach 2</b>	0.001	0.000	0.000	0.002	0.000	0.000			0.000	0.001	0.001
(0-5 conversion)	<b>2.235</b>	<b>0.584</b>	<b>0.918</b>	<b>5.000</b>	<b>1.368</b>	<b>0.370</b>	<b>0.000</b>	<b>0.000</b>	<b>0.860</b>	<b>2.712</b>	<b>3.839</b>

Table S13. The table presents the abbreviations of the behavioural categories analyzed using the EthoSeq Software to analyze the behavioral transitions and sequences.

<b>Behavior category</b>	<b>Behavior</b>	<b>Abbreviation</b>
<b>Non social behaviors</b>	Self-grooming	Selfg
	Scent Marking	Scent
	Solitary Play	Solplay
	Solitary Play Event	Solplaye
	Vocalizations	Vocal
	Scratch	Scratch
<b>Social behaviors</b>	Affiliation Initiator	Affi
	Infant Affiliation Provider	Affpinfant
	Sex Initiator	Sexi
	Play Initiator	Playi
	Parental Behaviour	Parent
	Hierarchy Mounting	Hiermountini
	Hair Pulling Initiator	Hairi
	Ritual Agonism Initiator	Ritagi
	Aggression Initiator	Aggri
	Ritual Submission Initiator	Ritsubi
	Effective Submission Initiator	Effsubi
	Affiliation Initiator Event	Affie
	Infant Affiliation Provider Event	Affpinfante
	Play Initiator Event	Playie
	Affiliative Receiver	Affir
	Infant Affiliation Receiver	Affrinfant
	Sex Receiver	Sexr
	Play Receiver	Playr
	Hair Pulling Receiver	Hairr
	Ritual Agonism Receiver	Ritagr
	Aggression Receiver	Aggrr
	Ritual Submission Received	Ritsubr
	Effective Submission Received	Effsubr
	Affiliative Receiver Event	Afire
	Infant Affiliation Receiver Event	Affrinfante
	Play Receiver Event	Playre
	Ritual Agonism Receiver Event	Ritagre
	Aggression Receiver Event	Aggrre
	Ritual Submission Received Event	Ritsubre
	Effective Submission Received Event	Effsubre
<b>Other behaviors</b>	Fear Related	OtherFear
	Wound Grooming	Wound
	Human interaction	Human
<b>Abnormal behaviors</b>	Abnormal Behavior	Abnorm
	Abnormal Behavior Event	Abnorme
<b>Arms reach</b>	Arms reach	AR

Table S14. EthoSeq summary results. In the first column are the behavioral categories that initiated a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the Mandrills as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only when that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the atypical transitions when compared with the transitions calculated for the group.

	<b>Group</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>
<b>Self-grooming (Sg)</b>	<b>Scratch</b> <b>38.10%</b>	Scratch 60.00%	Scratch 40.00%	Scratch 42.86%	Scratch 30.77%	Affi Ini 50.00%
<b>Scratch (Scratch)</b>	<b>EffeSubIni</b> <b>16.27%</b>	<25.00%	RitSubRec 28.57%	EffeSubIni 28.57%	Affi Rec 31.11%	EffeSubIni 37.50%
<b>Solitary Play (Solplay)</b>	<b>Scratch</b> <b>24.32%</b>	Scratch 100.00%	Scratch 50.00%	Play Ini 66.67%	RitSubIni 50.00%	Play Ini 33.33%
	<b>Play ini</b> <b>24.32%</b>		RitSubRec 50.00%	Scratch 33.33%	Affi Ini 50.00%	Scratch 33.33%
	<b>Affi Ini</b> <b>18.92%</b>					Play Rec 33.33%
<b>Vocalizations (Voc)</b>	<b>Scratch</b> <b>26.19%</b>	EffeSubRec 66.67%		Parent 33.33%	EffeSubRec 25.00%	Scratch 33.33%
	<b>Affi Rec</b> <b>14.29%</b>	Sg 33.33%		Affi Ini 33.33%	Affi Rec 25.00%	Affi Rec 33.33%
				Affi Rec 33.33%	Scratch 25.00%	EffeSubIni 33.33%
<b>Affiliation Initiator (Affi Ini)</b>	<b>Affi Rec</b> <b>21.6%</b>	<25.00%	RitSubRec 38.46%	Affi Rec 30.77%	Affi Rec 41.94%	Affi Rec 26.09%
	<b>Scratch</b> <b>16.40%</b>					
<b>Aggression Initiator (Aggr Ini)</b>	<b>EffeSubRec</b> <b>67.03%</b>	EffeSubRec 75.00%	EffeSubRec 50.00%	EffeSubRec 71.43%	EffeSubRec 92.86%	EffeSubRec 85.71%
			RitSubRec 33.33%			
<b>Effective Submission Initiator (Effe Sub Ini)</b>	<b>Scratch</b> <b>22.66%</b>	Scratch 40.00%			<25.00%	Affi Rec 24.24%
		EffeSubRec 40.00%				<25.00%
<b>Ritual Agonism Initiator (Rit Ag Ini)</b>	<b>EffeSubRec</b> <b>25.64%</b>	Affi Rec 33.33%	RitSubRec 55.56%	EffeSubRec 60.00%	EffeAgIni 50.00%	EffeSubRec 50.00%
	<b>RitSubRec</b> <b>17.95%</b>				RitSubIni 25.00%	RitAgRec 50.00%
					RitSubRec 25.00%	
<b>(Rit Sub Ini) Play Initiator (Play Ini)</b>	<b>EffeSubIni</b> <b>14.04%</b>					
	<b>AffiRec</b> <b>17.16%</b>	Affi Rec 100.00%		Scratch 50.00%	Affi Rec 31.58%	<25.00%
	<b>Affi Ini</b> <b>17.16%</b>			Play Rec 25.00%		
	<b>Play Rec</b> <b>15.67%</b>			EffeSubIni 25.00%		

Table S15. Continuation of table S16 (Continued on the next page).

	<b>Group</b>	<b>Camila</b>		<b>Kunta</b>		<b>Limbe</b>		<b>Lisala</b>		<b>Lolaya</b>		
<b>Sex Initiator (Sex Ini)</b>	<b>Scratch</b>	<b>38.46%</b>			Scratch	50.00%				<25.00%		
	<b>Affi Rec</b>	<b>15.38%</b>			Sg	50.00%						
<b>Hair Pulling Initiator (Hair Ini)</b>	<b>Affi Ini</b>	<b>28.57%</b>	Affi Rec	25.00%								
	<b>Voc</b>	<b>14.29%</b>	Affi Ini	25.00%								
	<b>EffeSubIni</b>	<b>14.29%</b>	EffeAgIni	25.00%								
	<b>Parent</b>	<b>14.29%</b>	Voc	25.00%								
<b>Hierarchy Mounting (hiermountini)</b>	<b>Affi Rec</b>	<b>50.00%</b>										
	<b>Play Ini</b>	<b>50.00%</b>										
<b>Other Fear Behavior (otherfear)</b>	<b>Affi Ini</b>	<b>28.57%</b>				EffeAgRec	50.00%					
	<b>EffeSubRec</b>	<b>14.29%</b>										
	<b>EffeSubIni</b>	<b>14.29%</b>										
	<b>Scratch</b>	<b>14.29%</b>										
	<b>EffeAgRec</b>	<b>14.29%</b>										
<b>Affiliation Receiver (Affi Rec)</b>	<b>Affi Ini</b>	<b>22.83%</b>	Affi Ini	44.00%	EffeAgIni	50.00%	EffeSubIni	28.57%		<25.00%	EffeSubIni	29.17%
	<b>EffeSubIni</b>	<b>20.47%</b>			Affi Ini	50.00%			(EffeSubIni	21.79%		
<b>Aggression Receiver (Aggr Rec)</b>	<b>EffeSubIni</b>	<b>68.57%</b>	Scratch	100.00%	Sg	33.33%	EffeSubIni	85.71%	EffeSubIni	66.67%	EffeSubIni	100.00%
					RitAgRec	33.33%						
					Affi Ini	33.33%						
<b>Effective Submission Receiver (Effe Sub Rec)</b>	<b>Scratch</b>	<b>16.06%</b>	Affi Rec	27.27%	Scratch	29.17%		<25.00%		<25.00%	RitAgIni	28.57%
	<b>Affi Rec</b>	<b>13.99%</b>			RitSubRec	29.17%			(Affi Rec	23.53%		
					Affi Ini	25.00%						
<b>Ritual Agonism Receiver (Rit Ag Rec)</b>	<b>EffeSubIni</b>	<b>29.41%</b>	Affi Rec	100.00%	Affi Ini	100.00%	EffeSubIni	100.00%	EffeAgIni	33.33%	EffeSubIni	42.86%
	<b>RitSubIni</b>	<b>23.53%</b>							RitSubIni	33.33%	EffeAgIni	28.57%
	<b>EffeAgIni</b>	<b>17.65%</b>							RitSubRec	33.33%	RitSubIni	28.57%
<b>Ritual Submission Receiver (Rit Sub Rec)</b>	<b>Affi Ini</b>	<b>52.44%</b>	Affi Ini	57.14%	Affi Ini	62.00%	EffeSubIni	50.00%	EffeSubRec	33.33%	Play Ini	50.00%
							EffeAgIni	25.00%			Affi Ini	50.00%
							Affi Ini	25.00%				
<b>Play Receiver (Play Rec)</b>	<b>Play Ini</b>	<b>27.66%</b>		<25.00%	Affi Ini	100.00%	EffeSubIni	50.00%		<25.00%	EffeSubIni	33.33%
	<b>Scratch</b>	<b>17.02%</b>					Affi Rec	50.00%			RitSubIni	33.33%
	<b>EffeSubIni</b>	<b>15.96%</b>									Play Ini	33.33%
<b>Hair Pulling Receiver (Hair Rec)</b>	<b>Affi Rec</b>	<b>50.00%</b>									Affi Ini	100.00%
	<b>EffeSubIni</b>	<b>14.29%</b>										
	<b>Affrinft</b>	<b>14.29%</b>										
<b>Abnormal Behavior (abnormal)</b>	<b>EffeSubIni</b>	<b>33.33%</b>	Scratch	100.00%								
	<b>Scratch</b>	<b>16.67%</b>										

Group	Camila	Kunta	Limbe	Lisala	Lolaya
Hairi	16.67%				
Voc	16.67%				
Sg	16.67%				

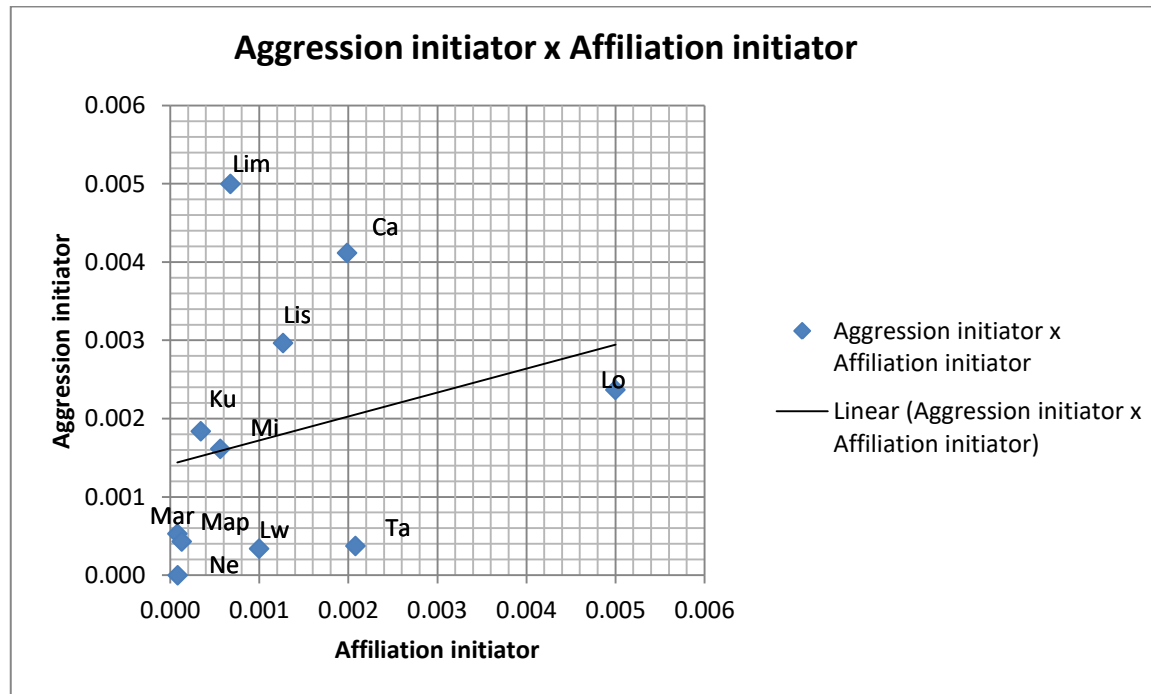


Figure S2. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Aggression initiator  $\times$  Affiliation



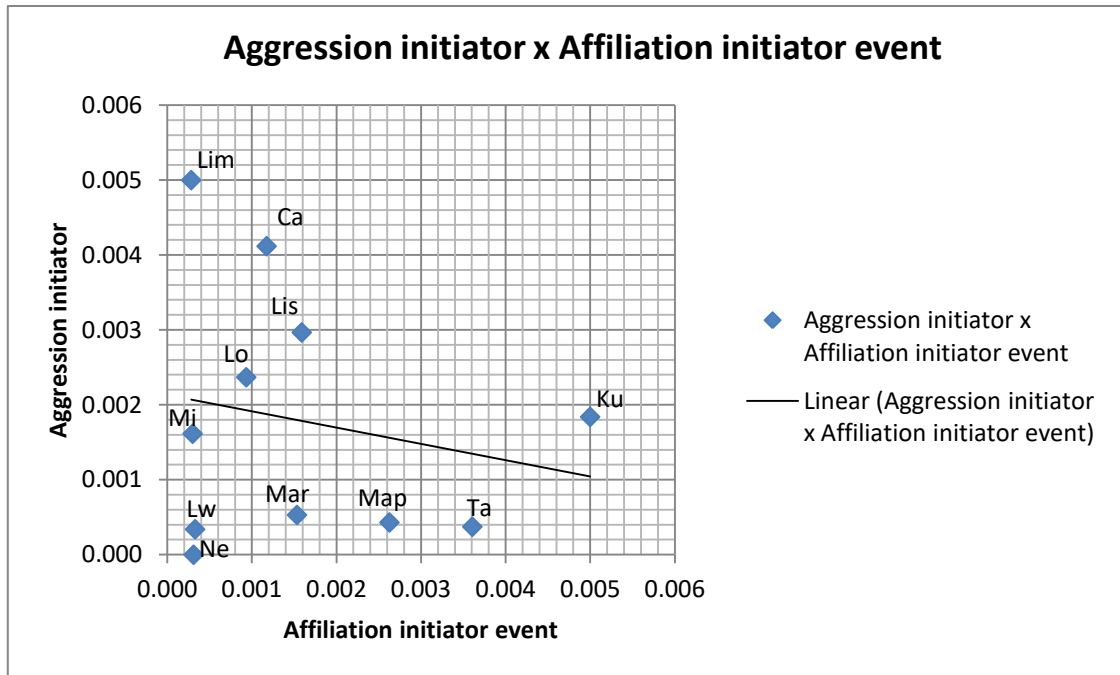


Figure S3. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Aggression initiator  $\times$  Affiliation initiator event

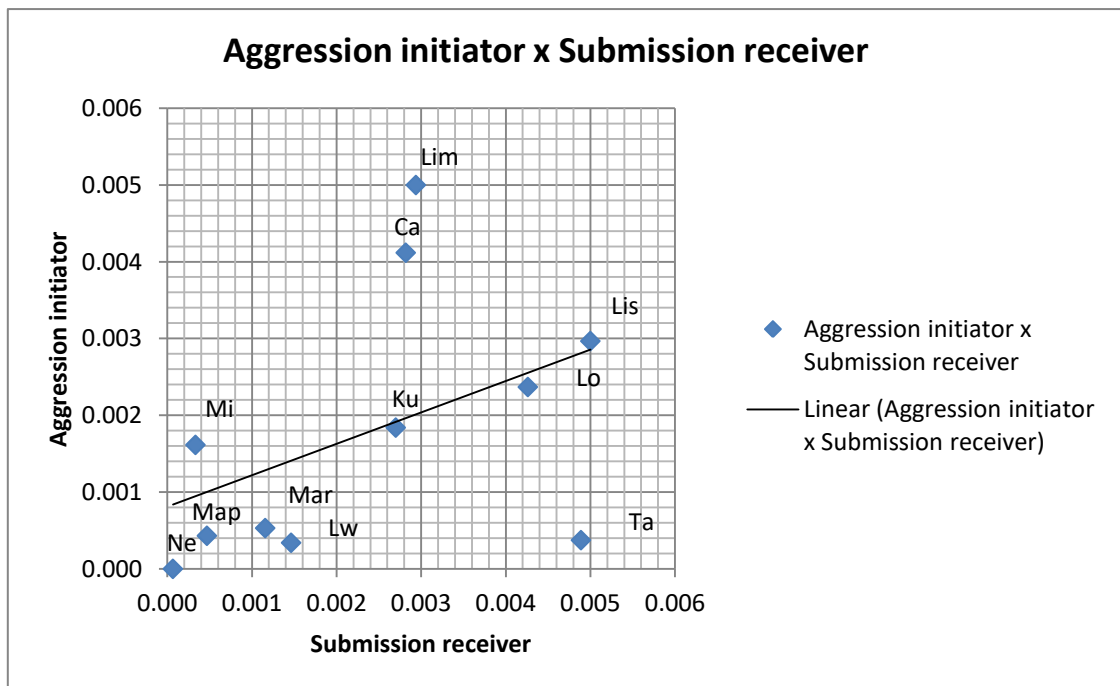


Figure S4. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Aggression initiator  $\times$  Submission receiver

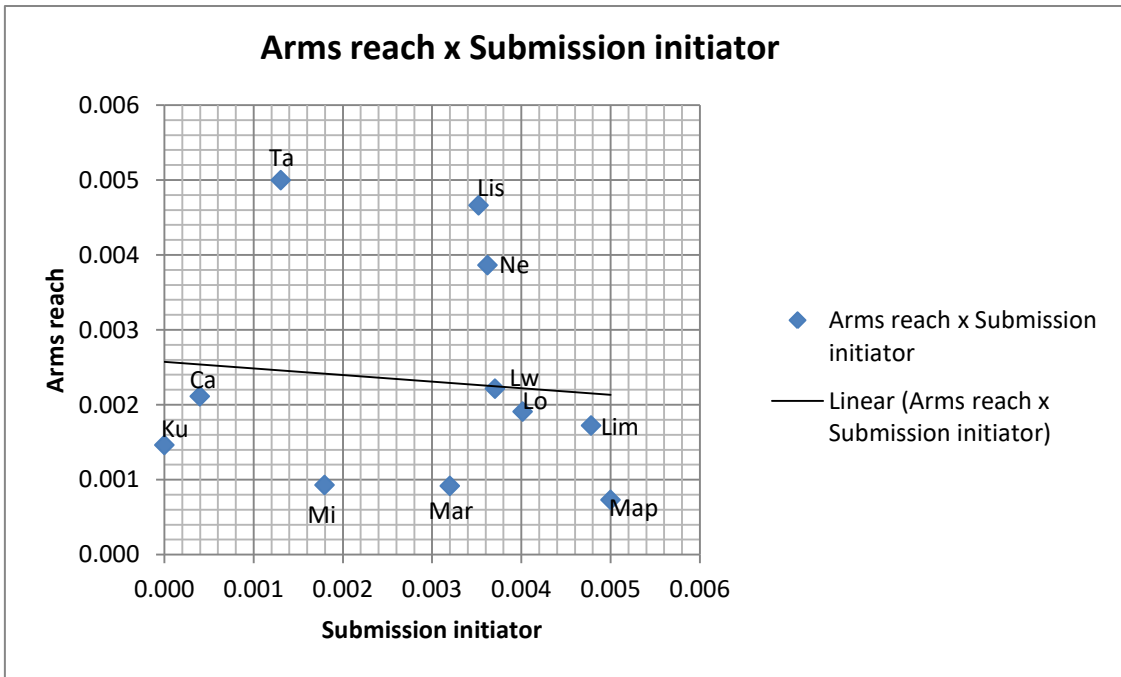


Figure S5. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Arms reach × Submission initiator

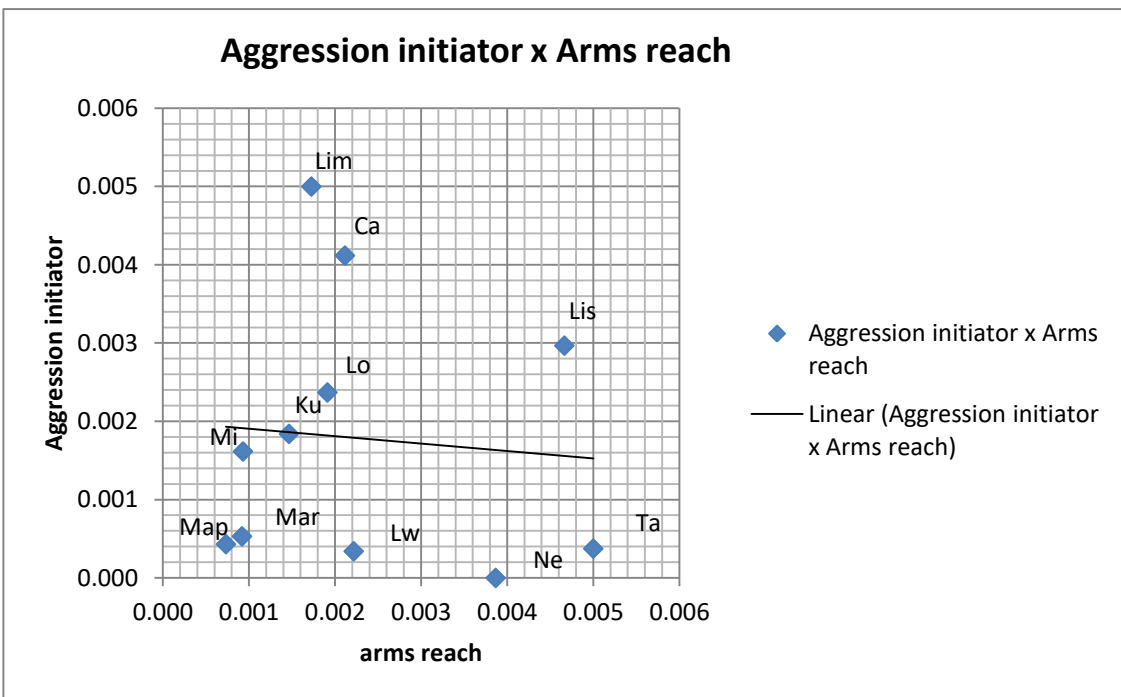


Figure S6. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Aggression initiator × Arms reach

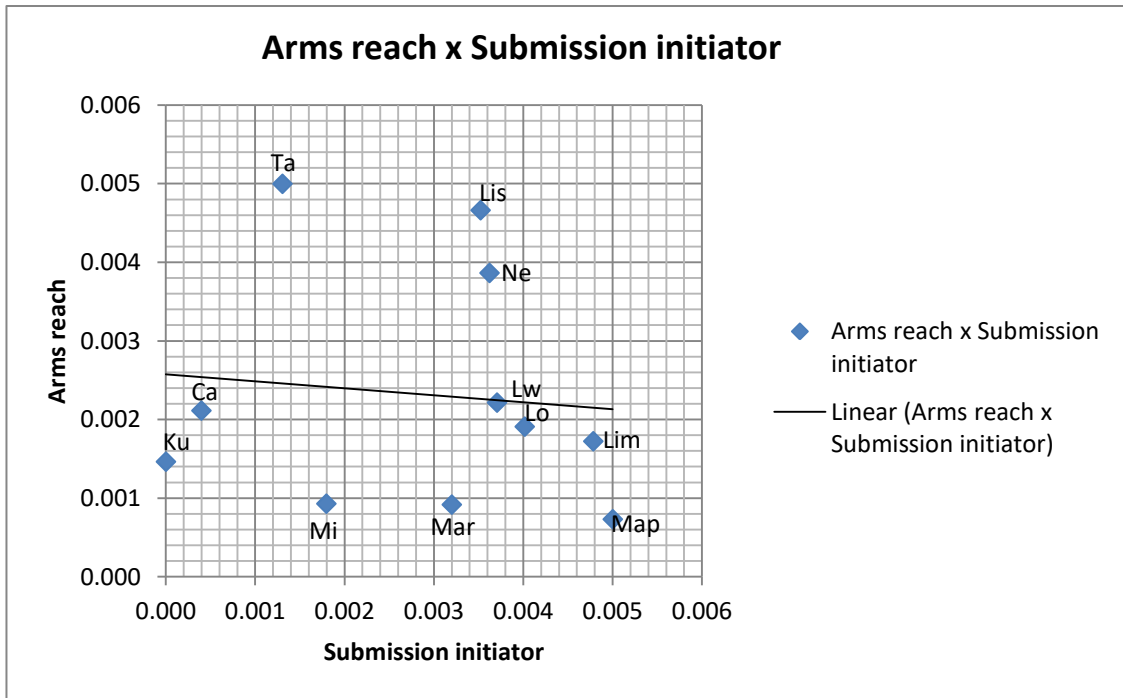


Figure S7. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Arms reach× Submission initiator

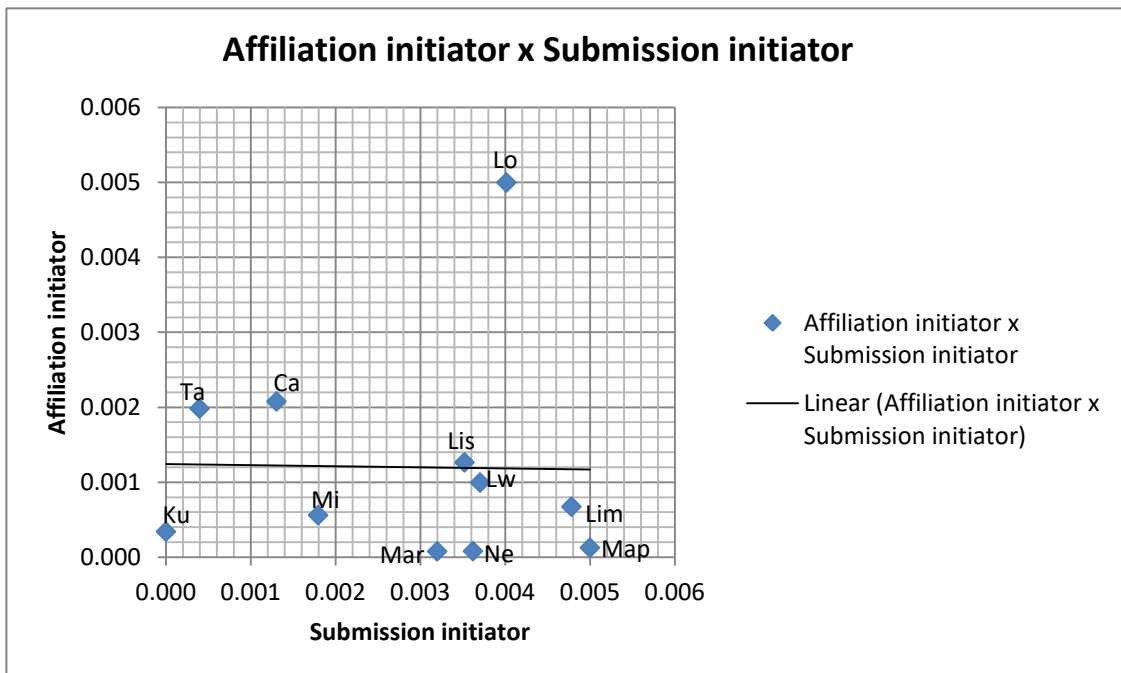


Figure S8. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Affiliation initiator× Submission initiator

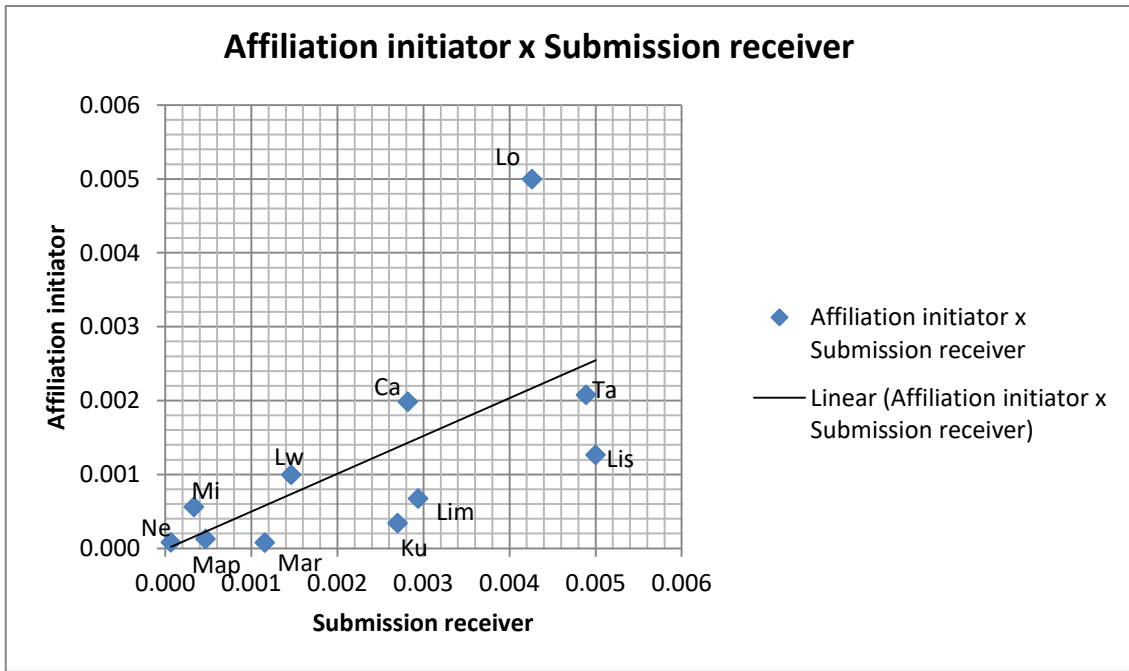


Figure S9. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Affiliation initiator× Submission receiver

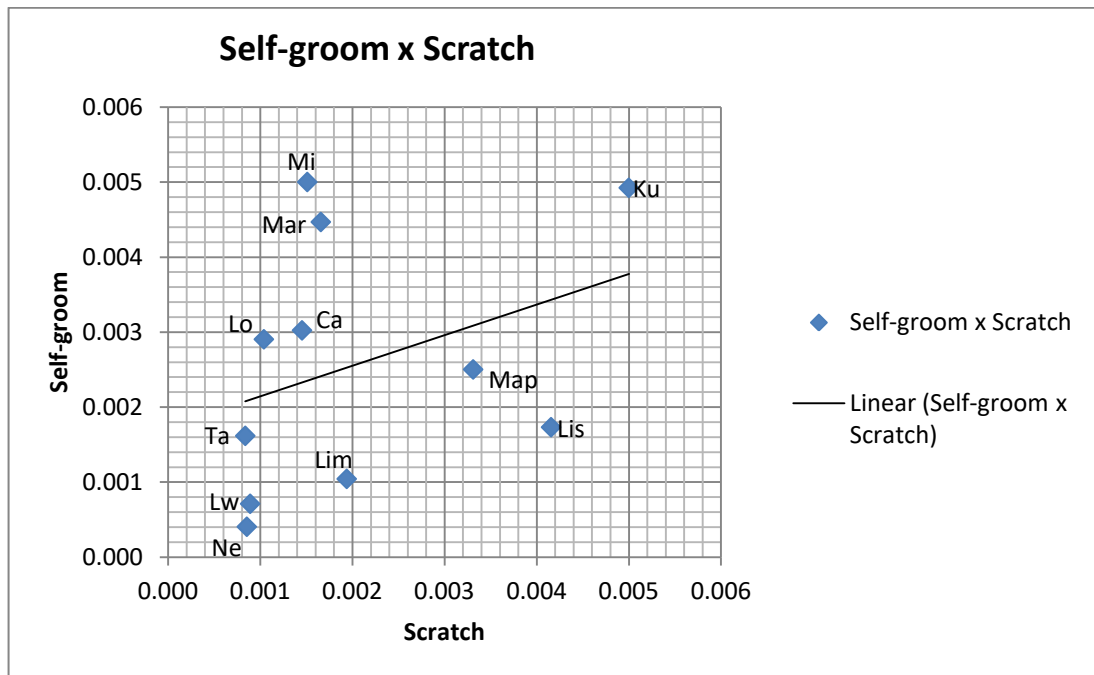


Figure S10. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-groom× Sractch

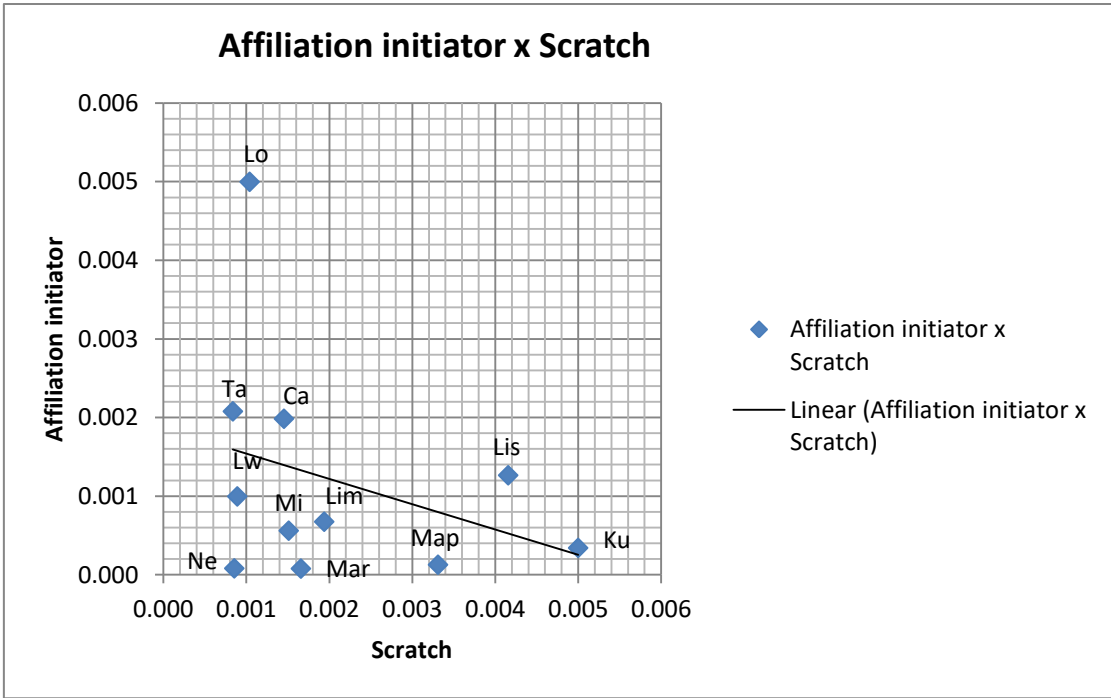


Figure S11. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Affiliation initiator× Scratch

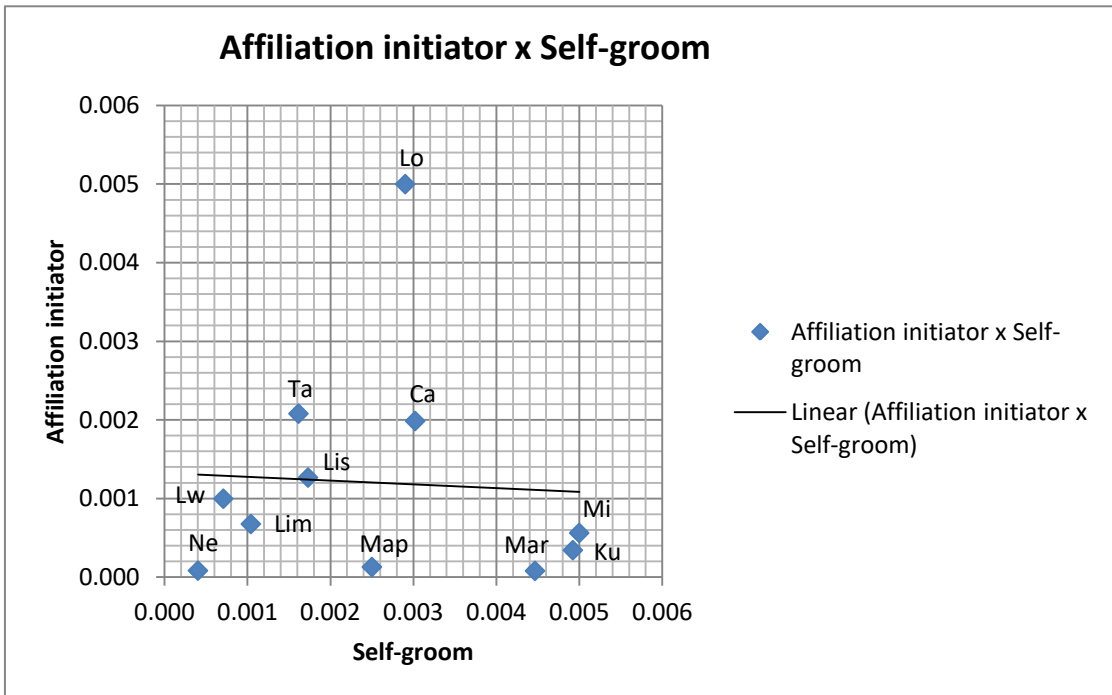


Figure S12. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Affiliation initiator× Self-groom

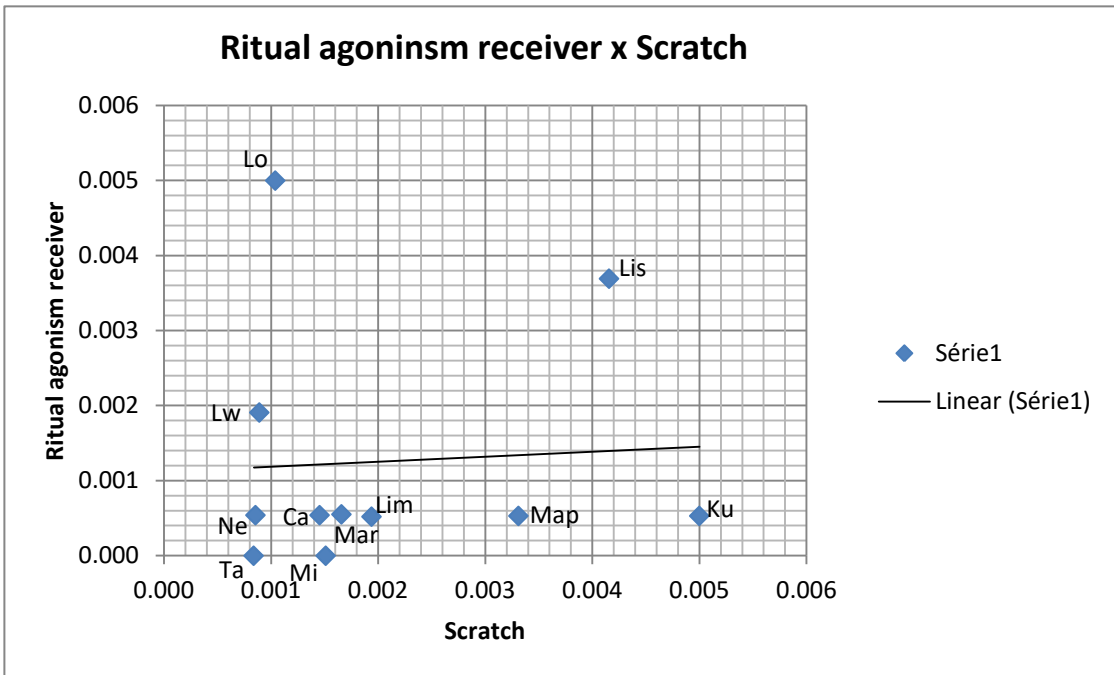


Figure S13. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Ritual agonism× Scratch

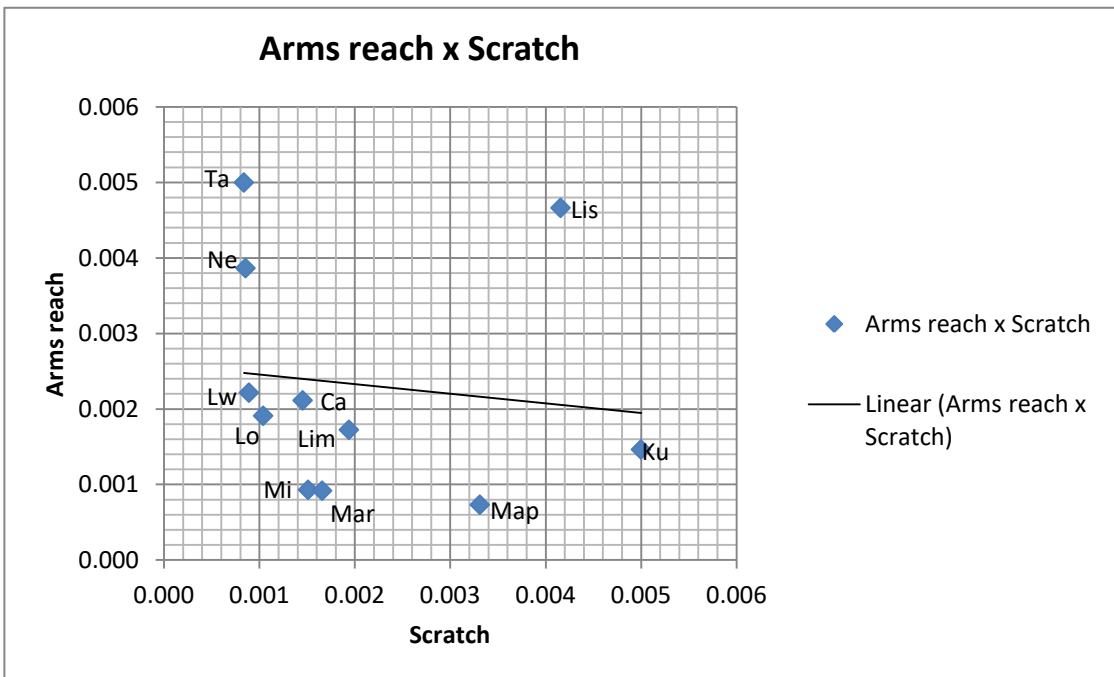


Figure S14. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Arms reach × Scratch

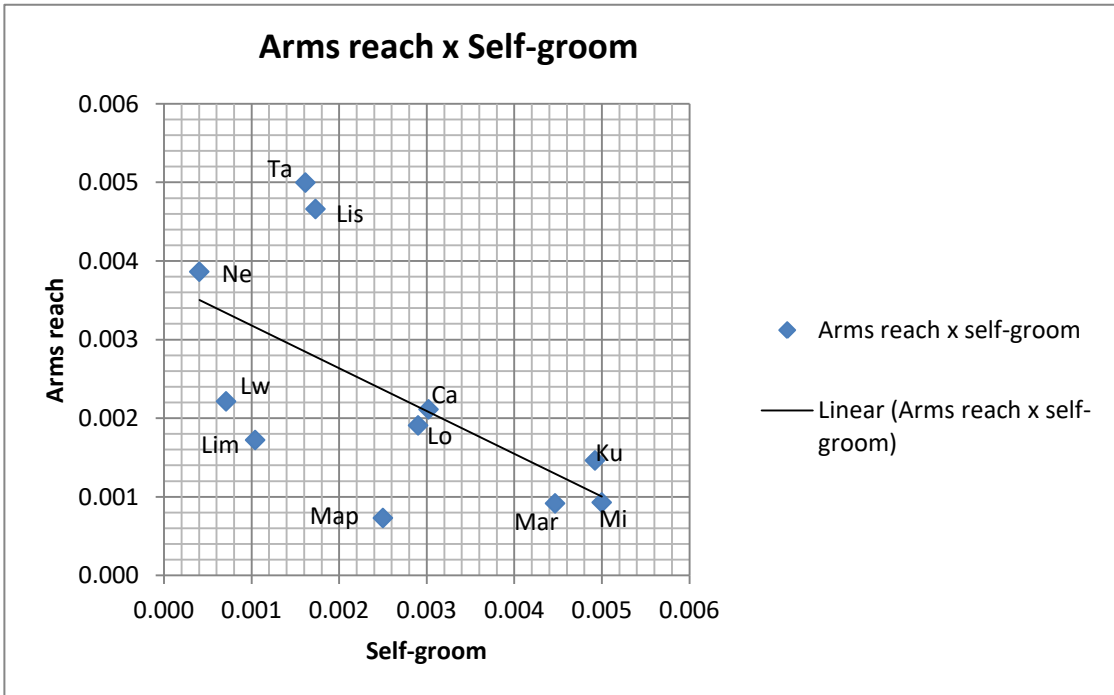


Figure S15. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Arms reach  $\times$  Self-groom

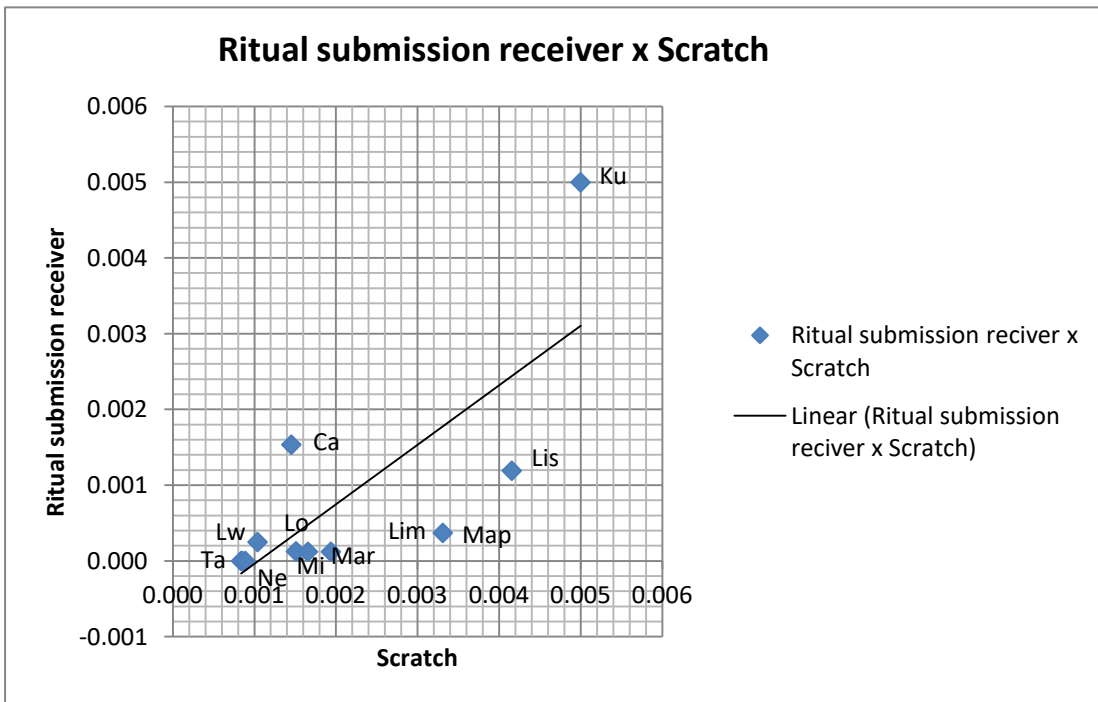


Figure S16. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Ritual submission  $\times$  Scratch

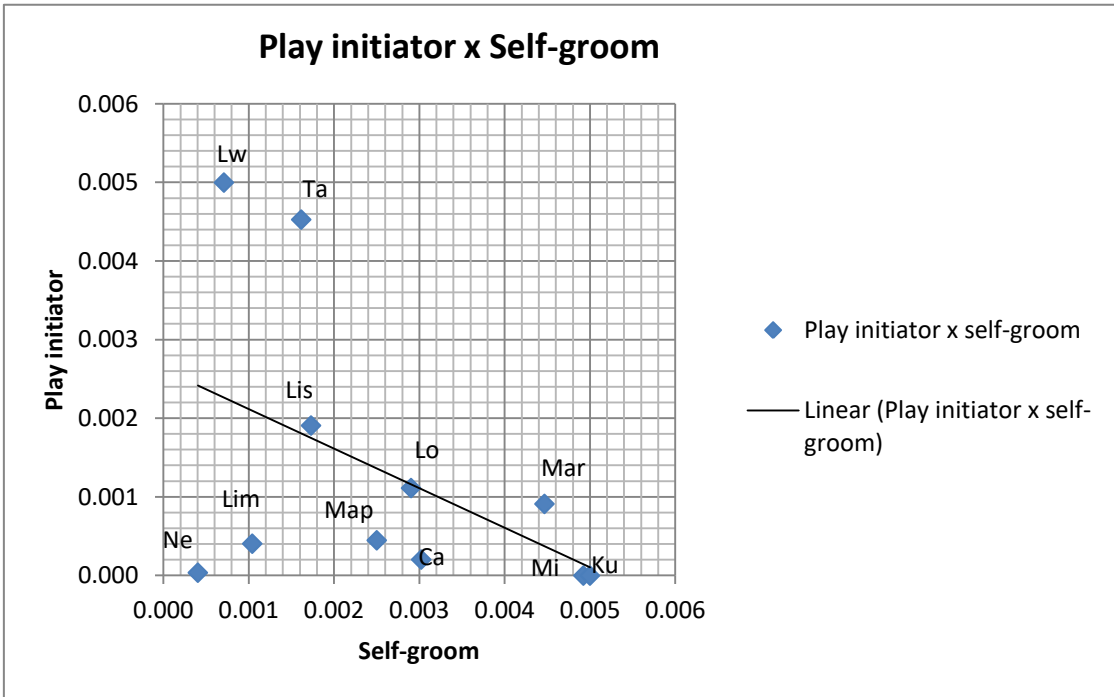


Figure S17. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Play initiator  $\times$  Self-groom

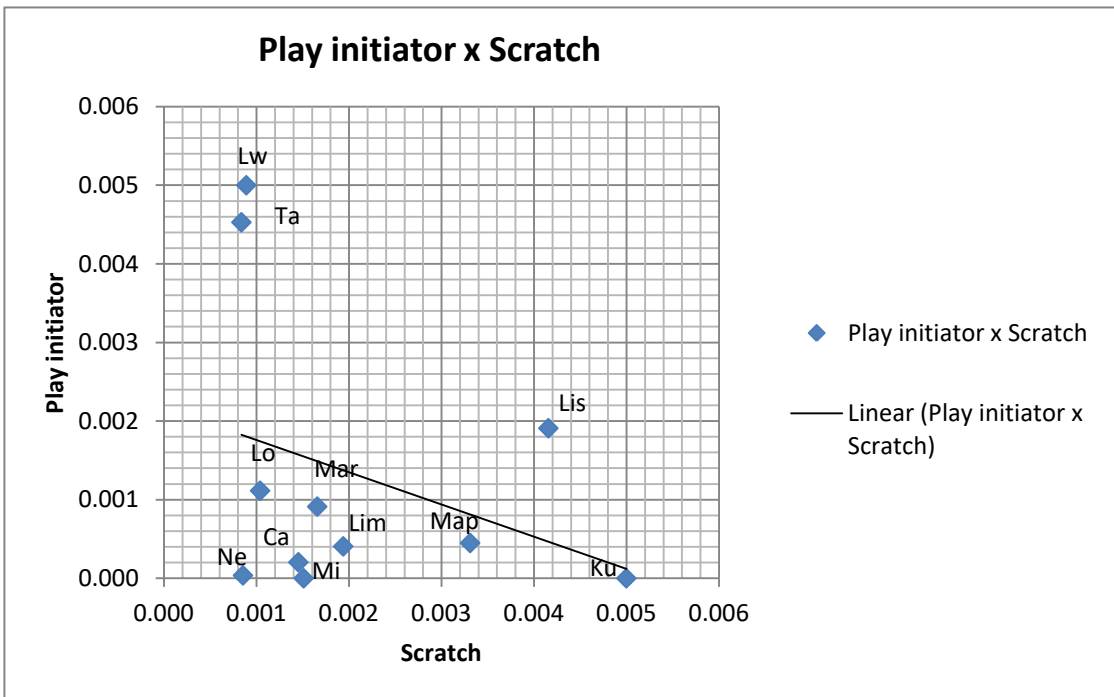


Figure S18. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Play initiator  $\times$  Scratch



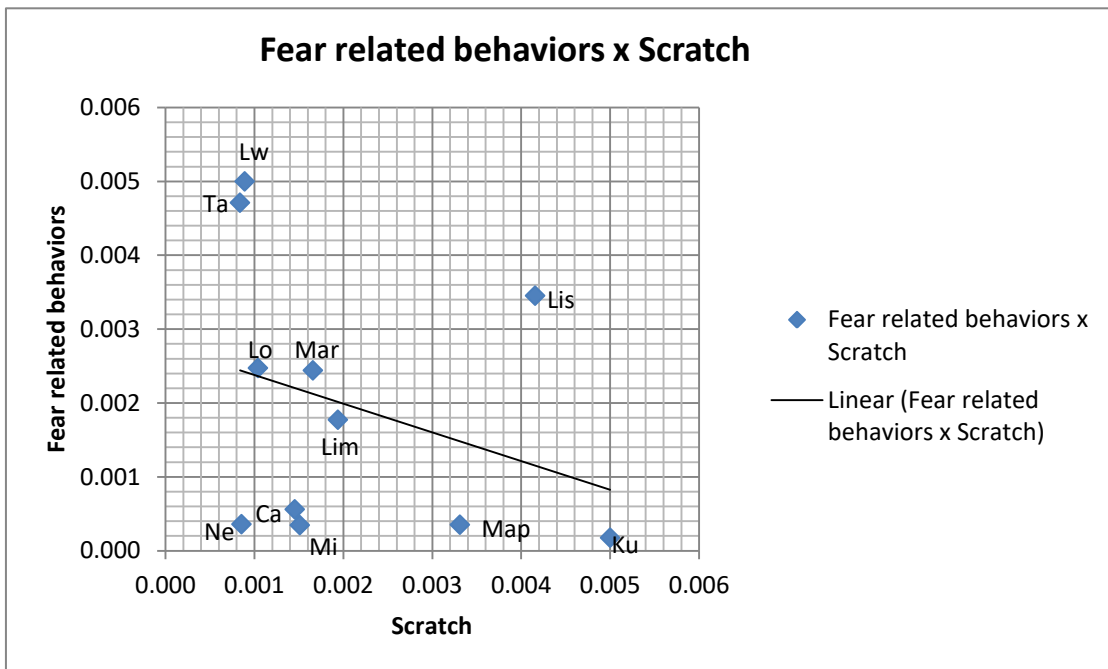


Figure S19. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Fear related behaviours × Scratch

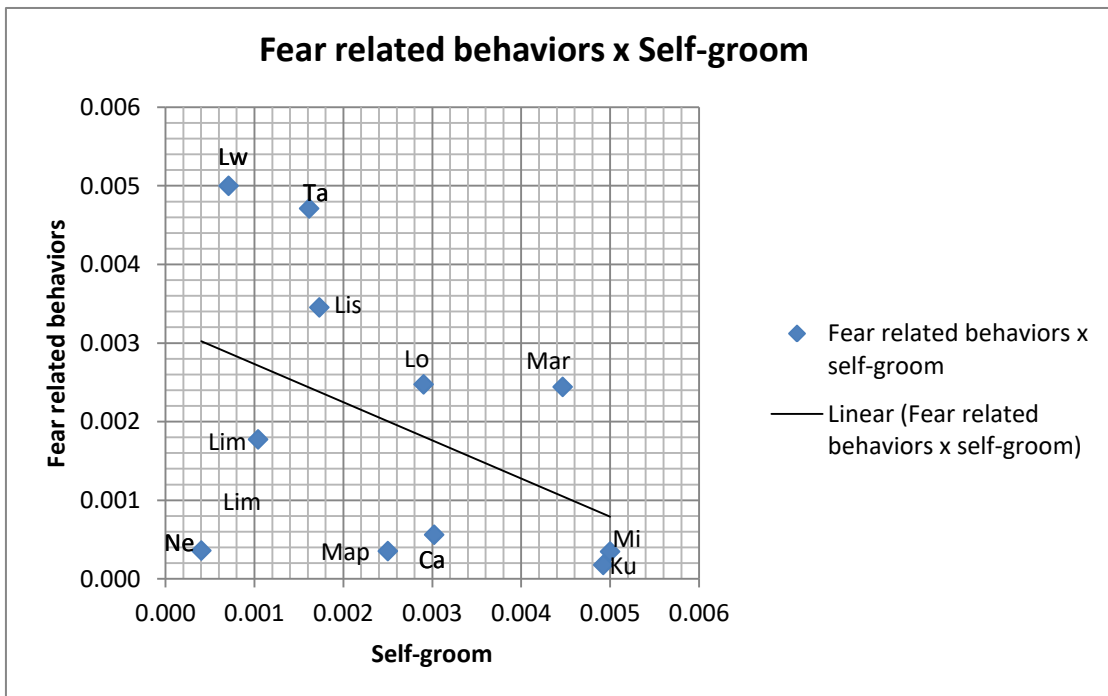


Figure S20. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Fear related behaviours × Self-groom

Table S16. The table presents the individual variability for the categories with variance different from zero in at least one of the animals in the group. The results for variance in each behavioral category were transformed into a 0-5 ratio scale, in which 5 represents the highest variance value obtained by any individual for that behavioral category, and 0 represents no variance across all the observation sessions. An individual's Mean Flexibility Score corresponds to the mean variance for that individual across all behavioral categories, after each variance score was transformed in the 0-5 ratio scale (Continued on the next page).

<b>Behavioral Categories</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>	<b>Lwiro</b>	<b>Mapendo</b>	<b>Martin</b>	<b>Mirinda</b>	<b>Nefertari</b>	<b>Tania</b>
<b>Self-grooming</b>	0.004	0.009	0.001	0.001	0.006	0.001	0.002	0.005	0.019	0.000	0.003
(0-5 conversion)	<b>1.053</b>	<b>2.368</b>	<b>0.263</b>	<b>0.263</b>	<b>1.579</b>	<b>0.263</b>	<b>0.526</b>	<b>1.316</b>	<b>5.000</b>	<b>0.000</b>	<b>0.789</b>
<b>Scratch</b>	0.000	0.011	0.002	0.005	0.000	0.000	0.001	0.000	0.001	0.000	0.000
(0-5 conversion)	<b>0.000</b>	<b>5.000</b>	<b>0.909</b>	<b>2.273</b>	<b>0.000</b>	<b>0.000</b>	<b>0.455</b>	<b>0.000</b>	<b>0.455</b>	<b>0.000</b>	<b>0.000</b>
<b>Solitary Play</b>	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000			0.000
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>Affiliation initiator</b>	0.019	0.000	0.007	0.013	0.082	0.014	0.000	0.000	0.003	0.000	0.010
(0-5 conversion)	<b>1.159</b>	<b>0.000</b>	<b>0.427</b>	<b>0.793</b>	<b>5.000</b>	<b>0.854</b>	<b>0.000</b>	<b>0.000</b>	<b>0.183</b>	<b>0.000</b>	<b>0.610</b>
<b>Play Initiator</b>	0.000		0.000	0.000	0.000	0.001	0.000	0.000		0.000	0.001
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>
<b>Hair pulling Initiator</b>	0.020								0.001	0.006	
(0-5 conversion)	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.250</b>	<b>1.500</b>	<b>0.000</b>
<b>Parental Behavior Initiator</b>			0.000							0.175	
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>
<b>Affiliative Receiver</b>	0.003	0.000	0.001	0.028	0.010	0.050	0.000	0.000	0.004	0.019	0.036
(0-5 conversion)	<b>0.300</b>	<b>0.000</b>	<b>0.100</b>	<b>2.800</b>	<b>1.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.400</b>	<b>1.900</b>	<b>3.600</b>
<b>Infant Affiliation</b>				0.000						0.028	0.004
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.714</b>
<b>Play Receiver</b>	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.001
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>
<b>Hair Pulling Receiver</b>				0.000	0.001					0.024	0.035

<b>Behavioral Categories</b>	<b>Camila</b>	<b>Kunta</b>	<b>Limbe</b>	<b>Lisala</b>	<b>Lolaya</b>	<b>Lwiro</b>	<b>Mapendo</b>	<b>Martin</b>	<b>Mirinda</b>	<b>Nefertari</b>	<b>Tania</b>
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.143</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>3.429</b>	<b>5.000</b>
<b>Other Behaviors Wound Grooming</b>				0.000			0.037				
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>Abnormal Behavior</b>	0.000							0.000	0.008	0.000	
(0-5 conversion)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>5.000</b>	<b>0.000</b>	<b>0.000</b>
<b>MFS</b>	<b>1.813</b>	<b>1.779</b>	<b>0.410</b>	<b>1.480</b>	<b>1.864</b>	<b>3.891</b>	<b>2.651</b>	<b>0.318</b>	<b>2.725</b>	<b>4.062</b>	<b>5.000</b>

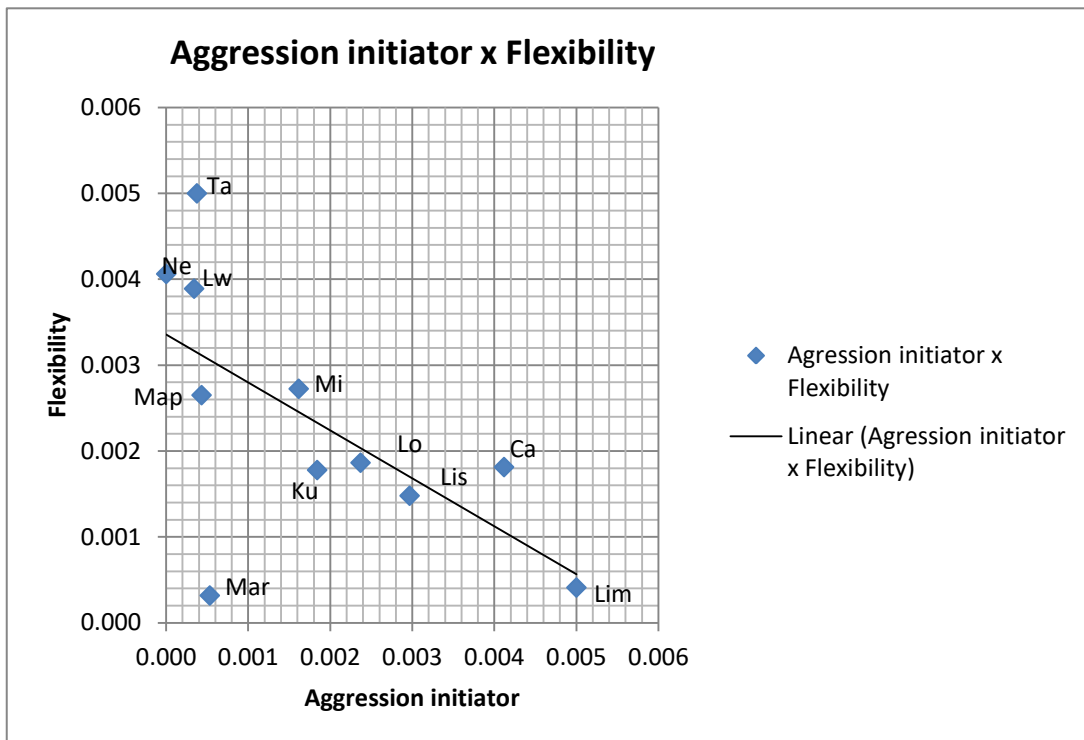


Figure S21. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Aggression initiator × Flexibility

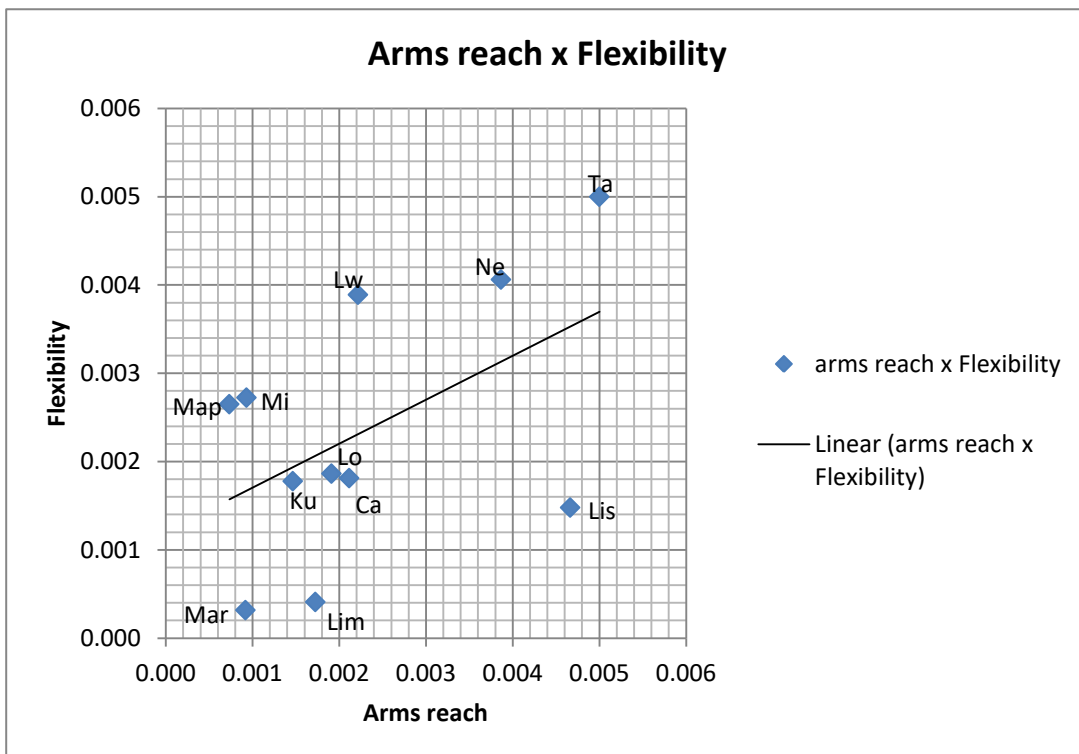


Figure S22. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Arms reach × Flexibility.

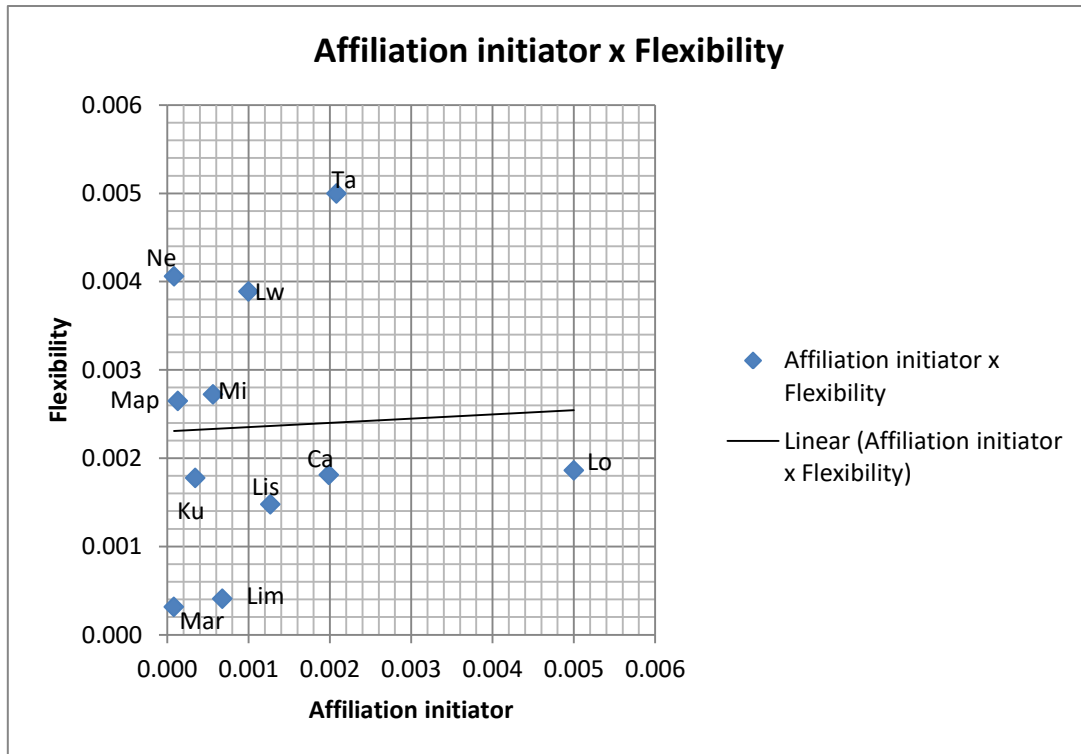


Figure S23. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Affiliation initiator  $\times$  Flexibility.

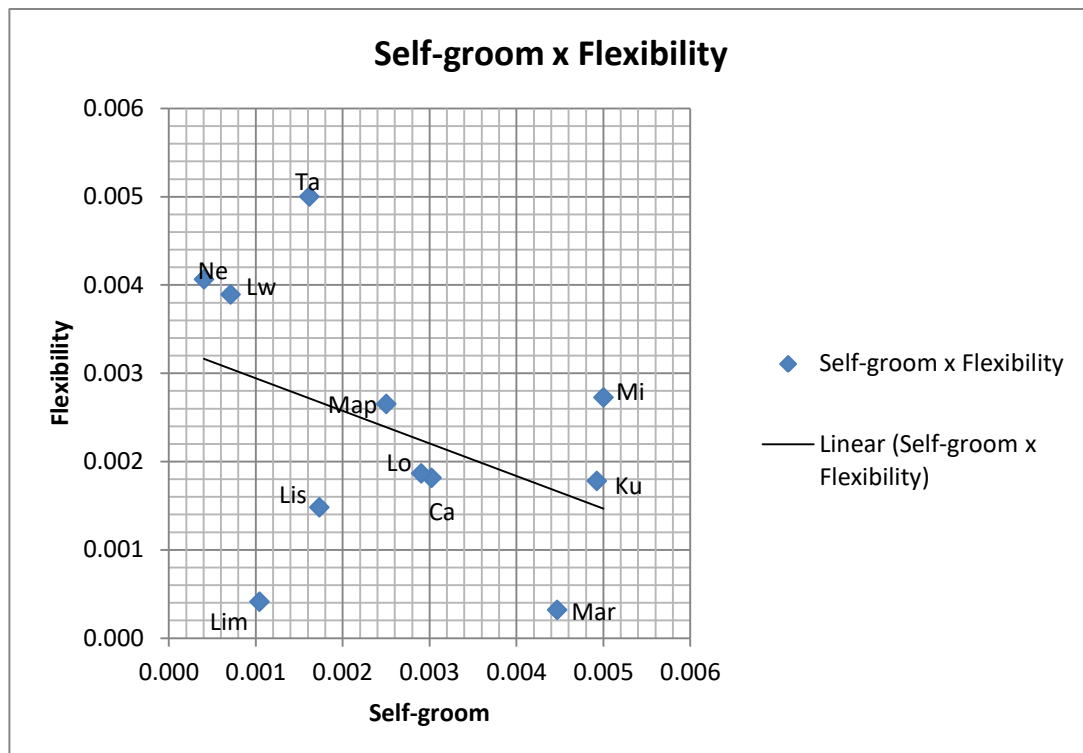


Figure S24. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Self-groom  $\times$  Flexibility.

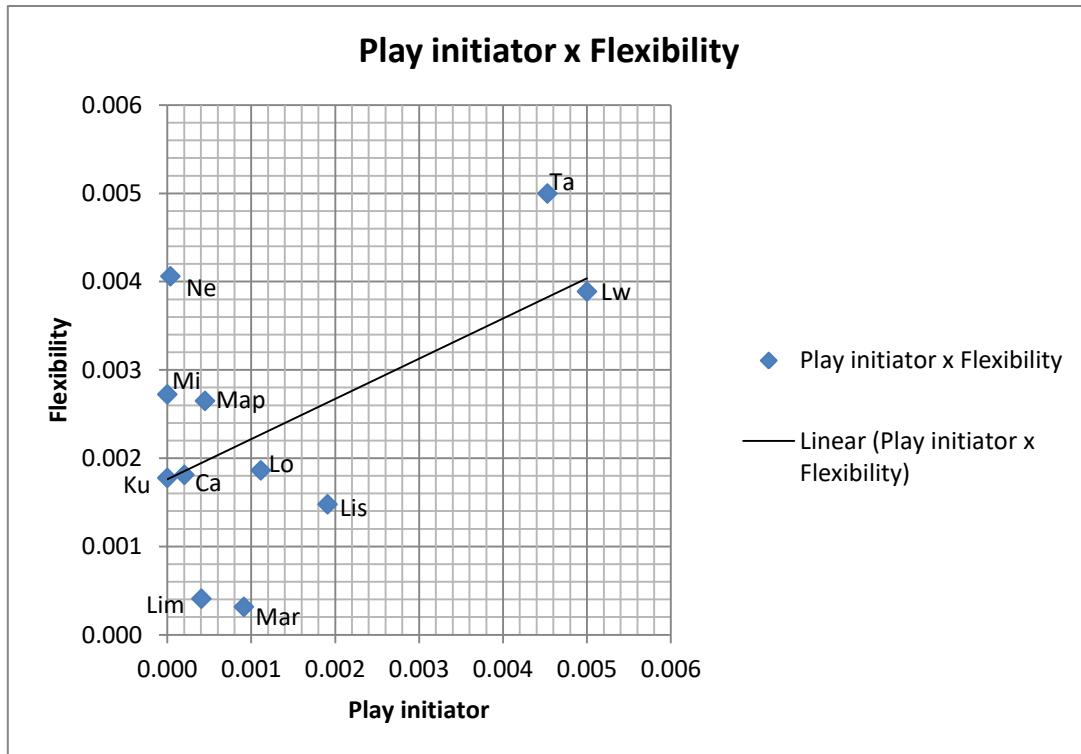


Figure S25. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Play Initiator × Flexibility

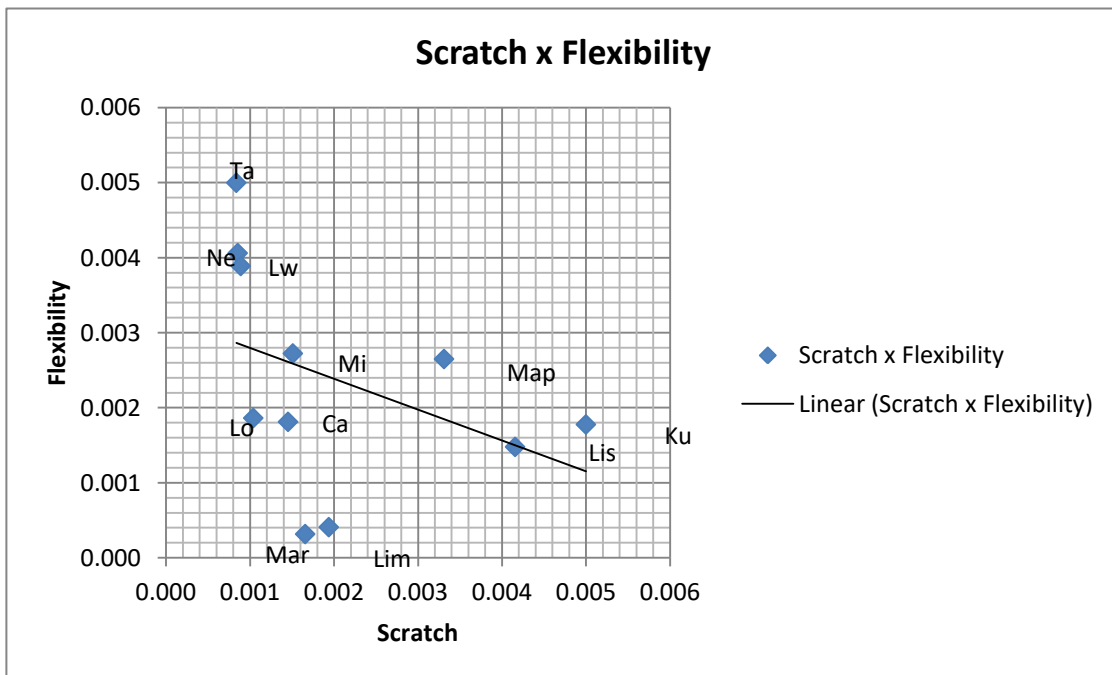


Figure S26. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Scratch × Flexibility

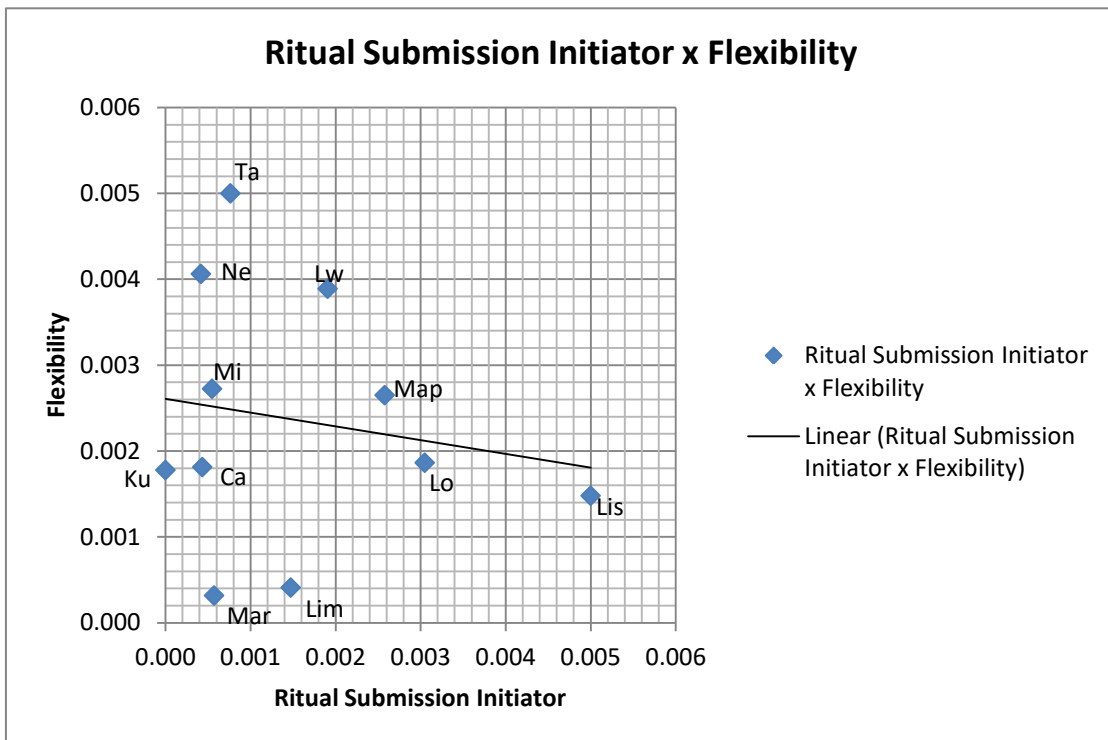


Figure S27. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Ritual Submission Initiator  $\times$  Flexibility

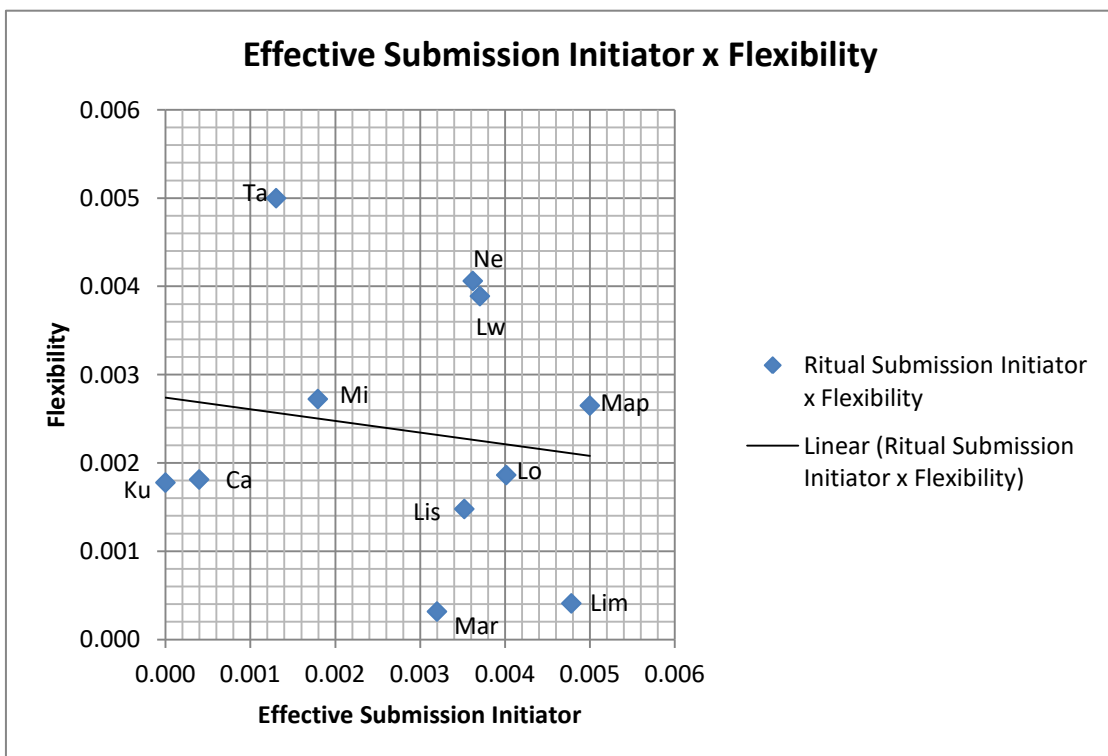


Figure S28. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Ritual Submission Initiator  $\times$  Flexibility

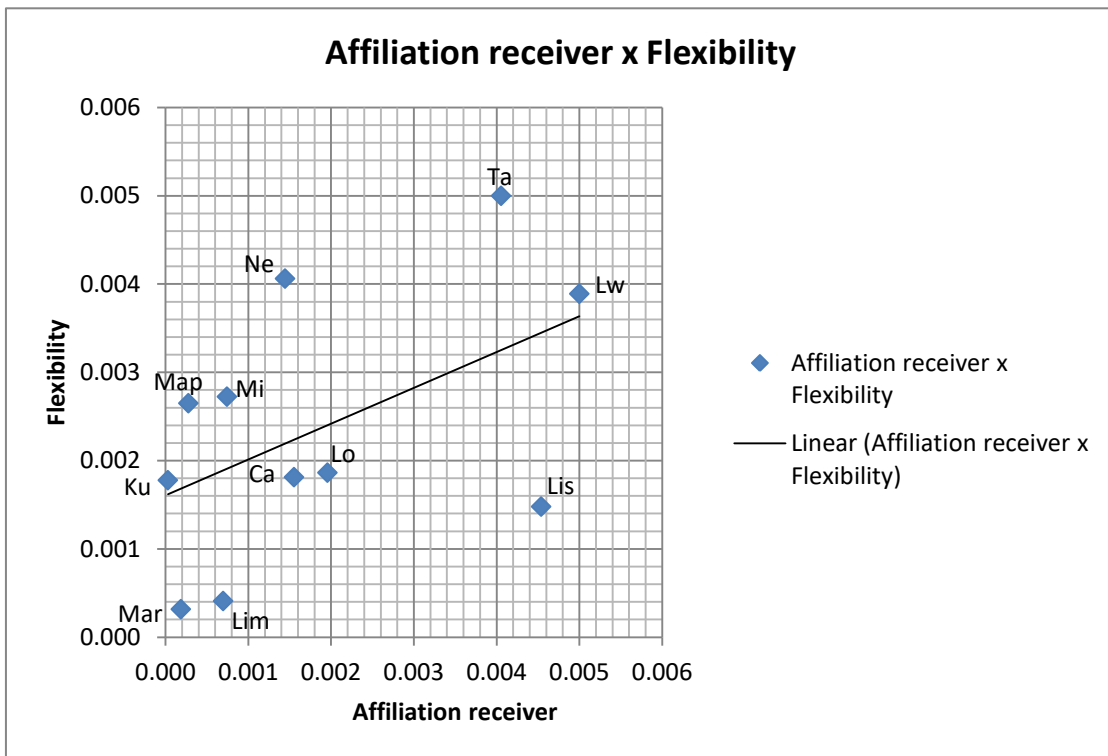


Figure S29. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Affiliation receiver  $\times$  Flexibility

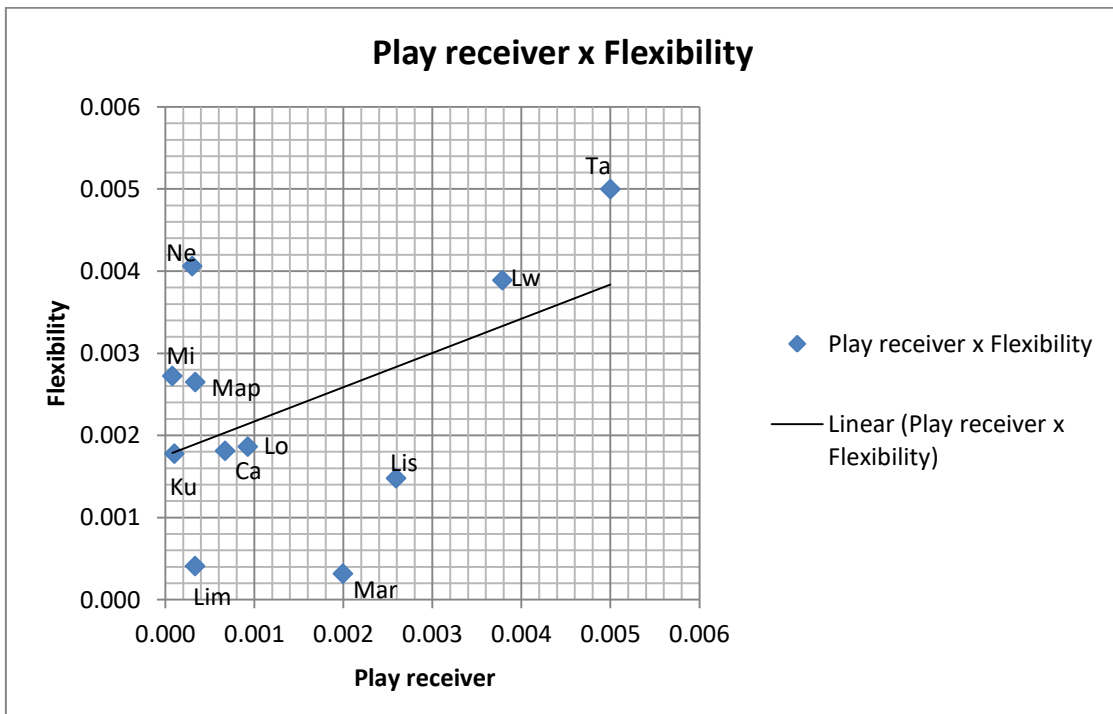


Figure S30. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Play receiver  $\times$  Flexibility



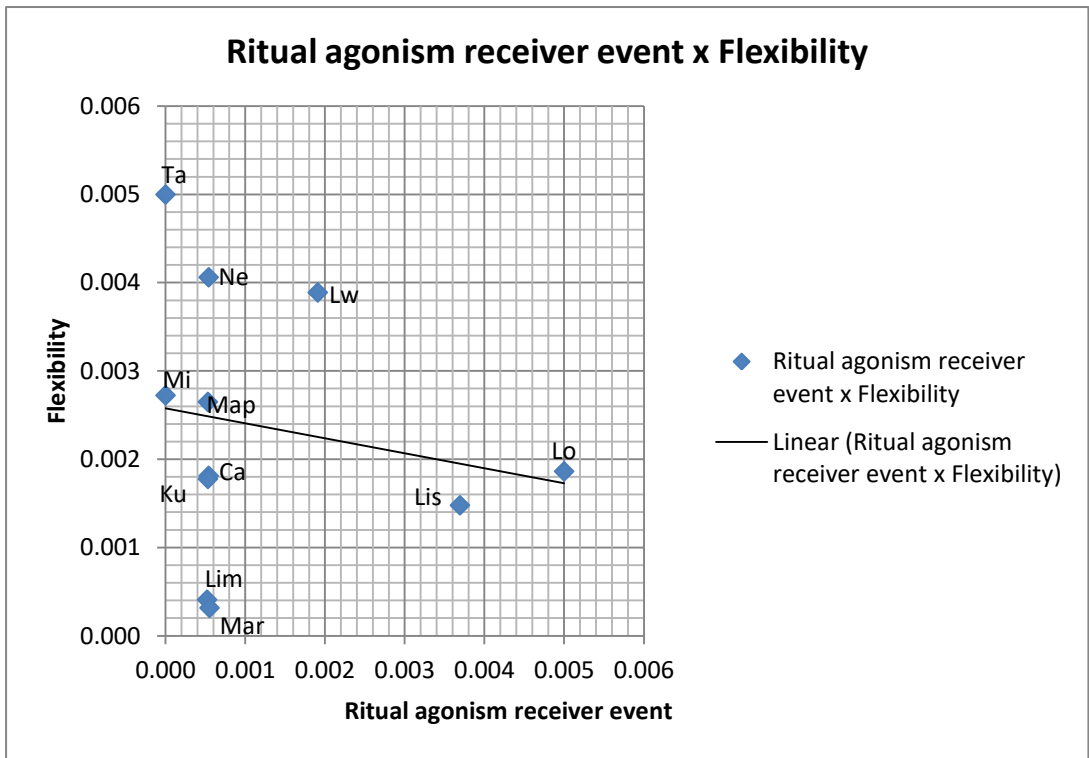


Figure S31. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Ritual agonism receiver event  $\times$  Flexibility

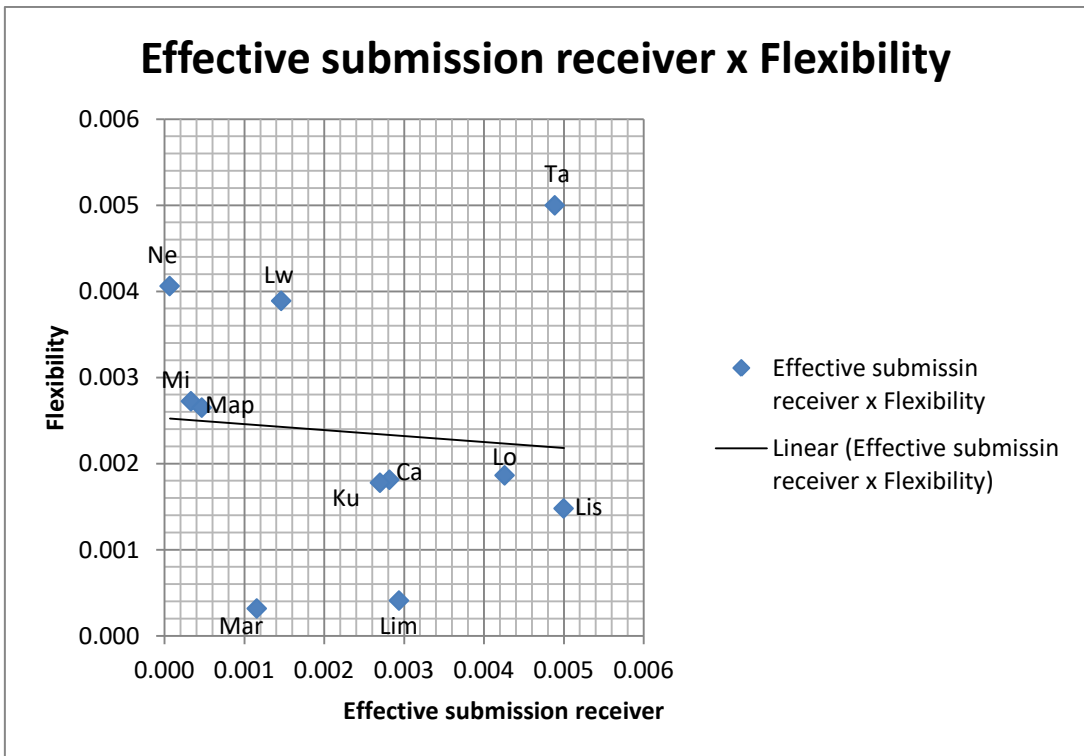


Figure S323. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Effective submission receiver × Flexibility

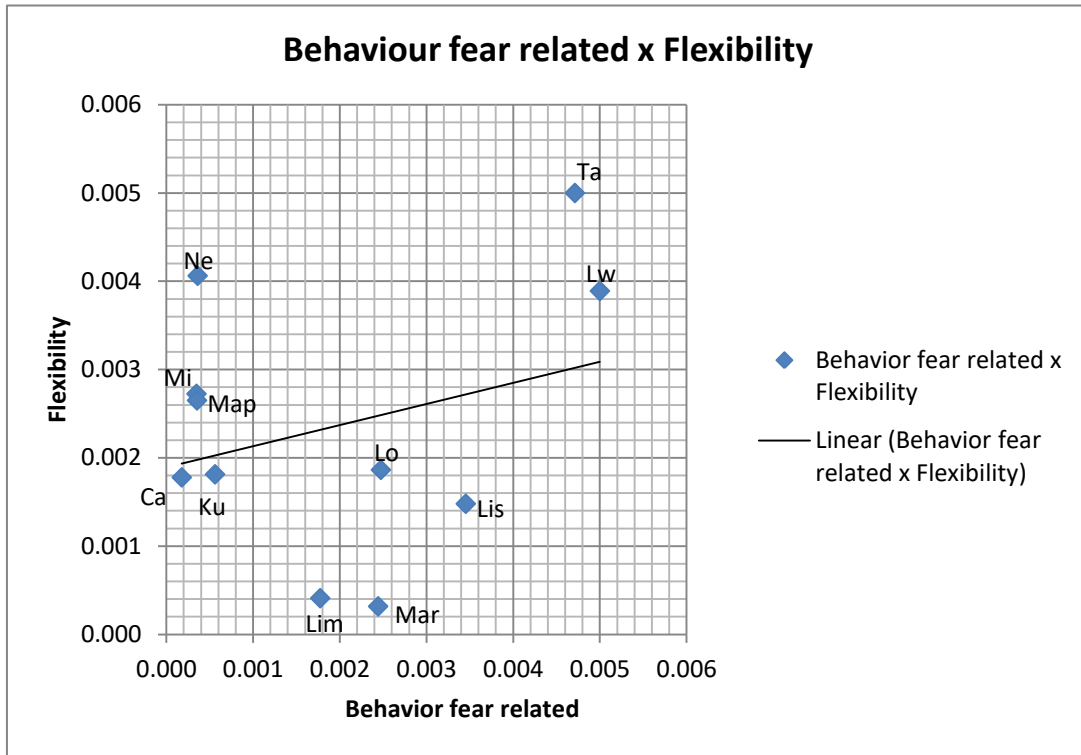


Figure S33. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Behaviour fear related × Flexibility

Table S17. The table presents the results for the complexity index, the four predictability indexes and the four unusual transition indices. For comparison purpose the results were transformed into a 0-5 ratio scale, in which 5 was the highest value obtained in the group for each index

	Camila	Kunta	Limbe	Lisala	Lolaya	Lwiro	Mapendo	Martin	Mirinda	Nefertari	Tânia
<b>complexity index</b>	0.164	0.199	0.182	0.159	0.211	0.142	0.217	0.203	0.170	0.164	0.180
	<b>3.779</b>	<b>4.585</b>	<b>4.194</b>	<b>3.664</b>	<b>4.862</b>	<b>3.272</b>	<b>5.000</b>	<b>4.677</b>	<b>3.917</b>	<b>3.779</b>	<b>4.147</b>
<b>predictability index</b>	0.672	0.591	0.555	0.427	0.484	0.512	0.608	0.618	0.577	0.617	0.501
	<b>5.000</b>	<b>4.398</b>	<b>4.125</b>	<b>3.172</b>	<b>3.601</b>	<b>3.811</b>	<b>4.519</b>	<b>4.595</b>	<b>4.295</b>	<b>4.590</b>	<b>3.724</b>
<b>predictability non-social index</b>	0.756	0.395	0.476	0.342	0.354	0.364	0.711	0.417	0.429	0.583	0.509
	<b>5.000</b>	<b>2.615</b>	<b>3.151</b>	<b>2.265</b>	<b>2.344</b>	<b>2.408</b>	<b>4.703</b>	<b>2.759</b>	<b>2.836</b>	<b>3.860</b>	<b>3.367</b>
<b>predictability social initiating index</b>	0.589	0.657	0.532	0.503	0.502	0.579	0.399	0.603	0.608	0.607	0.506
	<b>4.484</b>	<b>5.000</b>	<b>4.052</b>	<b>3.831</b>	<b>3.820</b>	<b>4.405</b>	<b>3.039</b>	<b>4.590</b>	<b>4.632</b>	<b>4.619</b>	<b>3.855</b>
<b>predictability social receiving index</b>	0.657	0.624	0.629	0.396	0.548	0.509	0.697	0.644	0.583	0.625	0.520
	<b>4.714</b>	<b>4.480</b>	<b>4.511</b>	<b>2.841</b>	<b>3.936</b>	<b>3.651</b>	<b>5.000</b>	<b>4.625</b>	<b>4.187</b>	<b>4.486</b>	<b>3.733</b>
<b>Unusual Transition Index</b>	46.589	44.614	39.396	47.273	40.185	41.029	40.522	46.032	36.989	42.027	39.001
	4.928	4.719	4.167	5.000	4.250	4.340	4.286	4.869	3.912	4.445	4.125
	<b>4.928</b>	<b>4.719</b>	<b>4.167</b>	<b>5.000</b>	<b>4.250</b>	<b>4.340</b>	<b>4.286</b>	<b>4.869</b>	<b>3.912</b>	<b>4.445</b>	<b>4.125</b>
<b>Unusual Non-Social Transition Index</b>	57.203	48.928	51.953	65.080	57.290	66.670	50.785	75.800	28.570	40.158	56.298
	<b>3.773</b>	<b>3.227</b>	<b>3.427</b>	<b>4.293</b>	<b>3.779</b>	<b>4.398</b>	<b>3.350</b>	<b>5.000</b>	<b>1.885</b>	<b>2.649</b>	<b>3.714</b>
<b>Unusual Social Initiating Transition Index</b>	37.017	34.914	30.874	38.676	35.017	38.000	41.856	40.599	35.778	57.229	40.963
	<b>3.234</b>	<b>3.050</b>	<b>2.697</b>	<b>3.379</b>	<b>3.059</b>	<b>3.320</b>	<b>3.657</b>	<b>3.547</b>	<b>3.126</b>	<b>5.000</b>	<b>3.579</b>
<b>Unusual Social Receiving Transition Index</b>	53.246	54.583	43.770	49.116	38.093	31.995	33.723	37.940	42.711	23.960	27.900
	<b>4.878</b>	<b>5.000</b>	<b>4.009</b>	<b>4.499</b>	<b>3.489</b>	<b>2.931</b>	<b>3.089</b>	<b>3.475</b>	<b>3.913</b>	<b>2.195</b>	<b>2.556</b>

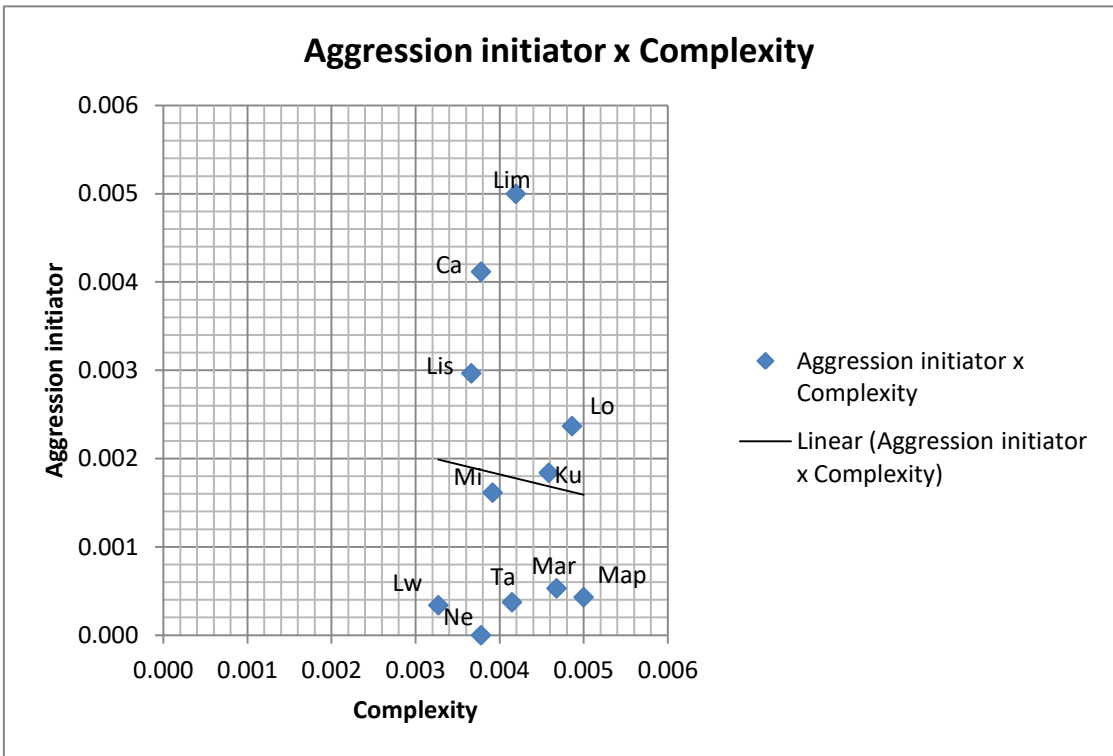


Figure S34. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Aggression initiator  $\times$  Complexity

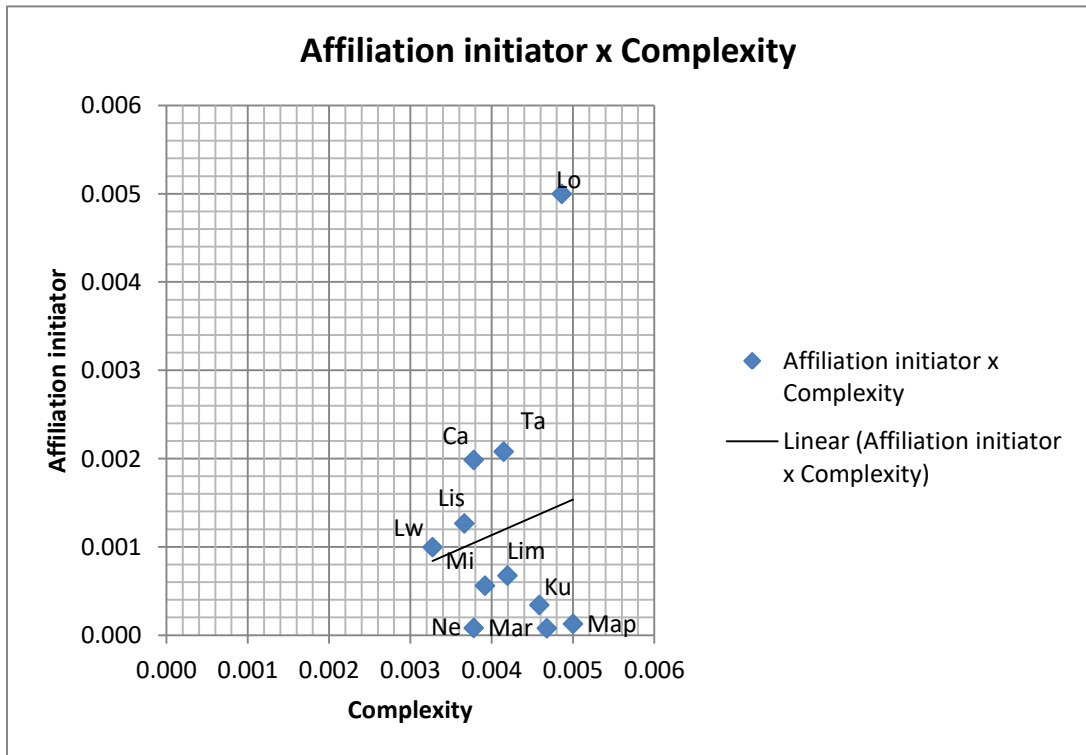


Figure S35. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Affiliation initiator  $\times$  Complexity

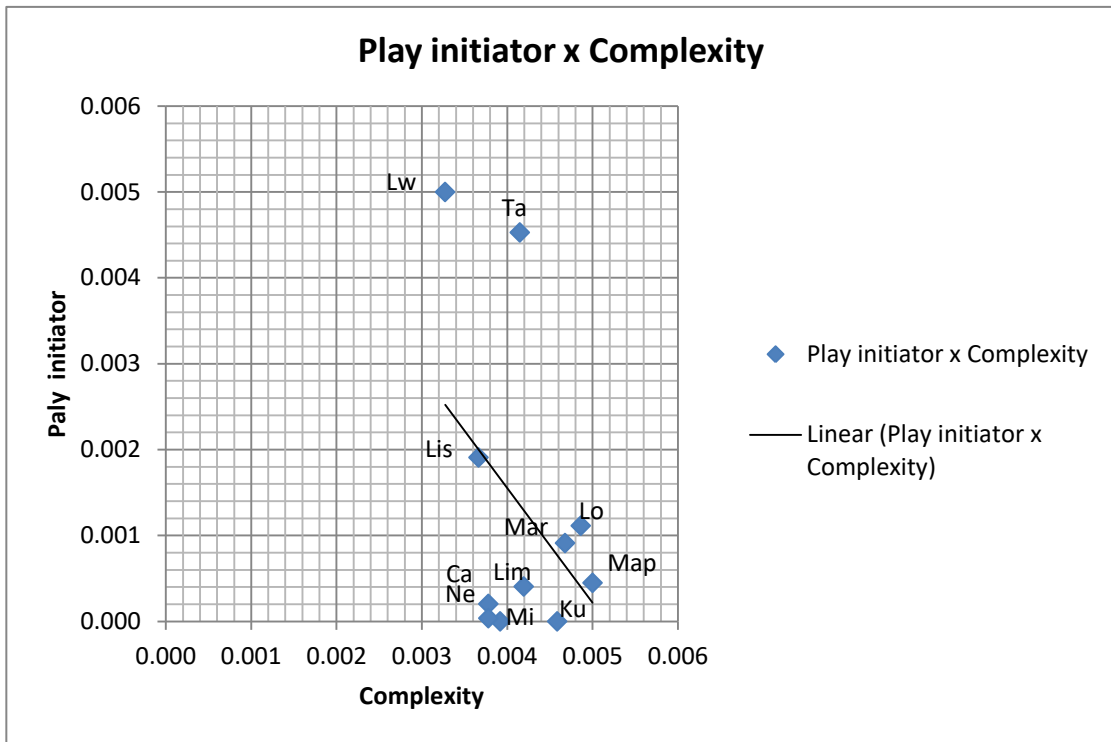


Figure S36. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Play initiator  $\times$  Complexity

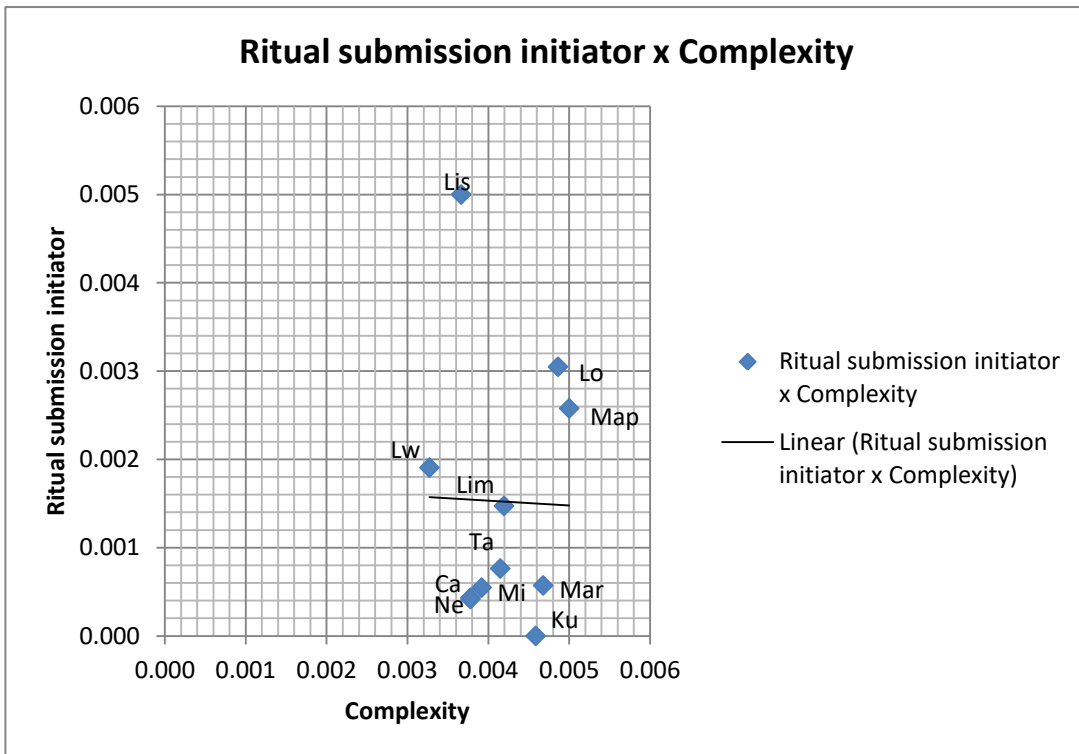


Figure S37. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Ritual submission initiator  $\times$  Complexity

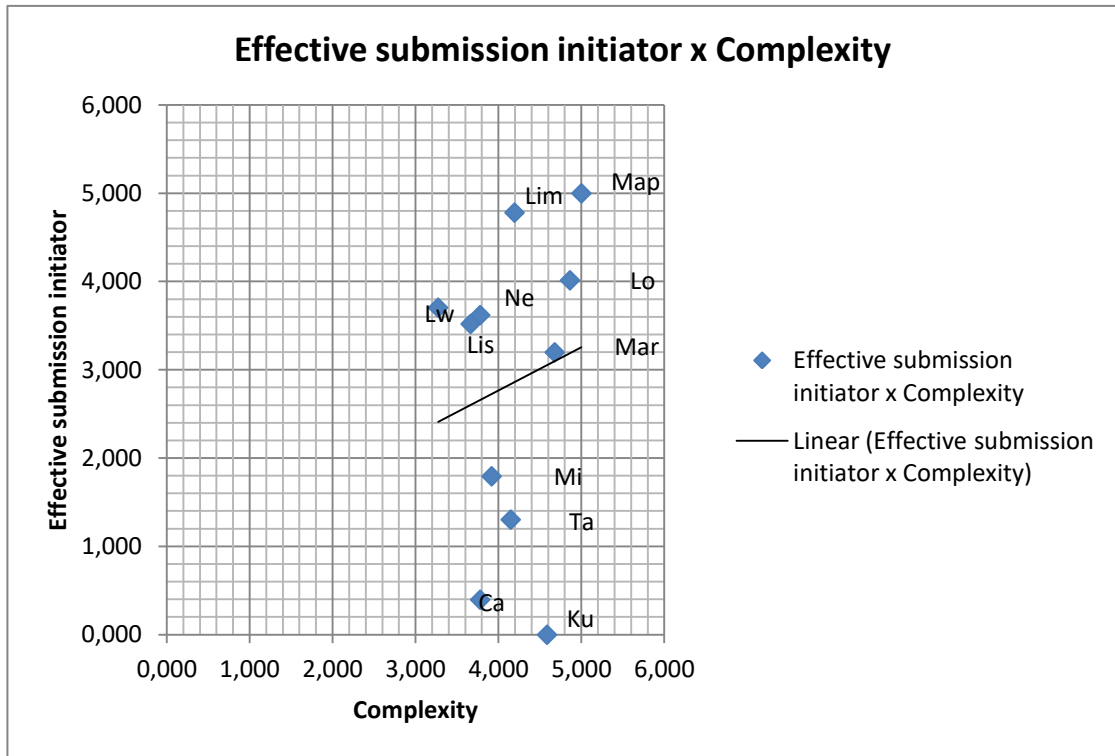


Figure S38. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Effective submission initiator × Complexity

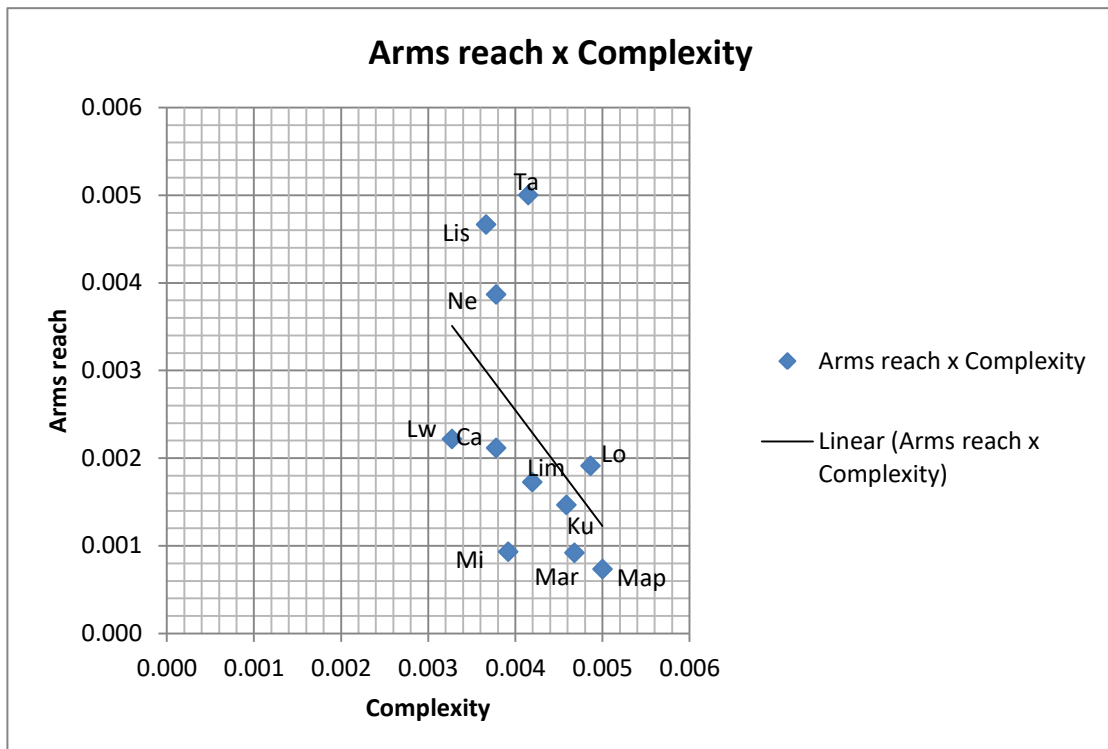


Figure S39. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Arms reach × Complexity

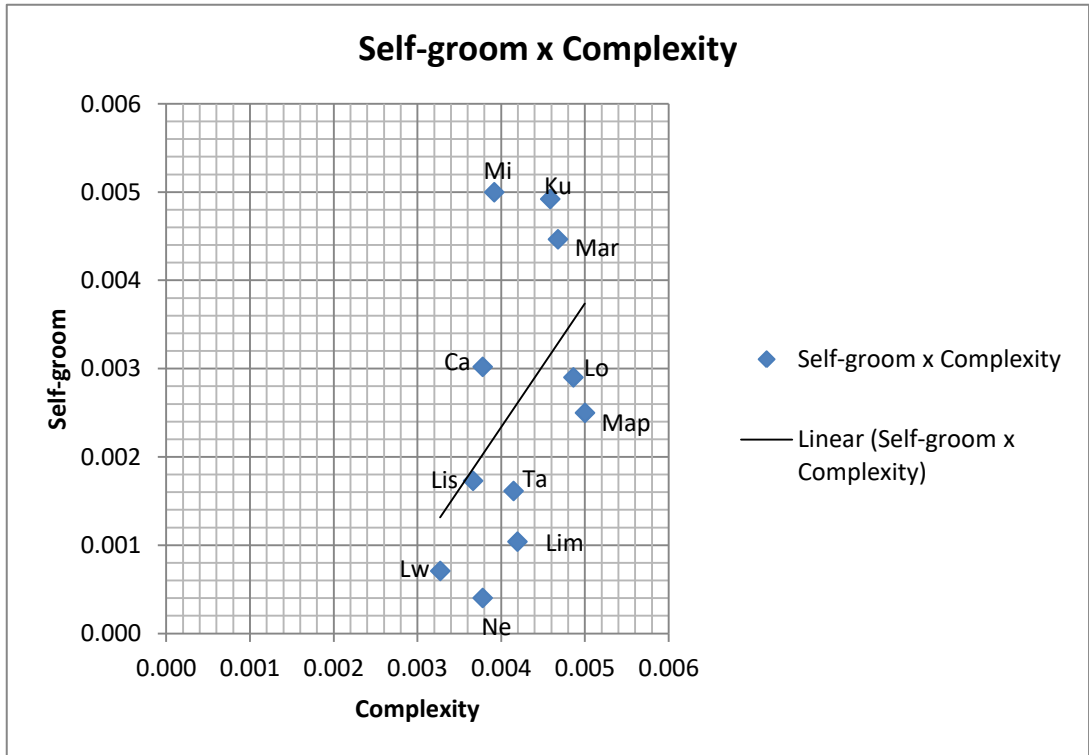


Figure S40. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Self-groom  $\times$  Complexity

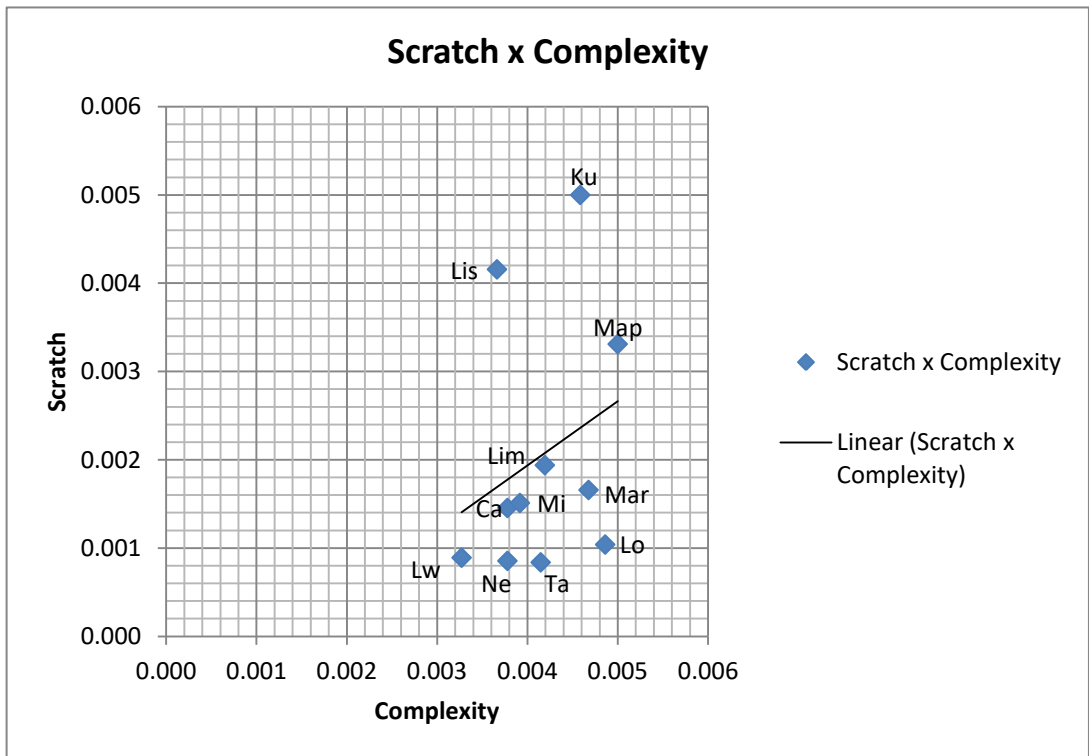


Figure S41. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale), Scratch  $\times$  Complexity

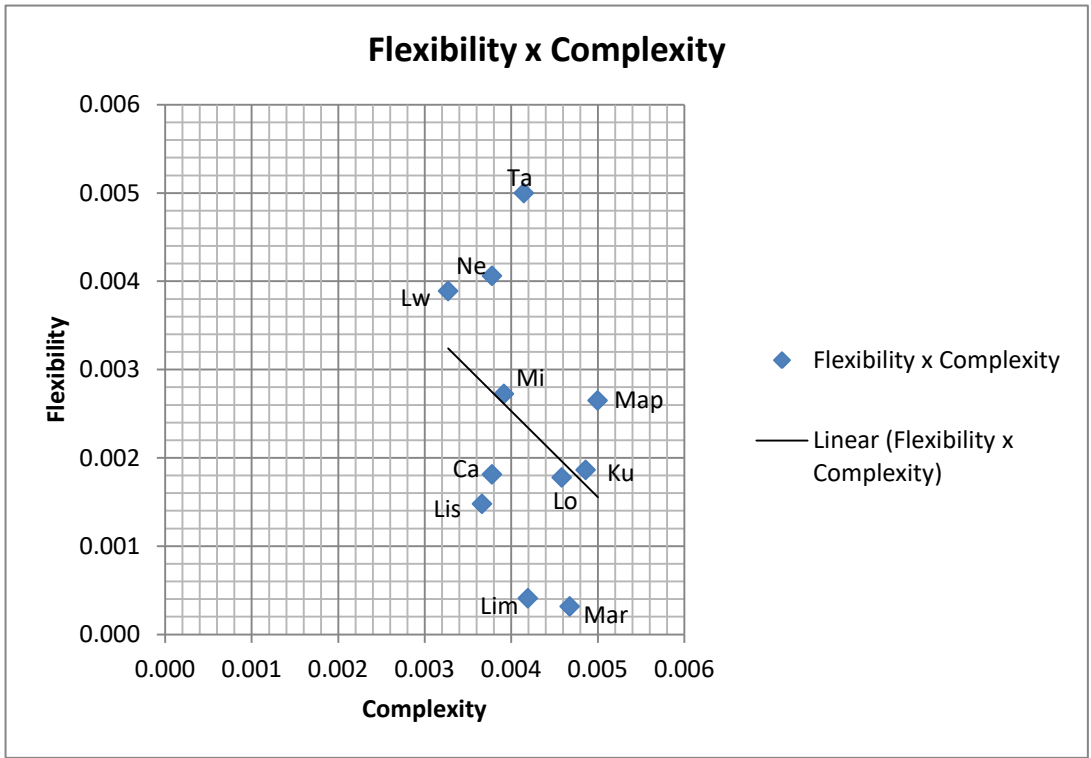


Figure S42. View of dispersion graphic constructed with flexibility results (after conversion in a 0-5 scale) and complexity index results (after conversion in a 0-5 scale).

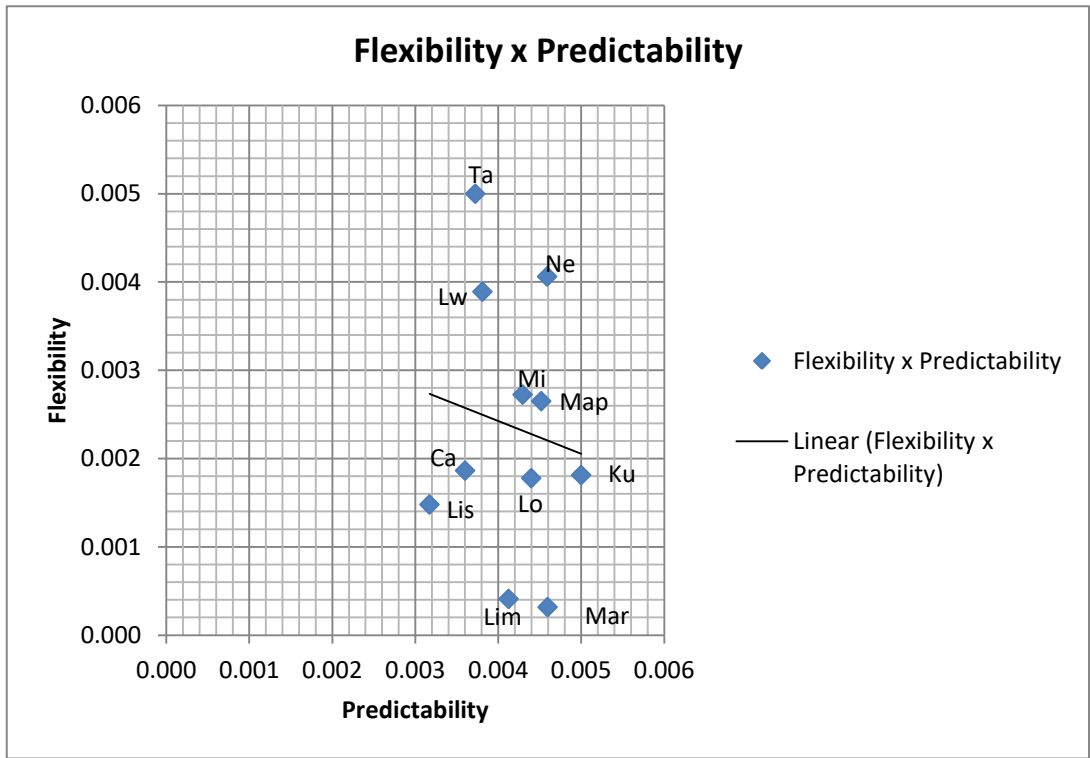


Figure S43. View of dispersion graphic constructed with flexibility results (after conversion in a 0-5 scale) and predictability index results (after conversion in a 0-5 scale).



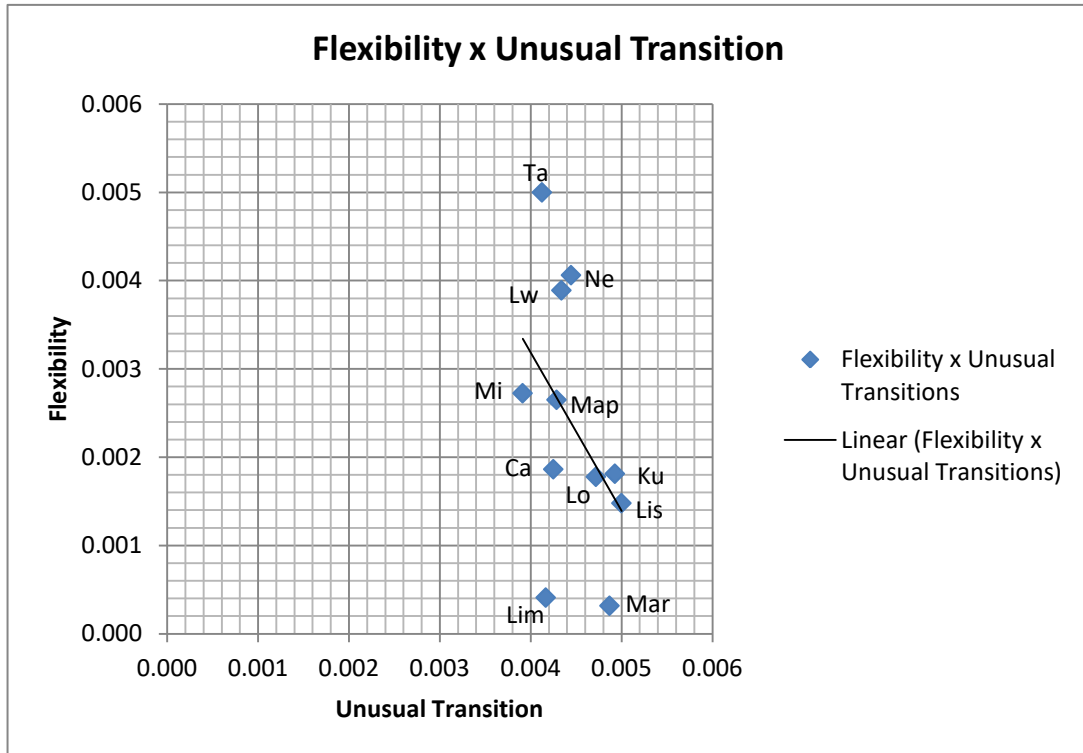


Figure S44. View of dispersion graphic constructed with flexibility results (after conversion in a 0-5 scale) and unusual transition index results (after conversion in a 0-5 scale).

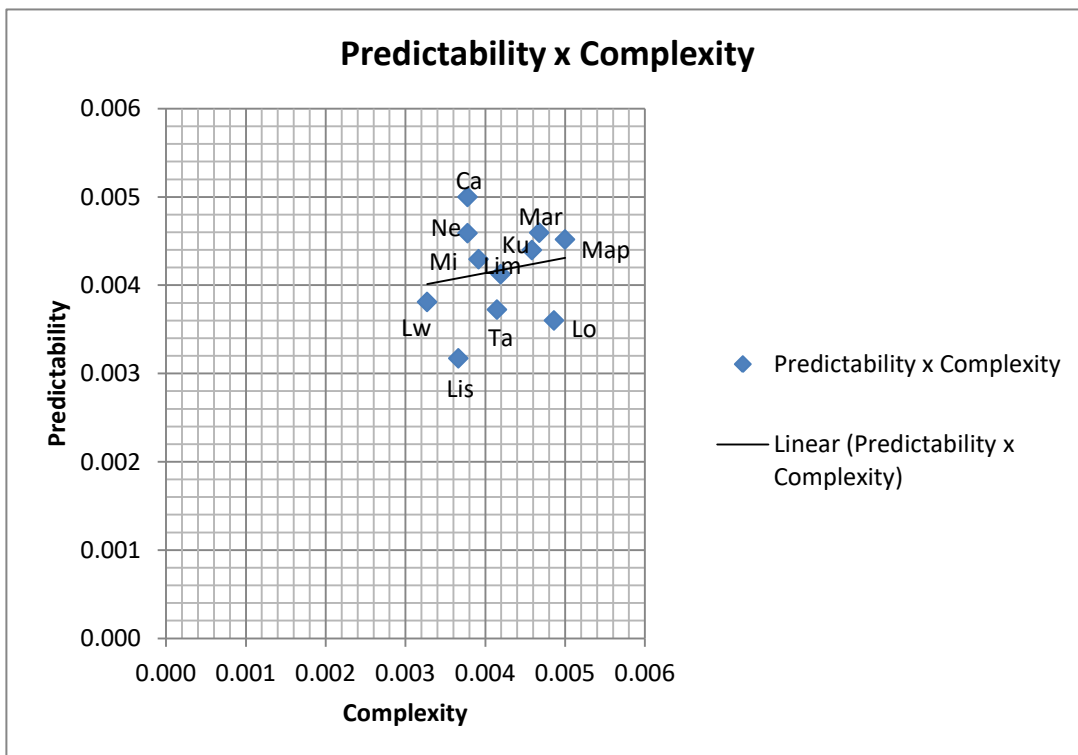


Figure S45. View of dispersion graphic constructed with predictability results (after conversion in a 0-5 scale) and complexity results (after conversion in a 0-5 scale).

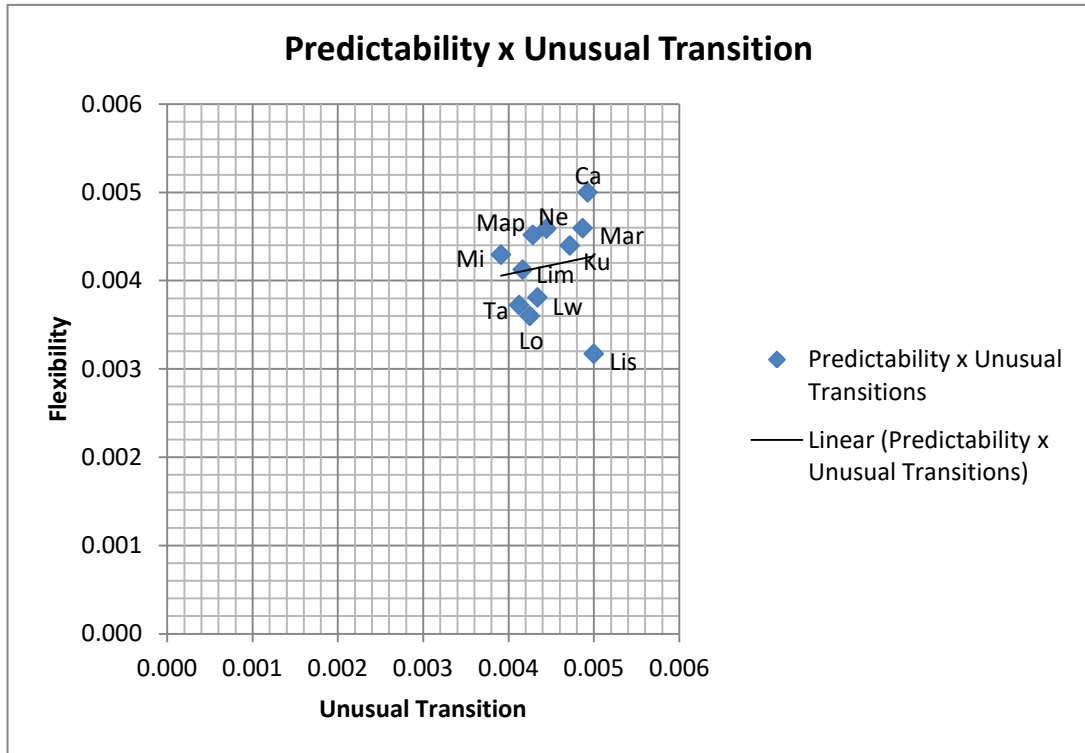


Figure S46. View of dispersion graphic constructed with unusual transition index results (after conversion in a 0-5 scale) and predictability results (after conversion in a 0-5 scale).

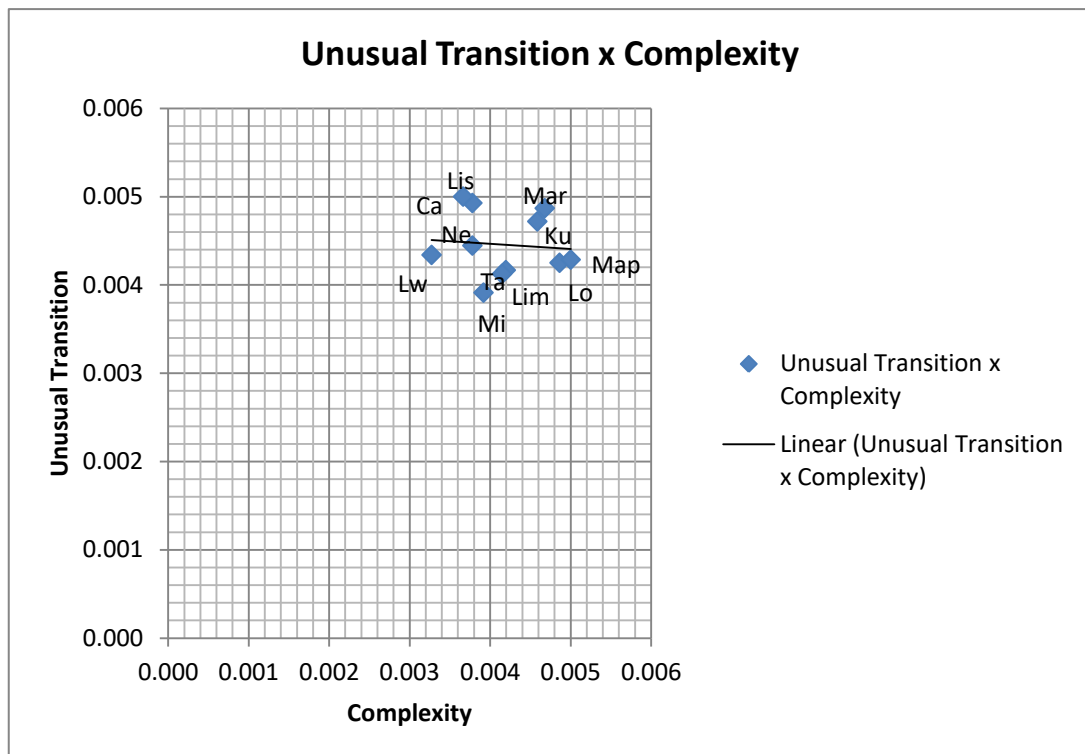


Figure S47. View of dispersion graphic constructed with unusual transition index results (after conversion in a 0-5 scale) and complexity results (after conversion in a 0-5 scale).

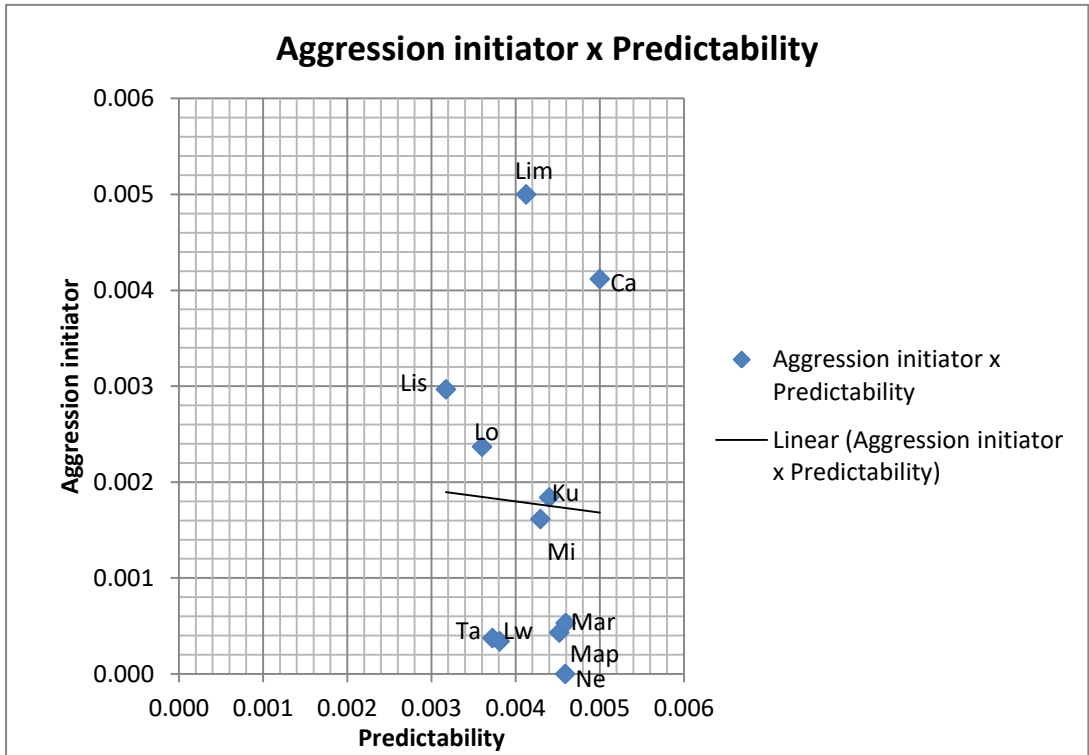


Figure S48. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and predictability index results (after conversion in a 0-5 scale).

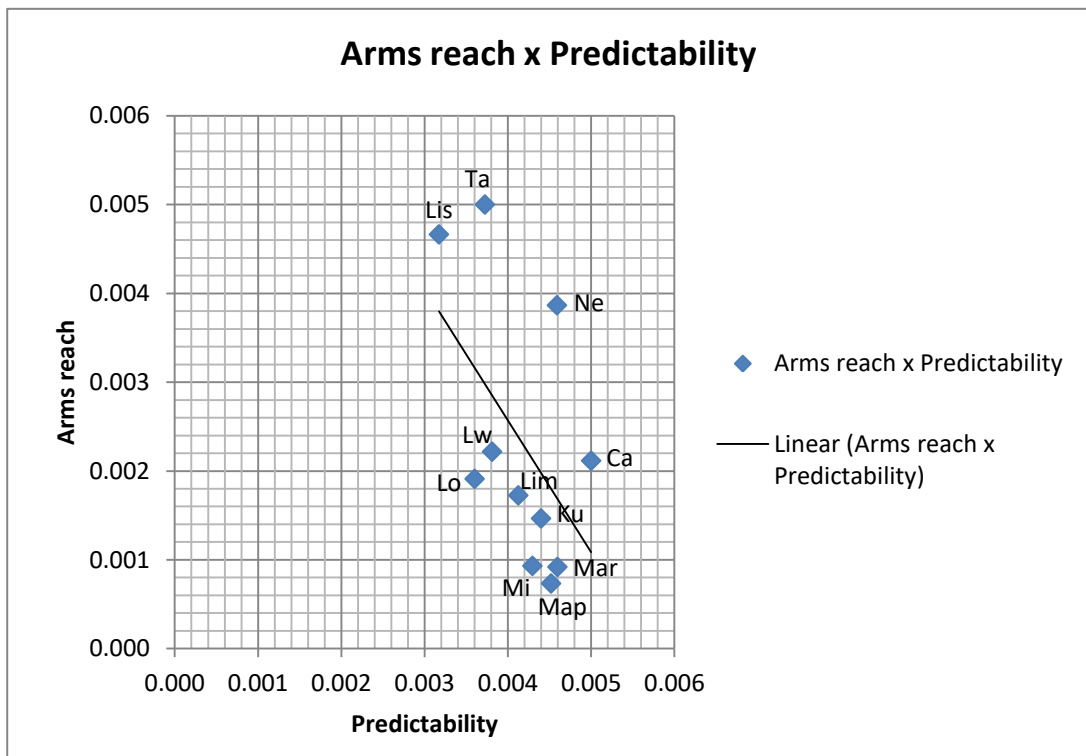


Figure S49. View of dispersion graphics constructed with arms reach results (REM analysis after conversion in a 0-5 scale) and predictability index results (after conversion in a 0-5 scale), Arms reach × Predictability

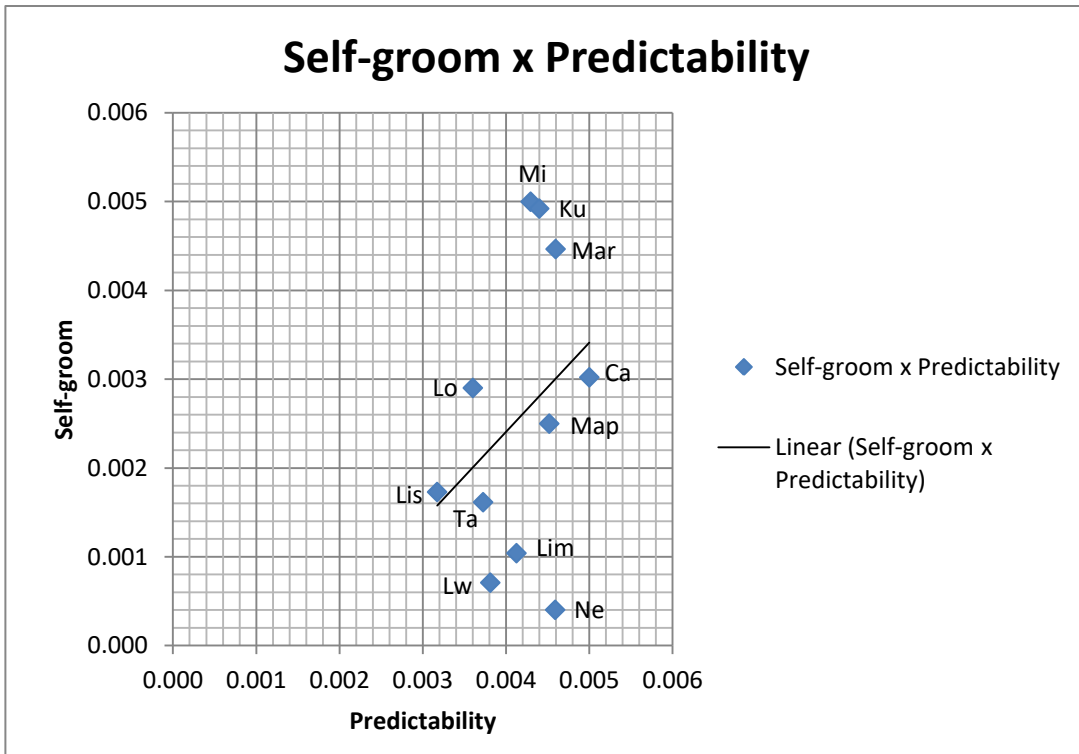


Figure S50. View of dispersion graphics constructed with arms reach results (REM analysis after conversion in a 0-5 scale) and predictability index results (after conversion in a 0-5 scale), Self-groom  $\times$  Predictability

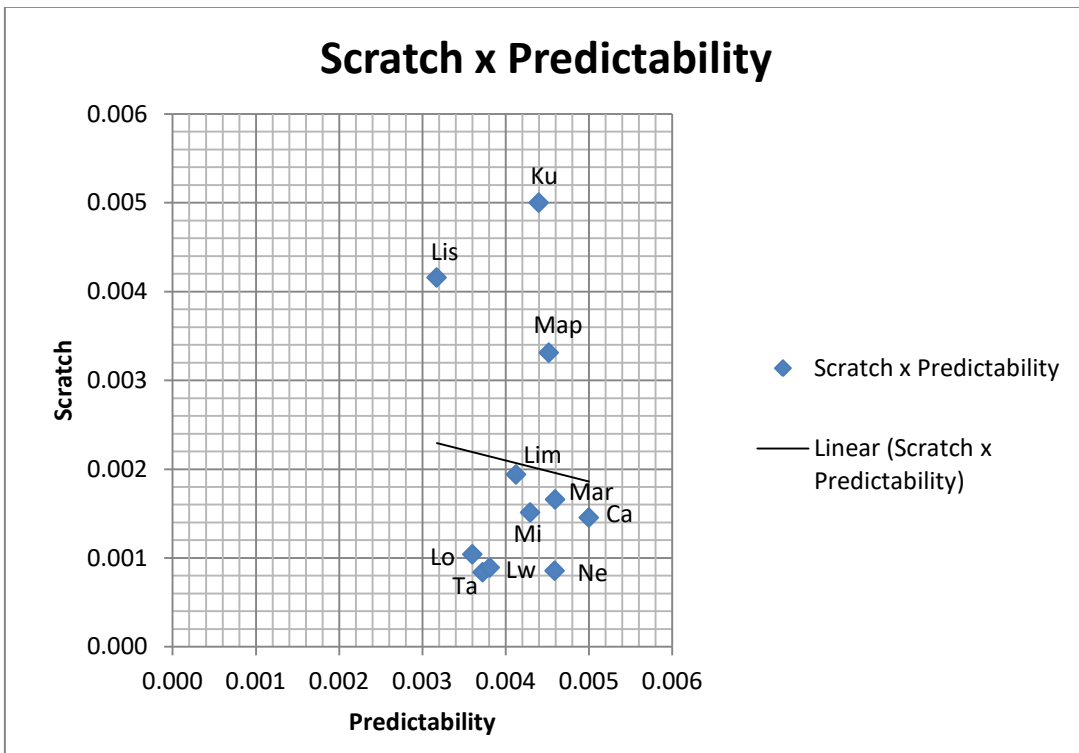


Figure S51. View of dispersion graphics constructed with arms reach results (REM analysis after conversion in a 0-5 scale) and predictability index results (after conversion in a 0-5 scale), Scratch  $\times$  Predictability

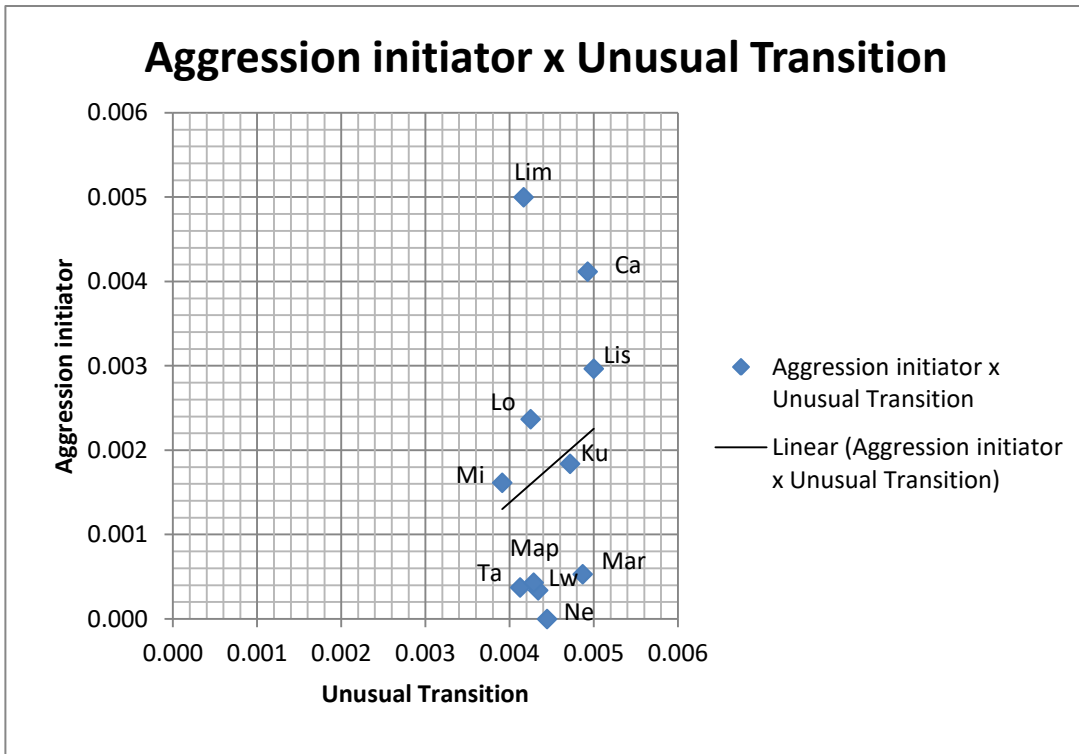


Figure S52. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and unusual transition index results (after conversion in a 0-5 scale), Aggression initiator  $\times$  Unusual Transition

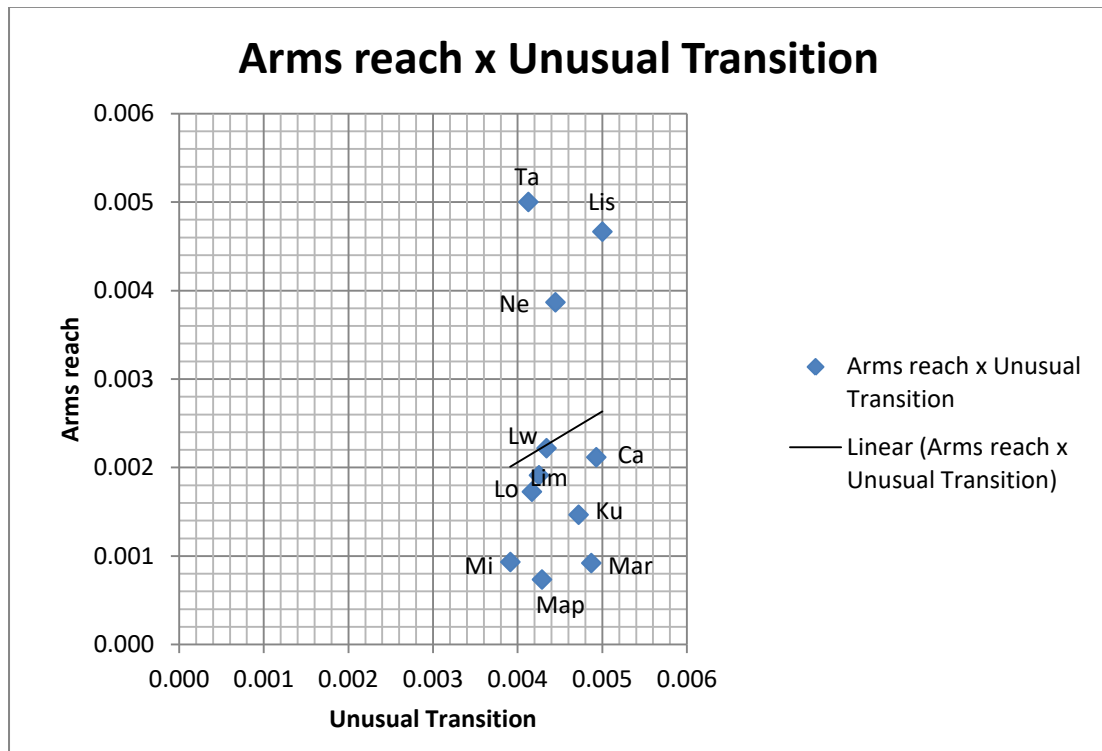


Figure S53. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and unusual transition index results (after conversion in a 0-5 scale), Arms reach  $\times$  Unusual Transition

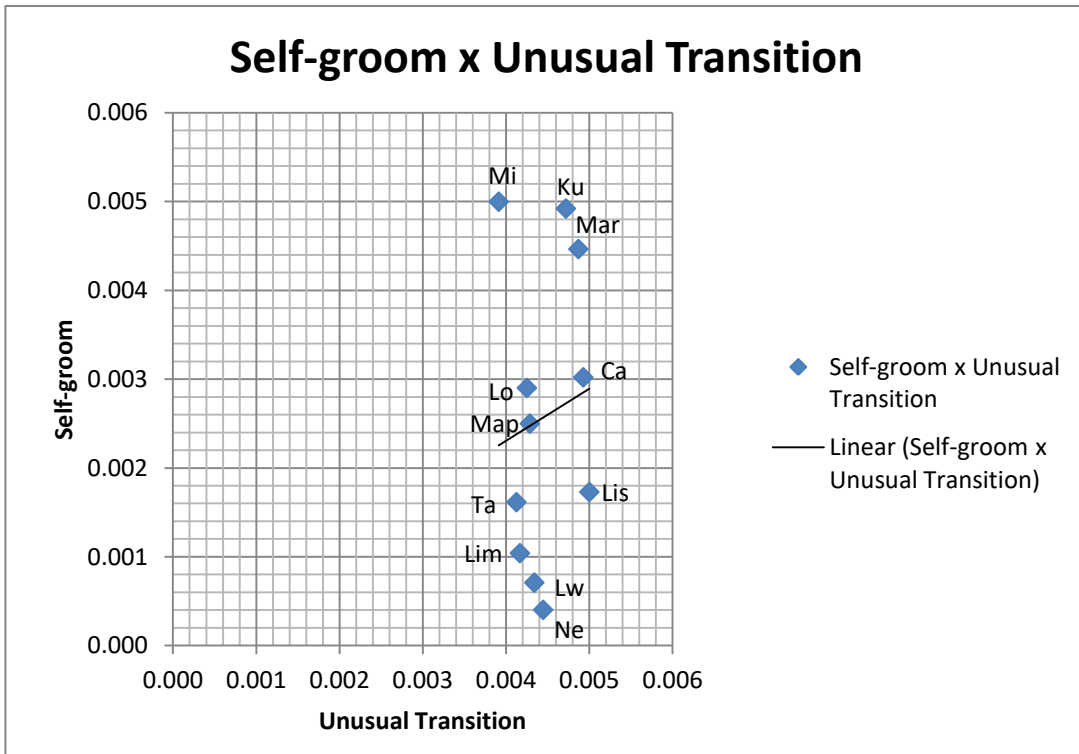


Figure S54. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and unusual transition index results (after conversion in a 0-5 scale), Self-groom  $\times$  Unusual Transition

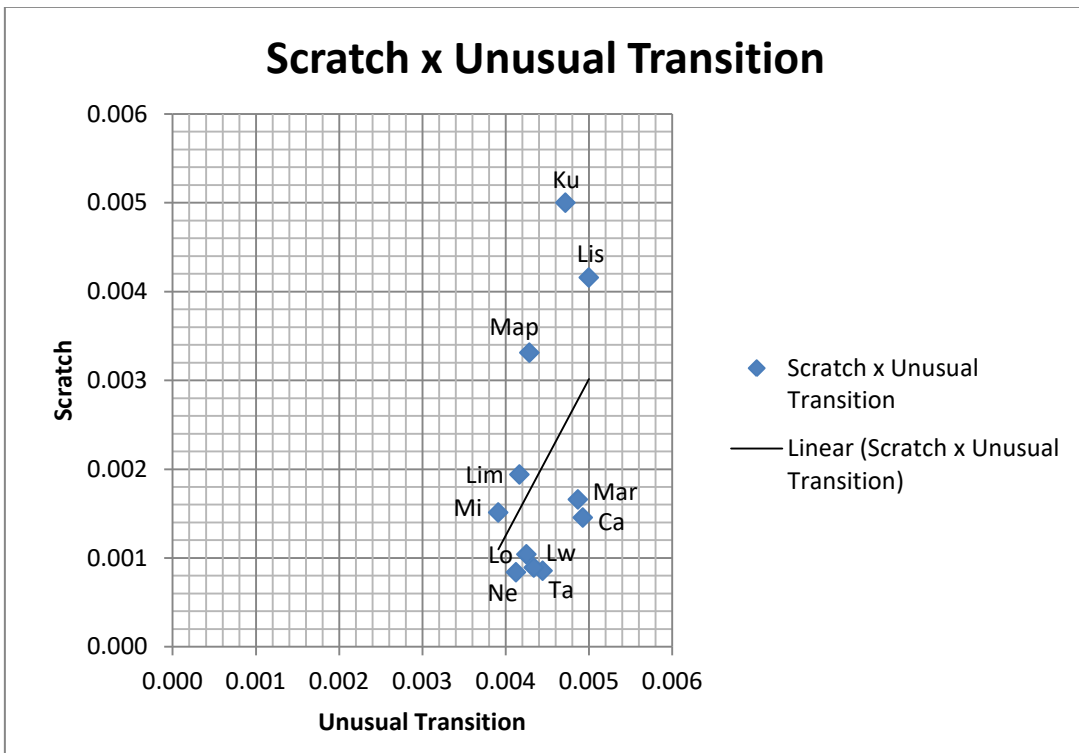
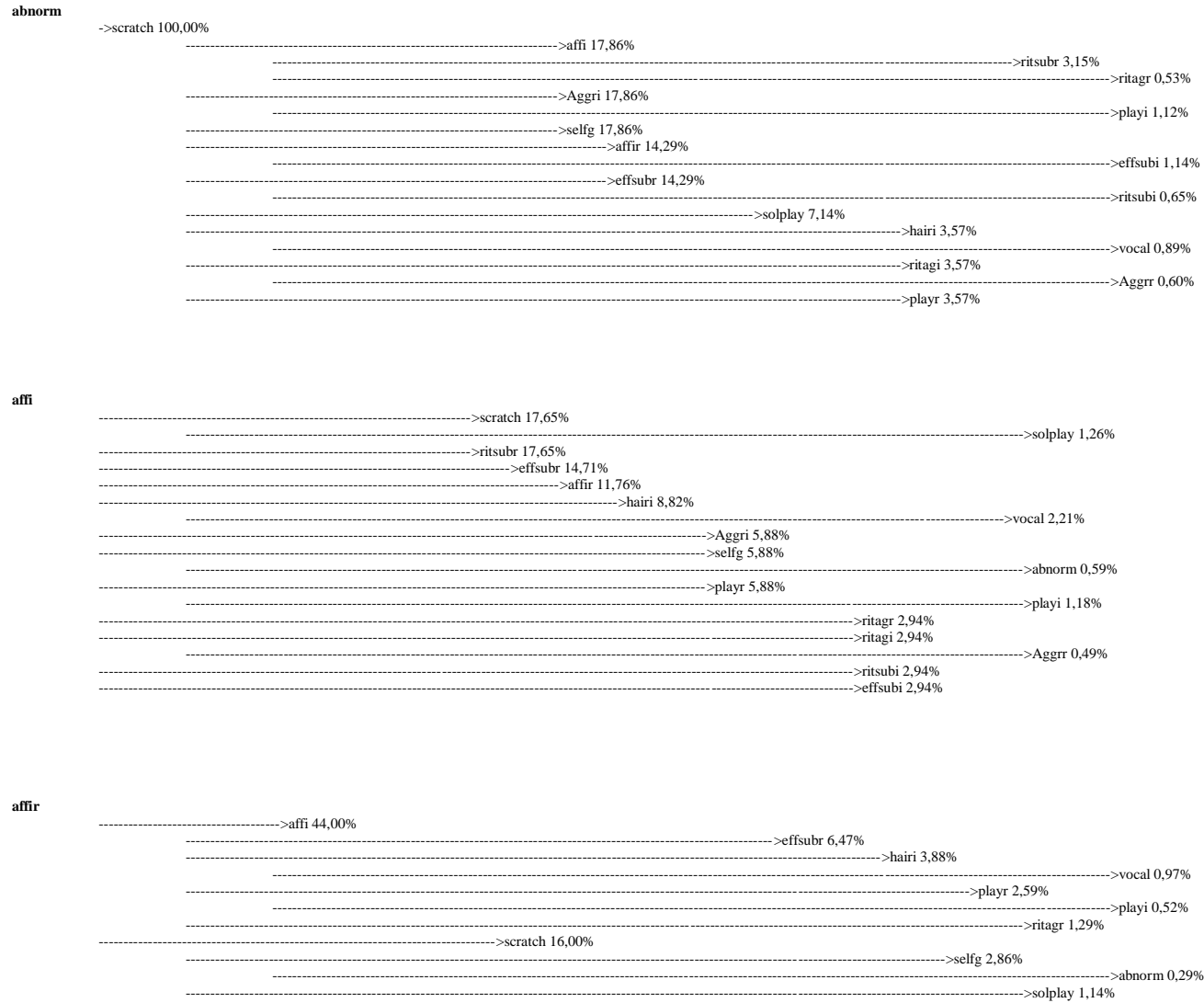


Figure S55. View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and unusual transition index results (after conversion in a 0-5 scale), Self-groom  $\times$  Unusual Transition

SE16. View of probability behavioral sequences of the behavioral transitions of Camila.



```

----->effsubi 8,00%
----->ritagi 8,00%
----->Aggrr 1,33%
----->ritsubr 8,00%
----->Aggri 8,00%
----->ritsubi 4,00%

```

**Aggri**

```

----->effsubr 75,00%
----->affir 20,45%
----->affi 9,00%
----->hairi 0,79%
----->ritagr 0,26%
----->scratch 6,82%
----->solplay 0,49%
----->selfg 6,82%
----->abnorm 0,68%
----->ritsubr 6,82%
----->effsubi 3,41%
----->vocal 3,41%
----->ritagi 3,41%
----->playr 0,57%
----->Aggrr 0,57%
----->ritsubi 3,41%
----->playi 6,25%

```

**Aggrr**

```

->scratch 100,00%
----->Aggri 17,86%
----->playi 1,12%
----->affi 17,86%
----->ritsubr 3,15%
----->ritagr 0,53%
----->selfg 17,86%
----->abnorm 1,79%
----->affir 14,29%
----->effsubi 1,14%
----->effsubr 14,29%
----->ritsubi 0,65%
----->solplay 7,14%
----->hairi 3,57%
----->vocal 0,89%
----->ritagi 3,57%
----->playr 3,57%

```

**effsubi**

```

----->scratch 40,00%

```



```

----->selfg 7,14%
----->solplay 2,86%----->abnorm 0,71%
----->hairi 1,43%
----->playr 1,43%
----->effsubr 40,00%
----->Aggri 9,09%
----->playi 0,57%
----->ritsubr 3,64%
----->ritsubi 1,82%
----->vocal 1,82%
----->ritagi 1,82%
----->Aggrr 0,30%
----->affir 20,00%
----->affi 8,80%
----->ritagr 0,26%

```

**effsubr**

```

----->affir 27,27%
----->affi 12,00%
----->hairi 1,06%
----->ritagr 0,35%
----->Aggri 22,73%
----->playi 1,42%
----->ritsubr 9,09%
----->selfg 9,09%
----->abnorm 0,91%
----->scratch 9,09%
----->solplay 0,65%
----->ritagi 4,55%
----->Aggrr 0,76%
----->playr 0,76%
----->effsubi 4,55%
----->ritsubi 4,55%
----->vocal 4,55%

```

**hairi**

```

----->affir 25,00%
----->effsubi 2,00%
----->ritagi 2,00%
----->Aggrr 0,33%
----->ritsubi 1,00%
----->affi 25,00%
----->ritsubr 4,41%
----->playr 1,47%
----->ritagr 0,74%
----->Aggri 25,00%

```

```

----->effsubr 18,75%
----->playi 1,56%
----->vocal 25,00%
----->selfg 8,33%
----->scratch 5,00%
----->solplay 0,36%
----->abnorm 0,83%

```

**playi**

```

->affir 100,00%
----->affi 44,00%
----->effsubr 6,47%
----->hairi 3,88%
----->vocal 0,97%
----->playr 2,59%
----->ritagr 1,29%
----->scratch 16,00%
----->selfg 2,86%
----->abnorm 0,29%
----->solplay 1,14%
----->effsubi 8,00%
----->ritagi 8,00%
----->Aggrr 1,33%
----->Aggri 8,00%
----->ritsubr 8,00%
----->ritsubi 4,00%

```

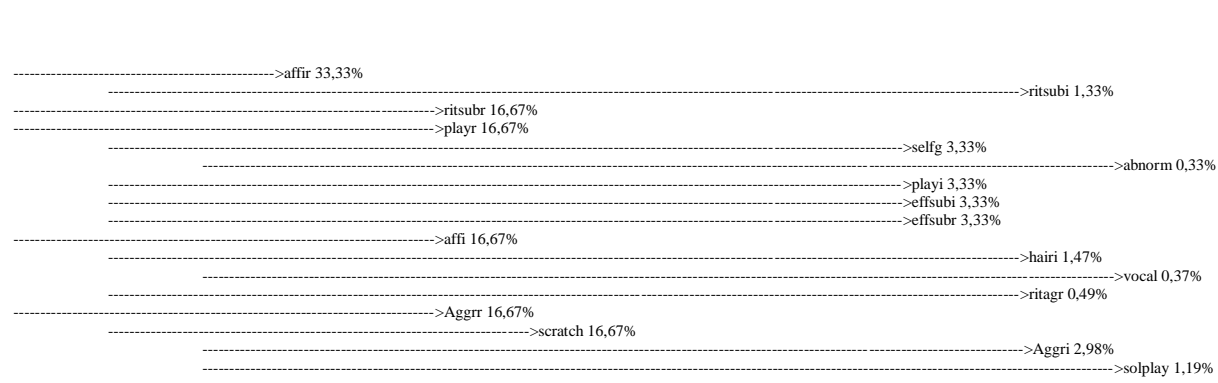
**playr**

```

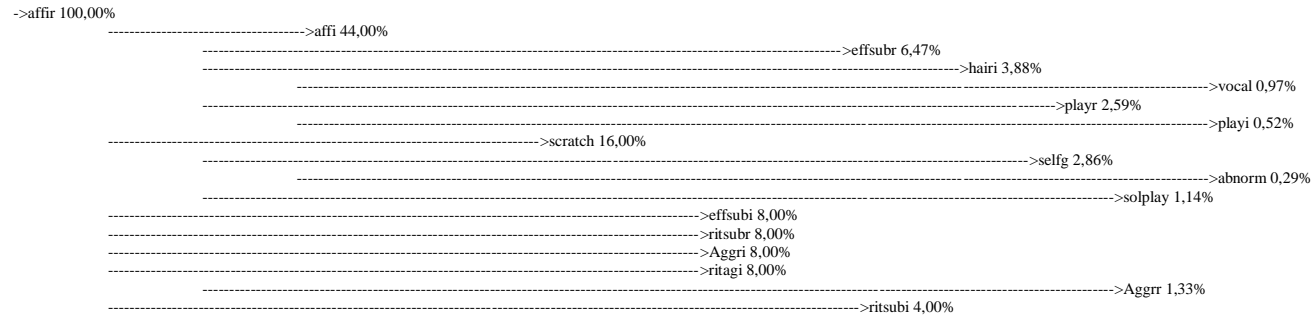
----->effsubr 20,00%
----->Aggri 4,55%
----->vocal 0,91%
----->ritsubi 0,91%
----->selfg 20,00%
----->scratch 12,00%
----->solplay 0,86%
----->ritagi 2,00%
----->Aggrr 0,33%
----->abnorm 2,00%
----->playi 20,00%
----->affir 20,00%
----->effsubi 20,00%
----->ritsubr 20,00%
----->affi 11,43%
----->ritagr 0,34%
----->hairi 1,43%

```

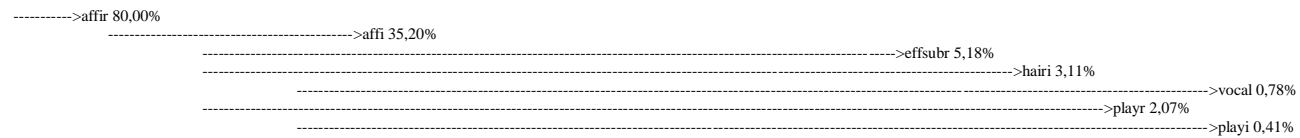
ritagi



ritagr



ritsubi



```

----->ritagr 1,04%
----->scratch 12,80%
----->selfg 2,29%
----->abnorm 0,23%
----->solplay 0,91%
----->effsubi 6,40%
----->Aggri 6,40%
----->ritagi 6,40%
----->Aggrr 1,07%
----->ritsubr 20,00%

```

**ritsubr**

```

----->affi 57,14%
----->selfg 3,36%
----->abnorm 0,34%
----->Aggri 3,36%
----->playr 3,36%
----->playi 0,67%
----->ritsubi 1,68%
----->effsubi 1,68%
----->ritagi 1,68%
----->Aggrr 0,28%
----->ritagr 1,68%
----->effsubr 14,29%
----->scratch 14,29%
----->solplay 1,02%
----->affir 7,14%
----->hairi 7,14%
----->vocal 1,79%

```

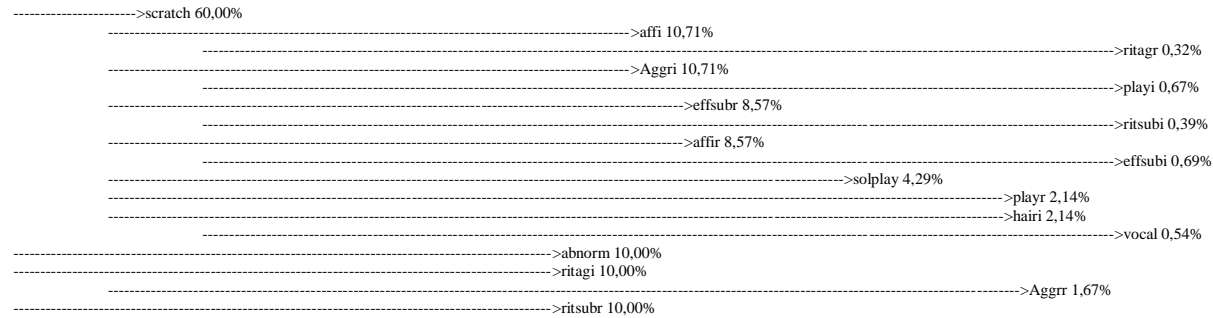
**scratch**

```

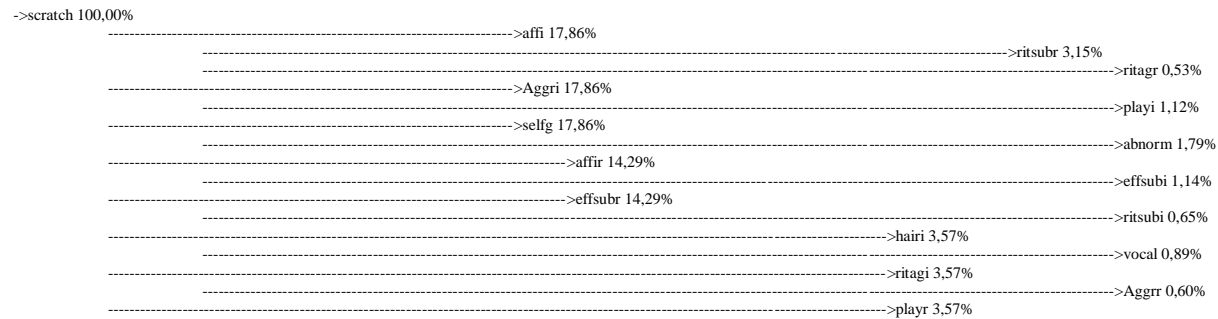
----->Aggri 17,86%
----->playi 1,12%
----->affi 17,86%
----->ritsubr 3,15%
----->ritagr 0,53%
----->selfg 17,86%
----->abnorm 1,79%
----->affir 14,29%
----->effsubi 1,14%
----->effsubr 14,29%
----->ritsubi 0,65%
----->solplay 7,14%
----->playr 3,57%
----->hairi 3,57%
----->vocal 0,89%
----->ritagi 3,57%
----->Aggrr 0,60%

```

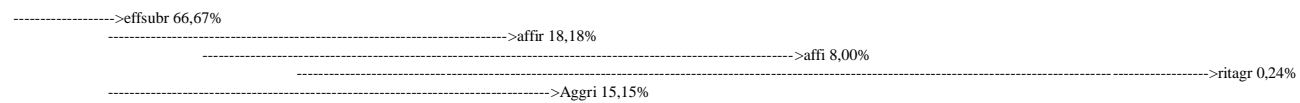
**selfg**

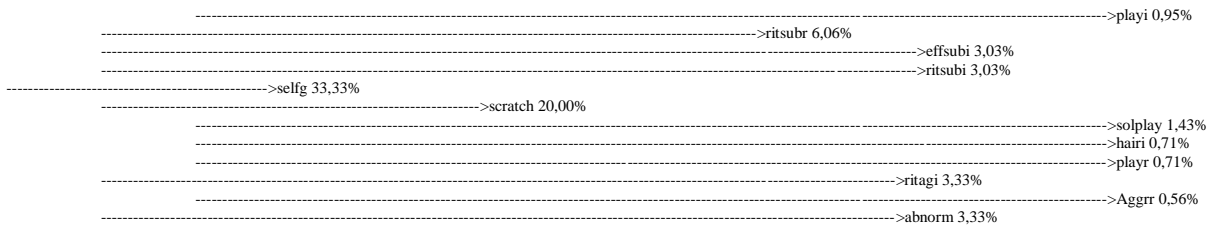


**solplay**



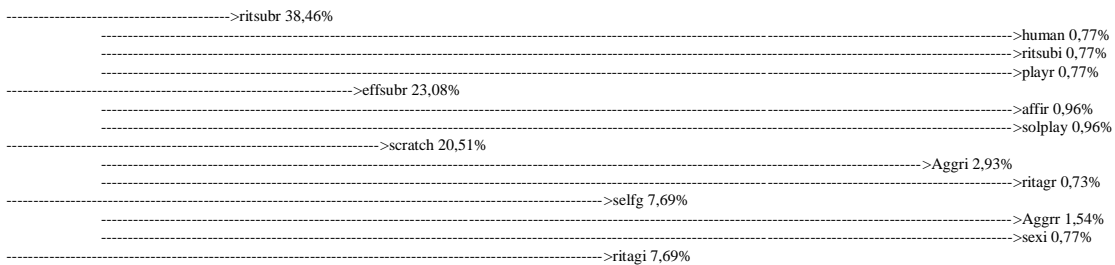
**vocal**



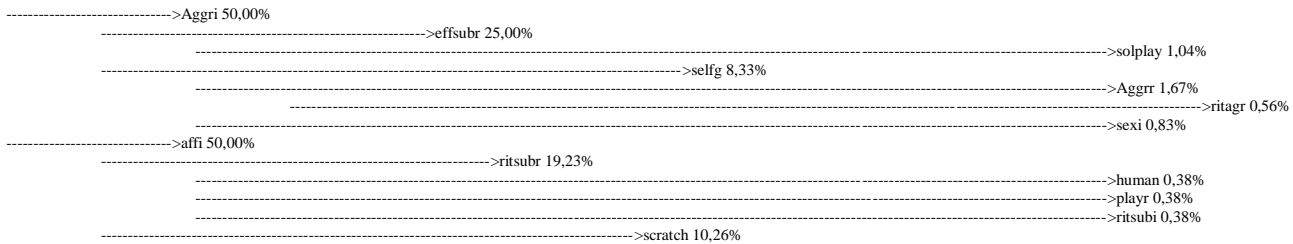


SE17. View of probability behavioral sequences of the behavioral transitions of Kunta.

affi



affir



----->ritagi 3,85%

**Aggri**

----->effsubr 50,00%  
----->scratch 14,58%  
----->affir 2,08%  
----->solplay 2,08%  
----->ritsubr 33,33%  
----->affi 20,67%  
----->ritagi 2,00%  
----->human 0,67%  
----->ritsubi 0,67%  
----->playr 0,67%  
----->selfg 16,67%  
----->Aggrr 3,33%  
----->ritagr 1,11%  
----->sexi 1,67%

**Aggrr**

----->selfg 33,33%  
----->scratch 13,33%  
----->playr 0,48%  
----->Aggri 3,33%  
----->sexi 3,33%  
----->affi 33,33%  
----->ritsubr 12,82%  
----->human 0,26%  
----->ritsubi 0,26%  
----->effsubr 7,69%  
----->affir 0,32%  
----->solplay 0,32%  
----->ritagi 2,56%  
----->ritagr 33,33%

**effsubr**

----->scratch 29,17%  
----->ritagi 2,08%  
----->sexi 1,04%  
----->ritagr 1,04%  
----->playr 1,04%  
----->ritsubr 29,17%  
----->ritsubi 0,58%  
----->Aggrr 0,58%

```

----->human 0,58%
----->selfg 1,92%
----->affi 25,00%
----->Aggri 8,33%
----->solplay 4,17%
----->affir 4,17%

```

**human**

```

->effsubr 100,00%
----->scratch 29,17%
----->ritagi 2,08%
----->playr 1,04%
----->ritagr 1,04%
----->sexi 1,04%
----->ritsubr 29,17%
----->ritsubi 0,58%
----->Aggrr 0,58%
----->affi 25,00%
----->selfg 1,92%
----->Aggri 8,33%
----->affir 4,17%
----->solplay 4,17%

```

**playr**

```

->affi 100,00%
----->ritsubr 38,46%
----->ritsubi 0,77%
----->human 0,77%
----->effsubr 23,08%
----->solplay 0,96%
----->affir 0,96%
----->scratch 20,51%
----->Aggri 2,93%
----->ritagr 0,73%
----->selfg 7,69%
----->Aggrr 1,54%
----->sexi 0,77%
----->ritagi 7,69%

```

**ritagi**

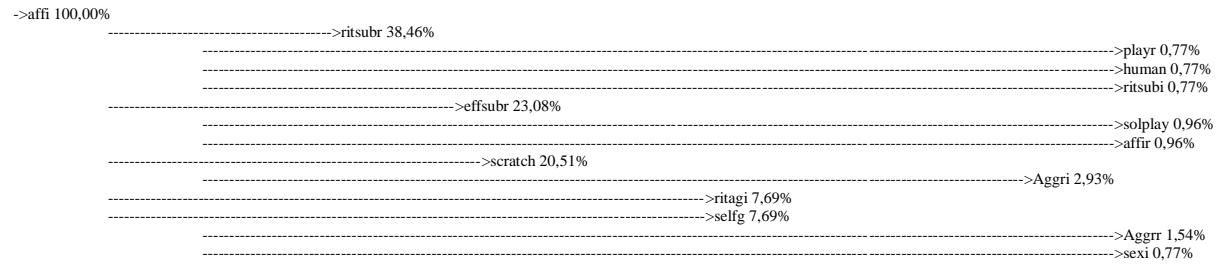
```

----->ritsubr 55,56%
----->affi 34,44%
----->selfg 2,65%
----->Aggri 3,33%
----->ritsubi 1,11%
----->Aggrr 1,11%
----->human 1,11%
----->playr 1,11%
----->solplay 1,11%
----->scratch 22,22%
----->sexi 0,79%
----->ritagr 0,79%
----->effsubr 22,22%
----->affir 0,93%

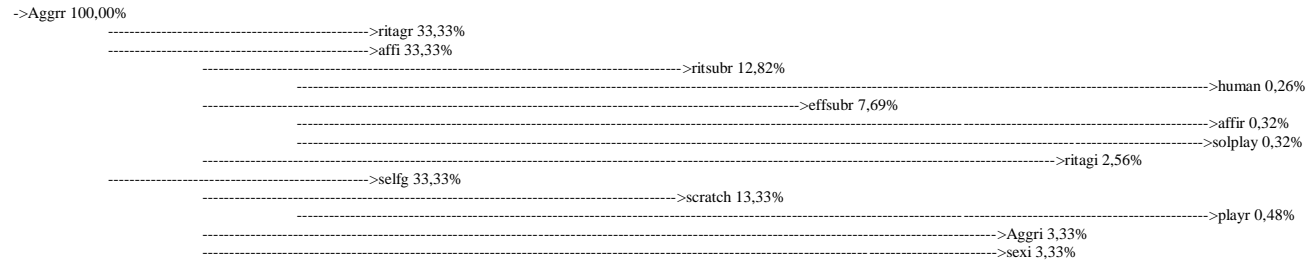
```



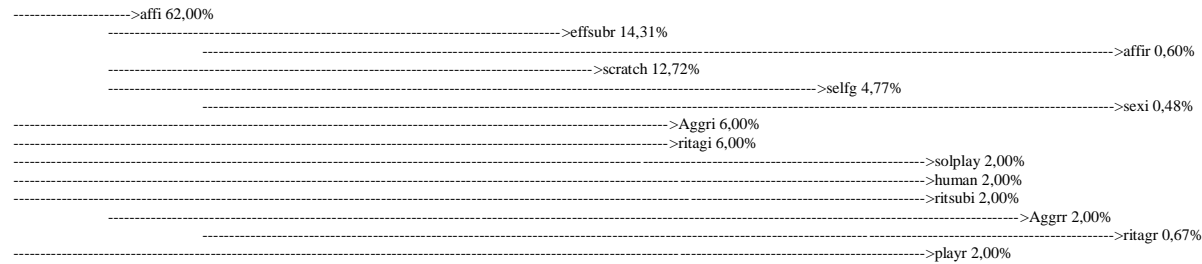
**ritagr**



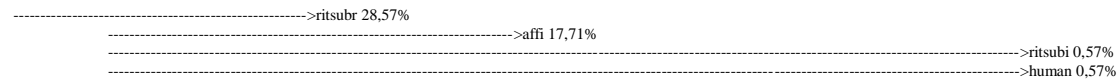
**ritsubi**



**ritsubr**



**scratch**



```

----->effsubr 21,43%
----->affir 0,89%
----->solplay 0,89%
----->Aggri 14,29%
----->ritagi 7,14%
----->selfg 3,57%
----->Aggrr 0,71%
----->sexi 3,57%
----->playr 3,57%
----->ritagr 3,57%

```

**selfg**

```

----->scratch 40,00%
----->effsubr 8,57%
----->affir 0,36%
----->ritagi 2,86%
----->playr 1,43%
----->ritsubr 20,00%
----->affi 12,40%
----->solplay 0,40%
----->human 0,40%
----->ritsubi 0,40%
----->Aggrr 20,00%
----->ritagr 6,67%
----->sexi 10,00%
----->Aggri 10,00%

```

**sexi**

```

----->scratch 50,00%
----->ritsubr 14,29%
----->affi 8,86%
----->human 0,29%
----->ritsubi 0,29%
----->effsubr 10,71%
----->solplay 0,45%
----->affir 0,45%
----->Aggri 7,14%
----->ritagi 3,57%
----->playr 1,79%
----->selfg 50,00%
----->Aggrr 10,00%
----->ritagr 3,33%

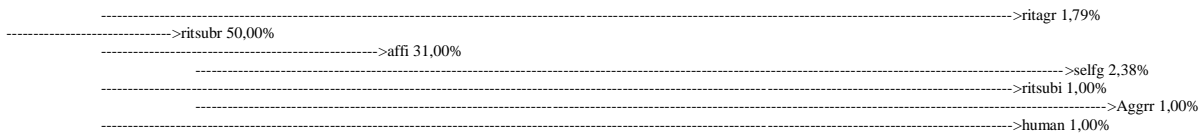
```

**solplay**

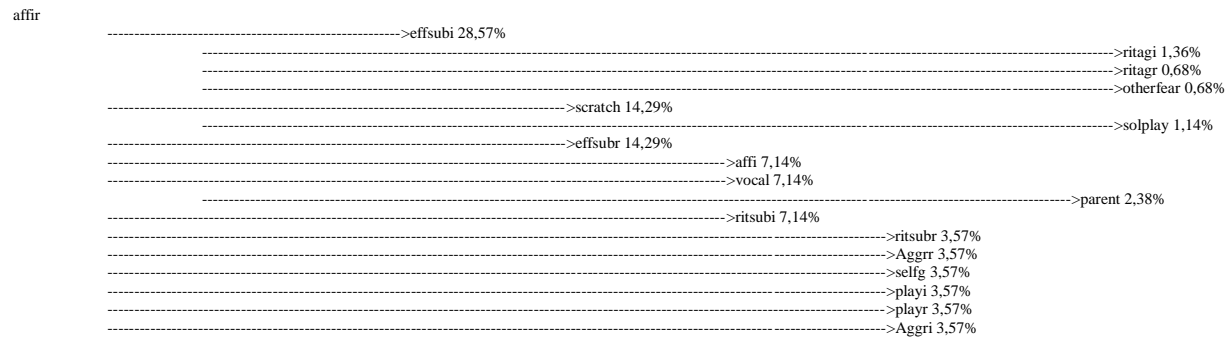
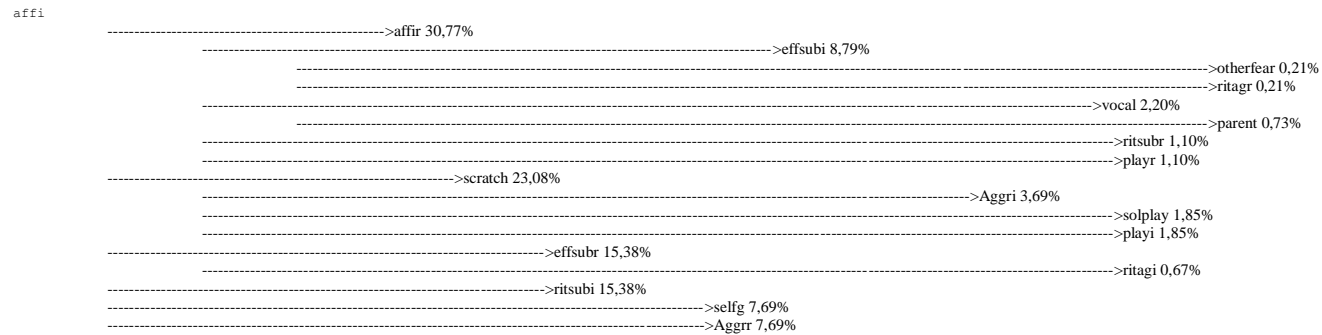
```

----->scratch 50,00%
----->effsubr 10,71%
----->affir 0,45%
----->Aggri 7,14%
----->ritagi 3,57%
----->playr 1,79%
----->sexi 1,79%

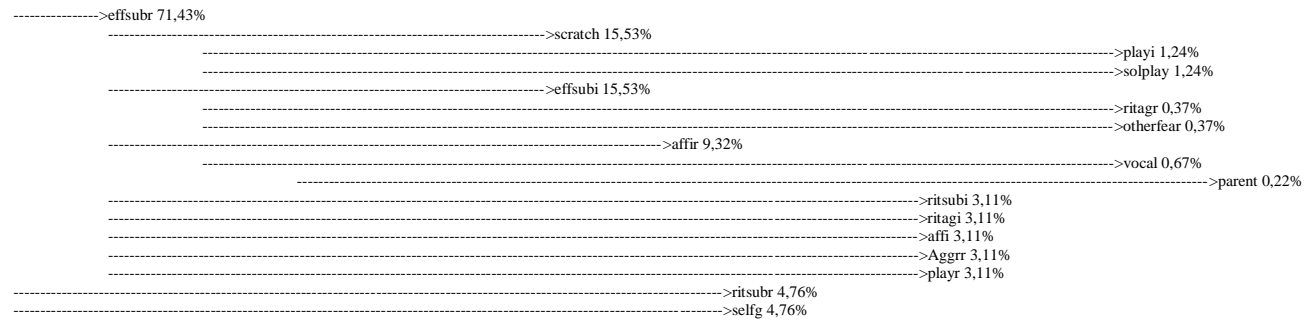
```



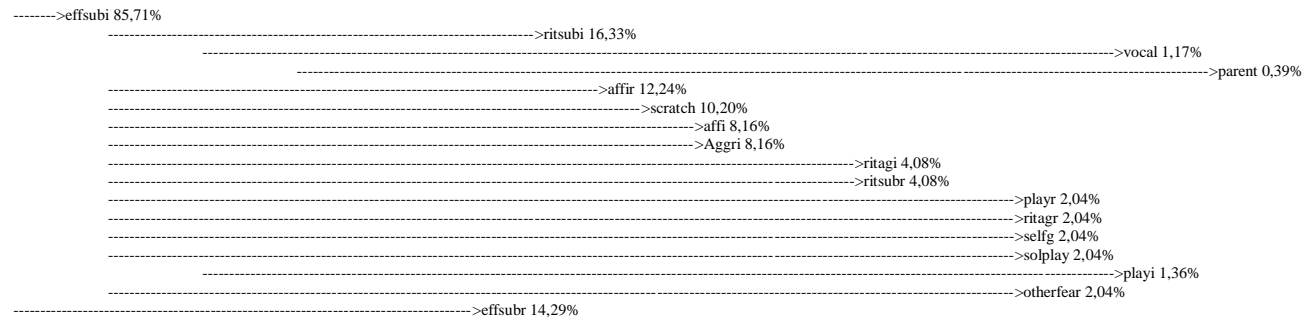
SE18. View of probability behavioral sequences of the behavioral transitions of Limbe.



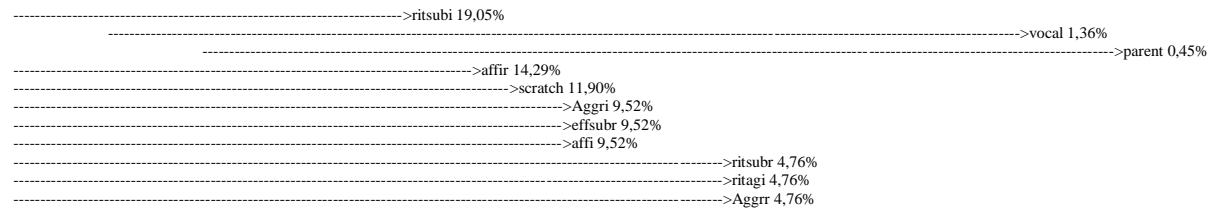
Aggri



Aggrr



effsubi



```

----->playr 2,38%
----->solplay 2,38%
----->playi 1,59%
----->otherfear 2,38%
----->selfg 2,38%
----->ritagr 2,38%

```

effsubr

```

----->Aggri 21,74%
----->ritsubr 1,04%
----->scratch 21,74%
----->solplay 1,74%
----->playi 1,74%
----->selfg 1,74%
----->effsubi 21,74%
----->ritagr 0,52%
----->otherfear 0,52%
----->affir 13,04%
----->vocal 0,93%
----->parent 0,31%
----->playr 4,35%
----->Aggrr 4,35%
----->ritsubi 4,35%
----->affi 4,35%
----->ritagi 4,35%

```

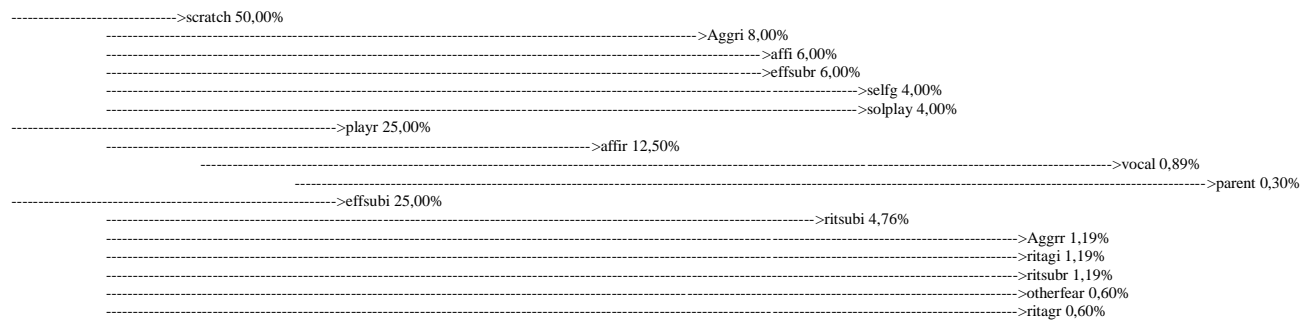
otherfear

```

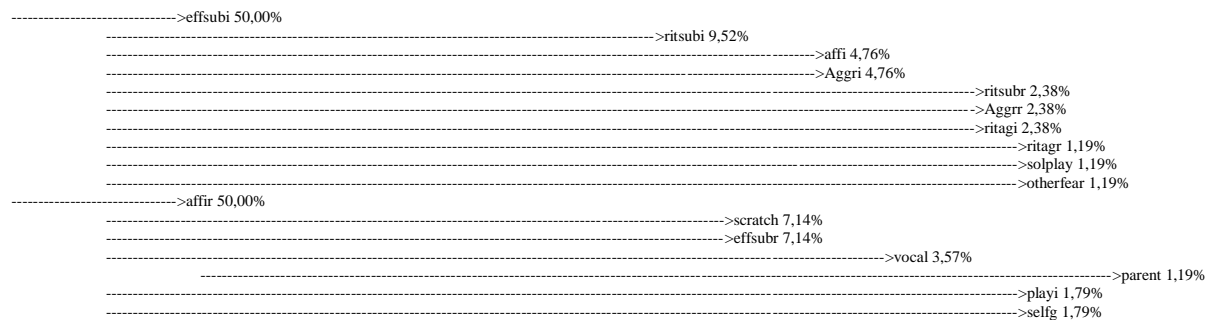
----->Aggrr 50,00%
----->effsubr 7,14%
----->effsubi 50,00%
----->ritsubi 9,52%
----->vocal 0,68%
----->parent 0,23%
----->affir 7,14%
----->scratch 5,95%
----->Aggri 4,76%
----->affi 4,76%
----->ritsubr 2,38%
----->ritagi 2,38%
----->selfg 1,19%
----->playr 1,19%
----->solplay 1,19%
----->playi 0,79%
----->ritagr 1,19%

```

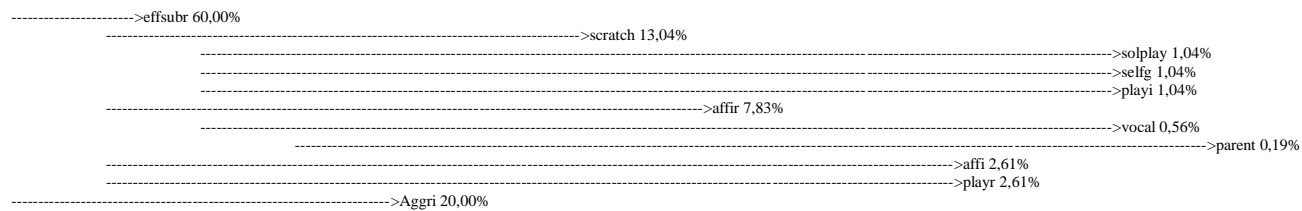
playi



playr



ritagi



```

----->ritsubr 0,95%
----->Aggrr 20,00%
----->effsubi 17,14%
----->ritsubi 3,27%
----->ritagr 0,41%
----->otherfear 0,41%

```

ritagr

```

->effsubi 100,00%
----->ritsubi 19,05%
----->vocal 1,36%
----->parent 0,45%
----->affir 14,29%
----->scratch 11,90%
----->effsubr 9,52%
----->affi 9,52%
----->Aggri 9,52%
----->Aggrr 4,76%
----->ritagi 4,76%
----->ritsubr 4,76%
----->playr 2,38%
----->otherfear 2,38%
----->solplay 2,38%
----->playi 1,59%
----->selfg 2,38%

```

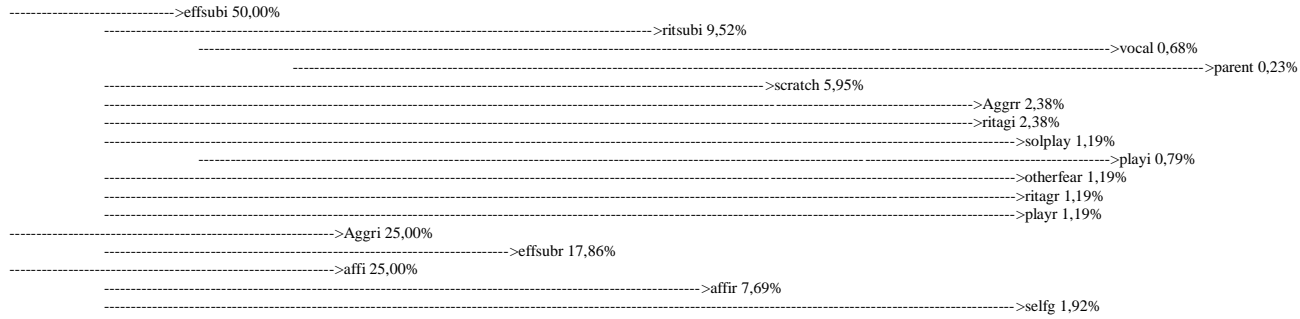
ritsubi

```

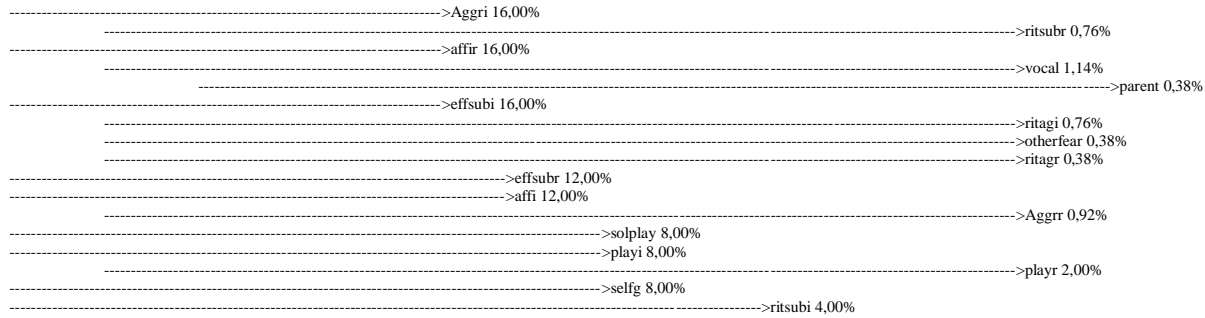
----->affir 57,14%
----->effsubi 16,33%
----->ritagi 0,78%
----->ritagr 0,39%
----->otherfear 0,39%
----->effsubr 8,16%
----->playi 2,04%
----->playr 2,04%
----->ritsubr 2,04%
----->Aggrr 2,04%
----->selfg 2,04%
----->scratch 14,29%
----->solplay 1,14%
----->affi 7,14%
----->Aggri 7,14%
----->vocal 7,14%
----->parent 2,38%

```

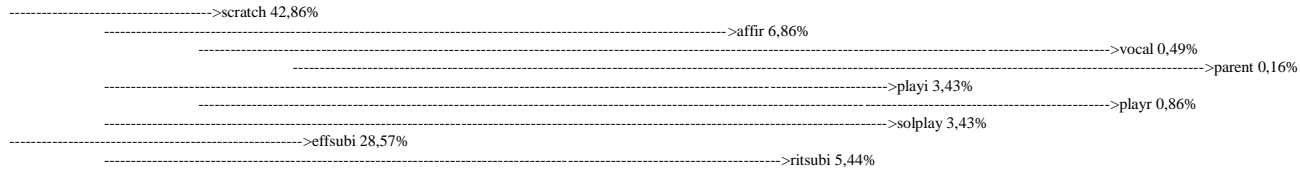
ritsubr



scratch



selfg





```

----->ritsubr 1,36%
----->ritagi 1,36%
----->Aggrr 1,36%
----->otherfear 0,68%
----->ritagr 0,68%
----->affi 14,29%
----->Aggri 14,29%
----->effsubr 10,20%

```

solplay

```

----->playi 66,67%
----->effsubi 16,67%
----->ritsubi 3,17%
----->Aggrr 0,79%
----->ritsubr 0,79%
----->ritagi 0,79%
----->otherfear 0,40%
----->ritagr 0,40%
----->playr 16,67%
----->affir 8,33%
----->vocal 0,60%

```

>parent 0,20%

```

----->scratch 33,33%
----->Aggri 5,33%
----->effsubr 4,00%
----->affi 4,00%
----->selfg 2,67%

```

vocal

```

----->parent 33,33%
----->affi 33,33%
----->scratch 7,69%
----->Aggri 1,23%
----->solplay 0,62%
----->ritsubi 5,13%
----->effsubr 5,13%
----->Aggrr 2,56%
----->selfg 2,56%
----->affir 33,33%
----->effsubi 9,52%
----->ritagi 0,45%
----->ritagr 0,23%
----->otherfear 0,23%
----->playr 1,19%

```

----->ritsubr 1,19%  
 ----->playi 1,19%

SE19. View of probability behavioral sequences of the behavioral transitions of Lisala.

**affi**

----->affir 41,94%  
 ----->effsubi 9,14%  
 ----->ritagi 0,55%  
 ----->Aggrr 1,08%  
 ----->scratch 19,35%  
 ----->selfg 1,72%  
 ----->playr 1,72%  
 ----->ritagr 0,43%  
 ----->solplay 0,43%  
 ----->effsubr 12,90%  
 ----->Aggri 1,77%  
 ----->playi 6,45%  
 ----->ritsubi 6,45%  
 ----->sexi 3,23%  
 ----->ritsubr 0,65%  
 ----->sexr 0,65%  
 ----->hairr 3,23%  
 ----->vocal 3,23%

**affir**

----->effsubi 21,79%  
 ----->ritagi 1,32%  
 ----->effsubr 16,67%  
 ----->vocal 1,32%  
 ----->affi 15,38%  
 ----->sexi 0,50%  
 ----->hairr 0,50%  
 ----->scratch 15,38%  
 ----->selfg 1,37%  
 ----->solplay 0,34%  
 ----->ritagr 0,34%  
 ----->ritsubi 10,26%  
 ----->playi 5,13%  
 ----->Aggri 3,85%  
 ----->playr 3,85%  
 ----->Aggrr 2,56%  
 ----->ritsubr 1,28%  
 ----->sexr 1,28%

**Aggri**

---->effsubr 92,86%  
----->affir 21,85%  
----->effsubi 4,76%  
----->sexr 0,28%  
----->scratch 16,39%  
----->playi 2,18%  
----->sexi 0,36%  
----->ritsubi 10,92%  
----->affi 9,10%  
----->vocal 0,29%  
----->hairr 0,29%  
----->playr 5,46%  
----->ritsubr 3,64%  
----->solplay 0,40%  
----->ritagi 1,82%  
----->ritagr 1,82%  
----->Aggrr 1,82%  
----->selfg 1,82%

**Aggrr**

----->effsubi 66,67%  
----->affir 16,16%  
----->affi 2,49%  
----->hairr 0,08%  
----->scratch 12,12%  
----->solplay 0,27%  
----->ritsubi 12,12%  
----->vocal 4,04%  
----->ritagi 4,04%  
----->ritagr 1,01%  
----->playr 4,04%  
----->sexr 2,02%  
----->sexi 0,51%  
----->playi 2,02%  
----->ritsubr 2,02%  
----->effsubr 11,11%  
----->Aggri 1,53%  
----->selfg 11,11%

**effsubi**

----->affir 24,24%  
----->effsubr 4,04%  
----->affi 3,73%  
----->hairr 0,12%  
----->Aggri 0,93%  
----->scratch 18,18%  
----->solplay 0,40%  
----->ritsubi 18,18%  
----->vocal 6,06%  
----->ritagi 6,06%  
----->ritagr 1,52%  
----->Aggrr 6,06%  
----->playr 6,06%  
----->playi 3,03%  
----->sexr 3,03%

----->sexi 0,76%  
 ----->ritsubr 3,03%  
 ----->selfg 3,03%

**effsubr**

----->affir 23,53%  
 ----->effsubi 5,13%  
 ----->sexr 0,30%  
 ----->scratch 17,65%  
 ----->playi 2,35%  
 ----->sexi 0,39%  
 ----->Aggri 13,73%  
 ----->ritsubi 11,76%  
 ----->affi 9,80%  
 ----->vocal 0,32%  
 ----->hairr 0,32%  
 ----->playr 5,88%  
 ----->ritsubr 3,92%  
 ----->solplay 0,44%  
 ----->ritagi 1,96%  
 ----->ritagr 1,96%  
 ----->Aggrr 1,96%  
 ----->selfg 1,96%

**playi**

----->affir 31,58%  
 ----->effsubi 6,88%  
 ----->ritsubi 3,24%  
 ----->affi 15,79%  
 ----->hairr 0,51%  
 ----->vocal 0,51%  
 ----->playr 10,53%  
 ----->ritagi 0,75%  
 ----->ritagr 0,75%  
 ----->scratch 10,53%  
 ----->selfg 0,94%  
 ----->effsubr 10,53%  
 ----->Aggri 1,44%  
 ----->ritsubr 5,26%  
 ----->solplay 0,58%  
 ----->Aggrr 5,26%  
 ----->sexr 5,26%  
 ----->sexi 1,32%

**playr**

----->ritsubi 21,43%  
 ----->affir 13,13%

```

----->scratch 14,29%
----->sexi 0,32%
----->solplay 0,32%
----->effsubr 14,29%
----->playi 7,14%
----->sexr 0,38%
----->Aggri 7,14%
----->selfg 7,14%
----->vocal 1,10%
----->Aggrr 0,55%
----->affi 7,14%
----->hairr 0,23%
----->ritagr 7,14%
----->ritsubr 2,38%
----->effsubi 7,14%
----->ritagi 7,14%

```

**ritagi**

```

----->effsubr 50,00%
----->affir 11,76%
----->effsubi 2,56%
----->sexr 0,15%
----->scratch 8,82%
----->playi 1,18%
----->sexi 0,20%
----->playr 2,94%
----->Aggrr 0,98%
----->ritagr 25,00%
----->Aggri 8,33%
----->ritsubi 8,33%
----->ritsubr 25,00%
----->affi 5,56%
----->hairr 0,18%
----->solplay 2,78%
----->selfg 2,78%
----->vocal 0,43%

```

**ritagr**

```

----->Aggri 33,33%
----->effsubr 30,95%
----->scratch 5,46%
----->playr 1,82%
----->Aggrr 0,61%
----->ritsubi 33,33%
----->affir 20,43%
----->effsubi 4,45%
----->sexr 0,26%
----->playi 3,23%
----->ritsubr 33,33%
----->affi 7,41%
----->sexi 0,24%
----->hairr 0,24%
----->ritagi 3,70%

```

----->solplay 3,70%  
 ----->selfg 3,70%  
 ----->vocal 0,57%

**ritsubi**

----->affir 61,29%  
 ----->effsubi 13,36%  
 ----->ritagi 0,81%  
 ----->effsubr 10,22%  
 ----->affi 9,43%  
 ----->hairr 0,30%  
 ----->sexi 0,30%  
 ----->scratch 9,43%  
 ----->ritagr 0,21%  
 ----->solplay 0,21%  
 ----->Aggri 2,36%  
 ----->playr 2,36%  
 ----->Aggrr 1,57%  
 ----->ritsubr 0,79%  
 ----->sexr 0,79%  
 ----->playi 9,68%  
 ----->selfg 9,68%  
 ----->vocal 1,49%

**ritsubr**

----->effsubr 33,33%  
 ----->scratch 5,88%  
 ----->Aggri 4,58%  
 ----->playr 1,96%  
 ----->affi 22,22%  
 ----->playi 1,43%  
 ----->sexi 0,72%  
 ----->sexr 0,14%  
 ----->hairr 0,72%  
 ----->affir 11,11%  
 ----->effsubi 2,42%  
 ----->solplay 11,11%  
 ----->ritsubi 5,56%  
 ----->selfg 11,11%  
 ----->vocal 1,71%  
 ----->Aggrr 0,85%  
 ----->ritagi 11,11%  
 ----->ritagr 2,78%

scratch

```
----->affir 31,11%
----->playi 13,33%
----->sexr 0,70%
----->playr 8,89%
----->ritagi 0,63%
----->effsubi 8,89%
----->selfg 8,89%
----->vocal 1,37%
----->effsubr 6,67%
----->affi 6,67%
----->hairr 0,22%
----->ritsubi 4,44%
----->Aggrr 2,22%
----->Aggri 2,22%
----->sexi 2,22%
----->ritagr 2,22%
----->ritsubr 0,74%
----->solplay 2,22%
```

selfg

```
----->scratch 30,77%
----->playi 4,10%
----->solplay 0,68%
----->ritagr 0,68%
----->sexi 0,68%
----->affir 23,08%
----->ritsubi 2,37%
----->sexr 0,30%
----->vocal 15,38%
----->Aggrr 7,69%
----->effsubi 5,13%
----->playr 7,69%
----->ritagi 0,55%
----->affi 7,69%
----->hairr 0,25%
----->effsubr 7,69%
----->Aggri 1,06%
----->ritsubr 0,30%
```

sexi

```
----->effsubi 20,00%
----->ritsubi 3,64%
----->vocal 1,21%
----->playr 1,21%
----->Aggrr 1,21%
----->affir 20,00%
----->ritsubr 20,00%
```

```

----->effsubr 6,67%
----->solplay 2,22%
----->selfg 2,22%
----->ritagi 2,22%
----->ritagr 0,56%
----->affi 20,00%
----->scratch 3,87%
----->hairr 0,65%
----->sexr 20,00%
----->Aggri 5,00%
----->playi 5,00%

```

**sexr**

```

----->sexi 25,00%
----->affi 5,00%
----->hairr 0,16%
----->ritsubr 5,00%
----->solplay 0,56%
----->Aggri 25,00%
----->effsubr 23,21%
----->ritagr 0,46%
----->effsubi 25,00%
----->ritsubi 4,55%
----->scratch 4,55%
----->ritagi 1,52%
----->Aggrr 1,52%
----->vocal 1,52%
----->selfg 0,76%
----->playi 25,00%
----->affir 7,89%
----->playr 2,63%

```

**solplay**

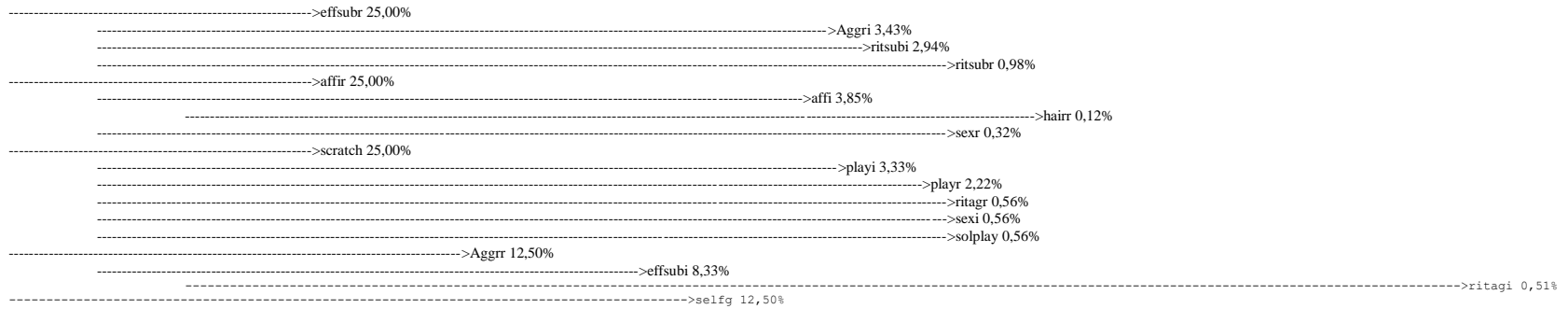
```

----->ritsubi 50,00%
----->affir 30,65%
----->effsubi 6,68%
----->ritagi 0,40%
----->playr 1,18%
----->Aggri 1,18%
----->Aggrr 0,79%
----->sexr 0,39%
----->ritsubr 0,39%
----->playi 4,84%
----->selfg 4,84%
----->affi 50,00%
----->scratch 9,68%
----->ritagr 0,22%
----->effsubr 6,45%
----->vocal 1,61%
----->hairr 1,61%
----->sexi 1,61%

```

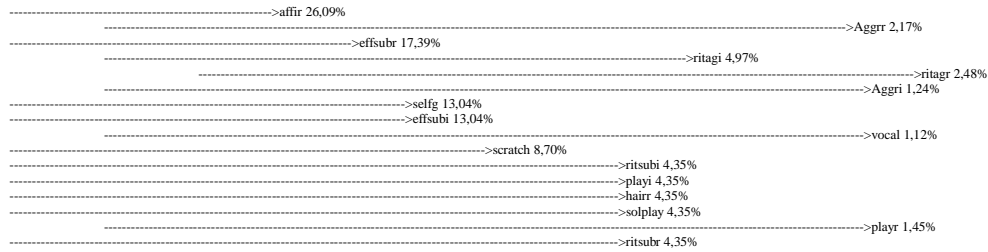


vocal



SE20. View of probability behavioral sequences of the behavioral transitions of Lolaya.

affi



affir



```

----->selfg 12,50%----->hairr 0,91%
----->Aggrr 8,33%
----->playi 8,33%
----->ritagi 1,11%
----->scratch 8,33%
----->ritsubi 8,33%
----->playr 4,17%

```

**Aggri**

```

----->effsubr 85,71%----->ritagi 24,49%
----->ritagr 12,24%----->effsubi 5,25%
----->scratch 12,24%
----->affi 12,24%
----->selfg 1,60%
----->solplay 0,53%
----->hairr 0,53%
----->playi 6,12%
----->affir 6,12%
----->ritsubr 6,12%
----->ritsubi 14,29%
----->vocal 0,79%
----->Aggrr 0,79%
----->playr 0,79%

```

**Aggrr**

```

->effsubi 100,00%
----->scratch 14,29%
----->affi 14,29%
----->hairr 0,62%
----->ritsubr 0,62%
----->ritsubi 14,29%
----->affir 8,57%
----->vocal 8,57%
----->playi 8,57%
----->Aggri 5,71%
----->effsubr 4,90%
----->ritagi 1,40%
----->playr 2,86%
----->solplay 2,86%
----->ritagr 2,86%
----->selfg 2,86%

```

**effsubi**

```

----->scratch 14,29%
----->affi 14,29%
----->ritsubr 0,62%
----->hairr 0,62%
----->ritsubi 14,29%
----->Aggrr 11,43%
----->playi 8,57%
----->affir 8,57%
----->vocal 8,57%
----->Aggri 5,71%
----->effsubr 4,90%

```

```

----->ritagi 1,40%
----->ritagr 2,86%
----->selfg 2,86%
----->playr 2,86%
----->solplay 2,86%

```

**effsubr**

```

----->ritagi 28,57%
----->ritagr 14,29%
----->effsubi 6,12%
----->affi 14,29%
----->selfg 1,86%
----->solplay 0,62%
----->hairr 0,62%
----->scratch 14,29%
----->Aggrr 0,89%
----->vocal 0,89%
----->playi 7,14%
----->ritsubi 7,14%
----->playr 0,40%
----->affir 7,14%
----->ritsubr 7,14%
----->Aggri 7,14%

```

**hairr**

```

->affi 100,00%
----->affir 26,09%
----->Aggrr 2,17%
----->effsubr 17,39%
----->ritagi 4,97%
----->ritagr 2,48%
----->Aggri 1,24%
----->selfg 13,04%
----->effsubi 13,04%
----->vocal 1,12%
----->scratch 8,70%
----->ritsubi 4,35%
----->playi 4,35%
----->solplay 4,35%
----->playr 1,45%
----->ritsubr 4,35%

```

**playi**

```

----->affir 20,00%
----->playr 0,83%
----->affi 20,00%
----->selfg 2,61%
----->hairr 0,87%
----->solplay 0,87%
----->effsubr 13,33%
----->ritsubr 0,95%
----->effsubi 13,33%
----->scratch 1,90%

```

```

----->vocal 1,14%
----->ritagi 13,33%
----->ritagr 6,67%
----->Aggri 1,90%
----->ritsubi 13,33%
----->Aggrr 6,67%

```

**playr**

```

----->effsubi 33,33%
----->scratch 4,76%
----->Aggrr 3,81%
----->vocal 2,86%
----->Aggri 1,90%
----->solplay 0,95%
----->ritsubi 33,33%
----->affir 12,96%
----->selfg 1,85%
----->playi 33,33%
----->affi 6,67%
----->hairr 0,29%
----->effsubr 4,44%
----->ritsubr 0,32%
----->ritagi 4,44%
----->ritagr 2,22%

```

**ritagi**

```

----->effsubr 50,00%
----->scratch 7,14%
----->affi 7,14%
----->selfg 0,93%
----->hairr 0,31%
----->ritsubr 3,57%
----->playi 3,57%
----->ritagr 50,00%
----->effsubi 21,43%
----->Aggrr 2,45%
----->vocal 1,84%
----->solplay 0,61%
----->Aggri 14,29%
----->ritsubi 14,29%
----->affir 5,56%
----->playr 0,79%

```

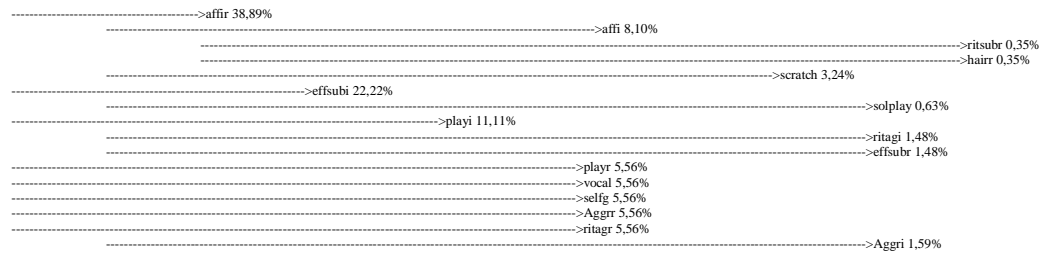
**ritagr**

```

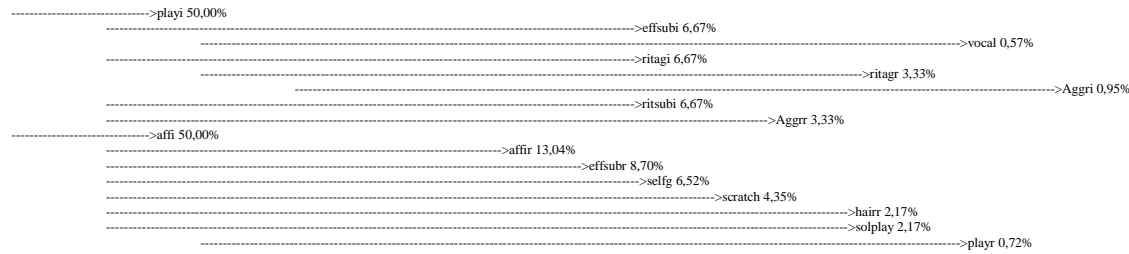
----->effsubi 42,86%
----->affi 6,12%
----->hairr 0,27%
----->scratch 6,12%
----->Aggrr 4,90%
----->playi 3,67%
----->vocal 3,67%
----->solplay 1,22%
----->Aggri 28,57%
----->effsubr 24,49%
----->ritagi 7,00%
----->ritsubr 1,75%
----->ritsubi 28,57%
----->affir 11,11%
----->playr 1,59%
----->selfg 1,59%

```

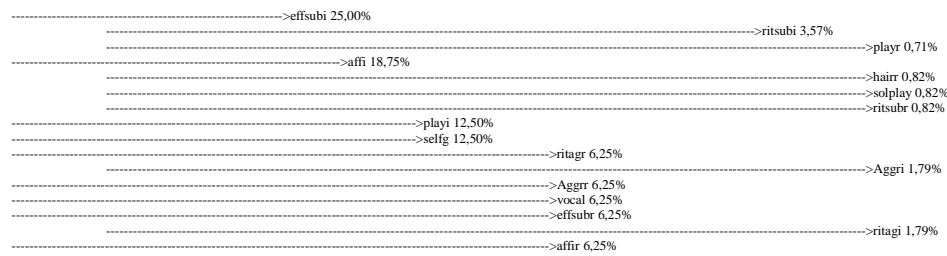
**ritsubi**



**ritsubr**



**scratch**



**selfg**



```

----->ritagi 2,48%
----->ritagr 1,24%
----->hairr 2,17%
----->ritsubr 2,17%
----->solplay 2,17%
----->effsubi 37,50%
----->ritsubi 5,36%
----->scratch 5,36%
----->Aggrr 4,29%
----->playi 3,21%
----->vocal 3,21%
----->Aggri 2,14%
----->playr 1,07%

```

**solplay**

```

----->playi 33,33%
----->affi 6,67%
----->hairr 0,29%
----->affir 6,67%
----->effsubr 4,44%
----->ritsubr 0,32%
----->ritagi 4,44%
----->ritagr 2,22%
----->Aggrr 2,22%
----->scratch 33,33%
----->selfg 4,17%
----->vocal 2,08%
----->playr 33,33%
----->ritsubi 11,11%
----->effsubi 11,11%
----->Aggri 0,63%

```

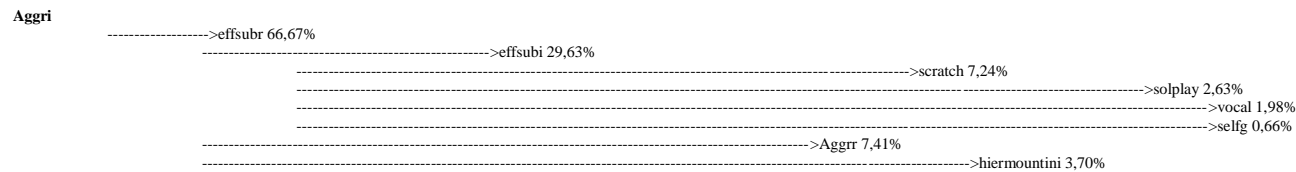
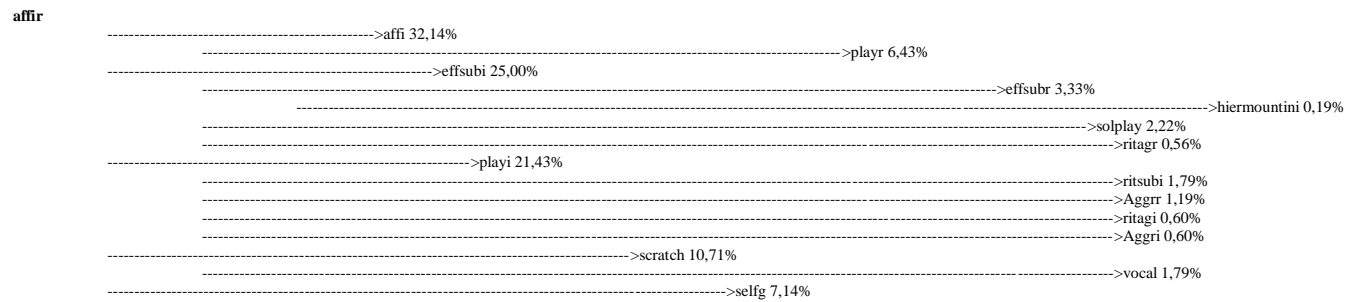
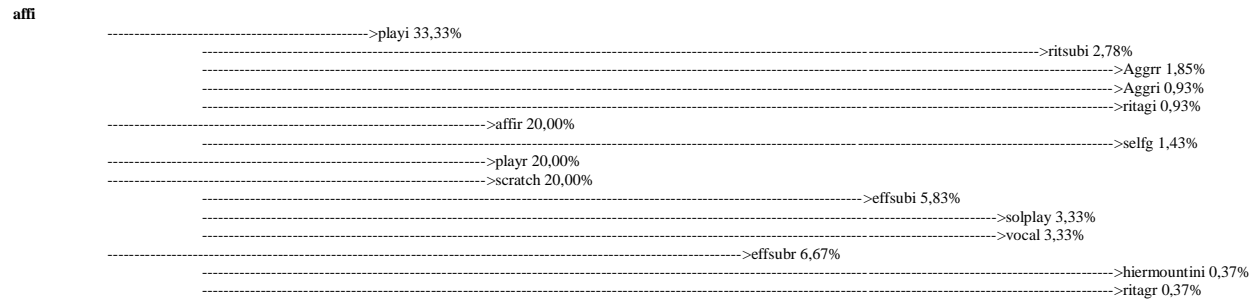
**vocal**

```

----->scratch 33,33%
----->selfg 4,17%
----->playi 4,17%
----->ritagr 2,08%
----->effsubr 2,08%
----->ritagi 0,60%
----->affir 33,33%
----->affi 6,94%
----->ritsubr 0,30%
----->hairr 0,30%
----->playr 1,39%
----->effsubi 33,33%
----->ritsubi 4,76%
----->Aggrr 3,81%
----->Aggri 1,90%
----->solplay 0,95%

```

SE21. View of probability behavioral sequences of the behavioral transitions of Lwiro.



```

----->ritagr 3,70%
----->ritagi 1,85%
----->playi 33,33%
----->affir 8,33%
----->affi 2,68%
----->playr 4,63%
----->ritsubi 2,78%

```

**Aggrr**

```

->effsubi 100,00%
----->scratch 24,44%
----->playr 13,33%
----->effsubr 13,33%
----->hiermountini 0,74%
----->playi 11,11%
----->solplay 8,89%
----->vocal 6,67%
----->affi 4,44%
----->affir 4,44%
----->ritsubi 4,44%
----->Aggri 2,22%
----->ritagr 2,22%
----->ritagi 1,11%
----->selfg 2,22%

```

**effsubi**

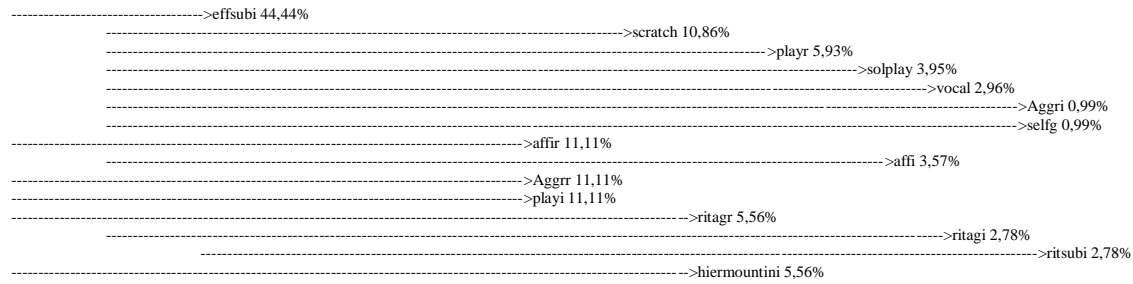
```

----->scratch 24,44%
----->playr 13,33%
----->effsubr 13,33%
----->hiermountini 0,74%
----->playi 11,11%
----->solplay 8,89%
----->vocal 6,67%
----->affi 4,44%
----->affir 4,44%
----->ritsubi 4,44%
----->ritagr 2,22%
----->ritagi 1,11%
----->selfg 2,22%
----->Aggri 2,22%
----->Aggrr 2,22%

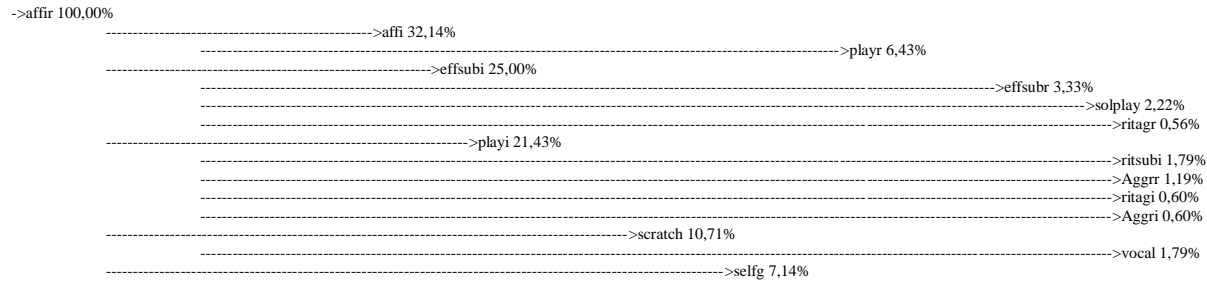
```



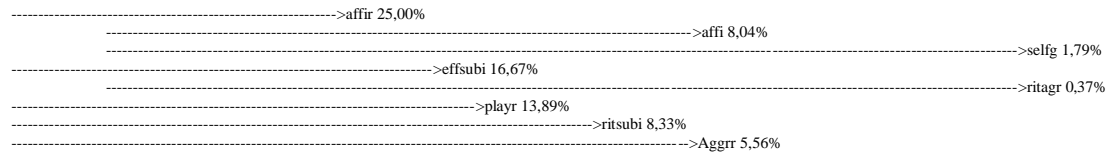
**effsubr**



**hiermountini**



**playi**



```

----->solplay 5,56%
----->effsubr 5,56%
----->hiermountini 0,31%
----->scratch 5,56%
----->Aggri 2,78%
----->vocal 2,78%
----->ritagi 2,78%

```

**playr**

```

----->playi 27,78%
----->ritsubi 2,31%
----->Aggrr 1,54%
----->ritagi 0,77%
----->Aggri 0,77%
----->affir 27,78%
----->affi 8,93%
----->effsubi 22,22%
----->effsubr 2,96%
----->hiermountini 0,16%
----->ritagr 0,49%
----->scratch 11,11%
----->vocal 1,85%
----->selfg 5,56%
----->solplay 5,56%

```

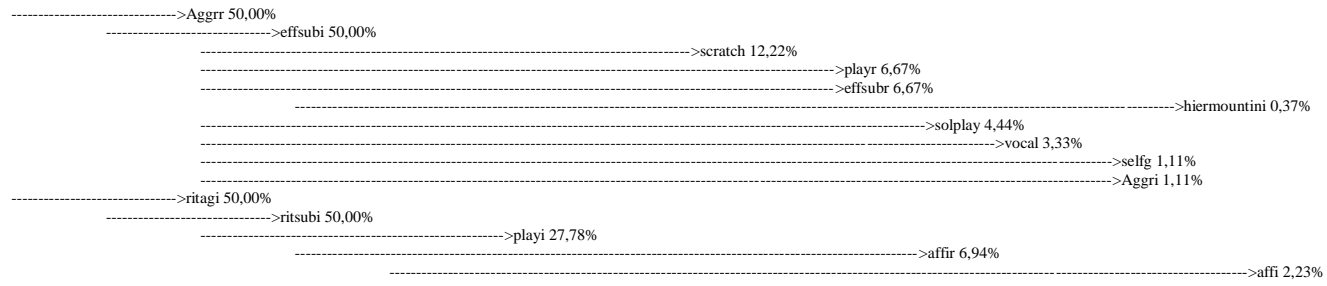
**ritagi**

```

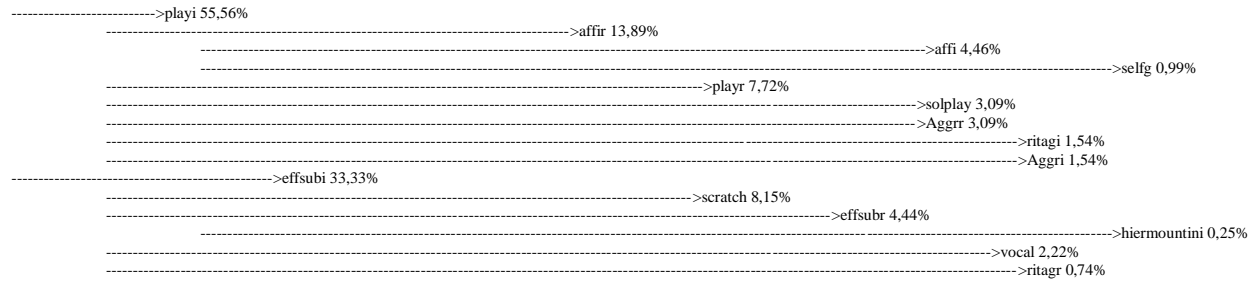
->ritsubi 100,00%
----->playi 55,56%
----->affir 13,89%
----->affi 4,46%
----->selfg 0,99%
----->playr 7,72%
----->solplay 3,09%
----->Aggrr 3,09%
----->Aggri 1,54%
----->effsubi 33,33%
----->scratch 8,15%
----->effsubr 4,44%
----->hiermountini 0,25%
----->vocal 2,22%
----->ritagr 0,74%

```

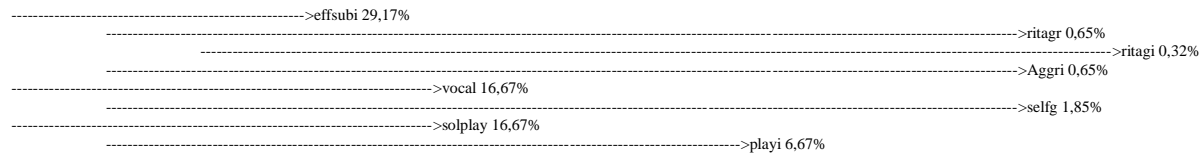
**ritagr**



**ritsubi**



**scratch**



----->affir 8,33%  
 ----->effsubr 8,33%  
 ----->hiermountini 0,46%  
 ----->playr 4,17%  
 ----->affi 4,17%  
 ----->ritsubi 4,17%  
 ----->Aggrr 4,17%

**selfg**

----->playr 40,00%  
 ----->scratch 4,44%  
 ----->vocal 0,74%  
 ----->solplay 2,22%  
 ----->affir 20,00%  
 ----->affi 6,43%  
 ----->effsubr 20,00%  
 ----->effsubi 8,89%  
 ----->Aggrr 2,22%  
 ----->hiermountini 1,11%  
 ----->ritagr 1,11%  
 ----->ritagi 0,56%  
 ----->playi 20,00%  
 ----->ritsubi 1,67%  
 ----->Aggri 0,56%

**solplay**

----->playi 40,00%  
 ----->effsubi 6,67%  
 ----->ritagr 0,15%  
 ----->playr 5,56%  
 ----->effsubr 2,22%  
 ----->hiermountini 0,12%  
 ----->Aggri 1,11%  
 ----->ritagi 1,11%  
 ----->scratch 20,00%  
 ----->affir 13,33%  
 ----->selfg 0,95%  
 ----->Aggrr 6,67%  
 ----->affi 6,67%  
 ----->vocal 6,67%  
 ----->ritsubi 6,67%

**vocal**

----->Aggrr 22,22%  
 ----->effsubi 22,22%  
 ----->playi 22,22%  
 ----->ritsubi 1,85%  
 ----->Aggri 0,62%  
 ----->ritagi 0,62%  
 ----->scratch 22,22%  
 ----->solplay 3,70%  
 ----->affir 11,11%  
 ----->affi 3,57%

```

----->selfg 11,11%
----->playr 4,44%
----->effsubr 11,11%
----->ritagr 0,62%
----->hiermountini 0,62%

```

SE22. View of probability behavioral sequences of the behavioral transitions of Mapendo.

**affi**

```

----->affir 42,86%
----->effsubi 17,14%
----->ritsubr 0,86%
----->sexi 0,86%
----->Aggri 0,86%
----->Aggrr 4,29%
----->playr 4,29%
----->effsubr 4,29%
----->vocal 0,61%
----->ritagr 0,61%
----->playi 4,29%
----->ritsubi 28,57%
----->selfg 5,71%
----->scratch 14,29%
----->ritagi 1,06%
----->solplay 0,53%

```

**affir**

```

----->effsubi 40,00%
----->scratch 12,00%
----->solplay 0,44%
----->ritsubi 8,00%
----->selfg 4,00%
----->ritsubr 2,00%
----->sexi 2,00%
----->ritagi 2,00%
----->Aggri 2,00%
----->playi 10,00%
----->Aggrr 10,00%
----->effsubr 10,00%
----->ritagr 1,43%
----->vocal 1,43%
----->affi 10,00%
----->playr 10,00%

```

**Aggri**

```
----->effsubr 50,00%
----->Aggrr 7,14%
----->affi 7,14%
----->vocal 7,14%
----->affir 7,14%
----->effsubi 7,14%
----->ritagr 7,14%
----->scratch 25,00%
----->ritsubi 6,48%
----->playr 1,85%
----->ritagi 1,85%
----->sexi 0,62%
----->solplay 0,93%
----->selfg 25,00%
----->playi 2,08%
----->ritsubr 0,42%
```

**Aggrr**

```
----->effsubi 75,00%
----->scratch 22,50%
----->playr 1,67%
----->solplay 0,83%
----->ritsubi 15,00%
----->affir 5,00%
----->affi 7,50%
----->selfg 7,50%
----->ritagi 3,75%
----->playi 3,75%
----->Aggri 3,75%
----->ritsubr 3,75%
----->sexi 3,75%
----->effsubr 25,00%
----->vocal 3,57%
----->ritagr 3,57%
```

**effsubi**

```
----->scratch 30,00%
----->playr 2,22%
----->vocal 1,11%
----->solplay 1,11%
----->ritsubi 20,00%
----->affir 6,67%
----->affi 10,00%
----->selfg 10,00%
----->effsubr 5,00%
----->ritagr 0,71%
----->playi 5,00%
----->Aggrr 5,00%
----->ritsubr 5,00%
```

```

----->sexi 5,00%
----->ritagi 5,00%
----->Aggri 5,00%

```

**effsubr**

```

----->effsubi 14,29%
----->Aggri 0,71%
----->ritsubr 0,71%
----->sexi 0,71%
----->affir 14,29%
----->playi 1,43%
----->playr 1,43%
----->scratch 14,29%
----->selfg 2,12%
----->ritagi 1,06%
----->solplay 0,53%
----->affi 14,29%
----->ritsubi 4,08%
----->ritagr 14,29%
----->vocal 14,29%
----->Aggrr 14,29%

```

**otherfear**

```

->Aggri 100,00%
----->effsubr 50,00%
----->vocal 7,14%
----->affi 7,14%
----->Aggrr 7,14%
----->effsubi 7,14%
----->ritagr 7,14%
----->affir 7,14%
----->scratch 25,00%
----->ritsubi 6,48%
----->playr 1,85%
----->ritagi 1,85%
----->sexi 0,62%
----->solplay 0,93%
----->selfg 25,00%
----->playi 2,08%
----->ritsubr 0,42%

```

**playi**

----->scratch 20,00%  
----->ritagi 1,48%  
----->playr 1,48%  
----->solplay 0,74%  
----->ritsubr 20,00%  
----->sexi 20,00%  
----->ritsubi 20,00%  
----->affir 6,67%  
----->selfg 4,00%  
----->effsubr 20,00%  
----->vocal 2,86%  
----->affi 2,86%  
----->Aggrr 2,86%  
----->ritagr 2,86%  
----->effsubi 20,00%  
----->Aggri 1,00%

**playr**

----->effsubi 33,33%  
----->affi 3,33%  
----->Aggrr 1,67%  
----->effsubr 1,67%  
----->ritagr 0,24%  
----->Aggri 1,67%  
----->playi 1,67%  
----->ritsubr 1,67%  
----->sexi 1,67%  
----->ritsubi 33,33%  
----->affir 11,11%  
----->selfg 6,67%  
----->scratch 33,33%  
----->ritagi 2,47%  
----->solplay 1,23%  
----->vocal 1,23%

**ritagi**

----->selfg 33,33%  
----->scratch 19,44%  
----->ritsubi 5,04%  
----->effsubi 5,04%  
----->Aggri 0,25%  
----->playr 1,44%  
----->solplay 0,72%  
----->sexi 33,33%  
----->playi 16,67%  
----->ritsubr 3,33%  
----->effsubr 33,33%  
----->vocal 4,76%



```

----->affi 4,76%
----->Aggrr 4,76%
----->affir 4,76%
----->ritagr 4,76%

```

**ritagr**

```

->effsubi 100,00%
----->scratch 30,00%
----->playr 2,22%
----->vocal 1,11%
----->solplay 1,11%
----->ritsubi 20,00%
----->affir 6,67%
----->selfg 10,00%
----->affi 10,00%
----->playi 5,00%
----->effsubr 5,00%
----->Aggri 5,00%
----->Aggrr 5,00%
----->ritagi 5,00%
----->ritsubr 5,00%
----->sexi 5,00%

```

**ritsubi**

```

----->affir 33,33%
----->effsubr 3,33%
----->ritagr 0,48%
----->playi 3,33%
----->Aggrr 3,33%
----->playr 3,33%
----->scratch 20,00%
----->ritagi 1,48%
----->solplay 0,74%
----->vocal 0,74%
----->effsubi 20,00%
----->Aggri 1,00%
----->ritsubr 1,00%
----->sexi 1,00%
----->selfg 20,00%
----->affi 6,67%

```

**ritsubr**

```
->sexi 100,00%
----->playi 50,00%
----->effsubr 10,00%
----->Aggrr 1,43%
----->ritagr 1,43%
----->scratch 50,00%
----->ritsubi 12,96%
----->affir 4,32%
----->effsubi 12,96%
----->Aggri 0,65%
----->selfg 7,41%
----->playr 3,70%
----->ritagi 3,70%
----->solplay 1,85%
----->affi 1,85%
----->vocal 1,85%
```

**scratch**

```
----->effsubi 25,93%
----->Aggri 1,30%
----->ritsubr 1,30%
----->Aggrr 1,30%
----->ritsubi 25,93%
----->affir 8,64%
----->selfg 14,81%
----->playr 7,41%
----->ritagi 7,41%
----->sexi 2,47%
----->effsubr 2,47%
----->ritagr 0,35%
----->affi 3,70%
----->solplay 3,70%
----->playi 3,70%
----->vocal 3,70%
```

**selfg**

```
----->scratch 58,33%
----->ritsubi 15,12%
----->effsubi 15,12%
----->Aggri 0,76%
----->ritagi 4,32%
----->playr 4,32%
----->vocal 2,16%
```

```

----->solplay 2,16%
----->affi 8,33%
----->playi 8,33%
----->ritsubr 1,67%
----->sexi 1,67%
----->affir 8,33%
----->effsubr 8,33%
----->ritagr 1,19%
----->Aggrr 1,19%

```

**sexi**

```

----->scratch 50,00%
----->ritsubi 12,96%
----->affir 4,32%
----->effsubi 12,96%
----->Aggri 0,65%
----->selfg 7,41%
----->ritagi 3,70%
----->playr 3,70%
----->affi 1,85%
----->solplay 1,85%
----->vocal 1,85%
----->playi 50,00%
----->effsubr 10,00%
----->ritagr 1,43%
----->Aggrr 1,43%
----->ritsubr 10,00%

```

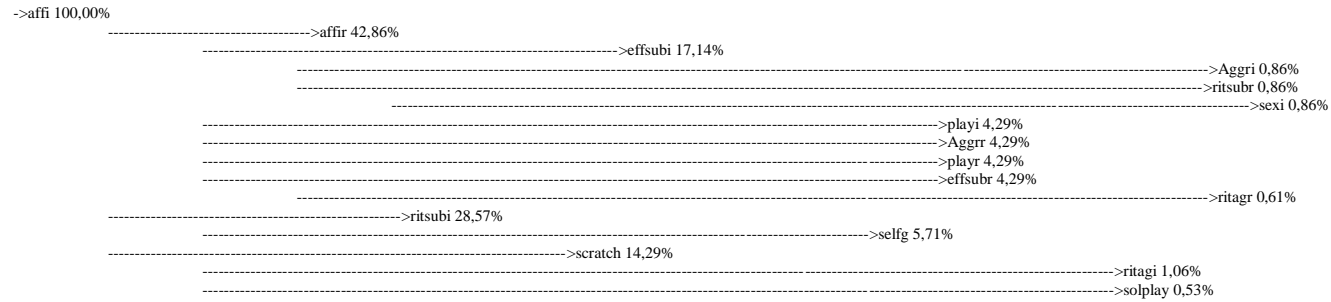
**solplay**

```

->affi 100,00%
----->affir 42,86%
----->effsubi 17,14%
----->Aggri 0,86%
----->ritsubr 0,86%
----->sexi 0,86%
----->playi 4,29%
----->Aggrr 4,29%
----->playr 4,29%
----->effsubr 4,29%
----->ritagr 0,61%
----->vocal 0,61%
----->ritsubi 28,57%
----->selfg 5,71%
----->scratch 14,29%
----->ritagi 1,06%

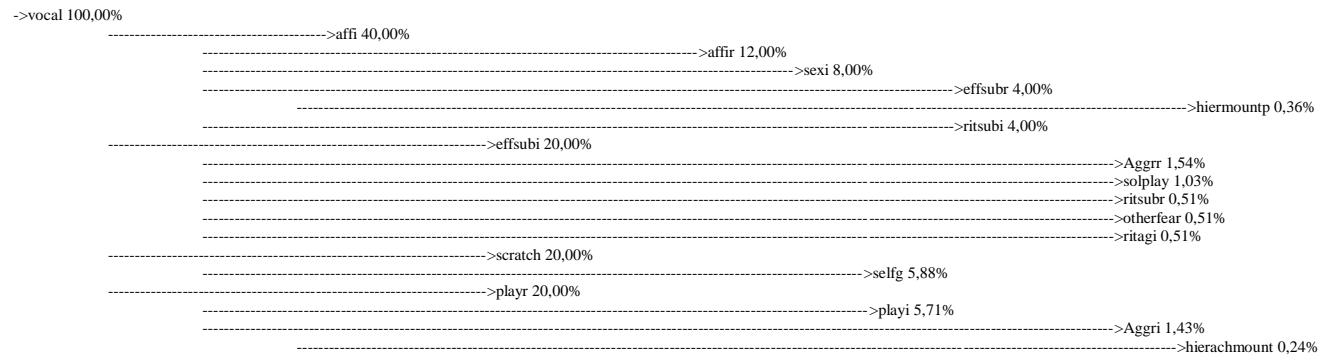
```

vocal



### SE23. View of probability behavioral sequences of the behavioral transitions of Martin.

abnorm



**affi**

```

----->affir 30,00%
----->playi 4,62%
----->playr 2,31%
----->sexi 20,00%
----->scratch 20,00%
----->vocal 1,18%
----->effsubi 10,00%
----->Aggrr 0,77%
----->solplay 0,51%
----->ritagi 0,26%
----->otherfear 0,26%
----->ritsubr 0,26%
----->abnorm 0,26%
----->ritsubi 10,00%
----->effsubr 10,00%
----->hiermountp 0,91%
----->Aggri 0,91%
----->hierachmount 0,15%
----->selfg 10,00%
```

**affir**

```

----->scratch 30,77%
----->vocal 1,81%
----->Aggri 0,90%
----->hierachmount 0,15%
----->selfg 15,38%
----->effsubi 15,38%
----->Aggrr 1,18%
----->solplay 0,79%
----->abnorm 0,39%
----->otherfear 0,39%
----->ritsubr 0,39%
----->ritagi 0,39%
----->playi 15,38%
----->ritsubi 1,28%
----->playr 7,69%
----->affi 7,69%
----->sexi 1,54%
----->effsubr 7,69%
----->hiermountp 0,70%
```

**Aggri**

```

----->Aggrr 33,33%
----->effsubi 33,33%
----->scratch 8,55%
----->affir 3,42%
----->ritsubi 2,56%
----->solplay 1,71%
----->vocal 1,71%
----->ritsubr 0,85%
----->ritagi 0,85%
```

```

----->otherfear 0,85%
----->abnorm 0,85%
----->effsubr 33,33%
----->affi 6,06%
----->hiermountp 3,03%
----->selfg 3,03%
----->hierachmount 16,67%
----->playi 16,67%
----->playr 5,56%
----->sexi 1,39%

```

**Aggrr**

```

->effsubi 100,00%
----->scratch 25,64%
----->playi 2,26%
----->affir 10,26%
----->selfg 7,69%
----->ritsubi 7,69%
----->effsubr 7,69%
----->hiermountp 0,70%
----->playr 7,69%
----->sexi 0,55%
----->vocal 5,13%
----->solplay 5,13%
----->abnorm 2,56%
----->ritagi 2,56%
----->affi 2,56%
----->Aggri 2,56%
----->hierachmount 0,43%
----->otherfear 2,56%
----->ritsubr 2,56%

```

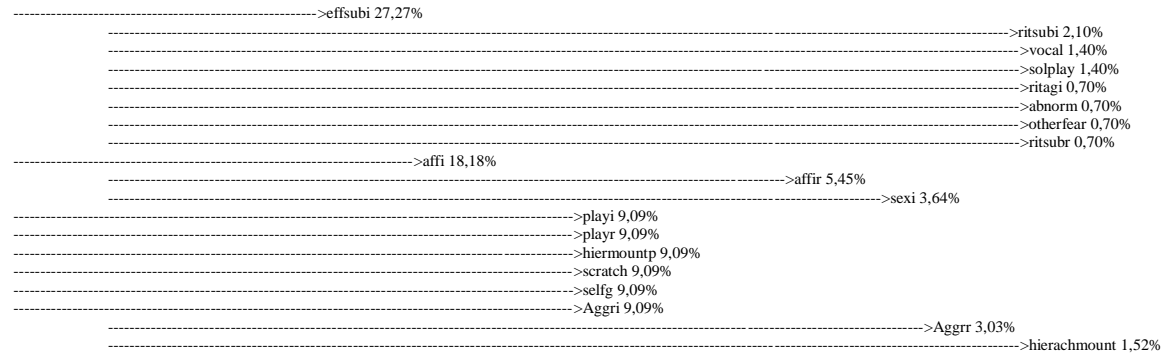
**effsubi**

```

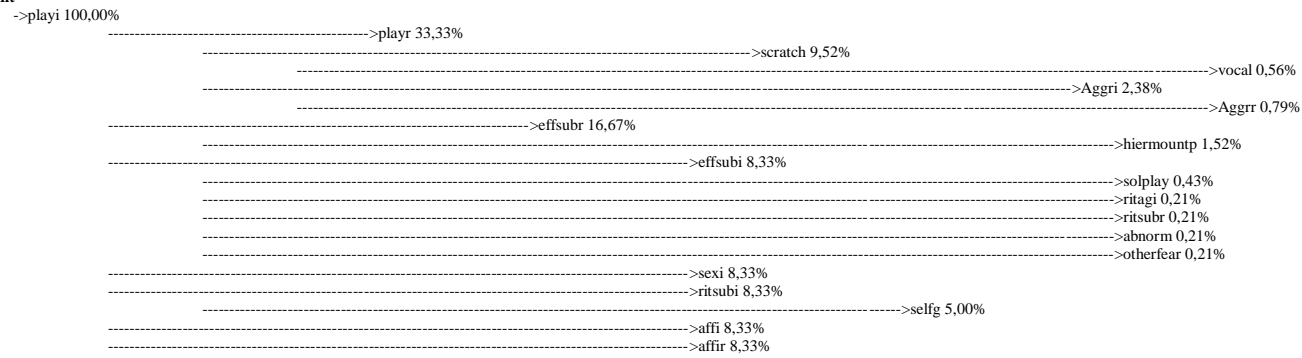
----->scratch 25,64%
----->playi 2,26%
----->affir 10,26%
----->effsubr 7,69%
----->hiermountp 0,70%
----->ritsubi 7,69%
----->Aggrr 7,69%
----->selfg 7,69%
----->playr 7,69%
----->sexi 0,55%
----->vocal 5,13%
----->solplay 5,13%
----->Aggri 2,56%
----->hierachmount 0,43%
----->abnorm 2,56%
----->otherfear 2,56%
----->affi 2,56%
----->ritagi 2,56%
----->ritsubr 2,56%

```

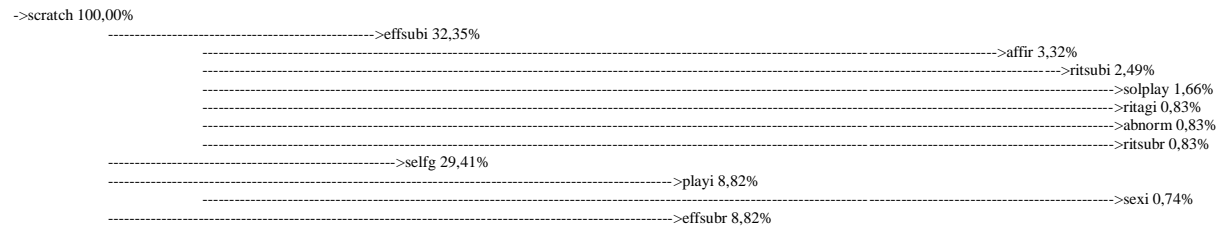
**effsubr**



**hierachmount**



**otherfear**



```

----->hiermountp 0,80%
----->vocal 5,88%
----->playr 5,88%
----->Aggrr 2,94%
----->affi 2,94%
----->Aggri 2,94%
----->hierachmount 0,49%

```

playi

```

----->playr 33,33%
----->scratch 9,52%
----->vocal 0,56%
----->Aggri 2,38%
----->Aggrr 0,79%
----->hierachmount 0,40%
----->effsubr 16,67%
----->hiermountp 1,52%
----->affi 8,33%
----->effsubi 8,33%
----->solplay 0,43%
----->otherfear 0,21%
----->abnorm 0,21%
----->ritagi 0,21%
----->ritsubr 0,21%
----->affir 8,33%
----->ritsubi 8,33%
----->selfg 5,00%
----->sexi 8,33%

```

playr

```

----->scratch 28,57%
----->effsubi 9,24%
----->solplay 0,47%
----->otherfear 0,24%
----->abnorm 0,24%
----->ritagi 0,24%
----->ritsubr 0,24%
----->selfg 8,40%
----->vocal 1,68%
----->playi 28,57%
----->effsubr 4,76%
----->hiermountp 0,43%
----->ritsubi 2,38%
----->affi 2,38%
----->affir 21,43%
----->Aggri 7,14%
----->Aggrr 2,38%
----->hierachmount 1,19%
----->sexi 7,14%

```



**ritagi**

```
->scratch 100,00%
----->effsubi 32,35%
----->affir 3,32%
----->ritsubi 2,49%
----->solplay 1,66%
----->otherfear 0,83%
----->abnorm 0,83%
----->ritsubr 0,83%
----->selfg 29,41%
----->playi 8,82%
----->sexi 0,74%
----->effsubr 8,82%
----->hiermountp 0,80%
----->vocal 5,88%
----->playr 5,88%
----->Aggrr 2,94%
----->affi 2,94%
----->Aggri 2,94%
----->hierachmount 0,49%
```

**ritagr**

```
->ritsubi 100,00%
----->selfg 60,00%
----->scratch 26,67%
----->playr 1,57%
----->Aggri 0,78%
----->hierachmount 0,13%
----->vocal 3,33%
----->effsubr 3,33%
----->hiermountp 0,30%
----->affi 3,33%
----->sexi 0,67%
----->affir 20,00%
----->playi 3,08%
----->effsubi 20,00%
----->Aggrr 1,54%
----->solplay 1,03%
----->abnorm 0,51%
----->otherfear 0,51%
----->ritsubr 0,51%
----->ritagi 0,51%
```

**ritsubi**

```
----->selfg 60,00%
----->scratch 26,67%
----->playr 1,57%
----->Aggri 0,78%
----->hierachmount 0,13%
----->affi 3,33%
----->sexi 0,67%
```

```

----->vocal 3,33%
----->effsubr 3,33%----->hiermountp 0,30%
----->effsubi 20,00%
----->Aggrr 1,54%
----->solplay 1,03%
----->abnorm 0,51%
----->ritagi 0,51%
----->otherfear 0,51%
----->ritsubr 0,51%
----->affir 20,00%
----->playi 3,08%

```

**ritsubr**

```

->Aggri 100,00%
----->effsubr 33,33%
----->affi 6,06%----->hiermountp 3,03%
----->selfg 3,03%
----->Aggrr 33,33%
----->effsubi 33,33%
----->scratch 8,55%----->affir 3,42%
----->ritsubi 2,56%
----->solplay 1,71%
----->vocal 1,71%
----->abnorm 0,85%
----->ritagi 0,85%
----->otherfear 0,85%
----->hierachmount 16,67%
----->playi 16,67%
----->playr 5,56%----->sexi 1,39%

```

**scratch**

```

----->effsubi 32,35%
----->affir 3,32%
----->ritsubi 2,49%
----->solplay 1,66%
----->ritsubr 0,83%
----->abnorm 0,83%
----->otherfear 0,83%
----->ritagi 0,83%
----->selfg 29,41%
----->playi 8,82%----->sexi 0,74%
----->effsubr 8,82%----->hiermountp 0,80%
----->vocal 5,88%
----->playr 5,88%
----->Aggrr 2,94%
----->Aggri 2,94%----->hierachmount 0,49%
----->affi 2,94%

```

selfg

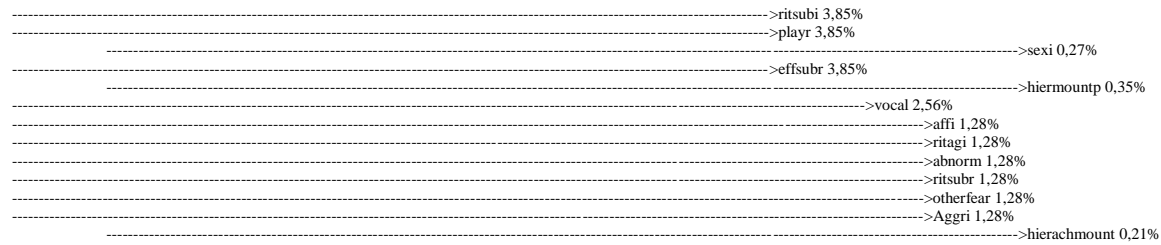
----->scratch 44,44%  
----->playi 3,92%  
----->playr 2,61%  
----->Aggri 1,31%  
----->hierachmount 0,22%  
----->effsubi 33,33%  
----->ritsubi 2,56%  
----->Aggrr 2,56%  
----->solplay 1,71%  
----->abnorm 0,85%  
----->ritsubr 0,85%  
----->otherfear 0,85%  
----->ritagi 0,85%  
----->affi 5,56%  
----->sexi 1,11%  
----->affir 5,56%  
----->effsubr 5,56%  
----->hiermountp 0,51%  
----->vocal 5,56%

sexi

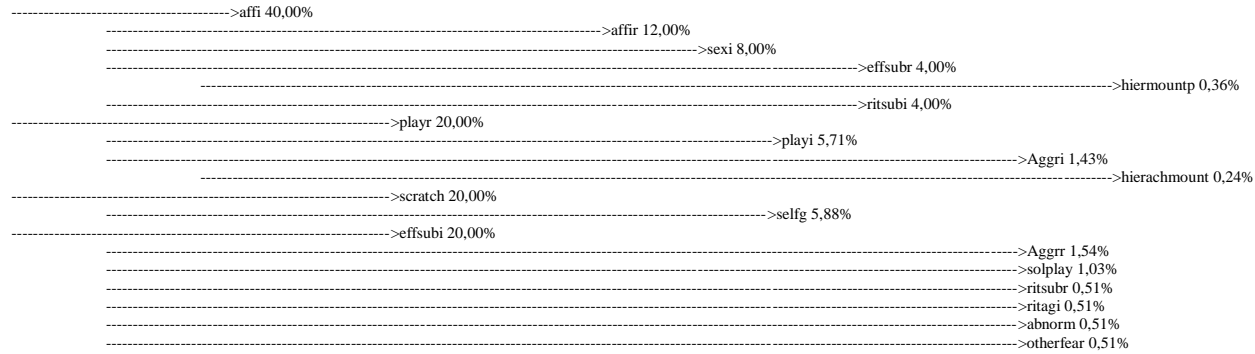
->scratch 100,00%  
----->effsubi 32,35%  
----->affir 3,32%  
----->ritsubi 2,49%  
----->solplay 1,66%  
----->otherfear 0,83%  
----->abnorm 0,83%  
----->ritagi 0,83%  
----->ritsubr 0,83%  
----->selfg 29,41%  
----->playi 8,82%  
----->effsubr 8,82%  
----->hiermountp 0,80%  
----->vocal 5,88%  
----->playr 5,88%  
----->Aggrr 2,94%  
----->affi 2,94%  
----->Aggri 2,94%  
----->hierachmount 0,49%

solplay

----->Aggrr 50,00%  
----->effsubi 50,00%  
----->scratch 12,82%  
----->playi 1,13%  
----->affir 5,13%  
----->selfg 3,85%

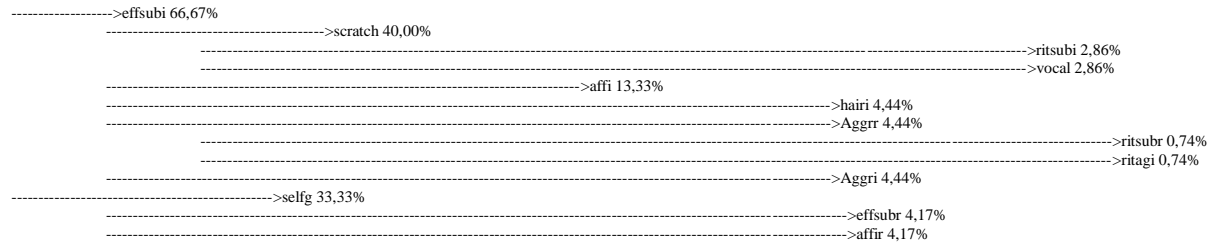


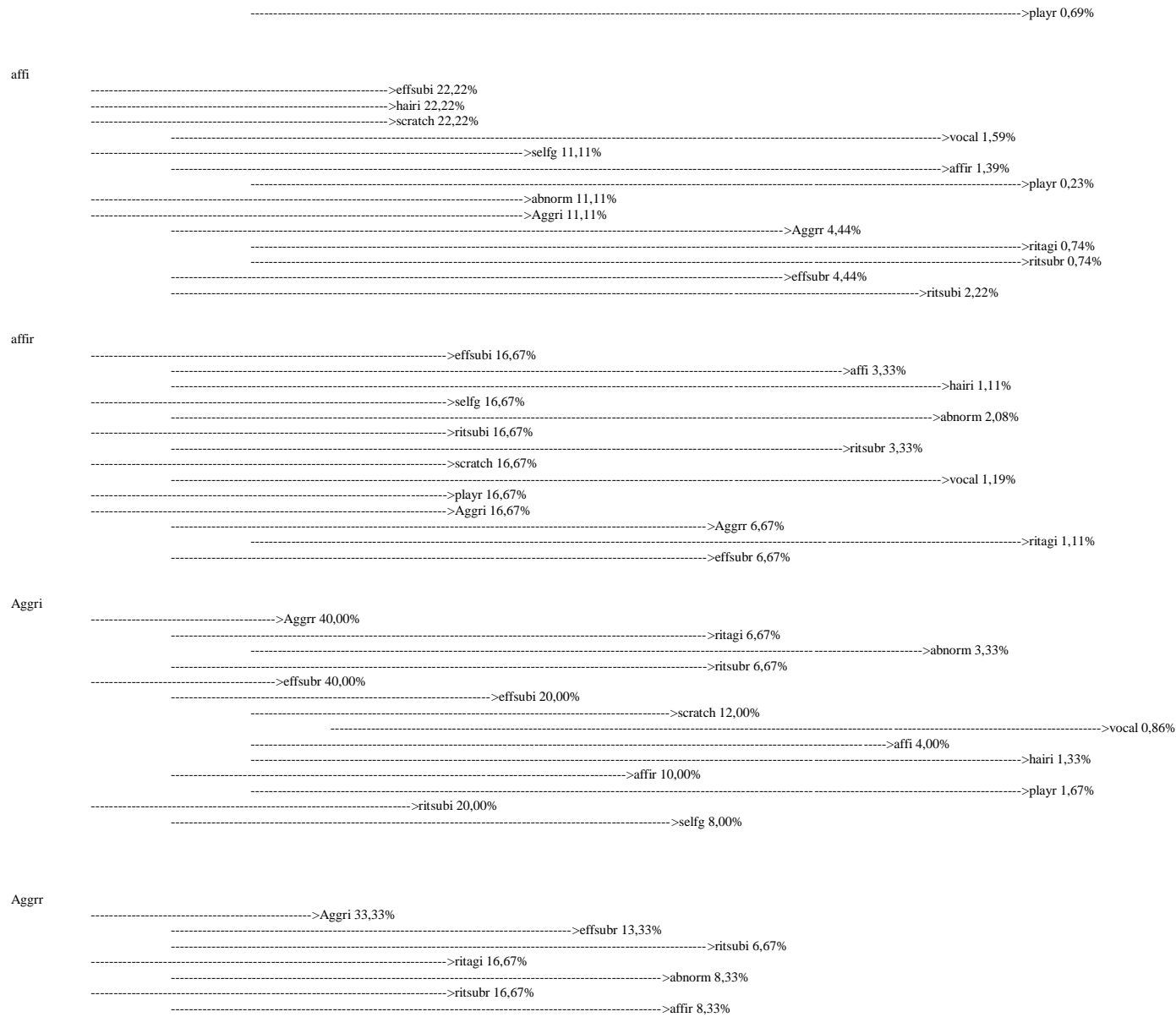
vocal



## SE24. View of probability behavioral sequences of the behavioral transitions of Mirinda.

abnorm





```

----->playr 1,39%
----->scratch 16,67%
----->selfg 4,76%
----->vocal 1,19%
----->effsubi 16,67%
----->affi 3,33%
----->hairi 1,11%

```

effsubi

```

----->scratch 60,00%
----->selfg 17,14%
----->affir 2,14%
----->playr 0,36%
----->ritsubi 4,29%
----->vocal 4,29%
----->effsubr 4,29%
----->affi 20,00%
----->abnorm 2,22%
----->Aggrr 6,67%
----->ritsubr 1,11%
----->ritagi 1,11%
----->hairi 6,67%
----->Aggri 6,67%

```

effsubr

```

----->effsubi 50,00%
----->scratch 30,00%
----->selfg 8,57%
----->vocal 2,14%
----->affi 10,00%
----->abnorm 1,11%
----->hairi 3,33%
----->Aggri 25,00%
----->Aggrr 10,00%
----->ritsubr 1,67%
----->ritagi 1,67%
----->ritsubi 5,00%
----->affir 25,00%
----->playr 4,17%

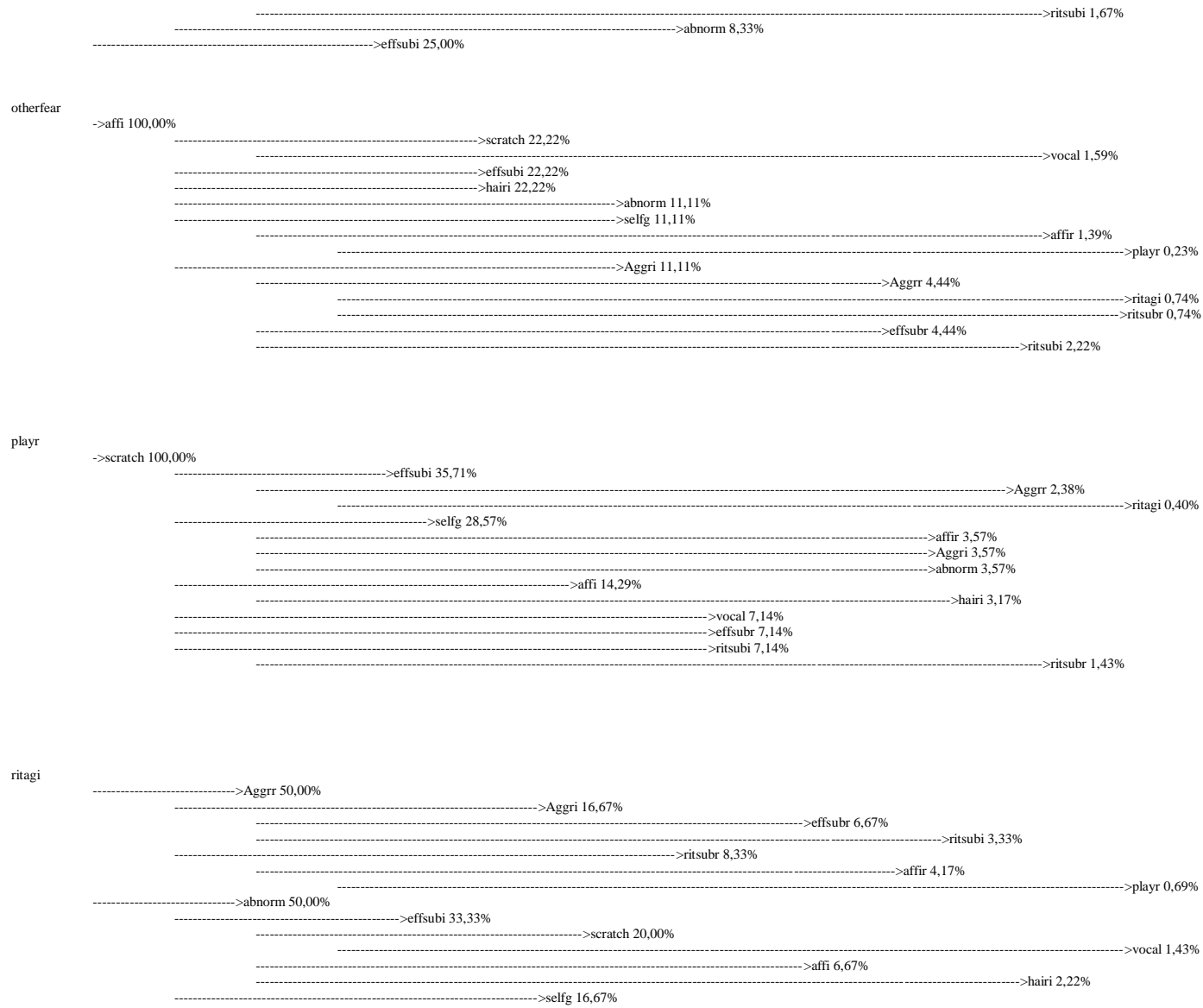
```

hairi

```

----->affi 75,00%
----->scratch 16,67%
----->vocal 1,19%
----->selfg 8,33%
----->affir 1,04%
----->playr 0,17%
----->Aggri 8,33%
----->Aggrr 3,33%
----->ritsubr 0,56%
----->ritagi 0,56%
----->effsubr 3,33%

```



ritsubi

```

----->selfg 40,00%
----->scratch 20,00%
----->vocal 1,43%
----->Aggri 5,00%
----->abnorm 5,00%
----->effsubr 5,00%
----->affir 20,00%
----->playr 3,33%
----->effsubi 20,00%
----->affi 4,00%
----->hairi 1,33%
----->ritsubr 20,00%
----->Aggrr 10,00%
----->ritagi 1,67%
```

ritsubr

```

----->affir 50,00%
----->selfg 8,33%
----->ritsubi 8,33%
----->playr 8,33%
----->Aggrr 50,00%
----->Aggri 16,67%
----->effsubr 6,67%
----->scratch 8,33%
----->vocal 0,60%
----->ritagi 8,33%
----->abnorm 4,17%
----->effsubi 8,33%
----->affi 1,67%
----->hairi 0,56%
```

scratch

```

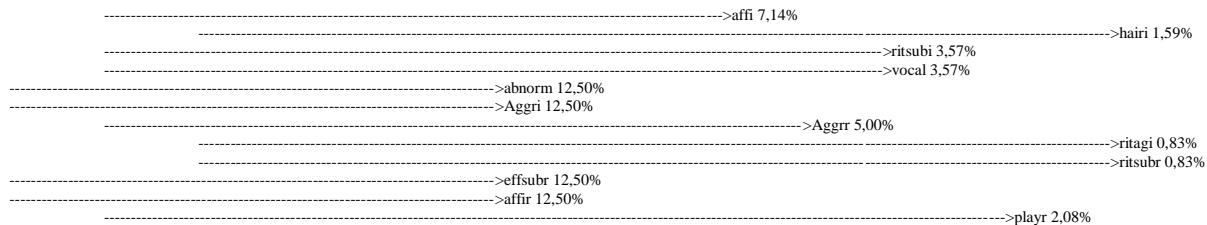
----->effsubi 35,71%
----->Aggrr 2,38%
----->ritagi 0,40%
----->selfg 28,57%
----->abnorm 3,57%
----->Aggri 3,57%
----->affir 3,57%
----->playr 0,60%
----->affi 14,29%
----->hairi 3,17%
----->vocal 7,14%
----->effsubr 7,14%
----->ritsubi 7,14%
----->ritsubr 1,43%
```

selfg

```

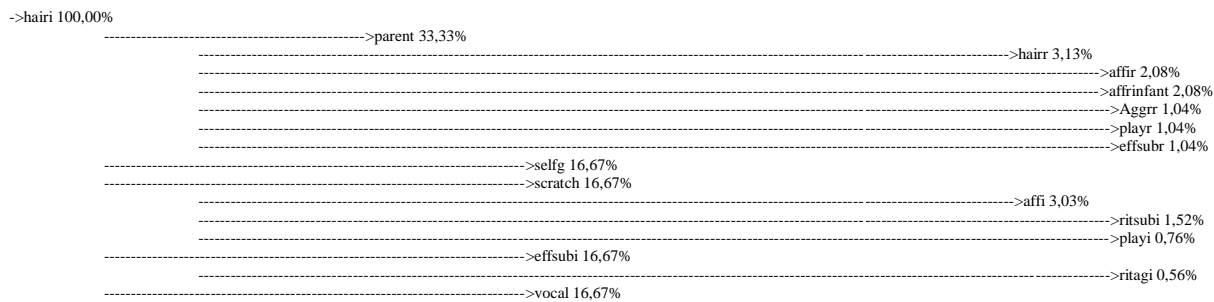
----->scratch 50,00%
----->effsubi 17,86%
```



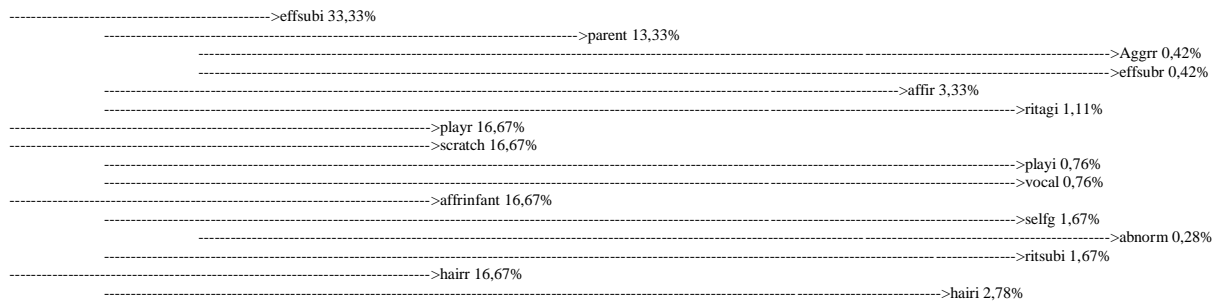


SE25. View of probability behavioral sequences of the behavioral transitions of Nefertari.

abnorm



affi



affir

```

----->effsubi 66,67%
----->scratch 11,11%
----->ritsubi 1,01%
----->playi 0,51%
----->hairi 4,44%
----->affrinfant 4,44%
----->hairr 4,44%
----->ritagi 2,22%
----->playr 2,22%
----->selfg 2,22%
----->abnorm 0,37%
----->affi 2,22%
----->parent 33,33%
----->vocal 1,04%
----->Aggrr 1,04%
----->effsubr 1,04%

```

affrinfant

```

----->parent 20,00%
----->effsubr 0,62%
----->Aggrr 0,62%
----->scratch 20,00%
----->affi 3,64%
----->vocal 0,91%
----->playi 0,91%
----->effsubi 20,00%
----->ritagi 0,67%
----->ritsubi 10,00%
----->affir 2,50%
----->selfg 10,00%
----->abnorm 1,67%
----->playr 10,00%
----->hairr 10,00%
----->hairi 1,67%

```

Aggrr

```

->effsubi 100,00%
----->parent 40,00%
----->vocal 1,25%
----->effsubr 1,25%
----->scratch 16,67%
----->ritsubi 1,52%
----->playi 0,76%

```

```

----->affir 10,00%
----->hairr 6,67%
----->affrinfant 6,67%
----->hairi 6,67%
----->affi 3,33%
----->playr 3,33%
----->ritagi 3,33%
----->selfg 3,33%
----->abnorm 0,56%

```

effsubi

```

----->parent 40,00%
----->Aggrr 1,25%
----->effsubr 1,25%
----->vocal 1,25%
----->scratch 16,67%
----->ritsubi 1,52%
----->playi 0,76%
----->affir 10,00%
----->affrinfant 6,67%
----->hairi 6,67%
----->hairr 6,67%
----->playr 3,33%
----->affi 3,33%
----->selfg 3,33%
----->abnorm 0,56%
----->ritagi 3,33%

```

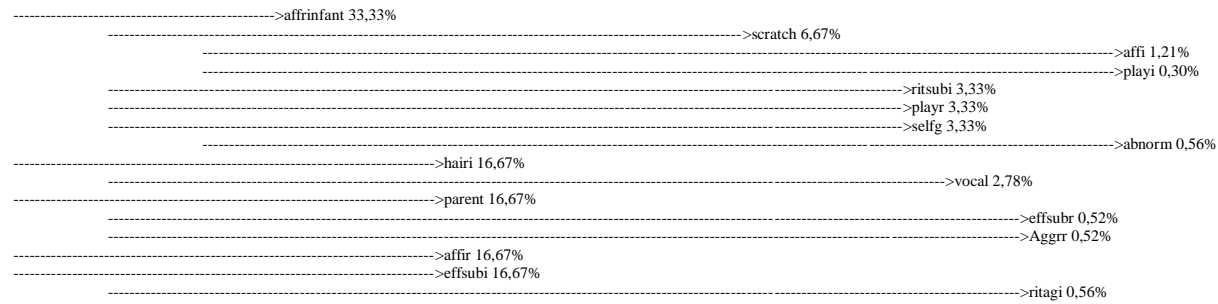
hairi

```

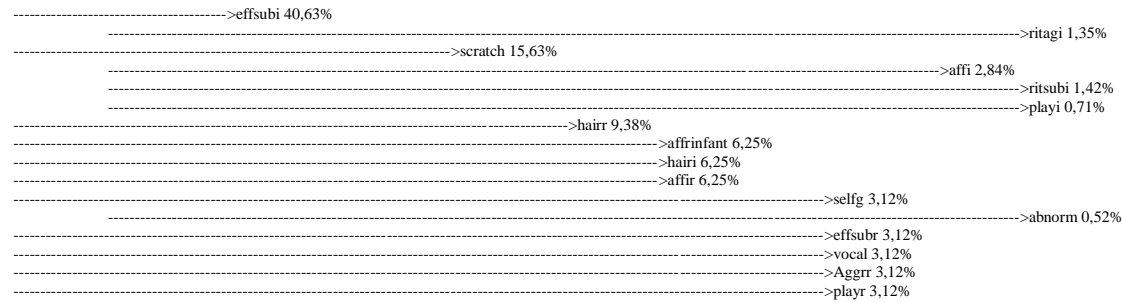
----->parent 33,33%
----->hairr 3,13%
----->affrinfant 2,08%
----->affir 2,08%
----->effsubr 1,04%
----->playr 1,04%
----->Aggrr 1,04%
----->vocal 16,67%
----->scratch 16,67%
----->affi 3,03%
----->ritsubi 1,52%
----->playi 0,76%
----->selfg 16,67%
----->abnorm 2,78%
----->effsubi 16,67%
----->ritagi 0,56%

```

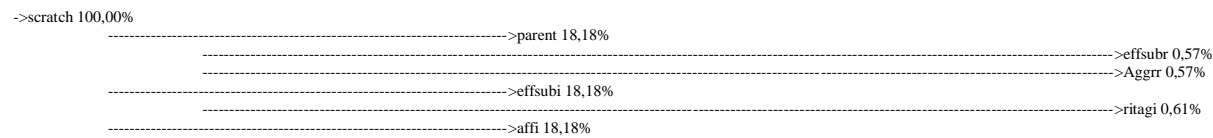
hairr



parent



playi



```

----->ritsubi 9,09%
----->affrinfant 4,55%
----->selfg 9,09%
----->abnorm 1,52%
----->hairi 1,52%
----->playr 4,55%
----->hairr 4,55%
----->affir 4,55%
----->vocal 4,55%

```

playr

```

----->effsubi 50,00%
----->parent 20,00%
----->effsubr 0,62%
----->Aggrr 0,62%
----->affir 5,00%
----->hairr 3,33%
----->hairi 3,33%
----->ritagi 1,67%
----->scratch 25,00%
----->affi 4,55%
----->playi 1,14%
----->vocal 1,14%
----->affrinfant 25,00%
----->ritsubi 2,50%
----->selfg 2,50%
----->abnorm 0,42%

```

ritagi

```

->effsubi 100,00%
----->parent 40,00%
----->Aggrr 1,25%
----->effsubr 1,25%
----->vocal 1,25%
----->scratch 16,67%
----->ritsubi 1,52%
----->playi 0,76%
----->affir 10,00%
----->affrinfant 6,67%
----->hairr 6,67%
----->hairi 6,67%
----->affi 3,33%
----->selfg 3,33%
----->abnorm 0,56%
----->playr 3,33%

```

ritsubi

```
----->affrinfant 50,00%
----->parent 10,00%
----->effsubr 0,31%
----->Aggrr 0,31%
----->playr 5,00%
----->selfg 5,00%
----->abnorm 0,83%
----->hairr 5,00%
----->affir 25,00%
----->effsubi 16,67%
----->hairi 1,11%
----->ritagi 0,56%
----->scratch 25,00%
----->affi 4,55%
----->vocal 1,14%
----->playi 1,14%
```

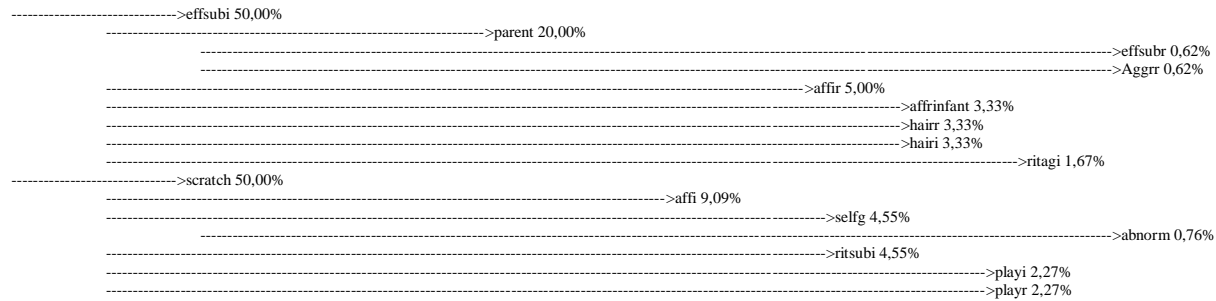
scratch

```
----->effsubi 18,18%
----->ritagi 0,61%
----->affi 18,18%
----->parent 18,18%
----->effsubr 0,57%
----->Aggrr 0,57%
----->selfg 9,09%
----->abnorm 1,52%
----->hairi 1,52%
----->ritsubi 9,09%
----->affrinfant 4,55%
----->hairr 4,55%
----->playi 4,55%
----->vocal 4,55%
----->affir 4,55%
----->playr 4,55%
```

selfg

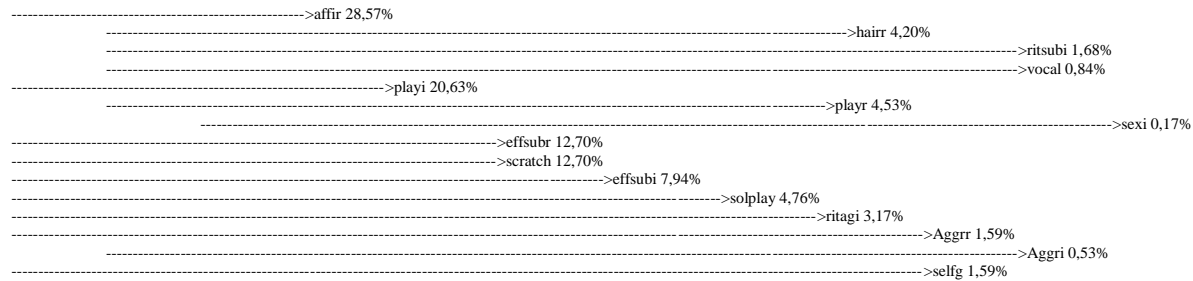
```
----->scratch 66,67%
----->effsubi 12,12%
----->ritagi 0,40%
----->affi 12,12%
----->ritsubi 6,06%
----->affrinfant 3,03%
----->affir 3,03%
----->vocal 3,03%
----->hairr 3,03%
----->playi 3,03%
----->playr 3,03%
----->parent 16,67%
----->effsubr 0,52%
----->Aggrr 0,52%
----->abnorm 16,67%
----->hairi 16,67%
```

vocal

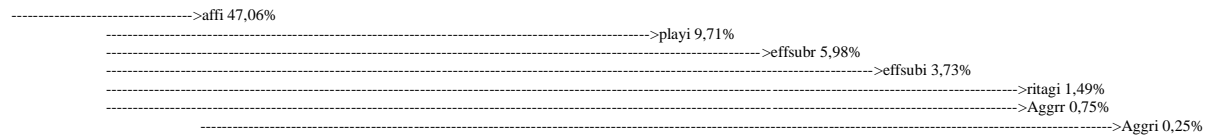


SE26. View of probability behavioral sequences of the behavioral transitions of Tania.

affi



affir



```

----->hairr 14,71%
----->scratch 8,82%
----->playr 8,82%
----->sexi 0,33%
----->ritsubi 5,88%
----->solplay 5,88%
----->vocal 2,94%
----->selfg 2,94%

```

**Aggri**

```

----->Aggrr 33,33%
----->effsubi 11,11%
----->affi 33,33%
----->affir 9,52%
----->hairr 1,40%
----->ritsubi 0,56%
----->vocal 0,28%
----->solplay 1,59%
----->ritagi 1,06%
----->selfg 0,53%
----->effsubr 33,33%
----->playi 7,02%
----->scratch 5,26%
----->playr 3,51%
----->sexi 0,13%

```

**Aggrr**

```

----->Aggri 33,33%
----->effsubr 11,11%
----->affi 33,33%
----->affir 9,52%
----->hairr 1,40%
----->ritsubi 0,56%
----->vocal 0,28%
----->solplay 1,59%
----->selfg 0,53%
----->effsubi 33,33%
----->playi 8,33%
----->scratch 6,67%
----->playr 3,33%
----->sexi 0,12%
----->ritagi 1,67%

```



**effsubi**

```
----->playi 25,00%----->solplay 1,22%
----->scratch 20,00%----->selfg 1,21%
----->affi 15,00%----->affir 10,00%----->hairr 1,47%
----->playr 10,00%----->sexi 0,37%
----->effsubr 10,00%----->vocal 0,37%
----->Aggrr 5,00%----->Aggri 1,67%
----->ritagi 5,00%----->ritsubi 1,67%
```

**effsubr**

```
----->affi 42,11%----->affir 12,03%----->hairr 1,77%
----->ritsubi 0,71%
----->solplay 2,01%
----->ritagi 1,34%
----->Aggrr 0,67%----->Aggri 0,22%
----->playi 21,05%
----->scratch 15,79%----->selfg 0,96%
----->playr 10,53%----->vocal 0,39%
----->sexi 0,39%
----->effsubi 10,53%
```

**hairr**

```
----->affir 85,71%
----->affi 40,34%----->playi 8,32%----->effsubr 5,12%
----->ritagi 1,28%
----->scratch 7,56%
----->playr 7,56%----->sexi 0,28%
----->ritsubi 5,04%
----->solplay 5,04%----->vocal 2,52%
----->selfg 2,52%
----->effsubi 14,29%
```

----->Aggrr 0,71%  
 ----->Aggri 0,24%

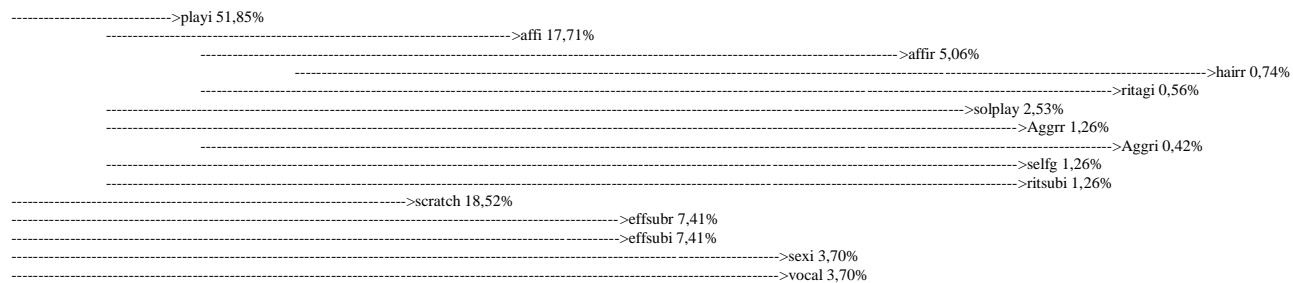
**otherfear**

->affi 100,00%  
 ----->affir 28,57%  
 ----->hairr 4,20%  
 ----->ritsubi 1,68%  
 ----->vocal 0,84%  
 ----->playi 20,63%  
 ----->playr 4,53%  
 ----->sexi 0,17%  
 ----->scratch 12,70%  
 ----->effsubr 12,70%  
 ----->effsubi 7,94%  
 ----->solplay 4,76%  
 ----->ritagi 3,17%  
 ----->selfg 1,59%  
 ----->Aggrr 1,59%  
 ----->Aggri 0,53%

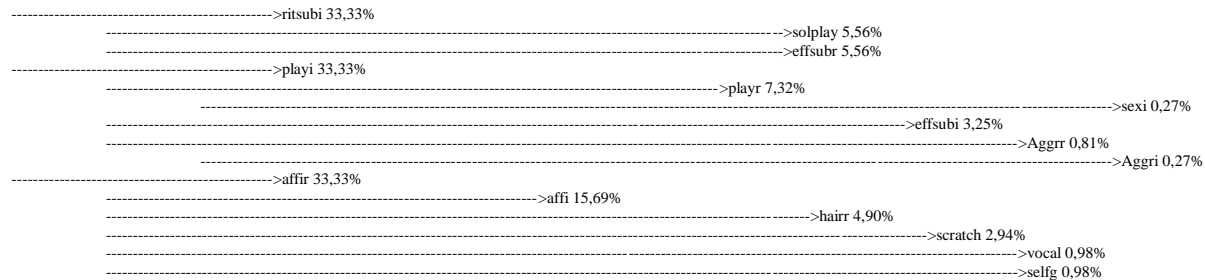
**playi**

----->affi 34,15%  
 ----->affir 9,76%  
 ----->hairr 1,43%  
 ----->scratch 4,34%  
 ----->ritagi 1,08%  
 ----->playr 21,95%  
 ----->vocal 0,81%  
 ----->sexi 0,81%  
 ----->effsubr 12,20%  
 ----->effsubi 9,76%  
 ----->solplay 4,88%  
 ----->ritsubi 2,44%  
 ----->selfg 2,44%  
 ----->Aggrr 2,44%  
 ----->Aggri 0,81%

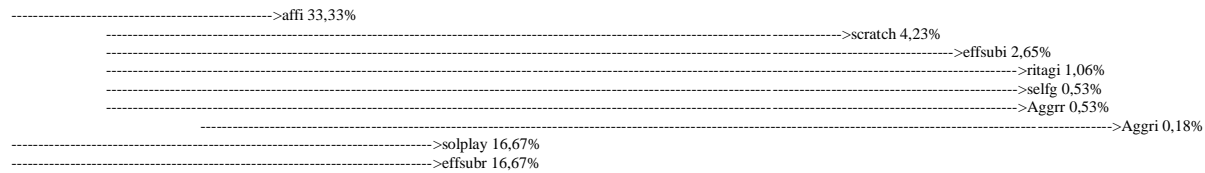
**playr**



**ritagi**



**ritsubi**



----->affir 16,67%  
 ----->hairr 2,45%  
 ----->vocal 0,49%  
 ----->playi 16,67%  
 ----->playr 3,66%  
 ----->sexi 0,14%

scratch

----->affi 36,36%  
 ----->effsubr 4,62%  
 ----->ritagi 1,15%  
 ----->Aggrr 0,58%  
 ----->Aggri 0,19%  
 ----->playr 18,18%  
 ----->sexi 0,67%  
 ----->affir 15,15%  
 ----->hairr 2,23%  
 ----->ritsubi 0,89%  
 ----->playi 12,12%  
 ----->selfg 6,06%  
 ----->vocal 1,52%  
 ----->effsubi 6,06%  
 ----->solplay 3,03%

selfg

----->affi 50,00%  
 ----->affir 14,29%  
 ----->hairr 2,10%  
 ----->ritsubi 0,84%  
 ----->playi 10,32%  
 ----->effsubr 6,35%  
 ----->solplay 2,38%  
 ----->ritagi 1,59%  
 ----->Aggrr 0,79%  
 ----->Aggri 0,26%  
 ----->vocal 25,00%  
 ----->scratch 15,00%  
 ----->effsubi 12,50%  
 ----->playr 12,50%  
 ----->sexi 0,46%

sexi

->affir 100,00%  
 ----->affi 47,06%  
 ----->playi 9,71%  
 ----->effsubr 5,98%  
 ----->effsubi 3,73%  
 ----->ritagi 1,49%  
 ----->Aggrr 0,75%  
 ----->Aggri 0,25%

```

----->hairr 14,71%
----->playr 8,82%
----->scratch 8,82%
----->ritsubi 5,88%
----->solplay 5,88%
----->selfg 2,94%
----->vocal 2,94%

```

**solplay**

```

----->affi 57,14%
----->affir 16,33%
----->hairr 2,40%
----->ritsubi 0,96%
----->playi 11,79%
----->effsubr 7,26%
----->effsubi 4,54%
----->ritagi 1,81%
----->selfg 0,91%
----->Aggrr 0,91%
----->Aggri 0,30%
----->playr 14,29%
----->vocal 0,53%
----->sexi 0,53%
----->scratch 14,29%

```

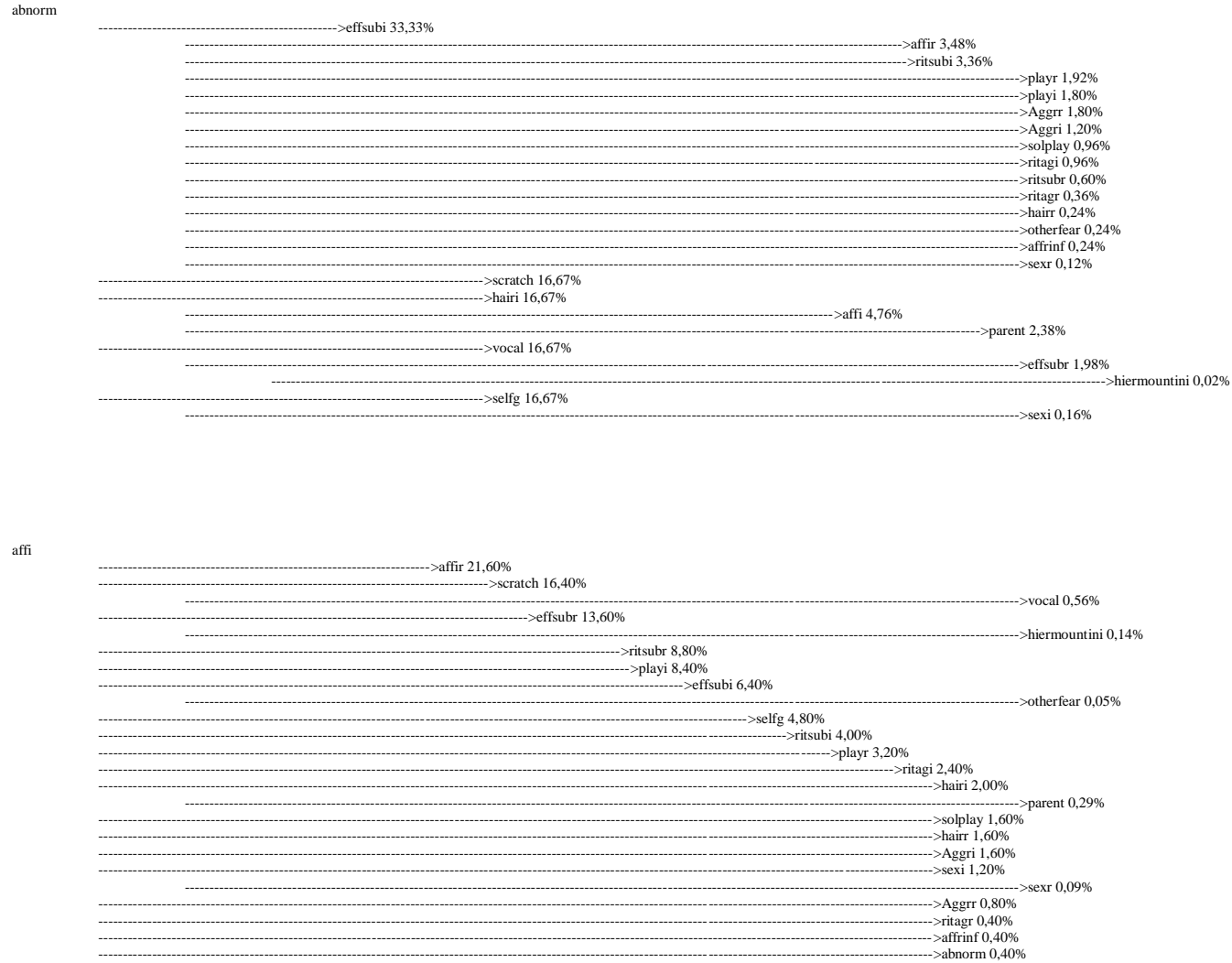
**vocal**

```

----->scratch 60,00%
----->affi 21,82%
----->effsubr 2,77%
----->ritagi 0,69%
----->Aggrr 0,35%
----->Aggri 0,12%
----->playr 10,91%
----->sexi 0,40%
----->affir 9,09%
----->hairr 1,34%
----->ritsubi 0,53%
----->playi 7,27%
----->effsubi 3,64%
----->solplay 1,82%
----->selfg 20,00%

```

SE27. View of probability behavioral sequences of the behavioral transitions of Mandrills' group.



affir

```
----->affi 22,83%----->ritsubr 2,01%
----->hairi 0,46%
----->sexi 0,27%
----->effsubi 20,47%----->parent 0,88%
----->ritagr 0,22%
----->otherfear 0,15%
----->scratch 13,39%----->effsubr 7,87%----->hiermountini 0,08%
----->playi 6,69%
----->ritsubi 6,30%----->playr 4,72%
----->selfg 4,33%----->abnorm 0,12%
----->Aggri 3,15%----->Aggrr 2,36%
----->hairr 1,97%----->affrinf 0,28%
----->vocal 1,57%
----->solplay 0,79%
----->ritagi 0,79%
----->sexr 0,39%
```

affrinf

```
----->effsubi 20,00%----->Aggrr 1,08%
----->vocal 0,72%
----->ritagi 0,58%
----->ritagr 0,22%
----->otherfear 0,14%
----->sexr 0,07%
----->scratch 20,00%----->affi 2,64%
----->effsubr 1,63%----->hiermountini 0,02%
----->Aggri 1,02%
----->solplay 0,68%
----->ritsubr 0,54%
----->parent 20,00%----->hairi 1,25%
----->selfg 10,00%----->abnorm 0,29%
----->hairr 10,00%----->affir 5,00%
----->ritsubi 10,00%
----->playr 10,00%----->playi 2,77%
----->sexi 0,21%
```

Aggri

```
----->effsubr 67,03%
----->scratch 10,77%
----->solplay 0,36%
----->affir 9,38%
----->hairr 0,18%
----->sexr 0,04%
----->affi 9,03%
----->hairi 0,18%
----->sexi 0,11%
----->effsubi 8,34%
----->parent 0,36%
----->otherfear 0,06%
----->affrinf 0,06%
----->playi 3,13%
----->playr 2,78%
----->ritagi 2,43%
----->ritagr 1,39%
----->vocal 0,69%
----->Aggrr 5,49%
----->ritsubr 5,49%
----->selfg 4,40%
----->abnorm 0,13%
----->ritsubi 3,30%
----->hiermountini 1,10%
```

Aggrr

```
----->effsubi 68,57%
----->scratch 15,54%
----->sexi 0,11%
----->affir 7,15%
----->ritsubi 6,91%
----->affi 5,43%
----->playr 3,95%
----->playi 3,70%
----->parent 2,96%
----->vocal 2,47%
----->solplay 1,97%
----->ritagi 1,97%
----->hairi 0,74%
----->otherfear 0,49%
----->hairr 0,49%
----->affrinf 0,49%
----->abnorm 0,25%
----->sexr 0,25%
----->effsubr 12,86%
```



```

----->hiermountini 0,13%
----->Aggri 4,29%
----->selfg 2,86%
----->ritsubr 1,43%
----->ritagr 1,43%

```

effsubi

```

----->scratch 22,66%
----->sexi 0,15%
----->affir 10,43%
----->ritsubi 10,07%
----->affi 7,91%
----->playr 5,76%
----->Aggrr 5,40%
----->playi 5,40%
----->effsubr 4,68%
----->hiermountini 0,05%
----->parent 4,32%
----->vocal 3,60%
----->selfg 3,60%
----->Aggri 3,60%
----->ritagi 2,88%
----->solplay 2,88%
----->ritsubr 1,80%
----->hairi 1,08%
----->ritagr 1,08%
----->affrinf 0,72%
----->hairr 0,72%
----->otherfear 0,72%
----->sexr 0,36%
----->abnorm 0,36%

```

effsubr

```

----->scratch 16,06%
----->solplay 0,54%
----->affir 13,99%
----->hairr 0,28%
----->sexr 0,06%
----->affi 13,47%
----->hairi 0,27%
----->sexi 0,16%
----->effsubi 12,44%
----->parent 0,54%
----->otherfear 0,09%
----->affrinf 0,09%
----->Aggri 11,40%
----->ritsubr 6,22%

```

----->ritsubi 4,66%  
 ----->playi 4,66%  
 ----->playr 4,15%  
 ----->ritagi 3,63%  
 ----->abnorm 0,09%  
 ----->Aggrr 2,59%  
 ----->selfg 2,07%  
 ----->ritagr 2,07%  
 ----->vocal 1,04%  
 ----->hiermountini 1,04%

hairi

----->affi 28,57%  
 ----->ritsubr 2,51%  
 ----->playi 2,40%  
 ----->playr 0,91%  
 ----->ritagi 0,69%  
 ----->solplay 0,46%  
 ----->sexi 0,34%  
 ----->vocal 14,29%  
 ----->Aggrr 1,02%  
 ----->effsubi 14,29%  
 ----->ritsubi 1,44%  
 ----->ritagr 0,15%  
 ----->otherfear 0,10%  
 ----->sexr 0,05%  
 ----->parent 14,29%  
 ----->hairr 1,34%  
 ----->affrinf 0,89%  
 ----->selfg 7,14%  
 ----->abnorm 0,20%  
 ----->Aggri 7,14%  
 ----->effsubr 4,79%  
 ----->scratch 7,14%  
 ----->hiermountini 0,08%  
 ----->affir 7,14%

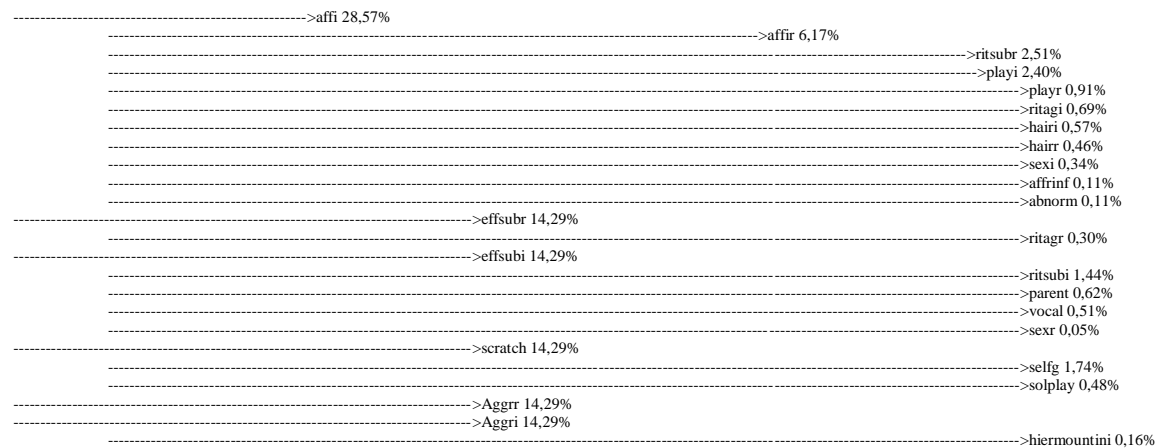
hairr

```
----->affir 50,00%
----->affi 11,42%
----->ritsubr 1,00%
----->sexi 0,14%
----->scratch 6,69%
----->effsubr 3,94%
----->hiermountini 0,04%
----->playi 3,35%
----->ritsubi 3,15%
----->playr 2,36%
----->selfg 2,17%
----->abnorm 0,06%
----->Aggri 1,57%
----->Aggrr 1,18%
----->sexr 0,20%
----->effsubi 14,29%
----->ritagi 0,41%
----->solplay 0,41%
----->ritagr 0,15%
----->otherfear 0,10%
----->affrinf 14,29%
----->hairi 7,14%
----->vocal 1,02%
----->parent 7,14%
```

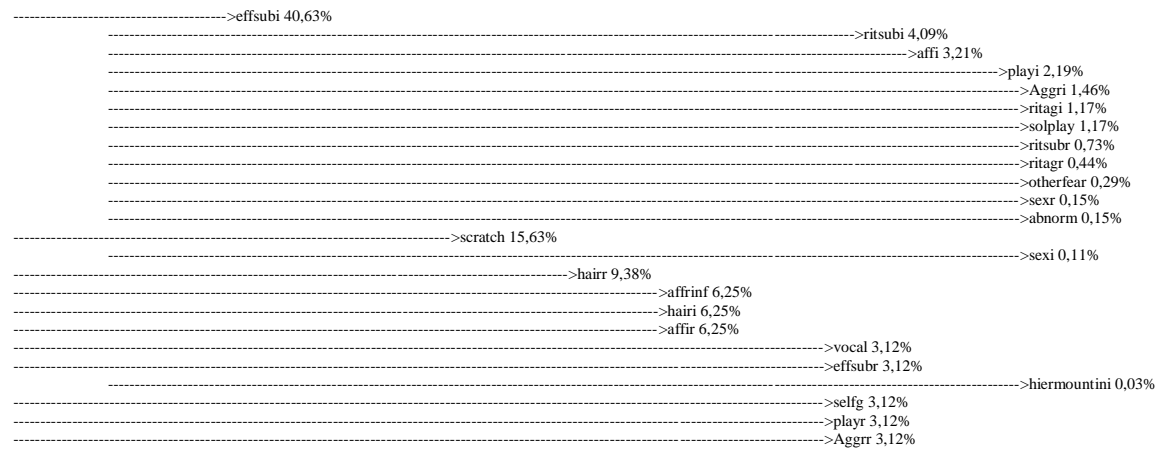
hiermountini

```
----->affir 50,00%
----->affi 11,42%
----->ritsubr 1,00%
----->hairi 0,23%
----->effsubi 10,24%
----->parent 0,44%
----->ritagr 0,11%
----->otherfear 0,07%
----->scratch 6,69%
----->ritsubi 3,15%
----->selfg 2,17%
----->abnorm 0,06%
----->Aggri 1,57%
----->hairr 0,98%
----->affrinf 0,14%
----->vocal 0,79%
----->playi 50,00%
----->playr 7,84%
----->effsubr 5,22%
----->Aggrr 1,87%
----->solplay 1,49%
----->ritagi 1,12%
----->sexr 0,37%
----->sexi 0,37%
```

otherfear



parent



playi

```
----->affir 17,16%
----->affi 17,16%
----->playr 15,67%
----->effsubi 11,94%
----->effsubr 10,45%
----->scratch 7,46%
----->ritsubi 5,97%
----->Aggrr 3,73%
----->solplay 2,99%
----->ritagi 2,24%
----->sexi 0,75%
----->sexr 0,75%
----->vocal 0,75%
----->hairr 0,34%
----->ritsubr 1,51%
----->hairi 0,34%
----->abnorm 0,07%
----->affrinf 0,17%
----->parent 0,52%
----->otherfear 0,09%
----->Aggri 1,19%
----->ritagr 0,22%
----->hiermountini 0,11%
----->selfg 0,91%
```

playr

```
----->playi 27,66%
----->affi 4,75%
----->Aggrr 1,03%
----->sexr 0,21%
----->scratch 17,02%
----->effsubi 15,96%
----->parent 0,69%
----->hairi 0,17%
----->otherfear 0,11%
----->affir 11,70%
----->hairr 0,23%
----->hiermountini 0,06%
----->selfg 3,19%
----->abnorm 0,09%
----->Aggri 2,13%
----->sexi 2,13%
----->vocal 1,06%
----->solplay 1,06%
----->ritagi 1,06%
----->affrinf 1,06%
----->ritagr 1,06%
----->ritsubr 1,06%
```

ritagi

----->effsubr 25,64%  
----->Aggri 2,92%  
----->hiermountini 0,27%  
----->ritsubr 17,95%  
----->affi 9,41%  
----->solplay 0,66%  
----->scratch 7,69%  
----->Aggrr 7,69%  
----->effsubi 5,27%  
----->parent 0,23%  
----->otherfear 0,04%  
----->affir 7,69%  
----->hairr 0,15%  
----->ritagr 7,69%  
----->ritsubi 5,13%  
----->affrinf 0,09%  
----->sexi 2,56%  
----->sexr 0,20%  
----->abnorm 2,56%  
----->hairi 0,43%  
----->vocal 0,43%  
----->playr 2,56%  
----->playi 2,56%  
----->selfg 2,56%

ritagr

----->effsubi 29,41%  
----->scratch 6,67%  
----->playr 1,69%  
----->parent 1,27%  
----->vocal 1,06%  
----->solplay 0,85%  
----->hairi 0,32%  
----->otherfear 0,21%  
----->hairr 0,21%  
----->sexr 0,11%  
----->ritsubi 23,53%  
----->affir 9,91%  
----->selfg 2,48%  
----->playi 2,27%  
----->affrinf 0,41%  
----->Aggri 17,65%  
----->effsubr 11,83%  
----->hiermountini 0,19%  
----->ritsubr 5,88%  
----->ritagi 5,88%  
----->sexi 0,15%  
----->abnorm 0,15%  
----->Aggrr 5,88%  
----->affi 5,88%

ritsubi

----->affir 42,11%  
----->affi 9,61%  
----->hairi 0,19%  
----->sexi 0,12%  
----->effsubr 3,32%  
----->hiermountini 0,03%  
----->playr 1,99%  
----->Aggri 1,33%  
----->hairr 0,83%  
----->sexr 0,17%  
----->effsubi 14,04%  
----->parent 0,61%  
----->ritagi 0,40%  
----->otherfear 0,10%  
----->selfg 10,53%  
----->abnorm 0,30%  
----->playi 9,65%  
----->scratch 6,14%  
----->Aggrr 2,63%  
----->ritsubr 1,75%  
----->affrinf 1,75%  
----->vocal 1,75%  
----->solplay 0,88%  
----->ritagr 0,88%

ritsubr

----->affi 52,44%  
----->affir 11,33%  
----->scratch 8,60%  
----->vocal 0,29%  
----->playi 4,40%  
----->effsubi 3,36%  
----->otherfear 0,02%  
----->selfg 2,52%  
----->ritsubi 2,10%  
----->playr 1,68%  
----->hairr 0,84%  
----->Aggrr 0,42%  
----->affrinf 0,21%  
----->abnorm 0,21%  
----->effsubr 13,41%  
----->hiermountini 0,14%  
----->Aggri 6,10%  
----->ritagi 4,88%  
----->ritagr 0,38%  
----->solplay 3,66%  
----->hairi 1,22%  
----->parent 0,17%  
----->sexi 1,22%  
----->sexr 0,09%

scratch

```
----->effsubi 16,27%
----->otherfear 0,12%
----->sexr 0,06%
----->affi 13,22%
----->selfg 12,20%
----->abnorm 0,35%
----->affir 10,85%
----->effsubr 8,14%
----->hiermountini 0,08%
----->playi 6,78%
----->playr 6,10%
----->Aggri 5,08%
----->ritsubi 4,75%
----->vocal 3,39%
----->solplay 3,39%
----->ritsubr 2,71%
----->ritagi 1,69%
----->Aggrr 1,36%
----->parent 1,36%
----->ritagr 1,02%
----->sexi 0,68%
----->hairi 0,34%
----->affrinf 0,34%
----->hairr 0,34%
```

selfg

```
----->scratch 38,10%
----->playi 2,58%
----->ritsubi 1,81%
----->solplay 1,29%
----->ritagr 0,39%
----->affrinf 0,13%
----->affi 12,38%
----->hairr 0,20%
----->effsubi 12,38%
----->otherfear 0,09%
----->affir 7,62%
----->effsubr 4,76%
----->hiermountini 0,05%
----->vocal 4,76%
----->playr 3,81%
----->Aggrr 2,86%
----->ritsubr 2,86%
----->Aggri 2,86%
----->abnorm 2,86%
----->hairi 0,48%
----->ritagi 0,95%
----->sexi 0,95%
----->sexr 0,07%
----->parent 0,95%
```



sexi

```

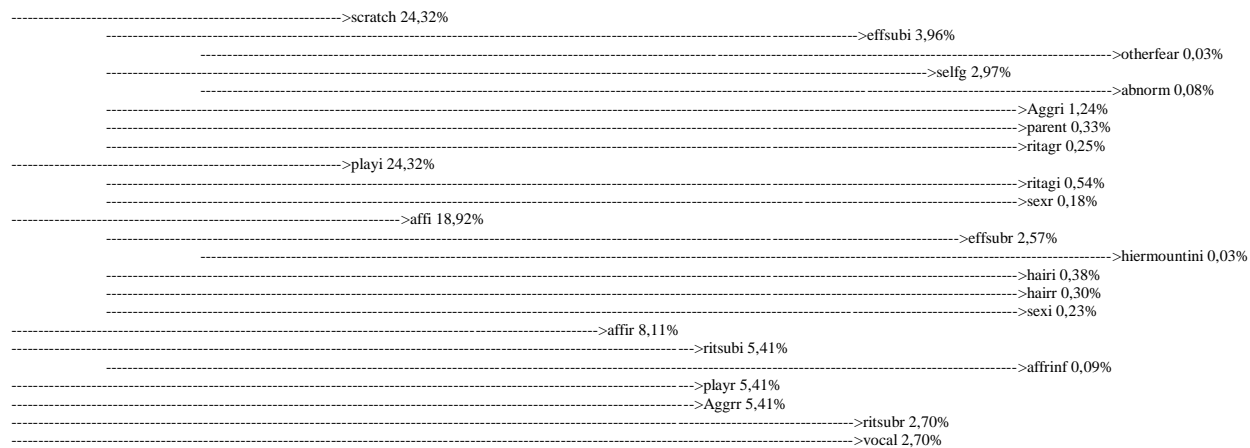
----->scratch 38,46%
----->effsubr 3,13%
----->hiermountini 0,03%
----->playr 2,35%
----->Aggri 1,96%
----->ritsubi 1,83%
----->solplay 1,30%
----->vocal 1,30%
----->ritagi 0,65%
----->parent 0,52%
----->Aggrr 0,52%
----->ritagr 0,39%
----->affrinf 0,13%
----->affir 15,38%
----->hairr 0,30%
----->effsubi 7,69%
----->otherfear 0,06%
----->affi 7,69%
----->hairi 0,15%
----->playi 7,69%
----->selfg 7,69%
----->abnorm 0,22%
----->ritsubr 7,69%
----->sexr 7,69%
```

sexr

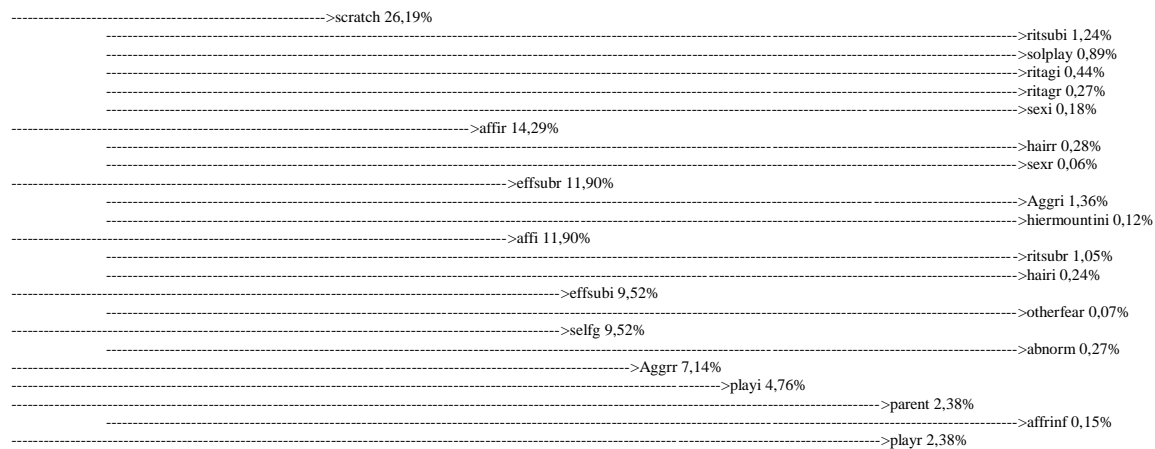
```

----->Aggri 25,00%
----->effsubr 16,76%
----->ritagr 0,35%
----->Aggrr 1,37%
----->hiermountini 0,27%
----->sexi 25,00%
----->scratch 9,62%
----->ritsubr 1,92%
----->selfg 1,92%
----->effsubi 25,00%
----->ritsubi 2,52%
----->parent 1,08%
----->vocal 0,90%
----->ritagi 0,72%
----->hairi 0,27%
----->hairr 0,18%
----->otherfear 0,18%
----->affrinf 0,18%
----->abnorm 0,09%
----->playi 25,00%
----->affi 4,29%
----->affir 4,29%
----->playr 3,92%
----->solplay 0,75%
```

solplay



vocal



### C. Lemurs' personalities: A comparative analysis between ring-tailed lemurs (*Lemur catta*) and red-ruffed lemurs (*Varecia rubra*)

Table S18. Ethogram of the ring-tailed lemurs' behaviors reported in this study. Although Affiliation category is very broad and certainly some behaviors included might show differences due to personality, we decided to maintain all into the same category group to prevent the increase of total number of variables to be observed, under the assumption that the differences in some of the behaviors included would not obscure potential differences in the broad category (Continued on the next page).

	<b>Behavior</b>	<b>Definition</b>
<b>Individual</b>	Self-grooming	Picking own dirt and ticks, brushing hair or skin with the mouth and/or hand(s). Self-groom of injuries are not included. May include fur rubbing and self-scratch.
	Scent marking	Rubbing anogenital area against surfaces (males and females) or rubbing chest, neck, chin and wrists area in their own tail (males). Males also leave visual and scent markings using the glands on their inner forearms. This is called "spur marking." They grasp the substrate, usually a small sapling, and drag the thorny nail which overlays the scent gland, cutting into the wood and spreading secretions (Jolly 1966; Merti-Millhollen 1988 in PIN).
	Solitary play	Repeated climbing and jumping off the same climbing structure, somersaulting, back flips and pushing piles of straw across the floor of the enclosure (Mellen et al., 1981). May include an alimentary item or manipulation of enrichment objects or other artificial device.
	Abnormal	Stereotypic (spinning, pacing and rocking), self-injurious (Hair pulling, mutilation/self-biting, head banging, stereotypic scratching, sucking fingers or hand, aggressive impulse), excessive self-grooming, coprophagy or aggressive interaction with objects (rail pulling, fence biting, ball biting).
<b>Social</b>	Affiliative	Allogrooming, liking, physical contact.
	Social play	Gnaw wrestling, wrestling or chasing another individual.
	Sexual behaviour	Mounting, genital inspection, masturbation, initiation copulation, sexual presentation.
	Agonistic ritualized	Threat display by "stink fight". Males anoint their tails by rubbing the end of the tails on the inside of their wrists and on their chest. They then arch their tails over their bodies and wave them at their opponent (in PIN).
	Effective agonism	Aggression with contact, rough behaviour, lunging, chasing, cuffing, grabbing, scratching, biting (in PIN).
	Effective submission	Submissive retreat, cowering, repeated glances (Hood, 1995), jumping away, fleeing and squealing (Jolly 1966; Taylor & Sussman 1985; Sauter et al. 1999 in PIN.), avoidance.
	Submission ritualized	Spat calling, spat grimace, submissive yips-chatters.
	Parental	Brest feeding, parental grooming, infant transport, restrain, allonursing.
	Huddling	Sitting or laying down together with several individuals in a cluster.
	Not Visible	Out of the observer's sight – observer can't disclose the behaviour that the individual is performing. Individual may be hiding.
Others	Any behaviour (social or individual) not described by this catalogue.	
Human interaction	Negative (throwing objects or dirt), vocal (trying to call people attention).	

Table S19. Ethogram of the red-ruffed lemurs' behaviors reported in this study. Although Affiliation category is very broad and certainly some behaviors included might show differences due to personality, we decided to maintain all into the same category group to prevent the increase of total number of variables to be observed, under the assumption that the differences in some of the behaviors included would not obscure potential differences in the broad category (Continued on the next page).

	<b>Behaviors</b>	<b>Definition</b>
<b>Individual</b>	Self-grooming	The individual forward scrapes with the toothcomb, beginning at the base of its hair follicles, and pushing through to the ends. Ruffed lemurs usually self-groom their limbs, feet, sides, genital regions and their tails. They lick their digits and scratched their heads, arms, feet and clean their ears with the toilet claw.
	Solitary play	The ruffed lemur does brisk and lively locomotors rotational movements of the whole body or just body parts that start and end abruptly; includes jumping bipedally and twist their bodies around their central axis while swinging their arms and rolling their heads.
	Scent marking	The lemur squats and drags its anogenital region back and forth or sideways along the surface being marked. The females do it only with the anogenital region and males use the chest, neck, and chin.
<b>Social</b>	Agonistic Effective Behaviour	Includes pounce on (jumping upon the opponent), scratch (injuring other individuals with its fingers or nail), bite (the individual does an oral seizure of pelage or limbs), charge (running toward while staring at a stationary group member) and push down (manual seizure of opponent's shoulders, forcing them down to the substrate)
	Agonistic Ritualized Behaviour	Includes chase (pursuing another ruffed lemur), threat (the animal produces some variations of the theme lunge-and-cuff), cuff (The individual executes a striking gesture with hand, from a tripod or bipedal position), lunge (thrusting of the upper part or whole body toward an opponent), feint-to-cuff (rapid raising of hand without cuffing motion), stare (directing a protracted gaze toward another with widening of eyes), and grimace (drawing back the lips, exposing the teeth, and keeping the mouth fairly closed).
	Submissive Effective Behaviour	Includes flee (rapid locomotion away from the opponent), flinch (the ruffed lemur adducts of their limbs and pulls the body away from an aggressor), and jump away (impelling the body with their feet away from the surface and the opponent)
	Submissive Ritualized Behaviour	Includes turn head (looking away from a threatening conspecific), back away (walking backwards, away from, but facing the opponent)
	Parental behaviour	Includes nursing (the infant approaches its mouth to the mother's nipple), parental grooming (allogrooming between the mother and their infants) and transport infants (the mothers transport their infants by mouth and park them).
	Social Play	Social play is an ensemble of social behaviours with characteristics similar to several social behaviours described in this ethogram, but whose identifying elements are the following: start and end abruptly, have several periods intercalated with several pauses to rest, minimal noise, don't cause injuries, and usually are variations of roles. Includes non-agonistic fighting (rough-and-tumble play), and chasing (approach-withdrawal play).
	Sexual behaviour	The individual interacts sexually, in which mounting, penile insertion, thrusting and ejaculation can occur. Usually, these interactions are initiated by females who approached and slap males.

	Social behaviour	Includes huddling (two or more lemurs sitting inactive, hunched or semihunched, in close or whole body contact), allogrooming (the individual forward scrapes with the toothcomb the fur of another conspecific), and greeting behaviours (during olfactory greeting the animal sniffs another's face, nose, mouth, arm pit, shoulders or anogenital region, and during tactile greeting the lemur approaches another and establishes body contact which could include sitting or standing side by side, varying degrees of manual contact or rubbing rhinaria).
	Vocalizations	Varecia subjects can use different calls in different contexts. Affiliative calls include roar/ shriek chorus, abrupt roar, pulsed squawk, bray/quack, huff and mew call. Agonistic calls include wail, growl, growl-snort, chatter and whine. Roar/shriek chorus with bray/quack vocalizations and whines can be produced during the breeding season
	Abnormal behaviour	Includes hair pulling (repeatedly pulling out hair from the body, while grooming), head twirling (repetitive movements with its head), pacing (walking in a fixed pattern repeatedly) and selfscratch (the lemur exaggeratedly scratch itself with their feet).
	Out of sight	The individual is located somewhere not visible for the researcher
	Other behaviors	The individual is performing other behaviour that is not specify in this catalogue

Table S20. Ring-tailed lemurs: descriptive statistics for categories for which significant relationships were found. Includes group means and group maximums, and each individual has its own mean and maximum per category. In bold are the highest means and the highest maximums, in grey are the lowest means.

Behavioral Categories	Group		Cot		Cos		Den		Jul		Maz		Min		Ore		Pul		Ron		Vel	
	mean	Max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.
Huddling	0.312	1.000	<b>0.045</b>	1.000	0.254	1.000	0.226	1.000	0.440	1.000	0.335	1.000	0.252	1.000	0.264	1.000	<b>0.588</b>	1.000	0.317	1.000	0.386	1.000
Vocalizations Event	0.001	0.030	0.001	0.010	0.002	0.013	0.002	0.017	0.002	0.025	<b>0.000</b>	0.006	0.001	0.022	<b>0.003</b>	<b>0.030</b>	0.001	0.017	0.000	0.004	0.001	0.009
Selfgrooming	0.035	0.558	0.055	0.239	0.017	0.093	0.026	<b>0.558</b>	0.053	0.225	0.052	0.299	<b>0.059</b>	0.335	0.028	0.147	<b>0.004</b>	0.033	0.032	0.253	0.023	0.123
Scratching	0.006	0.343	0.007	0.080	0.009	0.065	<b>0.018</b>	<b>0.343</b>	0.002	0.018	0.004	0.098	0.011	0.099	0.002	0.032	<b>0.001</b>	0.015	0.003	0.036	0.004	0.029
Affiliation Initiator	0.077	0.542	0.125	<b>0.542</b>	0.079	0.242	0.040	0.419	0.044	0.330	<b>0.135</b>	0.455	0.063	0.518	0.124	0.517	<b>0.036</b>	0.203	0.072	0.468	0.047	0.286
Effective Submission Initiator Event	0.000	0.007	0.000	0.003	<b>0.001</b>	<b>0.007</b>	0.000	0.002	0.000	0.003	<b>0.000</b>	0.002	0.000	0.002	0.000	0.003			0.000	0.004	<b>0.000</b>	0.002
Parental Behavior	0.167	1.000	0.001	0.028	0.007	0.059	0.006	0.103	0.000	0.012	0.014	0.224	0.002	0.047	0.009	0.127	<b>0.843</b>	<b>1.000</b>	<b>0.000</b>	0.002	0.778	<b>1.000</b>
Affiliation Receiver	0.078	0.827	0.080	0.472	0.038	0.195	<b>0.020</b>	0.147	0.044	0.560	0.044	0.435	0.031	0.170	0.064	0.409	0.153	<b>0.827</b>	0.057	0.452	<b>0.231</b>	0.810
Effective Agonism Receiver Event	0.000	0.003	<b>0.000</b>	0.002			0.000	0.002	0.000	0.003	0.000	0.002	0.000	0.002	<b>0.000</b>	<b>0.003</b>			<b>0.000</b>	0.002	0.000	0.002
Arms Reach	0.012	0.052	0.009	0.030	0.015	0.037	<b>0.007</b>	0.015	0.008	0.025	0.016	<b>0.052</b>	0.014	0.035	0.016	0.045	0.013	0.038	0.012	0.034	<b>0.018</b>	0.042
Arms Reach 1	0.006	0.028	0.005	0.018	0.005	0.015	0.004	0.012	<b>0.003</b>	0.015	<b>0.008</b>	0.026	0.006	0.020	0.007	<b>0.028</b>	0.006	<b>0.028</b>	0.005	0.018	0.007	0.018
Arms Reach 2	0.003	0.021	0.002	0.013	0.004	0.010	0.001	0.005	<b>0.001</b>	0.008	0.004	<b>0.021</b>	0.004	0.013	0.003	0.017	0.003	0.013	0.003	0.020	<b>0.005</b>	0.020
Arms Reach 3	0.002	0.013	0.001	0.008	<b>0.003</b>	0.012	<b>0.000</b>	0.005	0.001	0.007	0.002	0.012	0.002	0.011	0.002	<b>0.013</b>	0.001	0.010	0.001	0.011	0.002	0.010
Arms Reach 4	0.001	0.012	0.000	0.005	<b>0.002</b>	<b>0.012</b>	<b>0.000</b>	0.002	0.000	0.003	0.001	0.011	0.001	0.009	0.002	0.008	0.000	0.005	0.001	0.005	0.002	0.007
Arms Reach 5	0.002	0.011	<b>0.000</b>	0.005	0.001	0.005	0.001	0.007	<b>0.003</b>	0.010	0.002	<b>0.011</b>	0.001	0.008	0.001	0.007	0.002	0.005	0.002	0.007	0.002	0.007

Table S21. Red-ruffed lemurs: Descriptive statistics for categories for which significant relationships were found. Includes group means and group maximums, and each individual has its own mean and maximum per category. In bold are the highest means and the highest maximums, in grey are the lowest means.

Behavioral Categories	Group		Ft		Sf		Ma		Pn		Sh		Cl		Rs		Tx	
	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.	mean	max.
Self-grooming	0.053	0.332	0.063	0.303	<b>0.032</b>	0.313	<b>0.111</b>	<b>0.332</b>	0.090	0.243	0.081	0.273	0.034	0.307	0.055	0.254	0.033	0.188
Sent Marking	0.005	0.107	0.003	0.045	<b>0.000</b>	0.007	0.004	0.022			<b>0.016</b>	<b>0.107</b>	0.005	0.043	0.001	0.020	0.013	0.073
Effective Agonism Initiator Event	0.001	0.012	0.002	0.010	0.000	0.003	<b>0.000</b>	0.002			<b>0.002</b>	0.007	0.001	0.005	0.001	<b>0.012</b>	0.000	0.005
Affiliation Initiator	0.025	1.000	0.017	0.162	0.027	0.208	0.034	0.372	0.008	0.070	0.019	0.153	0.030	<b>1.000</b>	<b>0.043</b>	0.590	<b>0.006</b>	0.040
Effective Agonism Receiver Event	0.000	0.004	0.000	0.002	0.000	0.003					0.000	0.002	<b>0.000</b>	0.002	0.000	<b>0.004</b>	<b>0.001</b>	0.003
Affiliative Receiver	0.019	1.000	<b>0.002</b>	0.040	0.014	0.160	0.031	0.135	0.017	0.113	0.012	0.158	<b>0.035</b>	<b>1.000</b>	0.029	0.590	0.003	0.040
Arms Reach	0.010	0.042	0.006	0.018	0.008	0.020	0.011	0.028	0.014	0.030	<b>0.018</b>	0.033	0.009	0.025	0.015	<b>0.042</b>	<b>0.005</b>	0.017
Arms Reach 1	0.008	0.028	0.005	0.013	0.006	0.020	0.008	0.025	0.009	0.023	<b>0.013</b>	<b>0.028</b>	0.007	0.020	0.011	0.023	<b>0.004</b>	0.017
Arms Reach 2	0.002	0.019	0.001	0.008	0.001	0.007	0.002	0.007	0.003	0.010	<b>0.004</b>	0.012	0.001	0.011	0.003	<b>0.019</b>	<b>0.001</b>	0.008

Table S22. Ring-tailed lemurs: The table presents the group variance and individual variability for the categories with variance different from zero in at least one of the individuals in the group

Behavioral Categories	group variance	Cot	Cos	Den	Jul	Maz	Min	Ore	Pul	Ron	Vel
		Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Huddling	0.169	0.033	0.166	0.135	0.196	0.195	0.134	0.143	0.211	0.152	0.187
Selfgrooming	0.004	0.005	0.001	0.009	0.006	0.006	0.007	0.002	0.000	0.004	0.002
Scratching	0.001	0.000	0.000	0.004	0.000	0.000	0.001	0.000	0.000	0.000	0.000
Affiliation Initiator	0.013	0.026	0.007	0.008	0.008	0.021	0.016	0.016	0.003	0.009	0.006
Parental Behavior	0.127	0.000	0.000	0.001	0.000	0.002	0.000	0.001	0.094	0.000	0.122
Affiliation Receiver	0.020	0.016	0.004	0.002	0.012	0.007	0.002	0.01	0.047	0.009	0.045
Affiliation Receiver Event	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000

Table S23. Red-ruffed lemurs: The table presents the group variance and individual variability for the categories with variance different from zero in at least one of the individuals in the group.

		Ft	Sf	Ma	Pn	Sh	Cl	Rs	Tx
<b>Behavioral Categories</b>	<b>group variance</b>	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility	Individual Flexibility
Self-grooming	0.005	0.006	0.003	0.011	0.005	0.007	0.003	0.006	0.002
Solitary Play	0.004	0.000	0.000			0.000	0.015	0.000	0.000
Sent Marking	0.000	0.000	0.000	0.000		0.001	0.000	0.000	0.000
Vocalizations	0.000	0.001	0.000			0.000	0.000	0.000	0.000
Play Initiator	0.001	0.000	0.001	0.000	0.000	0.000	0.000	0.004	0.000
Sex Initiator	0.000		0.000			0.000		0.001	0.000
Affiliation Initiator	0.008	0.001	0.003	0.011	0.000	0.002	0.020	0.013	0.000
Affiliative Receiver	0.007	0.000	0.001	0.002	0.001	0.001	0.021	0.009	0.000



Table S24. The table presents the abbreviations of the behavioral categories analyzed using the EthoSeq Software to analyze the behavioral transitions and sequences.

<b>BEHAVIOR CATEGORY</b>	<b>BEHAVIOR</b>	<b>ABBREVIATION</b>
<b>NON SOCIAL BEHAVIORS</b>	Self-grooming	Selfg
	Scent Marking	Scent
	Solitary Play	Solplay
	Huddling	Hudd
	Vocalizations	Voc
<b>SOCIAL BEHAVIOR</b>	Affiliation Initiator	Affi
	Sex Initiator	Sexi
	Play Initiator	Playi
	Parental Behaviour	Parent
	Ritual Agonism Initiator	Ritagi
	Aggression Initiator	Effagi
	Ritual Submission Initiator	Ritsubi
	Effective Submission Initiator	Effsubi
	Affiliative Receiver	Affir
	Infant Affiliation Receiver	Affrinfant
	Sex Receiver	Sexr
	Play Receiver	Playr
	Ritual Agonism Receiver	Ritagr
	Aggression Receiver	Effagr
	Ritual Submission Received	Ritsubr
Effective Submission Received	Effsubr	
<b>RARE</b>	Abnormal Behavior	Abnorm

Table S25. Ring-tailed Lemurs. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S7). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group (Continued on the next pages).

	<b>Group</b>	<b>Cot</b>	<b>Cos</b>	<b>Den</b>	<b>Jul</b>	<b>Maz</b>	<b>Min</b>	<b>Ore</b>	<b>Pul</b>	<b>Ron</b>	<b>Vel</b>											
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>											
<b>Huddling</b> <b>(Hudd)</b>	Affi Ini	31.58 %	Affi Ini	33.33 %		Affi Ini	33.33 %	EffeA gRec	42.86 %	Affi Ini	40.00 %	Sg	80.00 %	Affi Ini	56.2 %	Affi Ini	40.00 %	Affi Ini	25.00 %	Affi Rec	66.67 %	
	Affi Rec	22.37 %	Scra	33.33 %		SM	66.67 %			Affi Rec	40.00 %					Affi Rec	40.00 %	Affi Rec	25.00 %			
	Sg	18.42 %	SM	33.33 %															Voc	25.00 %		
<b>Vocalizations</b> <b>(Voc)</b>	Affi Ini	32.14 %	Sg	42.86 %	Sg	27.27 %	Sg	27.27 %	Affi Ini	33.33 %	Affi Ini	33.33 %	Sg	66.67 %	Sg	27.7 %	Affi Rec	33.33 %	Sg	28.57 %	Affi Rec	44.44 %
	Sg	27.38 %	Affi Ini	28.57 %	Affi Ini	27.27 %	Affi Ini	63.64 %			Hud	33.33 %	SM	33.33 %	Affi Ini	33.3 %	Parent	33.33 %	Affi Ini	42.86 %		
	Affi Rec	19.05 %			Scr	27.27 %					EffeAg Ini	33.33 %			Affi Rec	33.3 %						
<b>Self-grooming</b> <b>(Sg)</b>	Affi Ini	32.35 %	Affi Ini	36.84 %	Affi Ini	44.44 %	Scr	42.86 %	Affi Ini	26.32 %	Affi Ini	52.00 %	Affi Ini	27.27 %	Affi Ini	55.0 %	Hudd	50.00 %	Affi Ini	42.11 %	Affi Rec	64.71 %
	Affi Rec	21.76 %					Voc	28.57 %					Scr	27.27 %	Voc	25.0 %	Affi Rec	33.33 %	Hudd	31.58 %		
	Scr	14.71 %																				
<b>Scratching</b> <b>(Scra)</b>	Sg	29.11 %	Affi Ini	27.27 %	Affi Ini	33.33 %	Voc	26.67 %	Sg	42.86 %	Affi Ini	40.00 %	Sg	50.00 %	Affi Ini	80.0 %	Voc	50.00 %	Affi Ini	37.50 %	Affi Rec	40.00 %
	Affi Ini	22.78 %	Sg	54.55 %					Voc	28.57 %	Affi Rec	60.00 %	SM	25.00 %			Sg	25.00 %			Parent	30.00 %
	Affi Rec	16.46 %							Hudd	28.57 %							Affi Rec	25.00 %				
<b>Sent Marking</b> <b>(SM)</b>	Affi Ini	30.00 %	Affi Ini	100.0 %	EffeSubIni	33.33 %	Sg	100.0 %	Voc	100.0 %	Affi Ini	50.00 %	Affi Ini	33.33 %	Affi Ini	50.0 %			Affi Ini	25.00 %		
					Parent	33.33 %					EffeAg Ini	50.00 %					Hudd	50.0 %		Affi Rec	25.00 %	
					RitAg Rec	33.33 %														Hudd	25.00 %	

	<b>Group</b>		<b>Cot</b>		<b>Cos</b>		<b>Den</b>		<b>Jul</b>		<b>Maz</b>		<b>Min</b>		<b>Ore</b>		<b>Pul</b>		<b>Ron</b>		<b>Vel</b>		
	<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		
																			Voc	25.00			
<b>Affiliation Initiator</b>	Affir Rec	40.93 %	Affi Re	41.94 %	Affi Rec	38.89 %	Affi Rec	37.50 %	Sg	33.33 %	Affi Rec	43.90 %	Affi Rec	26.67 %	Affi Rec	34.00 %	Affi Rec	61.90 %	Affi Rec	47.06 %	Affi Rec	47.62 %	
<b>(Affi ini)</b>	Sg	21.62 %			Voc	27.78 %	Scr	25.00 %	(Affi Rec	<25 %)	Sg	26.83 %	Sg	40.00 %				Sg	29.41 %				
<b>Play Initiator (Play ini)</b>	Parent	100.00 %			Parent	100.00 %																	
<b>Ritual Agonism Initiator</b>	Sg	30.00 %	Sg	66.67 %	Voc	50.00 %							EffeSu bRec	60.00 %									
<b>(Rit ag)</b>	EffeSubRec	30.00 %	EffeSubIni	33.33 %	RitAgRec	50.00 %																	
	RitAgRec	20.00 %																					
<b>Aggression Initiator (EffeAgIni)</b>	EffeSubRec	85.71 %										EffeSu bRec	100.00 %	EffeSu bRec	100.00 %			EffeSu bRec	100.00 %			EffeSu bRec	33.33 %
<b>Effective Submission Initiator (EffeSubIni)</b>	EffeAgIni	14.29 %																				EffeAgRec	66.67 %
	RitAgIni	21.05 %	RitAgIni	100.00 %	RitAgIni	50.00 %	Scr	100.00 %	Sg	75.00 %	AffiIni	100.00 %	RitAgIni	100.00 %	AffiIni	50.00 %			EffSu bRec	50.00 %	AffiRec	100.00 %	
	Sg	21.05 %			SM	50.00 %			Scr	25.00 %				Sg	25.00 %			AffiRec	50.00 %				
	AffiIni	15.79 %												SM	25.00 %								
	SM	15.79 %																					
<b>Parental Behavior (Parent)</b>	AffiRec	49.49 %			AffiIni	40.00 %	AffiRec	66.67 %	Sg	100.00 %	AffiRec	50.00 %	AffiRec	100.00 %	AffiRec	33.33 %	AffiRec	47.50 %	Hud	100.00 %	AffiRec	56.76 %	
	Hudd	17.17 %					Scr	33.33 %			Sg	25.00 %			AffiIni	33.33 %	Hudd	27.50 %					
															Sg	33.33 %							
<b>Affiliation</b>	Affi	45.97 %	AffiIni	54.17 %	Affi	38.46 %	Affi	27.27 %	Affi	62.50 %	AffiIni	52.94 %	AffiIni	45.45 %	Affi	58.6 %	Parent	28.57 %	Affi	69.70 %	AffiIni	34.00 %	

	Group 1st trans.		Cot 1st trans.		Cos 1st trans.		Den 1st trans.		Jul 1st trans.		Maz 1st trans.		Min 1st trans.		Ore 1st trans.		Pul 1st trans.		Ron 1st trans.		Vel 1st trans.		
<b>n Receiver (Affi Rec)</b>	Ini	%	%	Ini	%	Ini	%	Ini	%	%	%	Ini	2%	%	Ini	%	Ini	%	%				
						Sg	27.27%				SM	45.45%		(Affi Ini	<25%)								
						Scr	36.36%																
<b>Sex Receiver (Sex Rec)</b>	Play Rec	100.00%									Play Rec	100.00%											
<b>Play Receiver (Play Rec)</b>	Affi Rec	40.00%		Play Ini	100.00%					Affi Ini	50.00%	EffeAg Ini	100.00%				Affi Rec	100.00%					
	Affi Ini	20.00%								Affi Rec	50.00%												
	Play Ini	20.00%																					
	EffeAg Ini	20.00%																					
<b>Ritual Agonism Receiver (RitAg Rec)</b>	EffeSub Ini	50.00%	Voc	100.00%	EffeSub Ini	66.67%						EffeSub Ini	50.00%										
	SM	16.67%			SM	33.33%						EffeSub Rec	50.00%										
	Voc	16.67%																					
	EffeSub Rec	16.67%																					
<b>Aggression Receiver (EffeAg Rec)</b>	EffeSub Ini	75.00%					EffeSub Ini	100.00%	EffeSub Ini	100.00%	Affi Rec	100.00%	Affi Rec	100.00%	EffeSub Ini	80.00%		EffeSub Ini	100.00%	EffeSub Ini	100.00%	EffeSub Ini	50.00%
																						EffeSub Rec	50.00%
<b>Effective Submission</b>	Affi Rec	27.78%	Affi Ini	100.00%							Affi Ini	50.00%	RitAgIni	44.44%			Affi Rec	100.00%	EffeSub Ini	100.00%	Affi Rec	100.00%	

	<b>Group</b>	<b>Cot</b>	<b>Cos</b>	<b>Den</b>	<b>Jul</b>	<b>Maz</b>	<b>Min</b>	<b>Ore</b>	<b>Pul</b>	<b>Ron</b>	<b>Vel</b>
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>
<b>Receiver</b>	Affi Ini	22.22				Affi	50.00				
<b>(EffeSui)</b>	RitAgIn	22.22				Rec	%				
<b>bRec)</b>	i	%									

Table S26. Red-ruffed Lemurs. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S7). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group (Continued on the next pages).

	<b>Group</b>	<b>Ft</b>	<b>Sf</b>	<b>Ma</b>	<b>Pn</b>	<b>Sh</b>	<b>Cl</b>	<b>Rs</b>	<b>Tx</b>				
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>				
<b>Selfgrooming</b>	Affi Ini	26.92	36.36	32.00	Affi	28.57	Affi	50.00					
<b>(Sg)</b>	Affi Rec	16.03	27.27		Rec	%	Rec	%					
	EffeAgIni	14.10	36.36				Affi	33.33					
		%	%				Ini	%					
<b>Solitary Play</b>	SM	28.07		100.00			EffeAgIni	100.00	EffeAgIni	33.33		37.93	40.00
<b>(SoliPlay)</b>	Affi Ini	21.05			Affi Rec	%		%	Affi Ini	%		Affi Ini	%
	EffeAgIni	17.54							Sex Ini	%			
		%											
<b>Sent Marking</b>	Soliplay	27.63	33.33	50.00	Sg	60.00		41.67	SoliPlay	90.91		33.33	26.92
<b>(SM)</b>	Sg	19.74		50.00		%		%		%		33.33	26.92
	Affi Ini	15.79			Play Ini	%						Sg	%
		%										33.33	%
												SoliPlay	%
<b>Vocalizations</b>	Sg	35.90		25.00				33.33		40.00		60.00	40.00
<b>(Voc)</b>	Affi Ini	20.51		62.50	Affi Ini	%		Affi Ini	%	Sg	%	Sg	%
		%		%								SM	%
					Sg	%		Sg	%				

	<b>Group</b>	<b>Ft</b>	<b>Sf</b>	<b>Ma</b>	<b>Pn</b>	<b>Sh</b>	<b>Cl</b>	<b>Rs</b>	<b>Tx</b>									
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>									
	SM	15.38 %																
<b>Ritual Agonism</b>	Sg	28.57 %	Affi Ini %	66.67 %			37.50 %	50.00 %	EffeAgI ni %	100.00 %								
<b>Initiator</b>	Voc	21.43 %	Voc %	33.33 %			25.00 %	50.00 %										
<b>(RitAgIni)</b>	Affi Ini EffeAgI ni	14.29 % 14.29 %																
<b>Aggression Initiator</b>	Sg	32.35 %	Sg %	38.46 %	Sg %	25.00 %	Affi Rec %	100.00 %	40.00 %	26.32 %	Sg %	33.33 %						
<b>(EffeAgIni)</b>				Voc %	Affi Ini EffeAgR ec %	25.00 %			26.32 %									
<b>Ritual Submission</b>	EffeAgR ec	50.00 %							100.00 %		EffeAgR ec	100.00 %						
<b>Initiator</b>	Sg	50.00 %																
<b>(RitSubIni)</b>																		
<b>Effective Submission</b>	Sg	40.00 %	Sg %	33.33 %	Sg %	100.00 %			Affi Rec %	100.00 %	Sg %	100.00 %	Affi Ini %	33.33 %				
<b>Initiator</b>	Voc	20.00 %	Voc %	66.67 %									SM EffeAgI ni %	33.33 %				
<b>(EffeSubIni)</b>																		
<b>Play Initiator</b>	Affi Ini	31.25 %	Affi Rec %	50.00 %	Affi Rec %	30.00 %			Sg %	100.00 %	Sg %	60.00 %	EffeAgR ec %	33.33 %	Affi Ini %	61.11 %	SM %	100.00 %
<b>(PlayIni)</b>	Sg	27.08 %	EffeAgI ni %	50.00 %	Affi Ini %	30.00 %												
<b>Sex Initiator</b>	EffeAgR ec	30.00 %			SM %	33.33 %			Affi Rec %	100.00 %					Affi Rec %	25.00 %	SM %	100.00 %
<b>(SexIni)</b>	SM	30.00 %			EffeAgR ec %	66.67 %									EffeAgR ec %	25.00 %		
	Play Ini	20.00 %													Play Ini %	50.00 %		

	<b>Group</b>	<b>Ft</b>	<b>Sf</b>	<b>Ma</b>	<b>Pn</b>	<b>Sh</b>	<b>Cl</b>	<b>Rs</b>	<b>Tx</b>									
	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>	<b>1st trans.</b>									
	Affi Rec	20.00 %																
<b>Affiliation</b>	Affi Rec	26.52 %	Sg	27.27 %	Sg	34.62 %	<25.00 %	Affi Rec	100.00 %	Sg	45.45 %	Affi Rec	33.33 %	Sg	26.47 %	SM	47.06 %	
<b>Initiator</b>	Affi Rec	26.52 %				38.46 %				Sg		Affi Rec	33.33 %					
<b>(Affi ini)</b>	Sg			Affi Rec		(Sg	20%)					SoliPlay						
<b>Ritual Agonism</b>	Sg	27.78 %	EffeAgI ni	25.00 %		Affi Rec	66.67 %			EffeAgI ni	28.57 %	EffeAgI ni	50.00 %			Voc	50.00 %	
<b>Receiver</b>	EffeAgI ni	22.22 %	Affi Ini	25.00 %		Affi Ini	33.33 %			Sg	42.86 %	Affi Rec	50.00 %			EffeAgR ec	50.00 %	
<b>(RitAgRec)</b>	Affi Rec	22.22 %	Sg	50.00 %														
	Affi Ini	16.67 %																
<b>Aggression</b>	Affi Ini	24.00 %	EffeAgI ni	66.67 %						Sg	100.00 %	RitAgRe c	100.00 %	Sg	33.33 %	Sg	25.00 %	
<b>Receiver</b>	Affi Ini	16%	EffeSub Ini	33.33 %										Affi Ini	33.33 %	Sm	25.00 %	
<b>(EffeAgRec)</b>																		
<b>Effective Submission</b>	Affi Ini	50.00 %												Sg	50.00 %			
<b>Receiver</b>	Sg	50.00 %												Affi li	50.00 %			
<b>(EffeSubRec)</b>																		
<b>Affiliative</b>	Affi Ini	31.71 %	SM	50%	Affi Ini	35.71 %	Affi Ini	37.50 %	Affi ini	40.00 %	Sg	25.00 %	Sg	31.58 %	Affi Ini	42.86 %	Sg	75.00 %
<b>Receiver</b>	Affi Ini	23.17 %					Sg	50.00 %			EffeAgI ni	25.00 %						
<b>(AffiRec)</b>																		

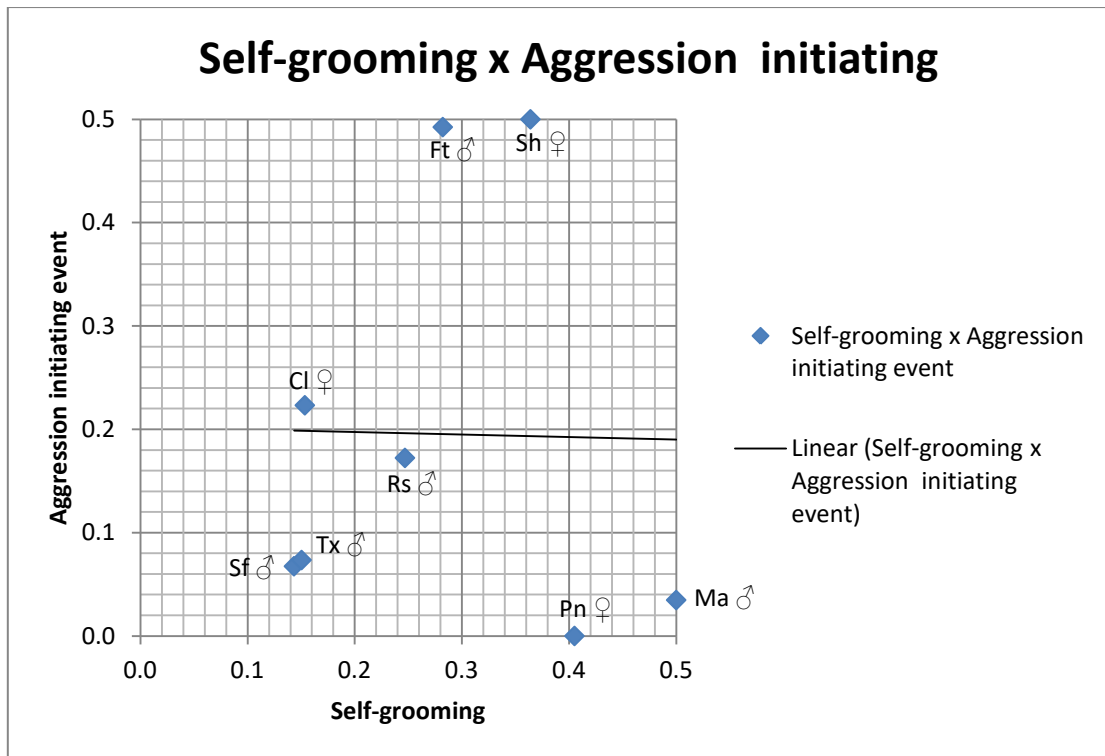


Figure S56. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Aggression initiating

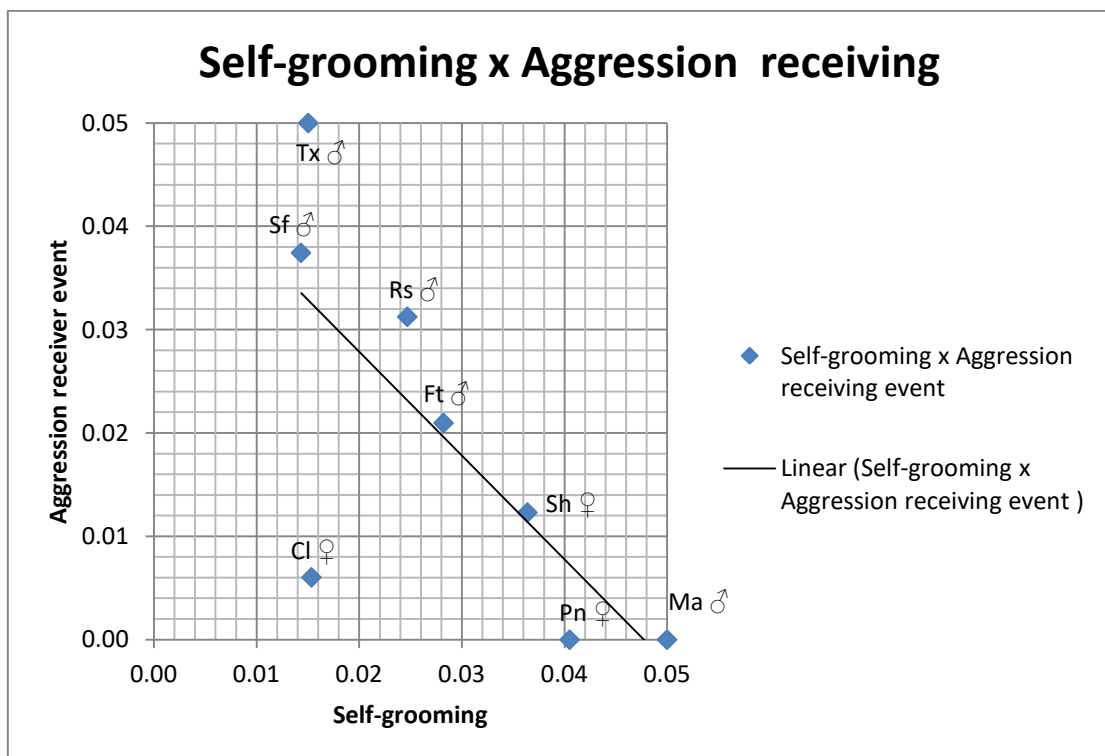


Figure S57. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Aggression receiving



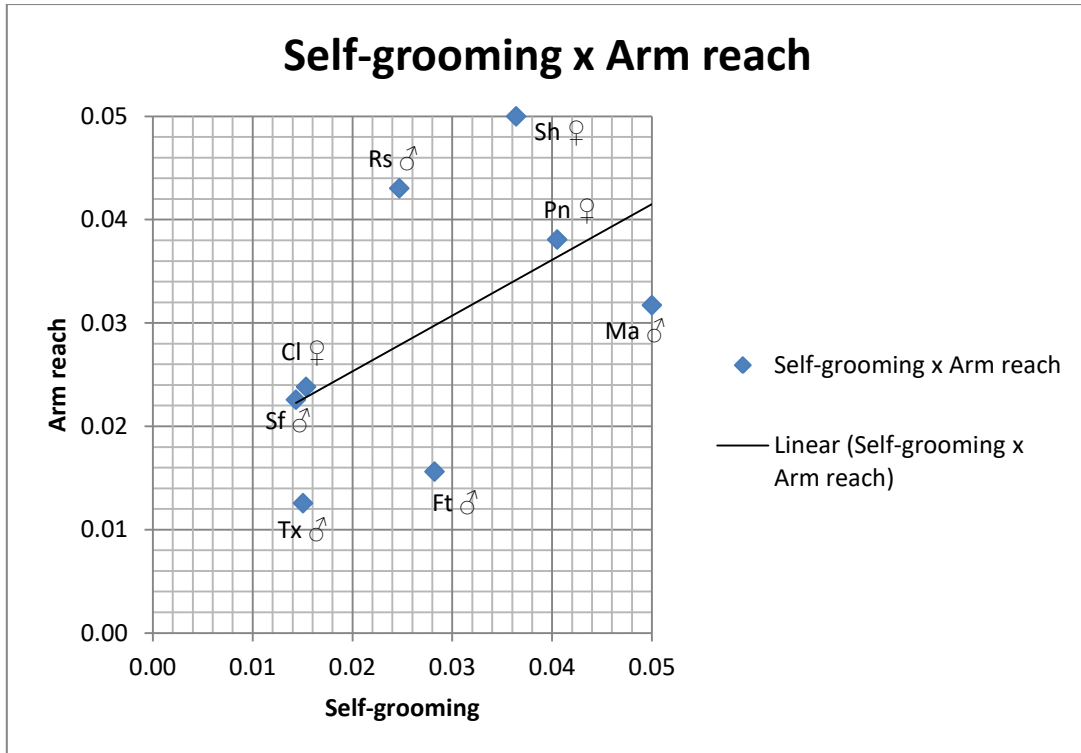


Figure S58. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming  $\times$  Arm reach

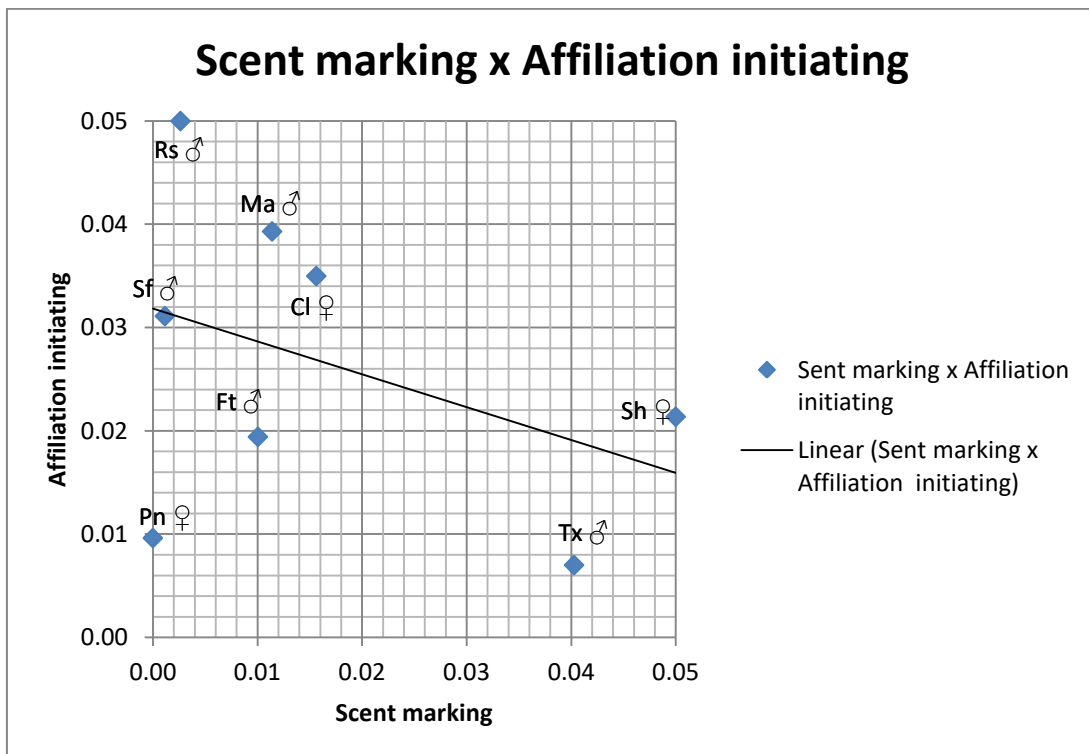


Figure S59. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Scent marking  $\times$  Affiliation initiating

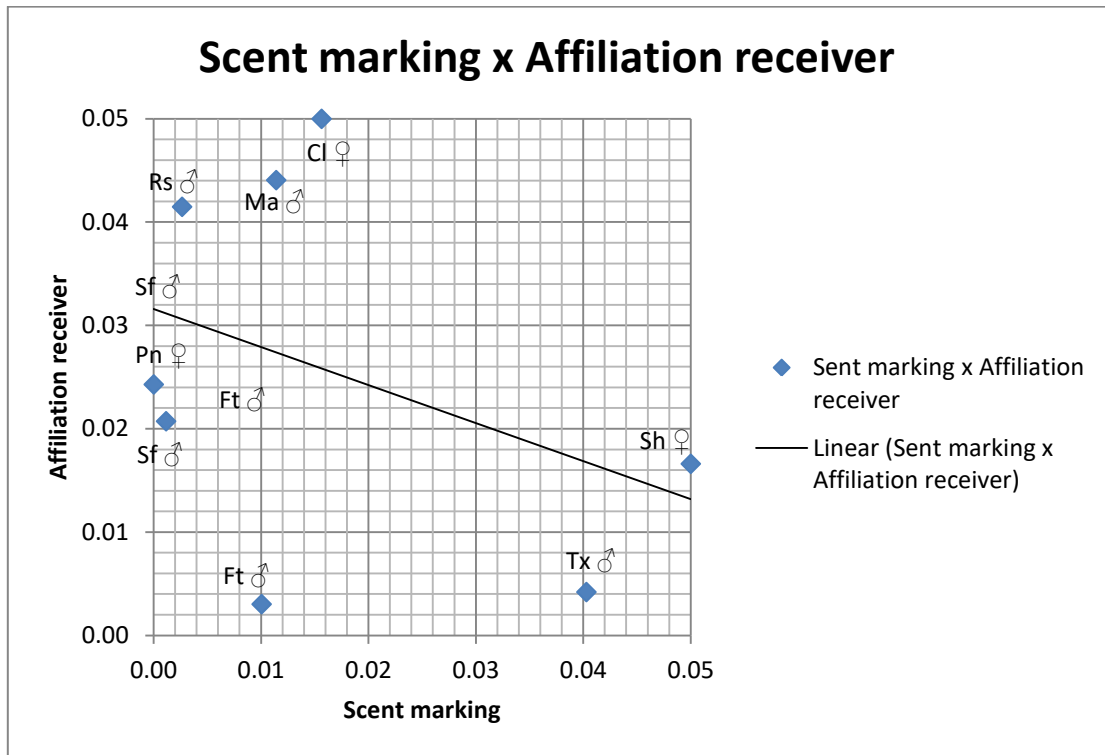


Figure S60. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Scent marking  $\times$  Affiliation receiver

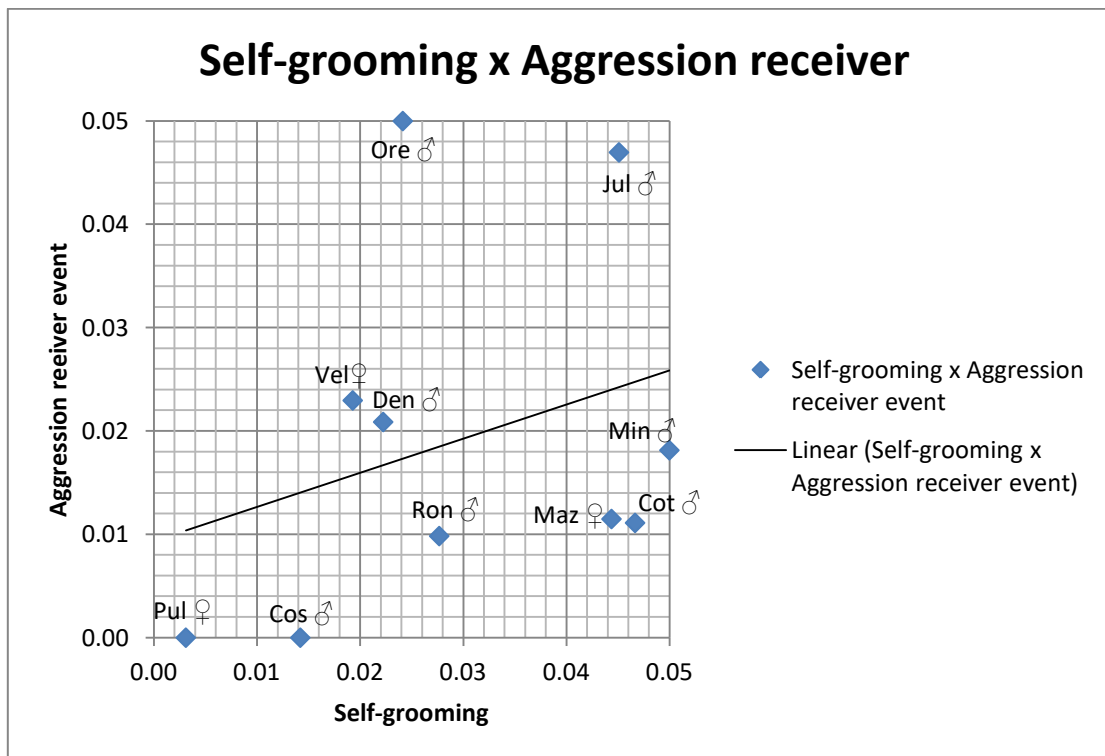


Figure S61. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming  $\times$  Affiliation receiver

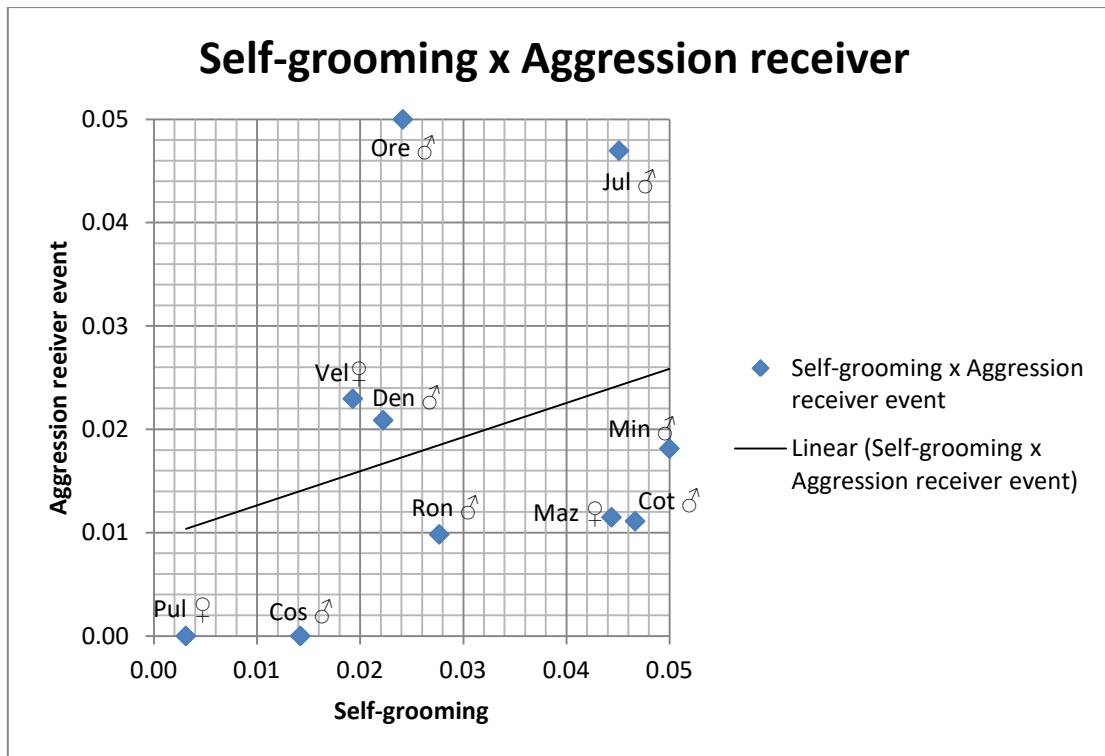


Figure S62. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Aggression receiver

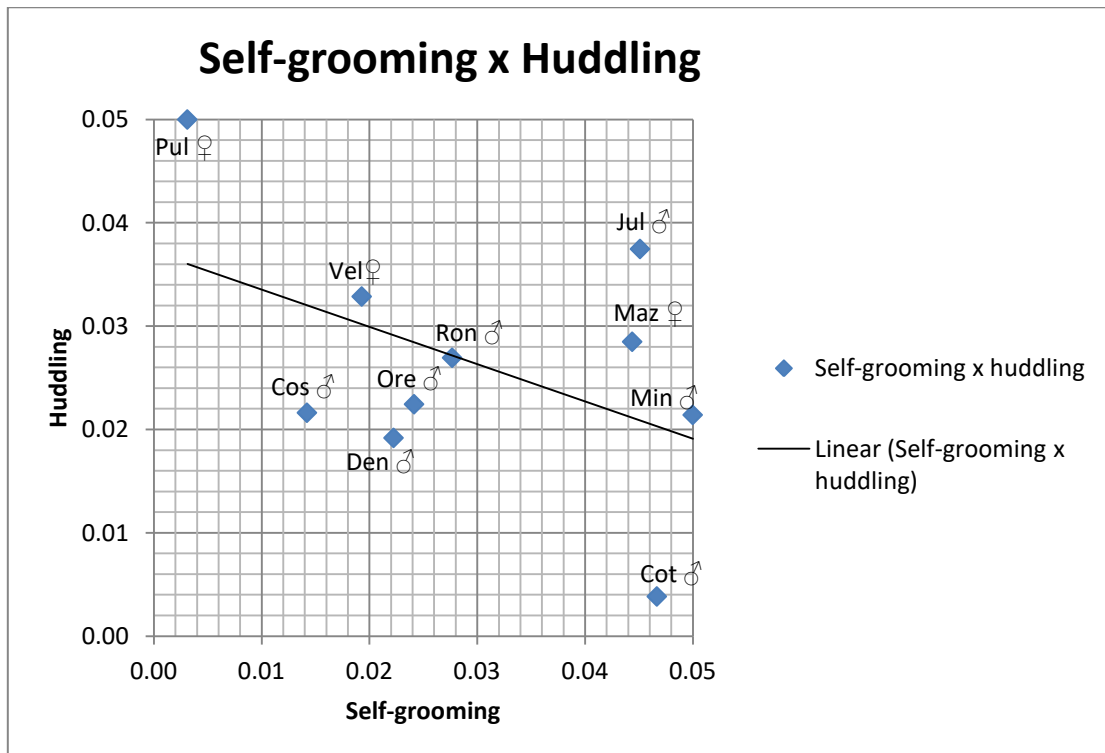


Figure S63. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Huddling

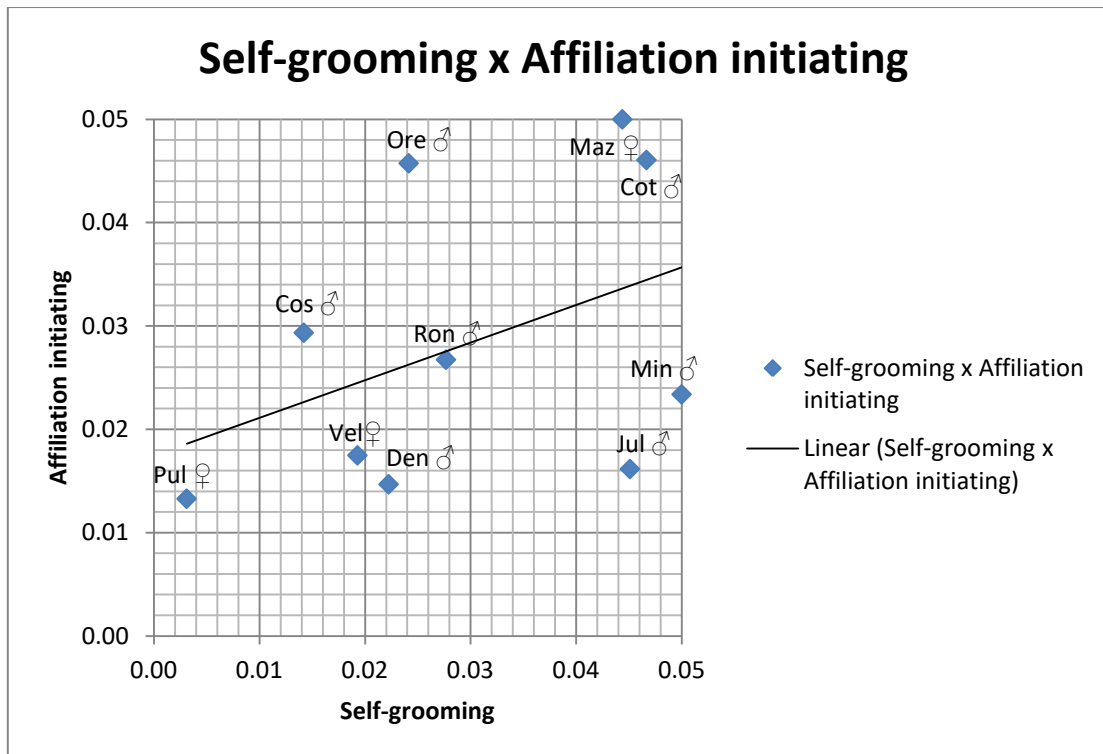


Figure S64. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Affiliation initiating

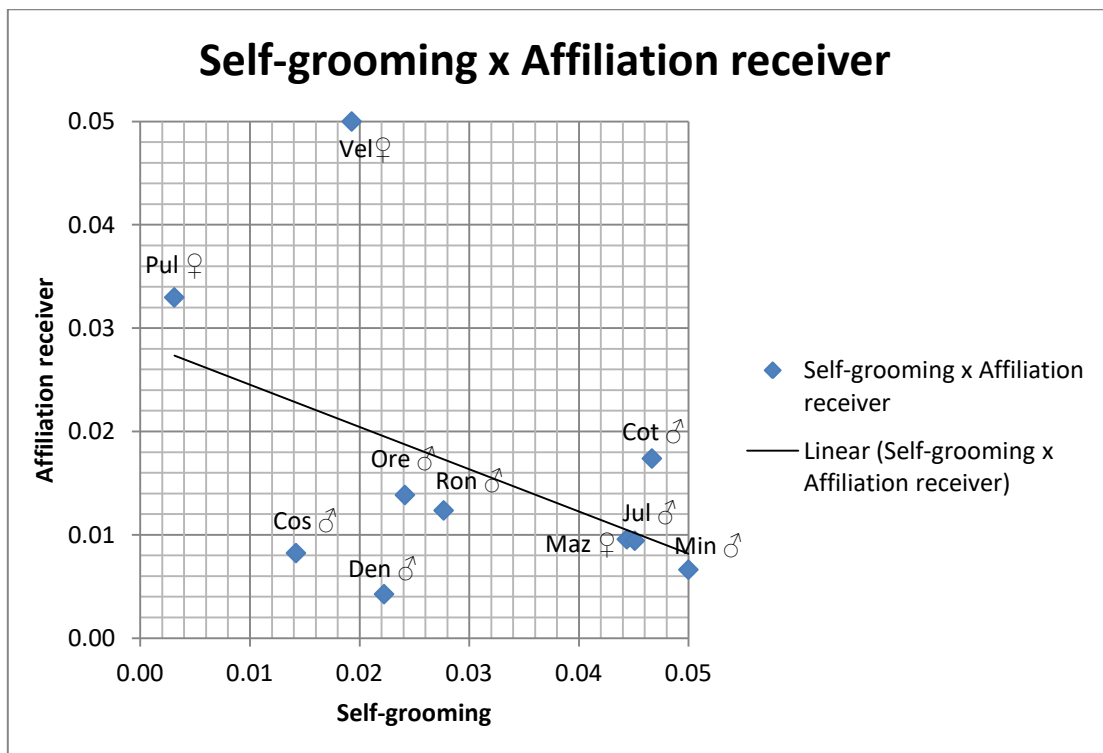


Figure S65. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Affiliation receiver

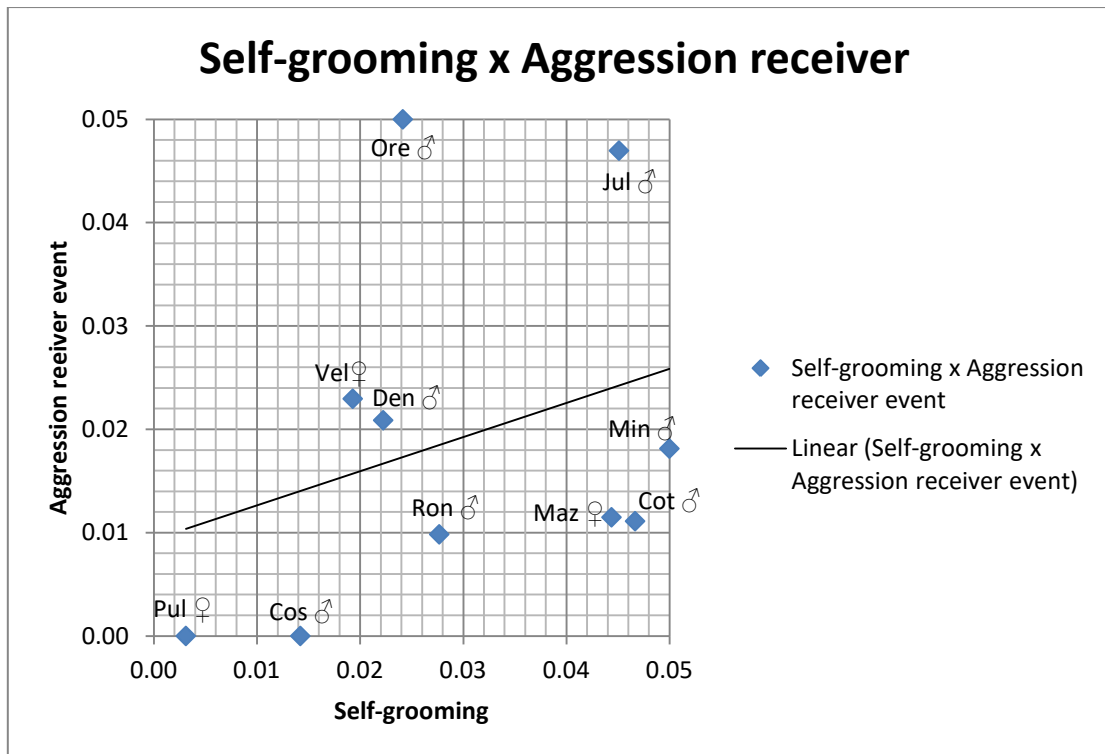


Figure S66. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Aggression receiver

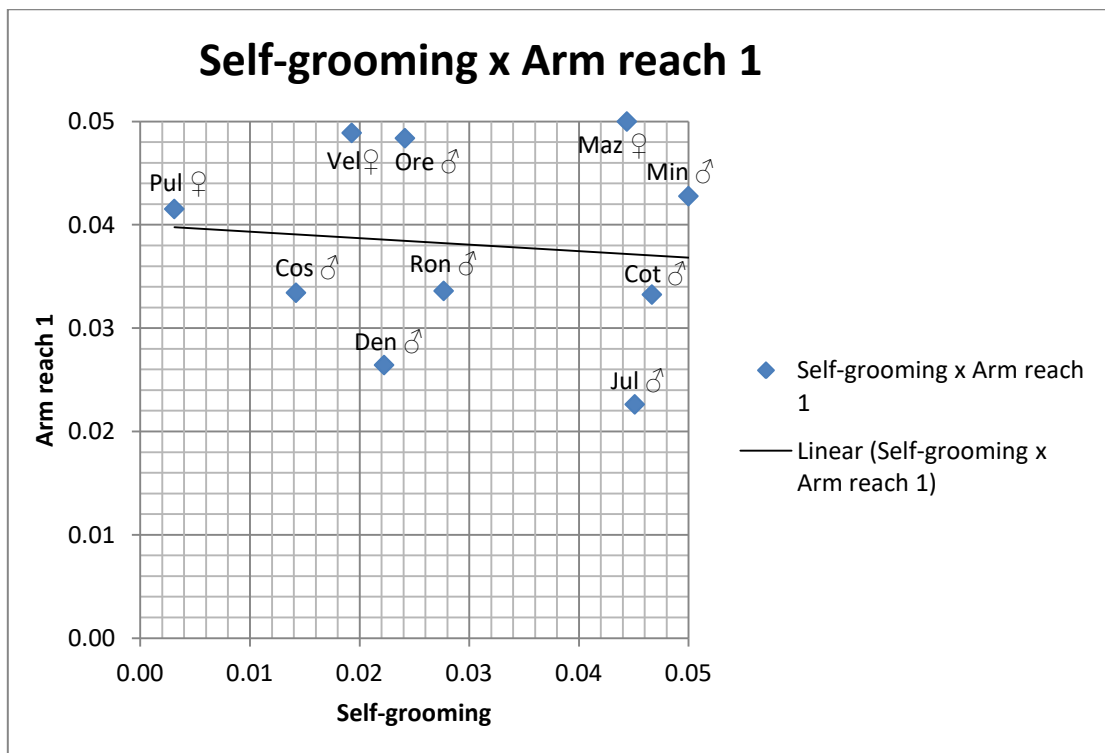


Figure S67. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Arm reach 1

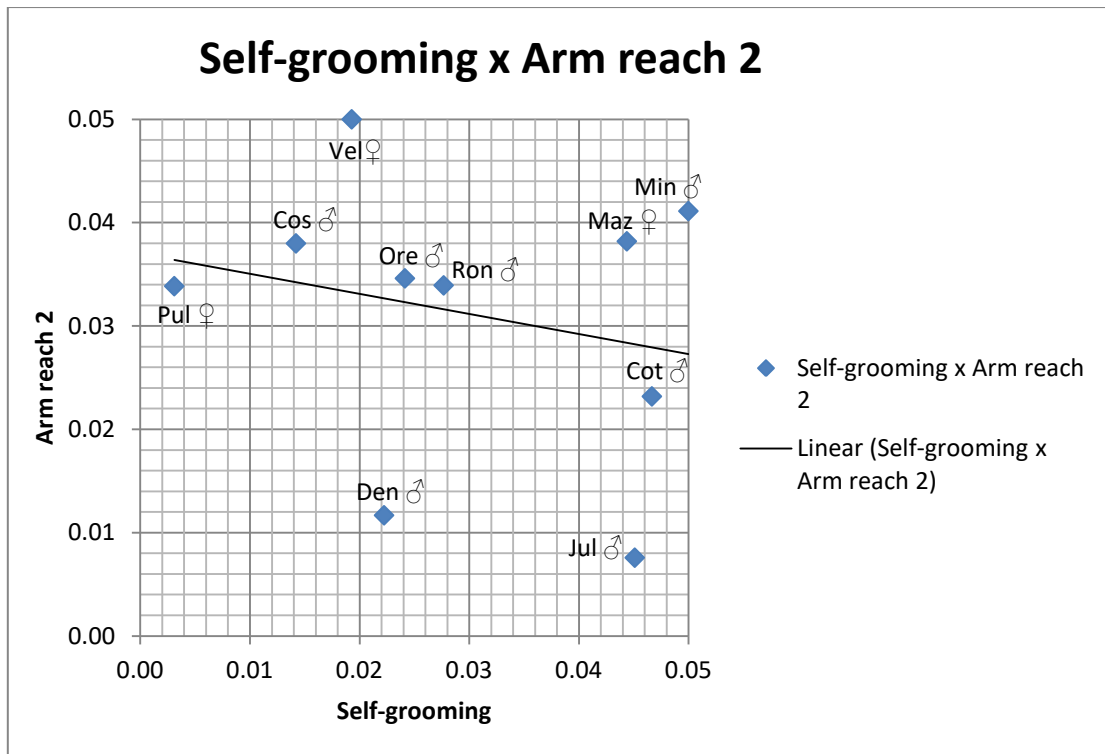


Figure S68. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Arm reach 2

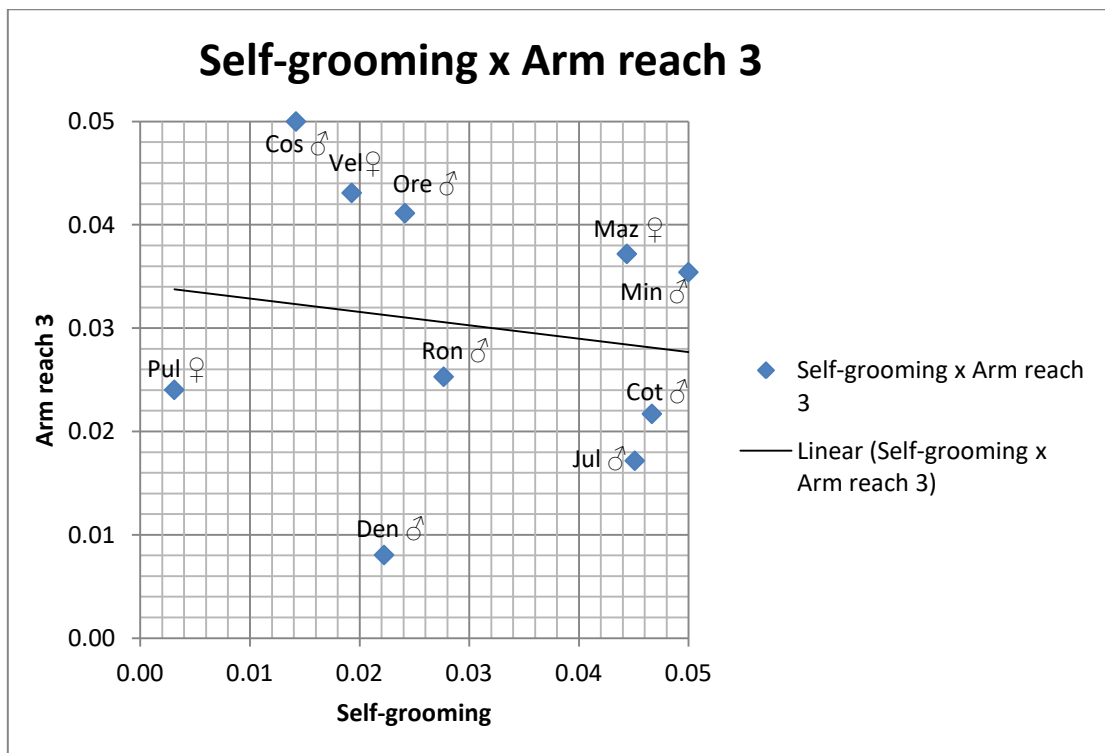


Figure S69. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Arm reach 3

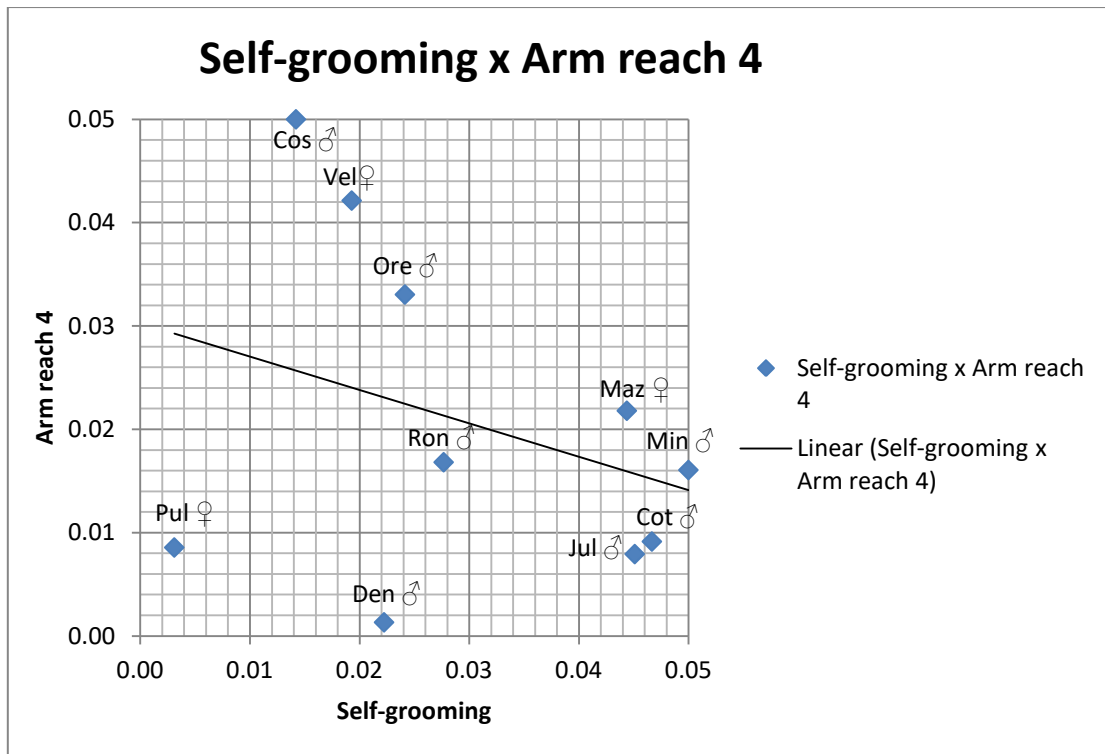


Figure S70. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Arm reach 4

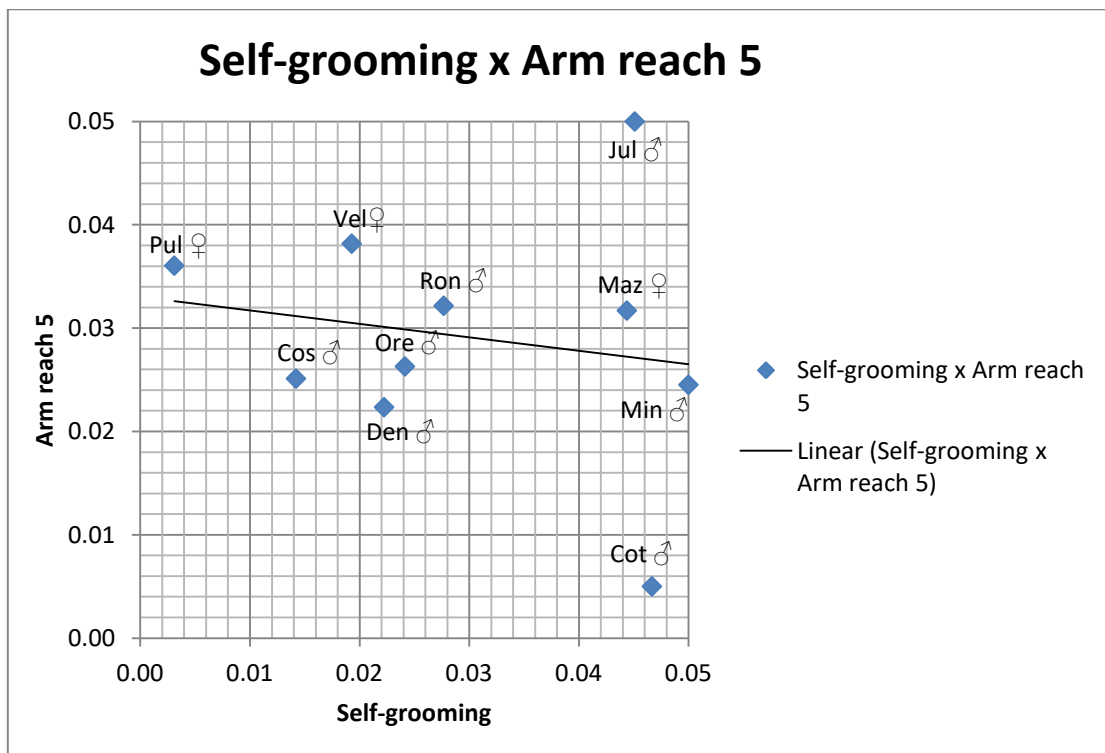


Figure S71. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Arm reach 5

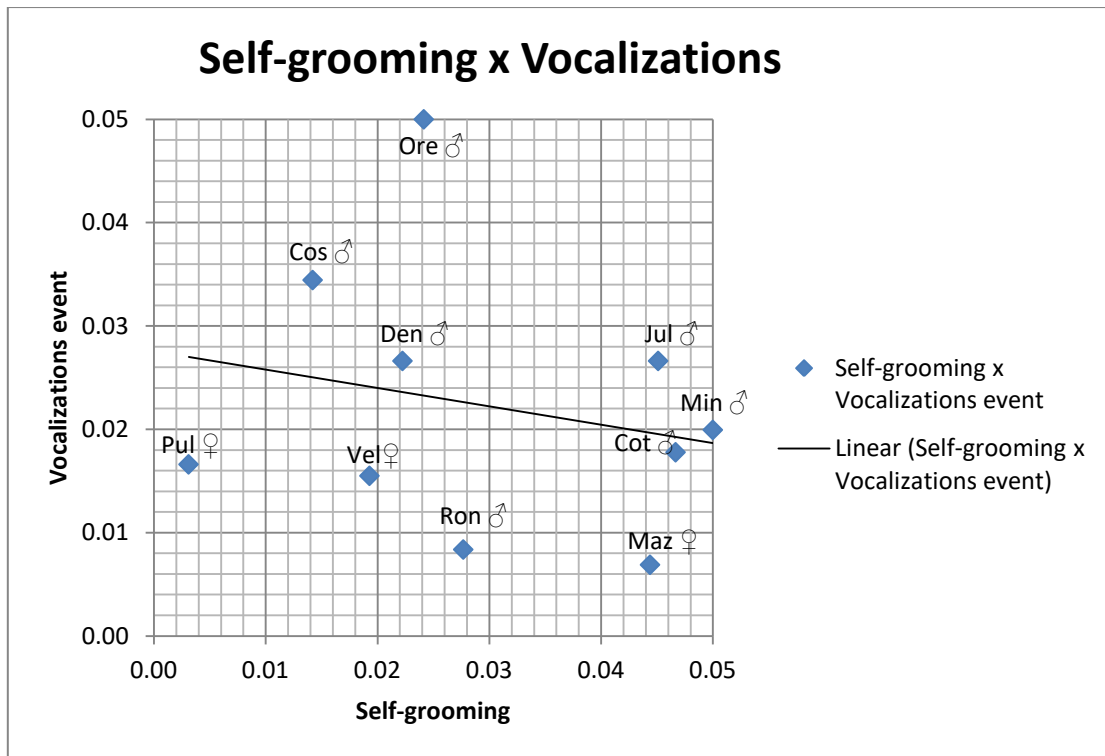


Figure S72. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Vocalizations

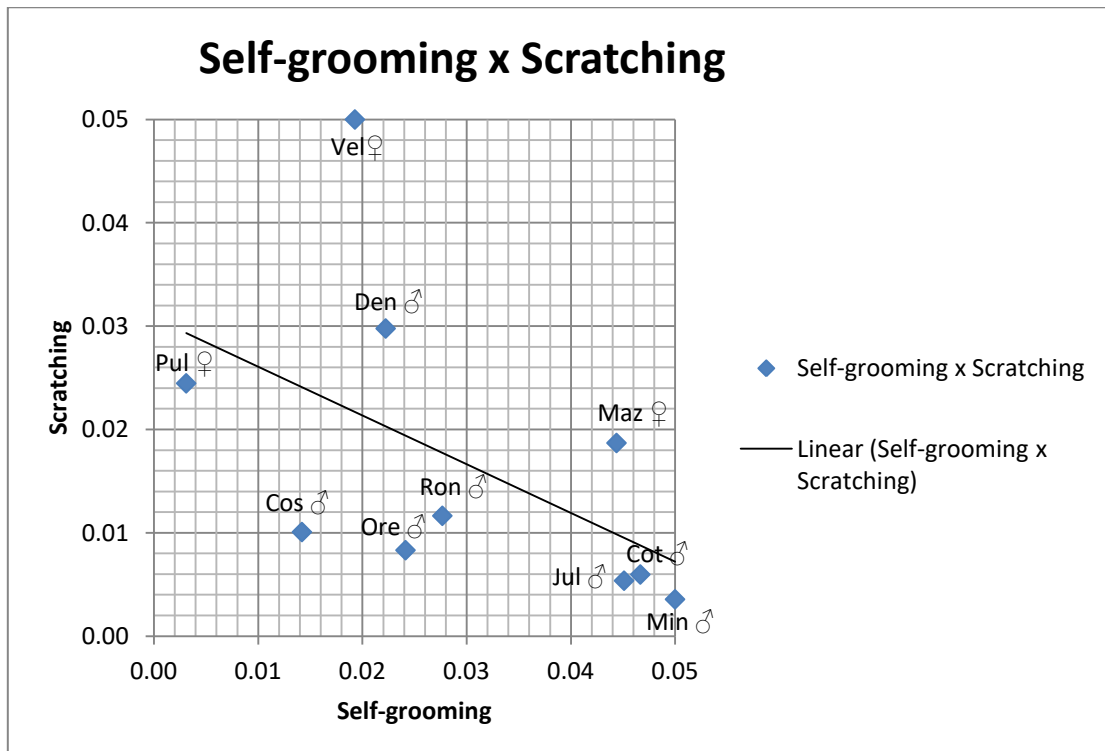


Figure S 73. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Self-grooming × Scratching



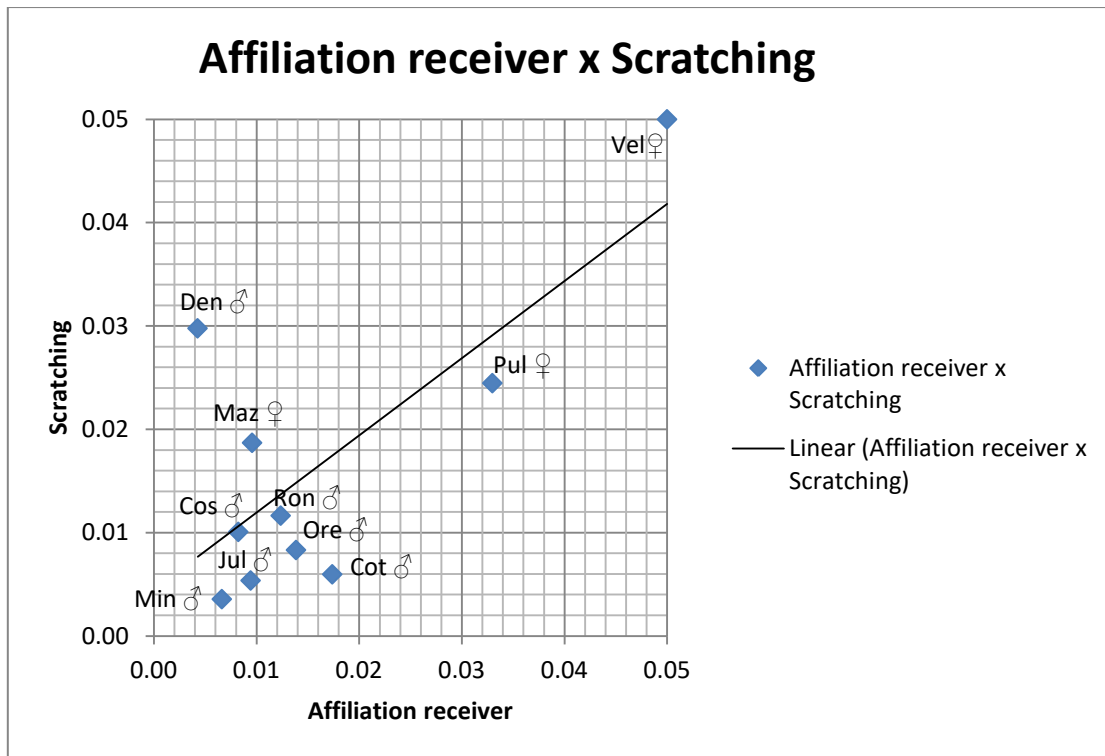


Figure S74. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Affiliation receiver  $\times$  Scratching

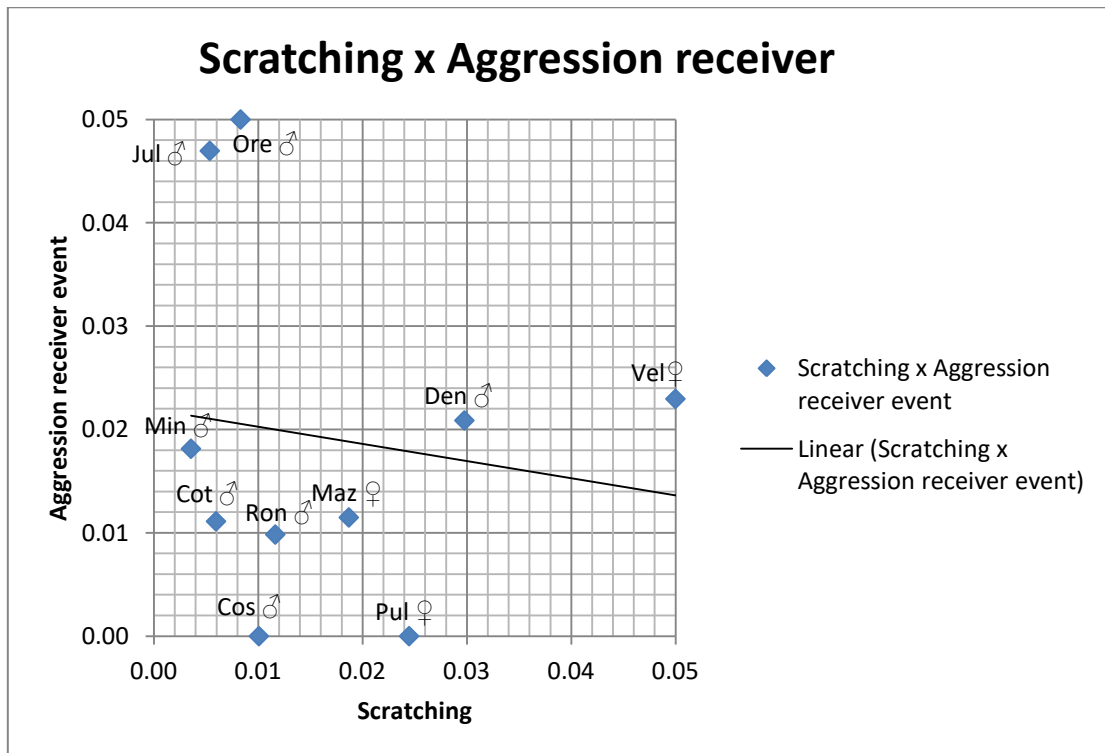


Figure S75. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Scratching  $\times$  Aggression receiver

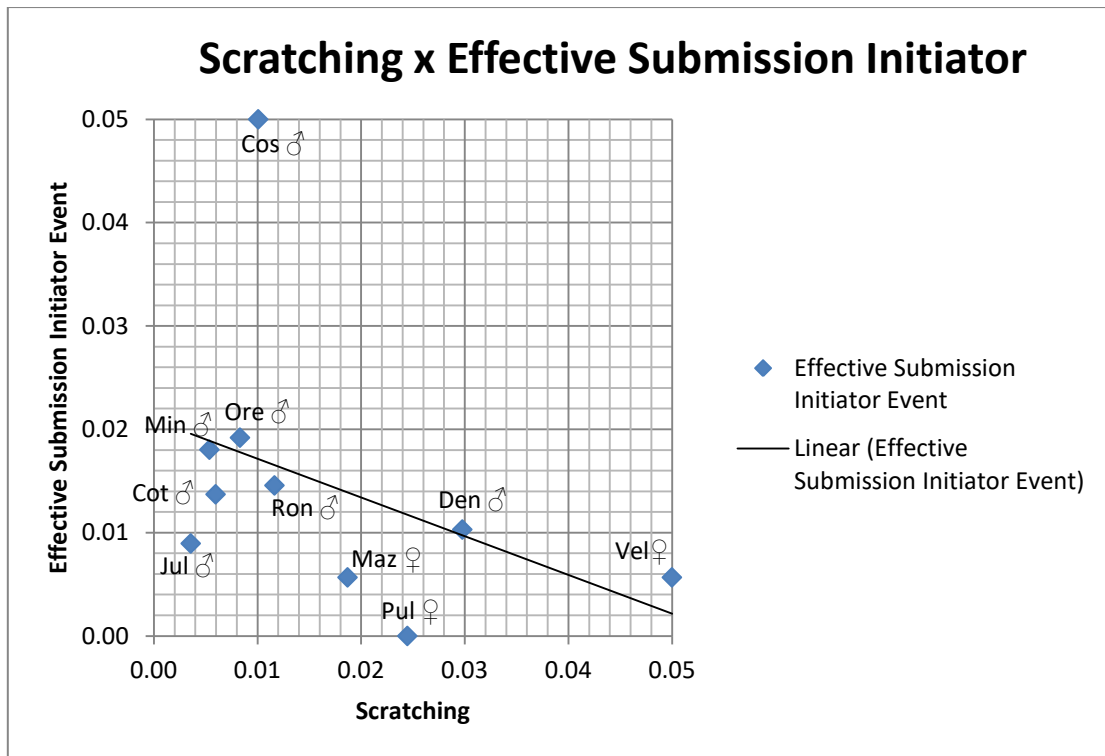


Figure S76. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Scratching × Effective Submission Initiator

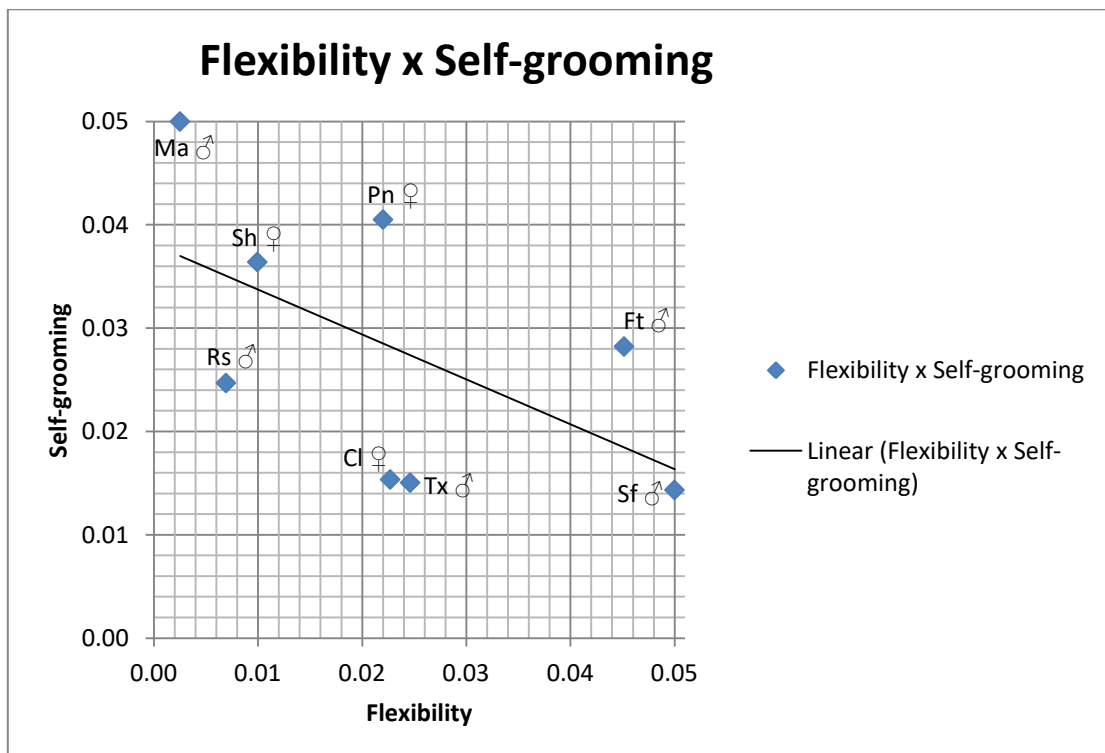


Figure S77. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale), Flexibility × Self-grooming

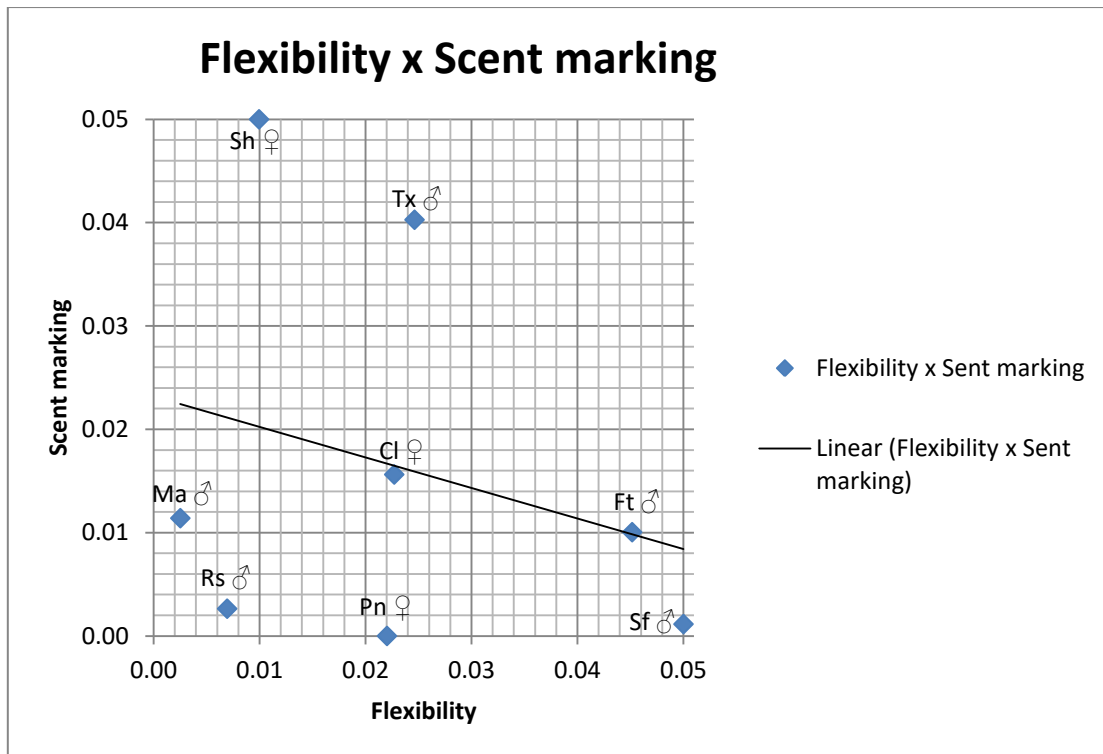


Figure S78. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility × Scent marking

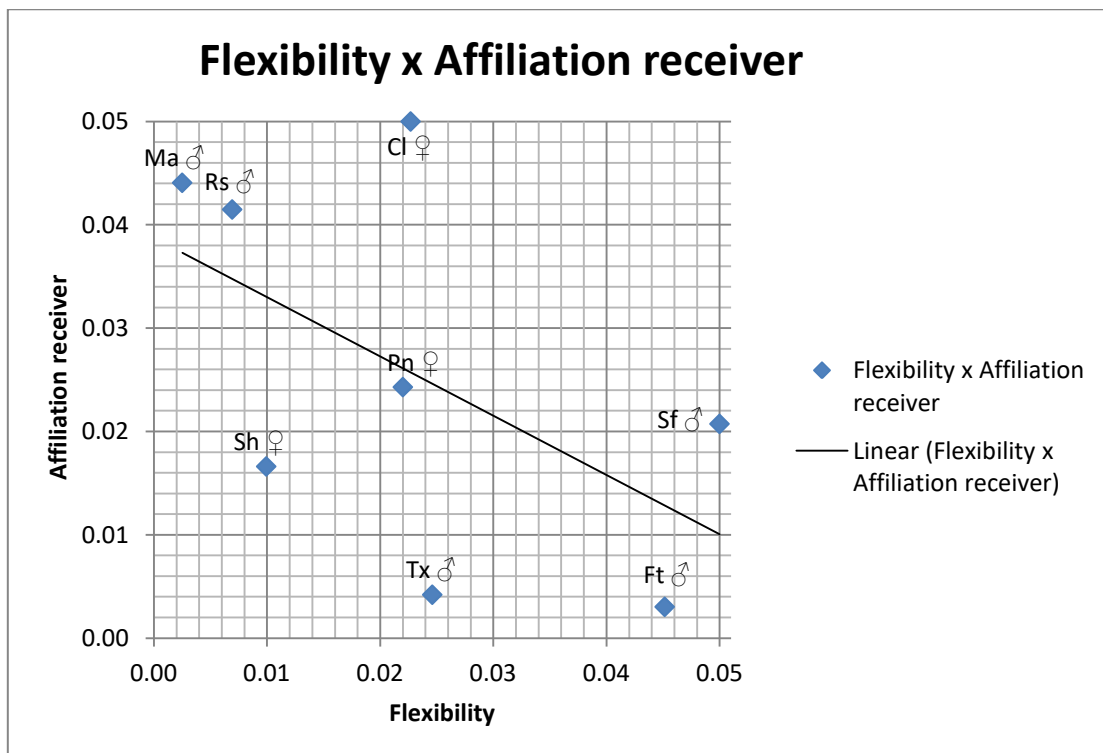


Figure S79. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility × Affiliation receiver

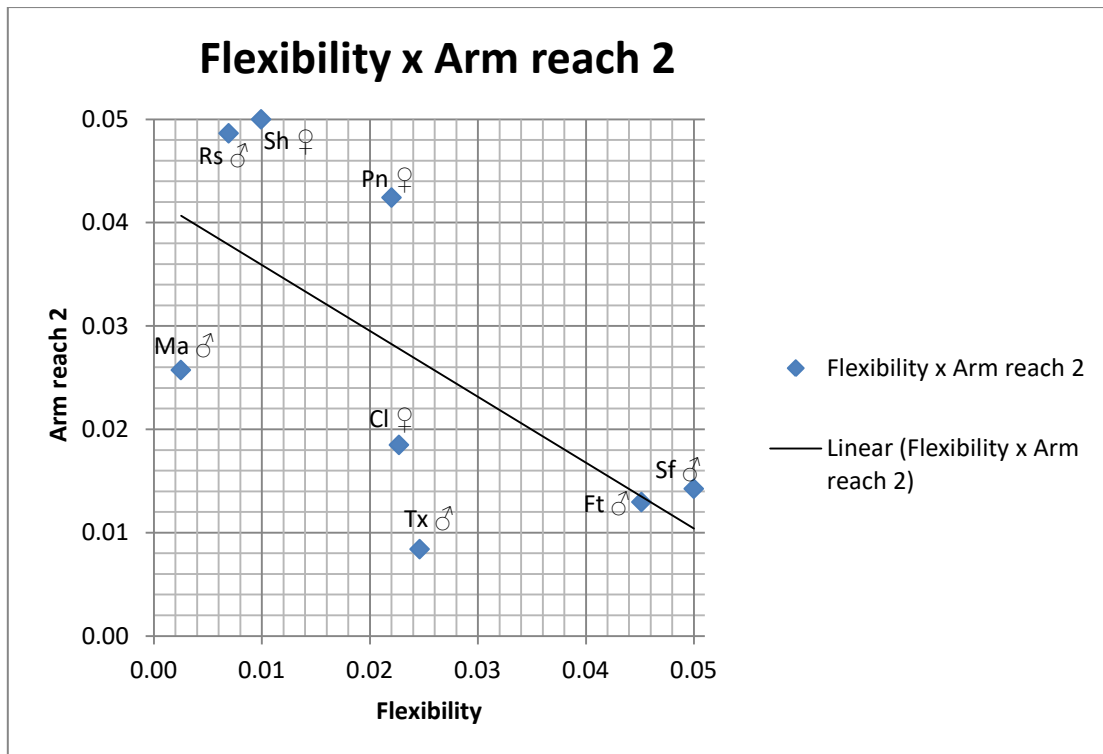


Figure S80. Red-ruffed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility  $\times$  Arm reach 2

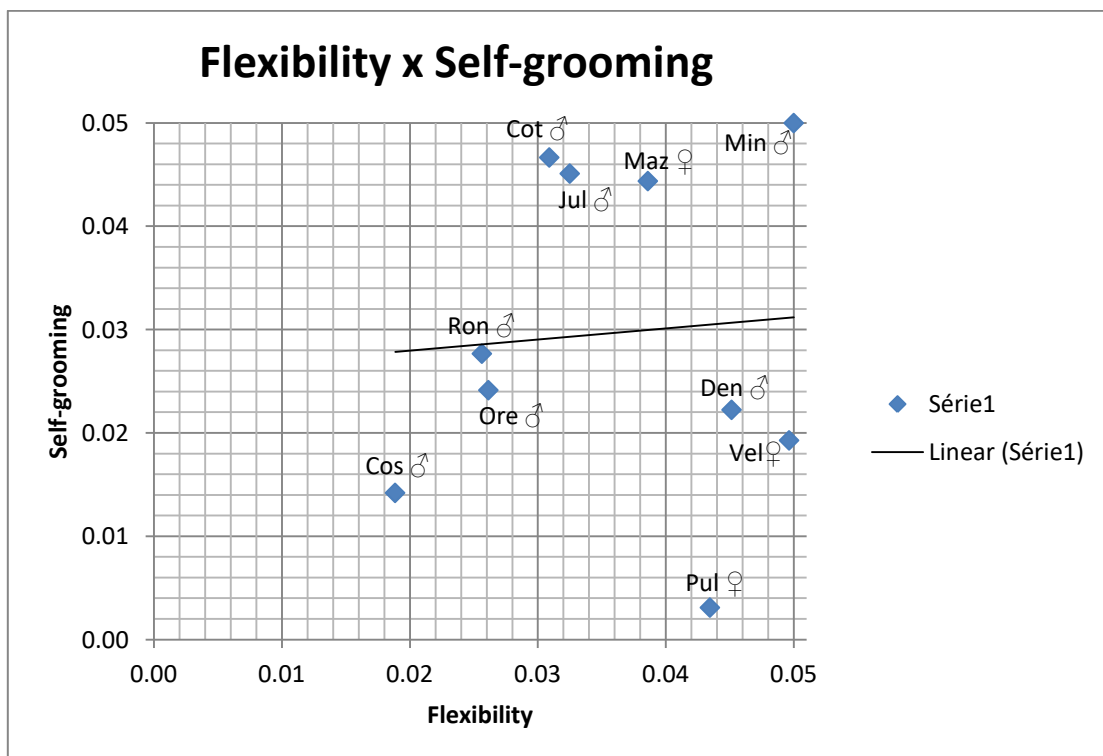


Figure S81. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility  $\times$  Self-grooming

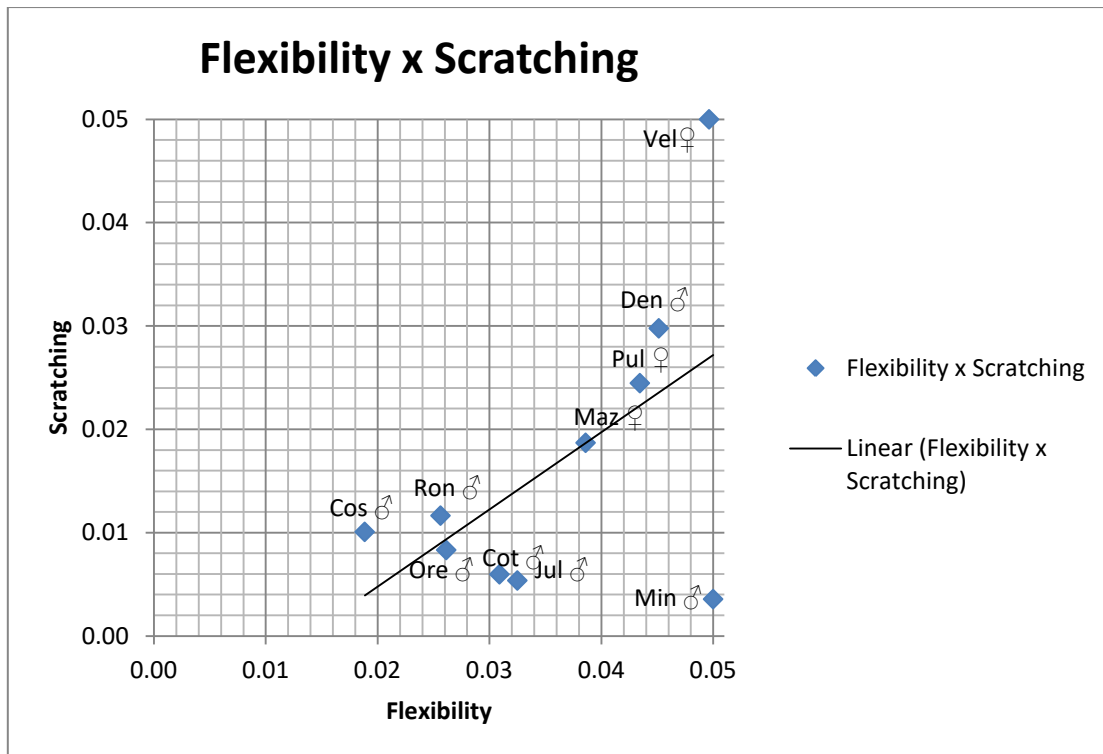


Figure S82. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility  $\times$  Scratching

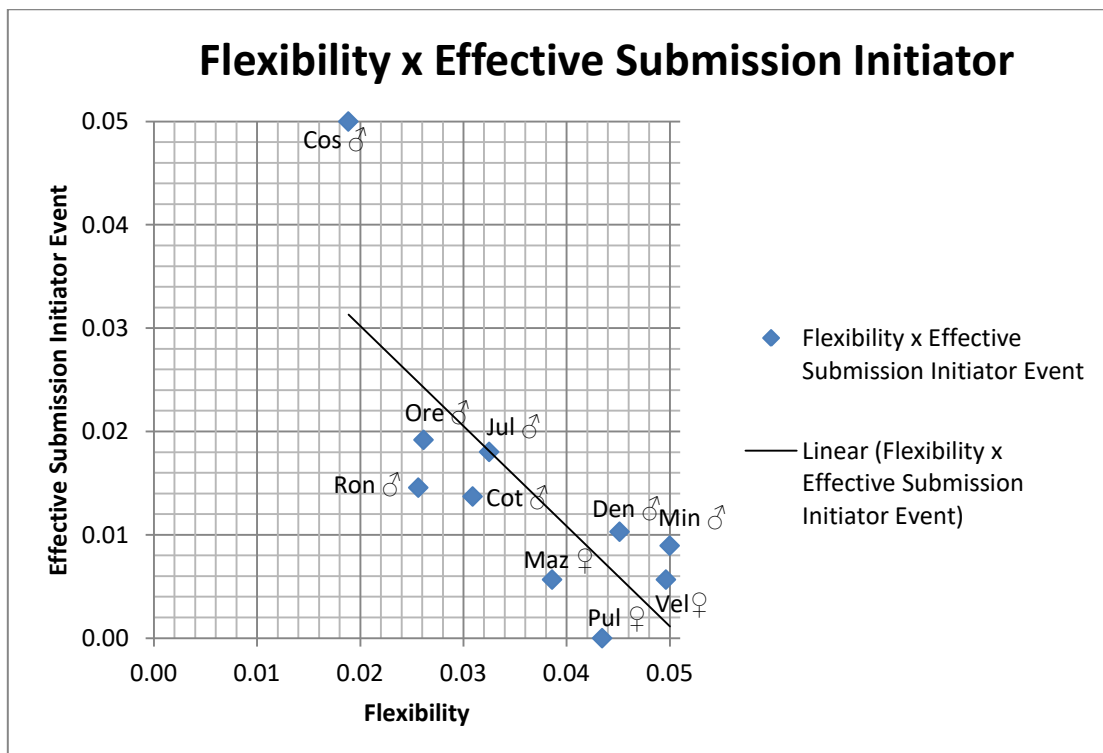


Figure S83. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility  $\times$  Effective Submission Initiator

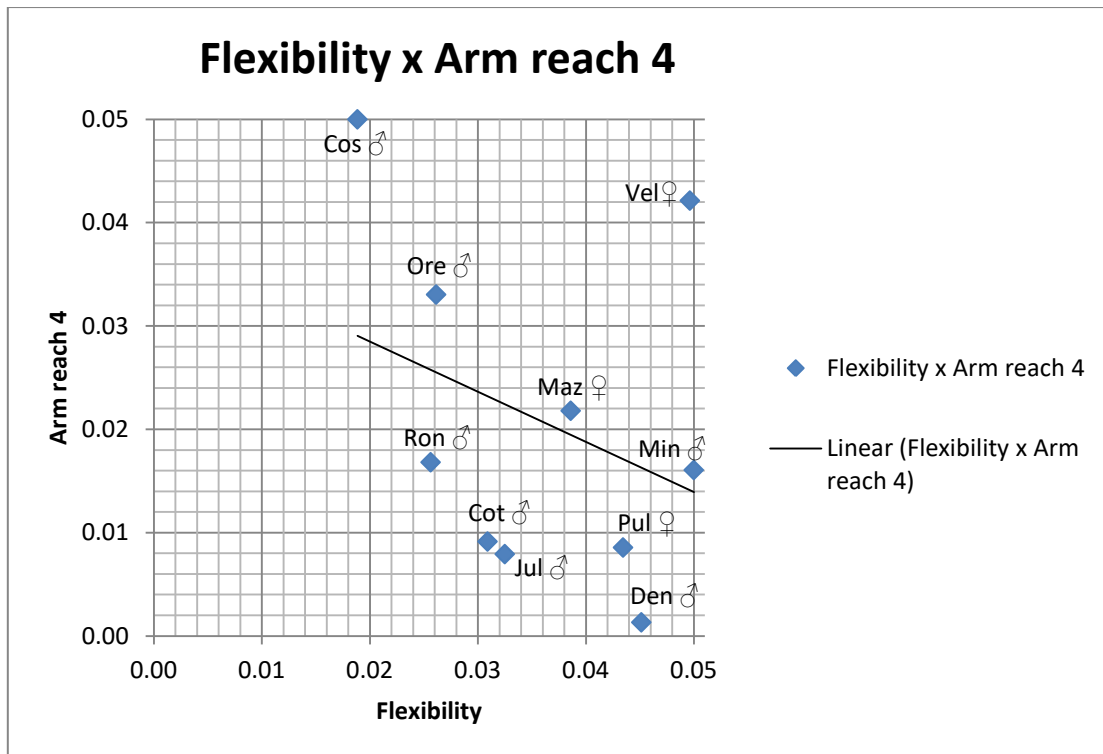


Figure S84. Ring-tailed lemurs: View of dispersion graphics constructed with diversity results (REM analysis after conversion in a 0-5 scale) and flexibility results (after conversion in a 0-5 scale), Flexibility  $\times$  Arm reach 4

Table S27. EthoSeq Schematic Matrices for ring-tailed lemurs.

	abnorm	affip	affir	Effagp	effagr	effsubp	effsubr	hud	humint	parent	playp	playr	ritagp	ritagr	ritsubp	ritsubr	sm	scra	selfg	sexp	sexr	soliplay	Vocal		
abnorm																									
affip																									
affir																									
effagp																									
effagr																									
effsubp																									
effsubr																									
hud																									
humint																									
parent																									
playp																									
playr																									
ritagp																									
ritagr																									
ritsubp																									
ritsubr																									
sm																									
scra																									
selfg																									
sexp																									
sexr																									
soliplay																									
Vocal																									

Table S28. EthoSeq Schematic Matrices for red-ruffed lemurs.

	AC	AgEfe	AgEfr	AgRite	AgRitr	EST	Jsociale	JSolit	Outros	ScentM	Sex	Soce	Socr	SubEfe	SubEfr	SubRite	SubRitr	Voc	
AC																			
AgEfe																			
AgEfr																			
AgRite																			
AgRitr																			
EST																			
Jsociale																			
JSolit																			
Outros																			
ScentM																			
Sex																			
Soce																			
Socr																			
SubEfe																			
SubEfr																			
SubRite																			
SubRitr																			
Voc																			



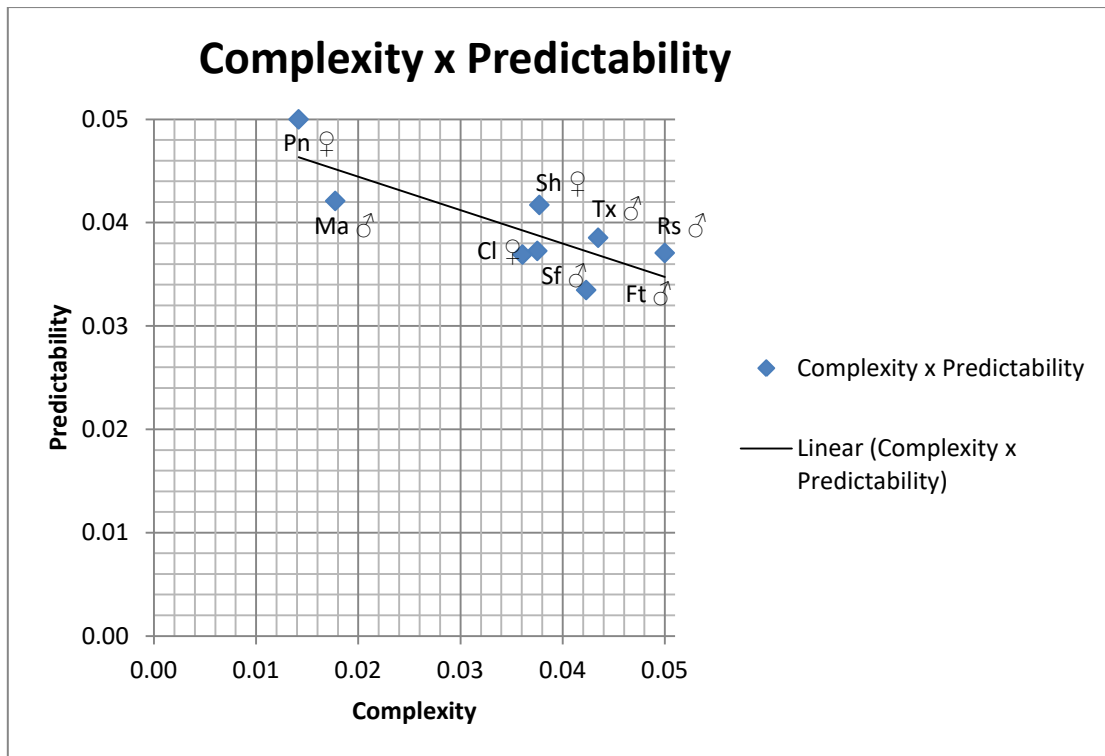


Figure S85. Red-ruffed lemurs: View of dispersion graphics constructed with complexity and predictability index

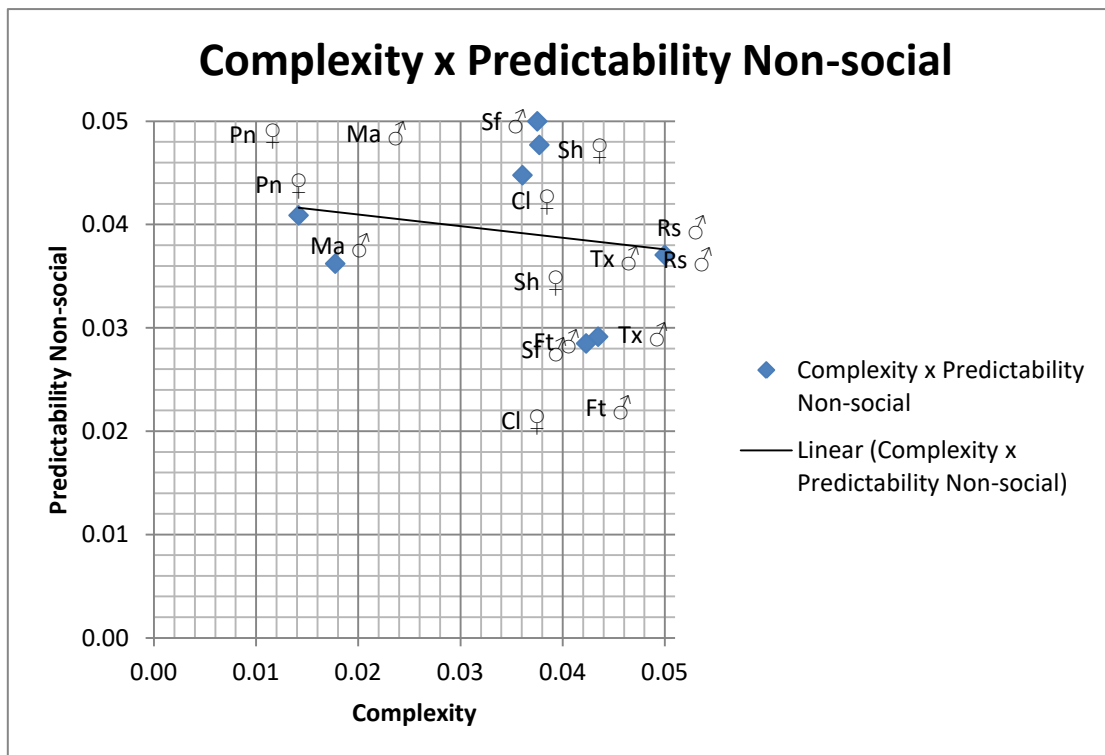


Figure S86. Red-ruffed lemurs: View of dispersion graphics constructed with complexity and predictability non-social index

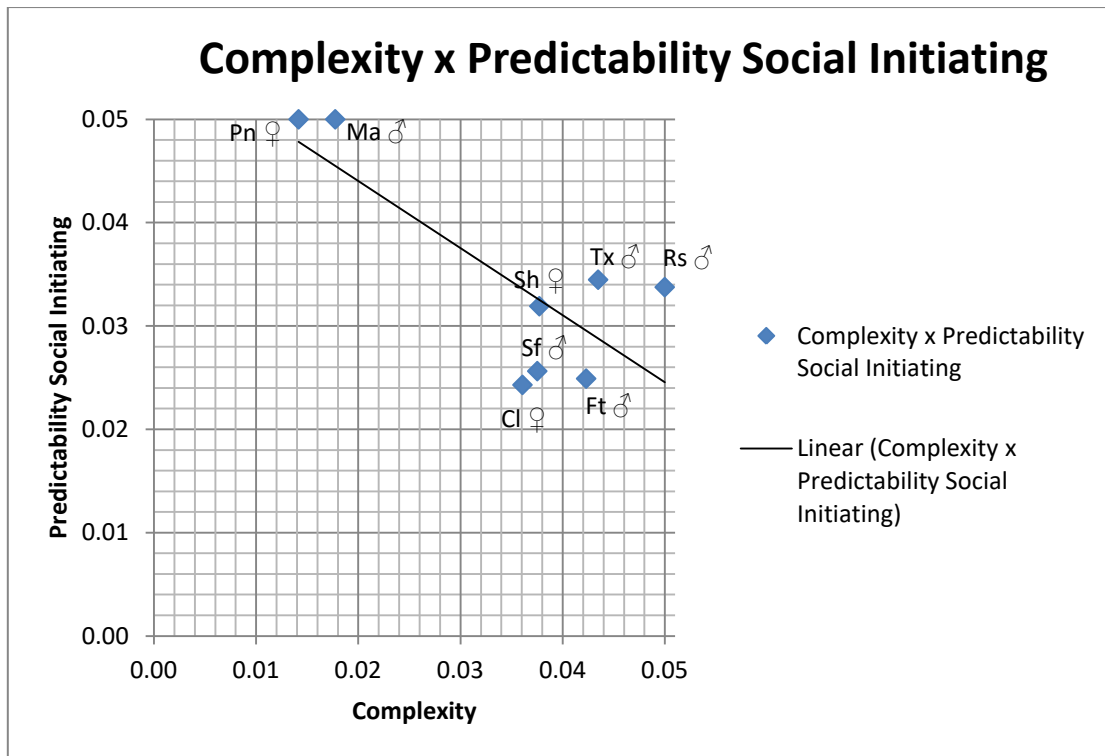


Figure S87. Red-ruffed lemurs: View of dispersion graphics constructed with complexity and predictability social initiating index

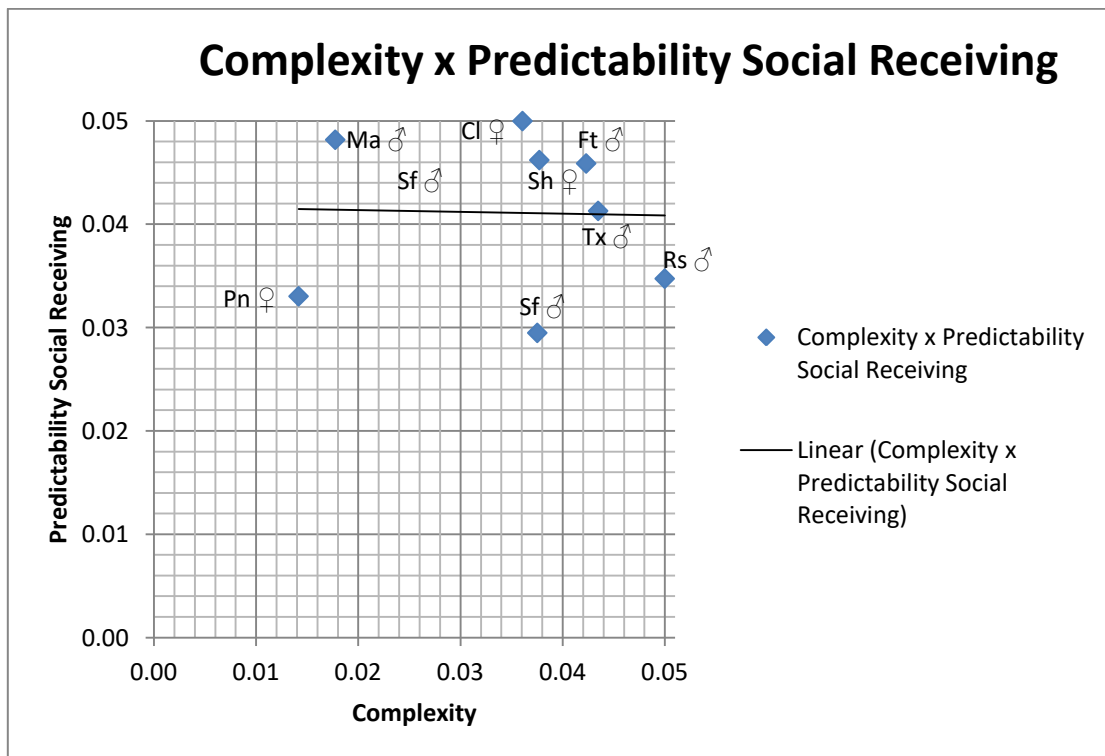


Figure S88. Red-ruffed lemurs: View of dispersion graphics constructed with complexity and predictability social receiving index

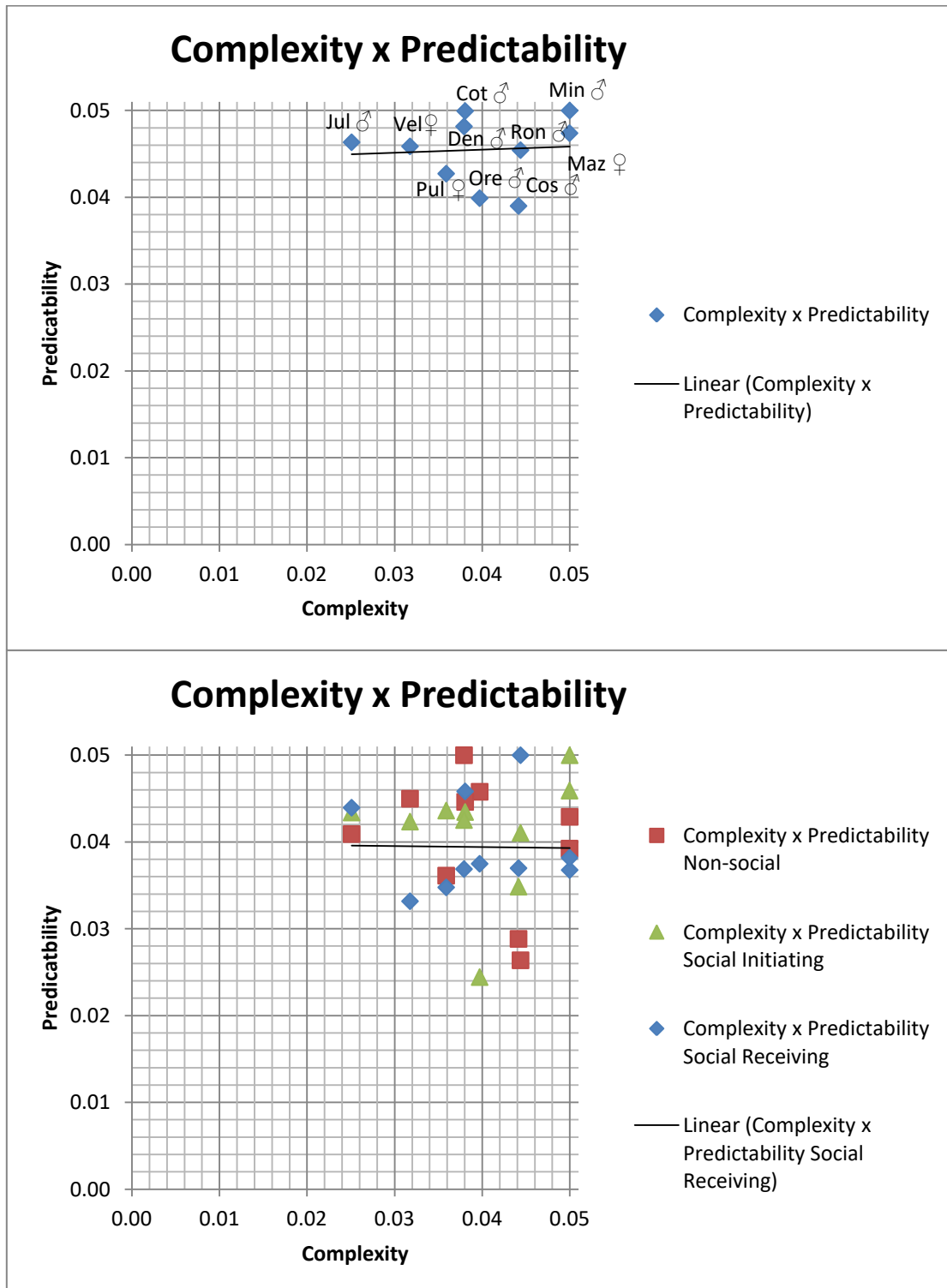


Figure S89. Ring-tailed lemurs: View of dispersion graphics constructed with complexity and predictability index

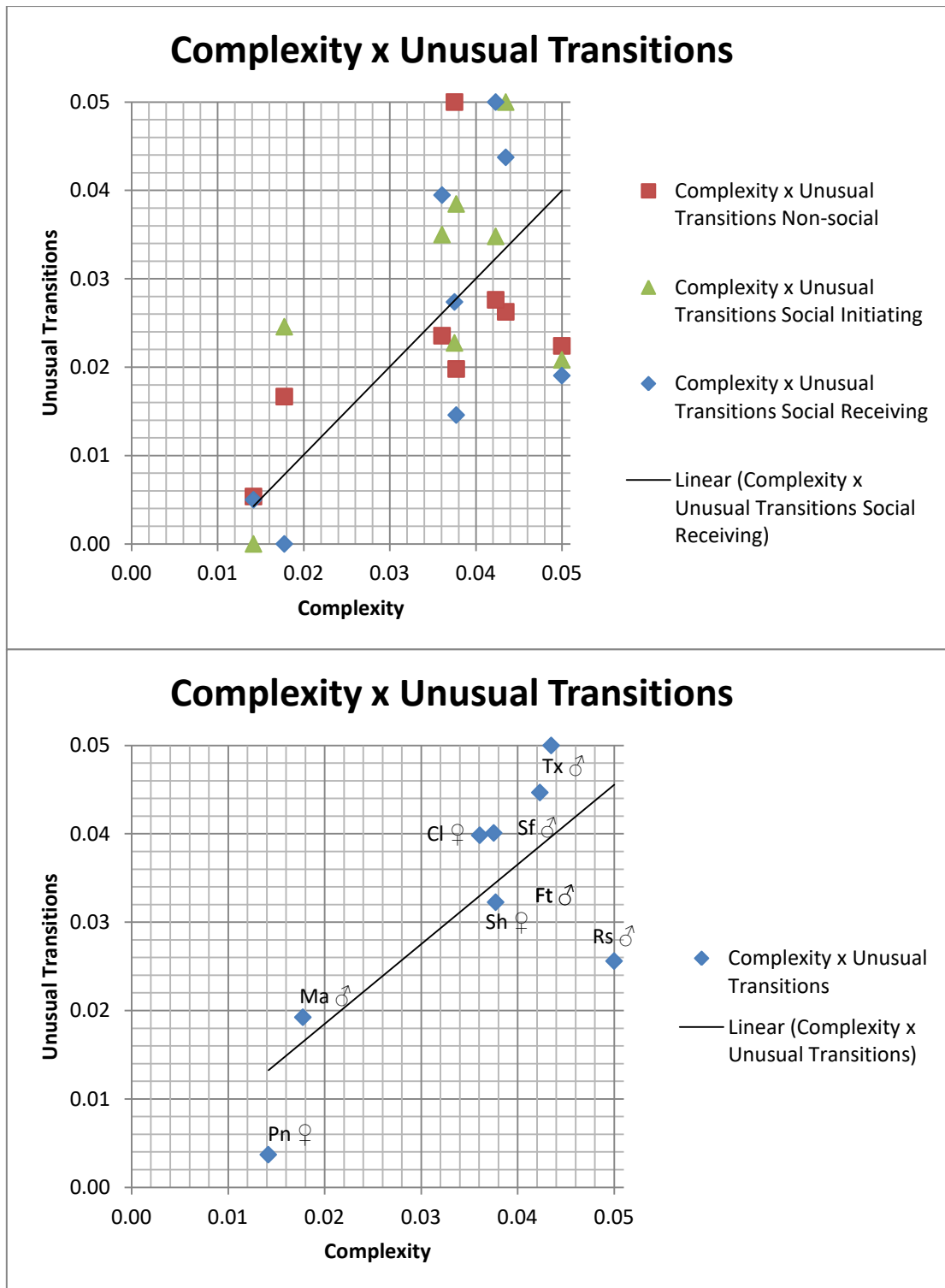


Figure S90. Red-ruffed lemurs: View of dispersion graphic constructed with complexity and unusual transition indices

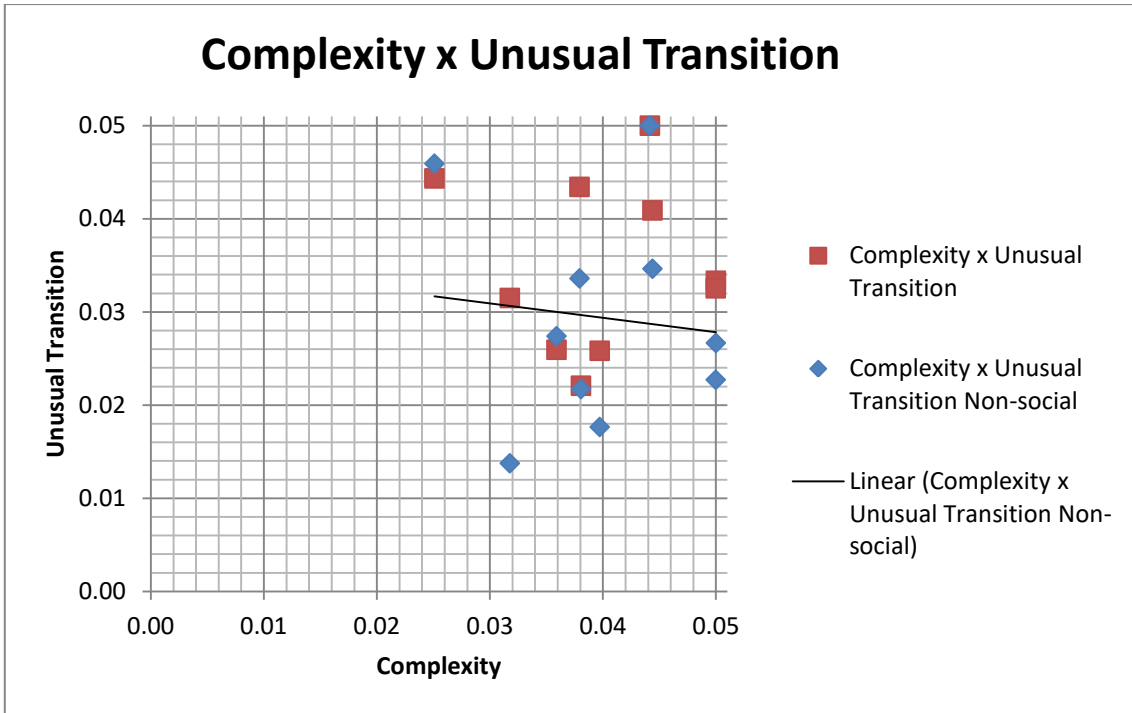


Figure S91. Ring-tailed lemurs: View of dispersion graphic constructed with complexity and unusual transition index.

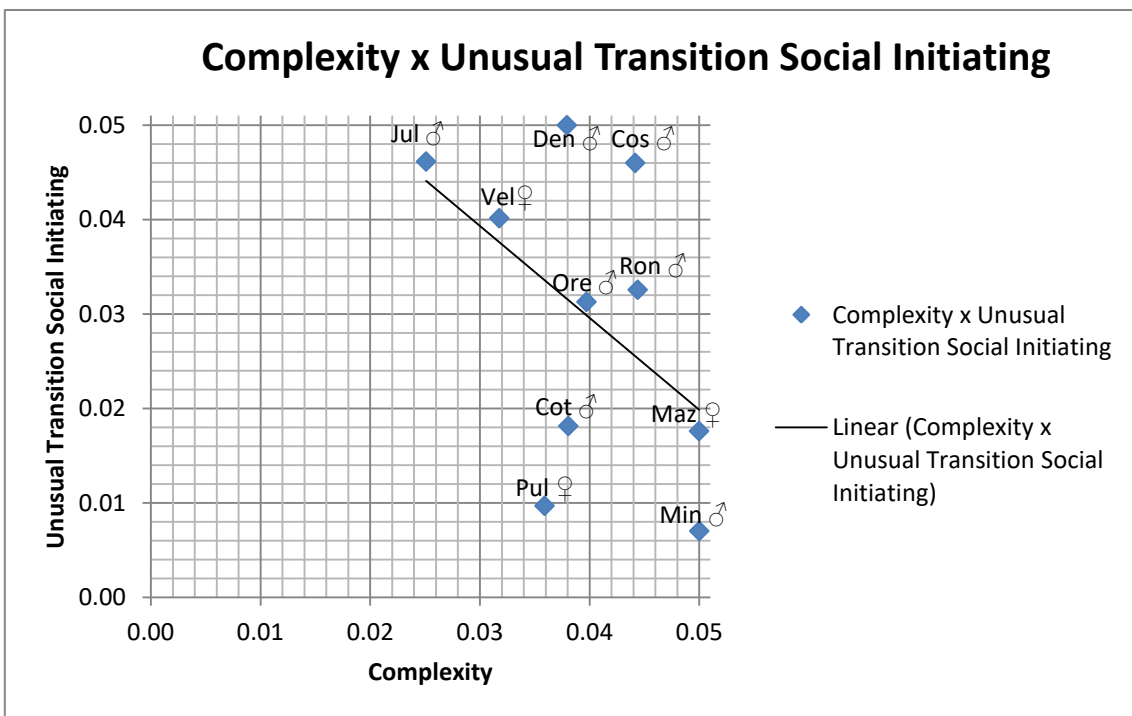


Figure S92. Ring-tailed lemurs: View of dispersion graphic constructed with complexity and unusual transition social initiating index.

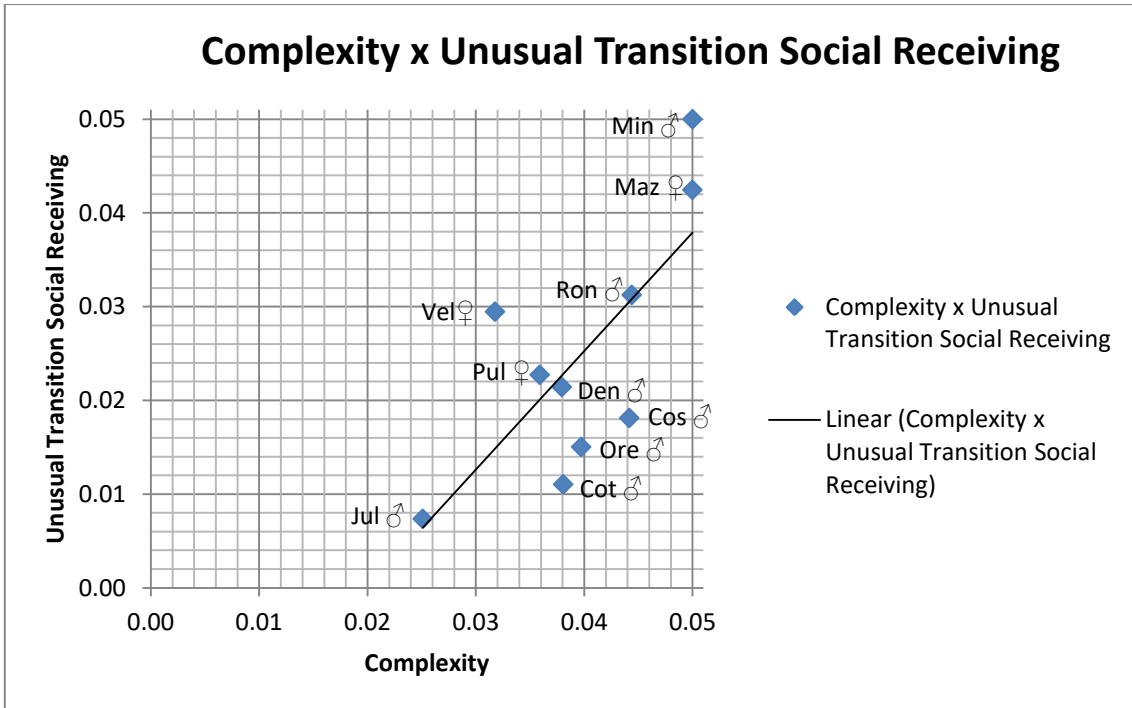
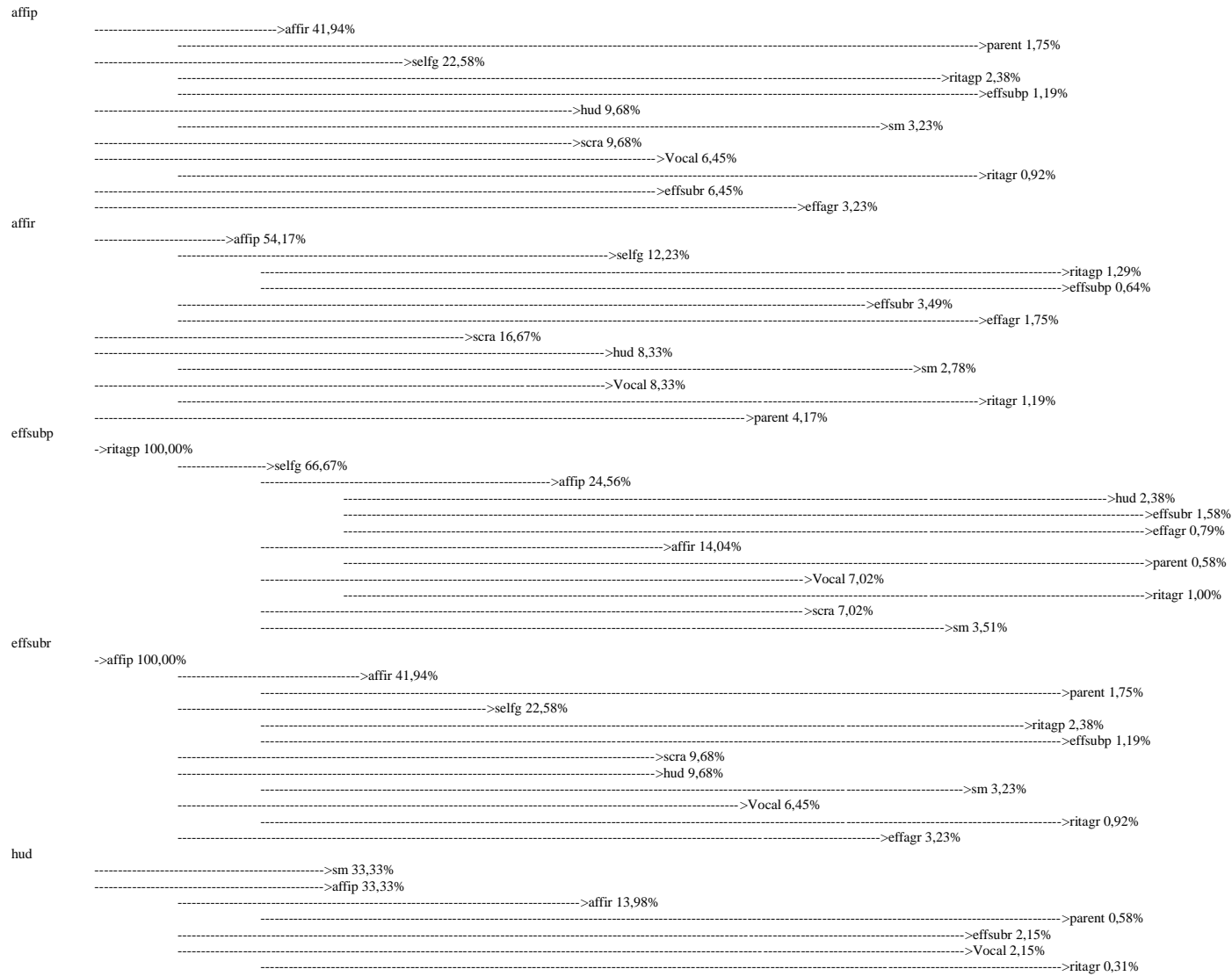
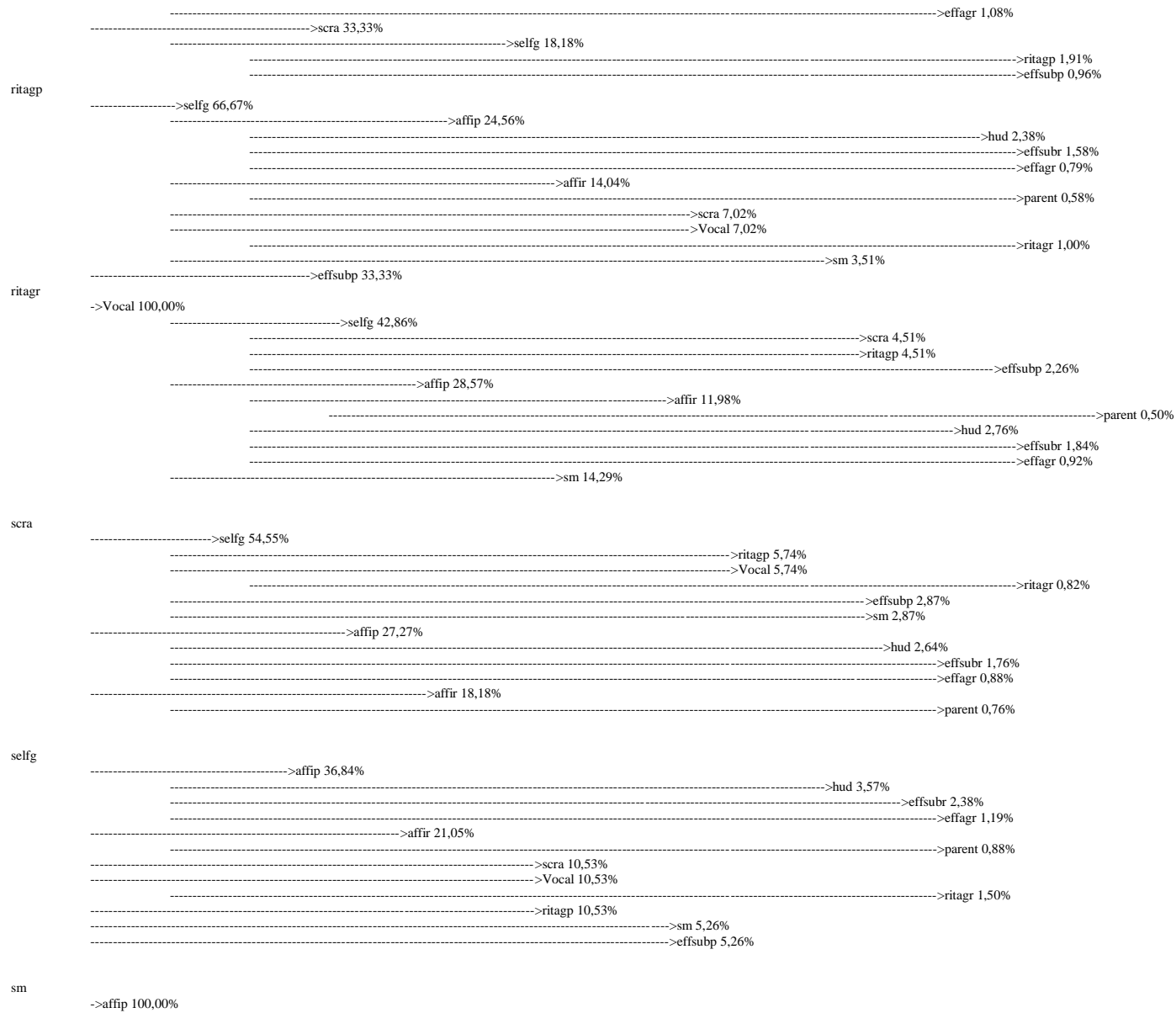


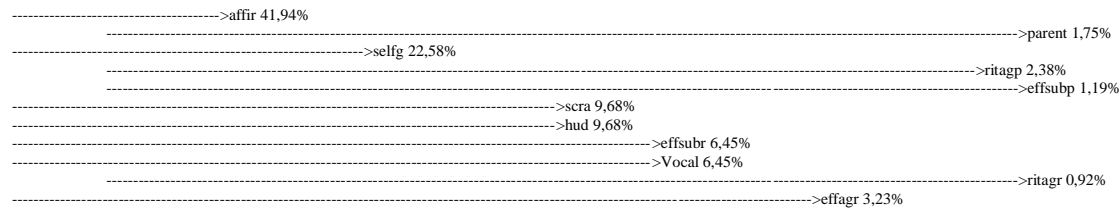
Figure S93. Ring-tailed lemurs: View of dispersion graphic constructed with complexity and unusual transition social receiving index

SE28. View of probability behavioral sequences of the behavioral transitions of Cot.

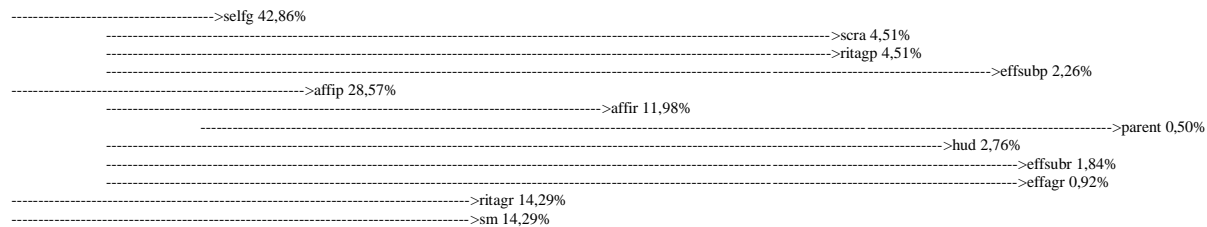






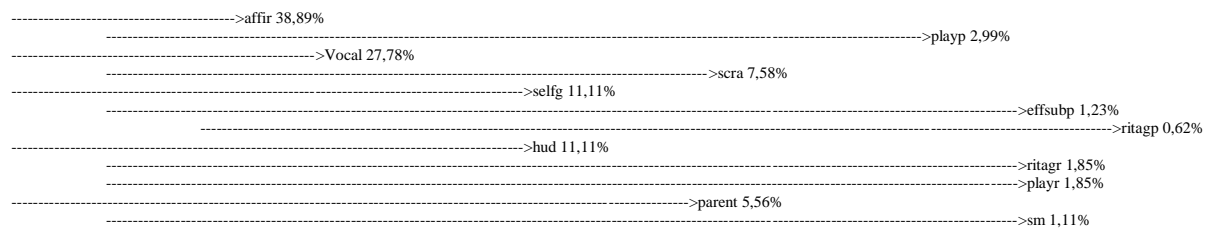


Vocal

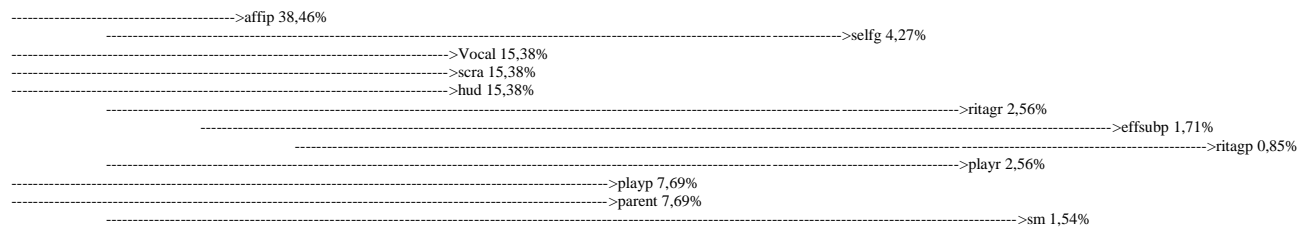


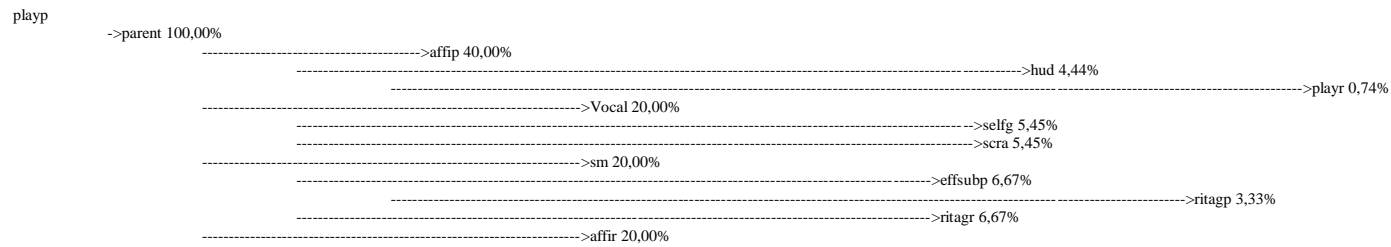
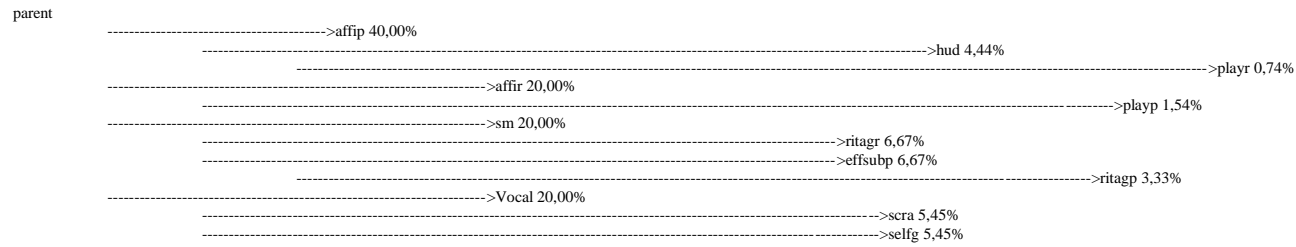
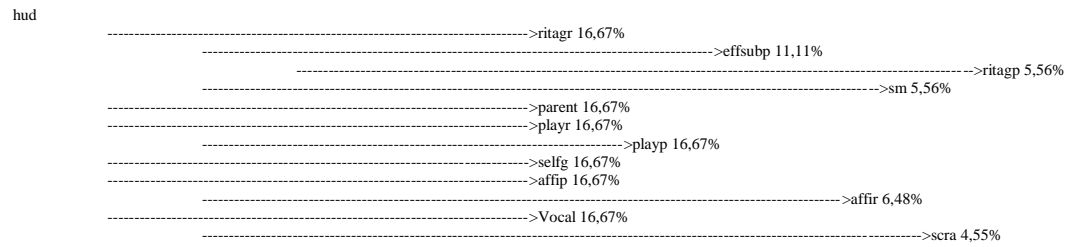
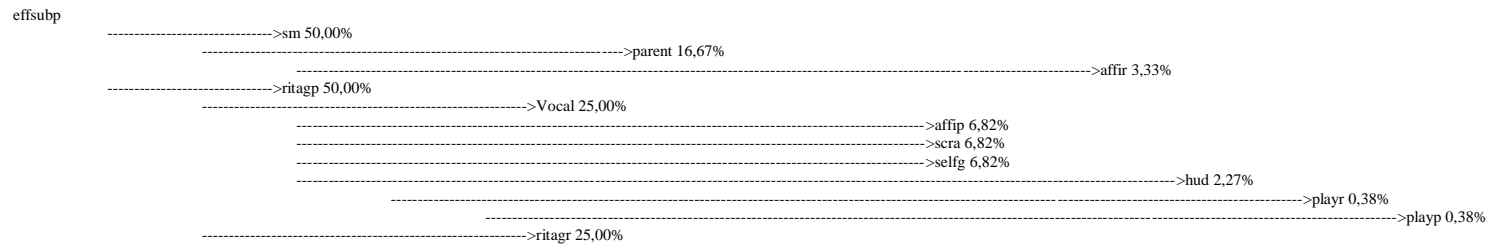
## SE29. View of probability behavioral sequences of the behavioral transitions of Cos.

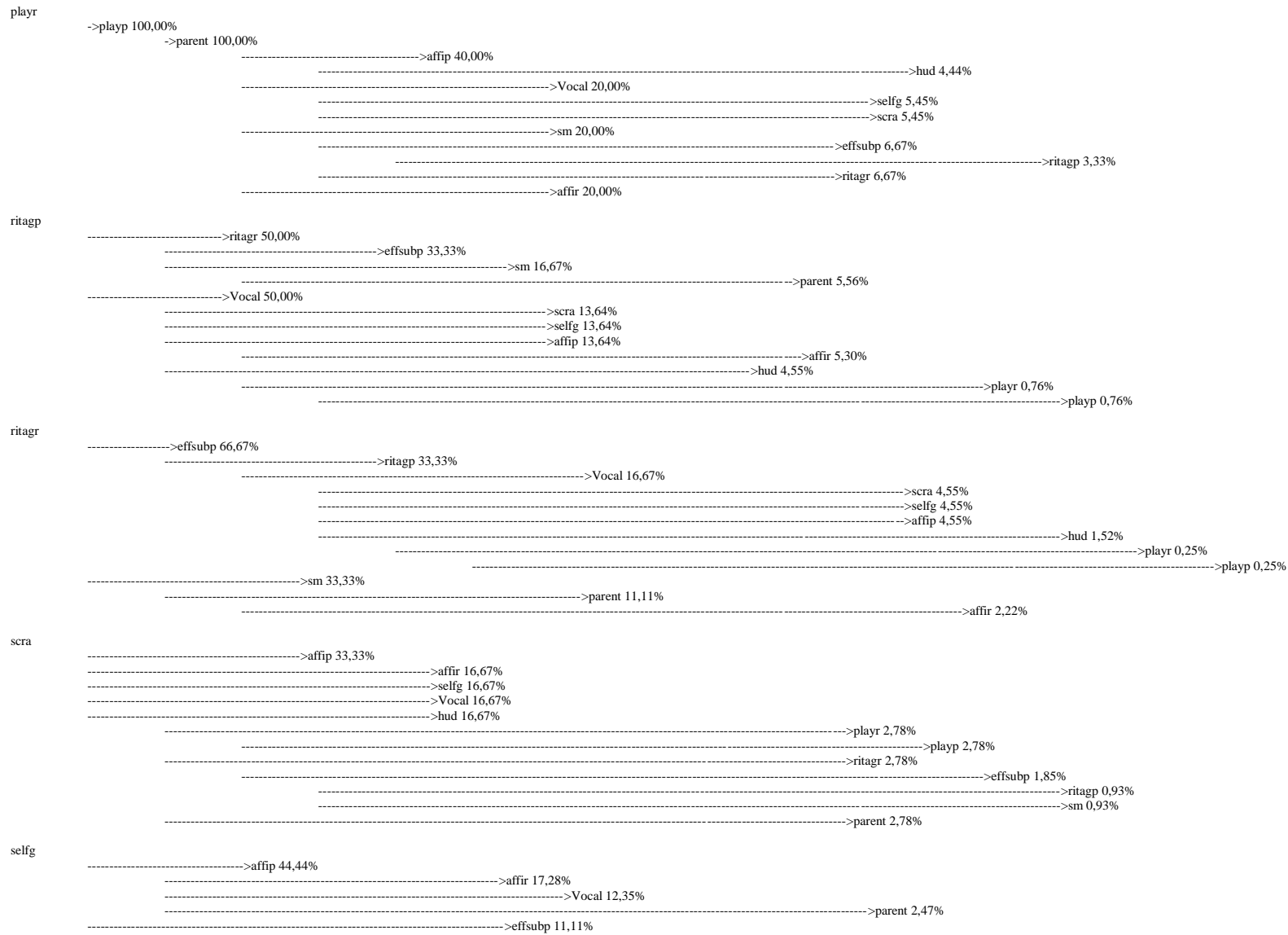
affip

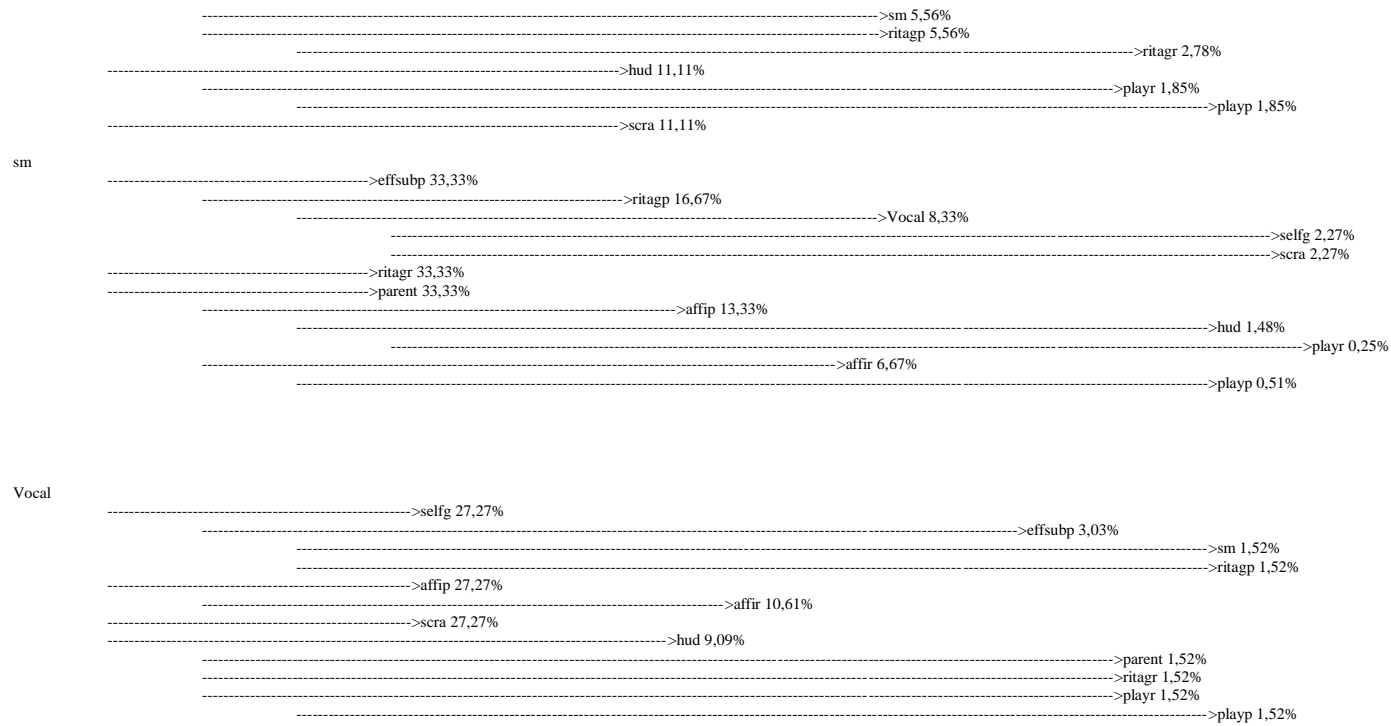


affir

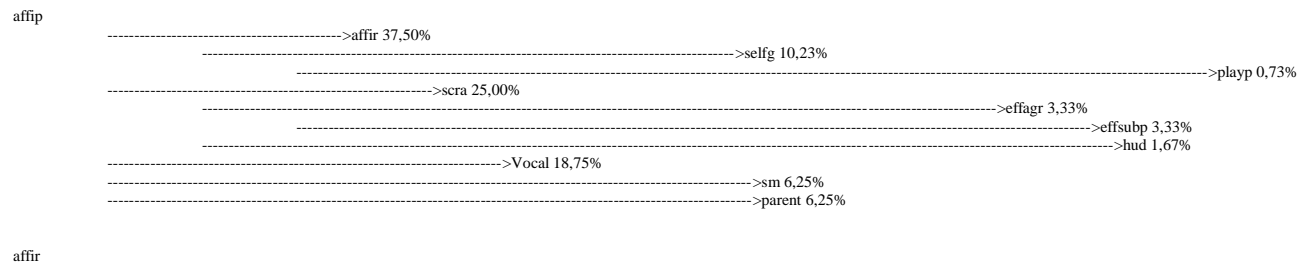


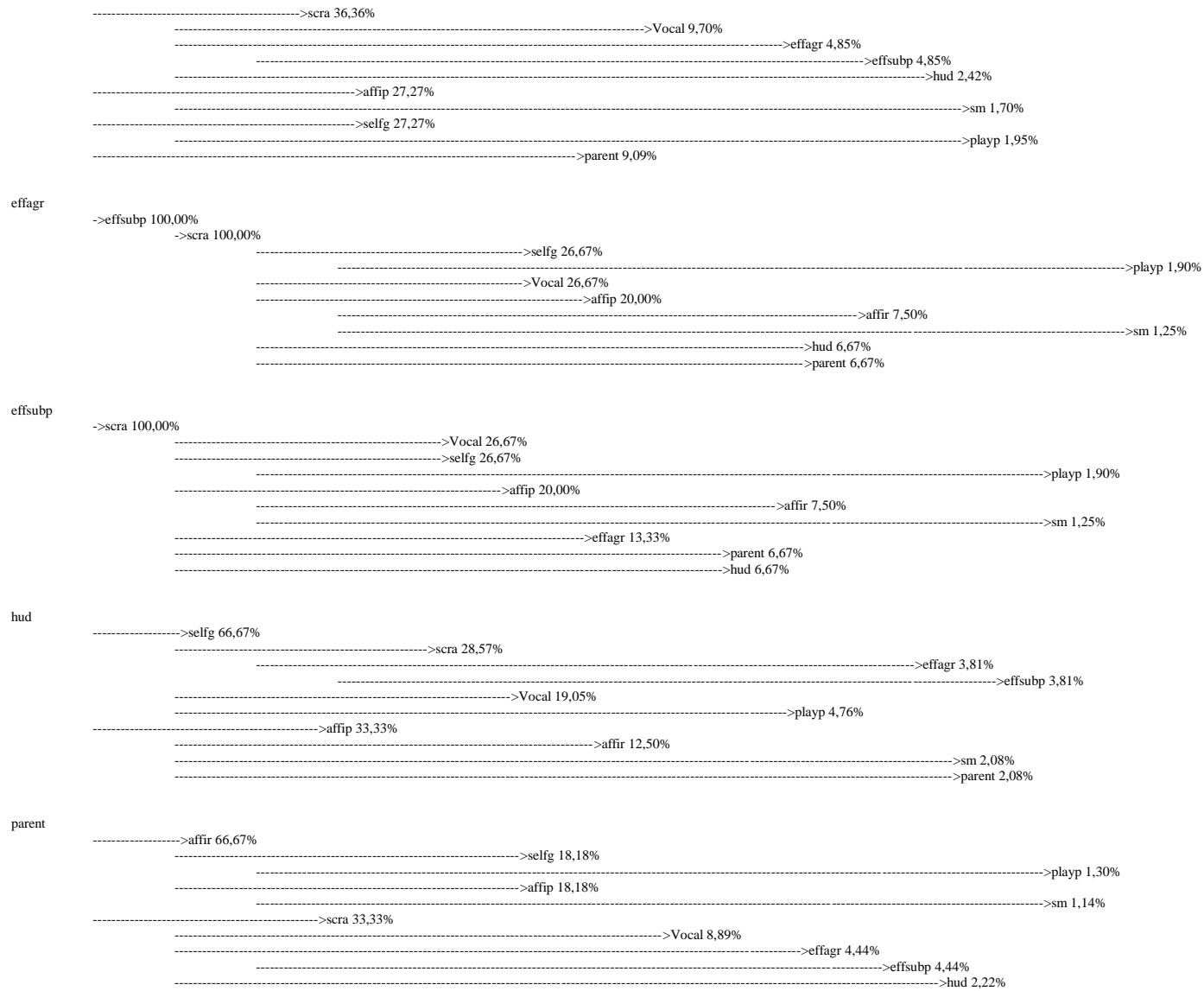


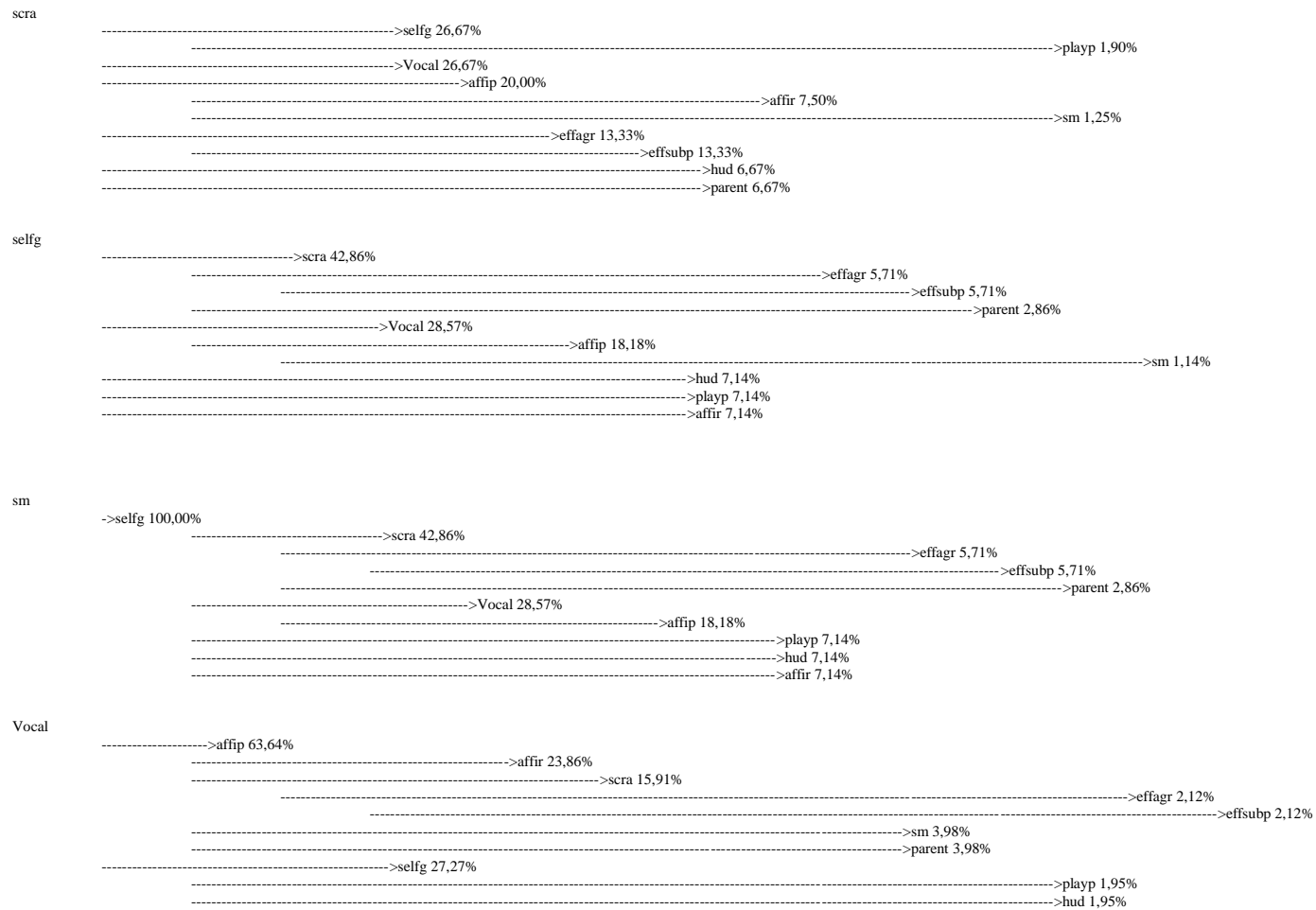




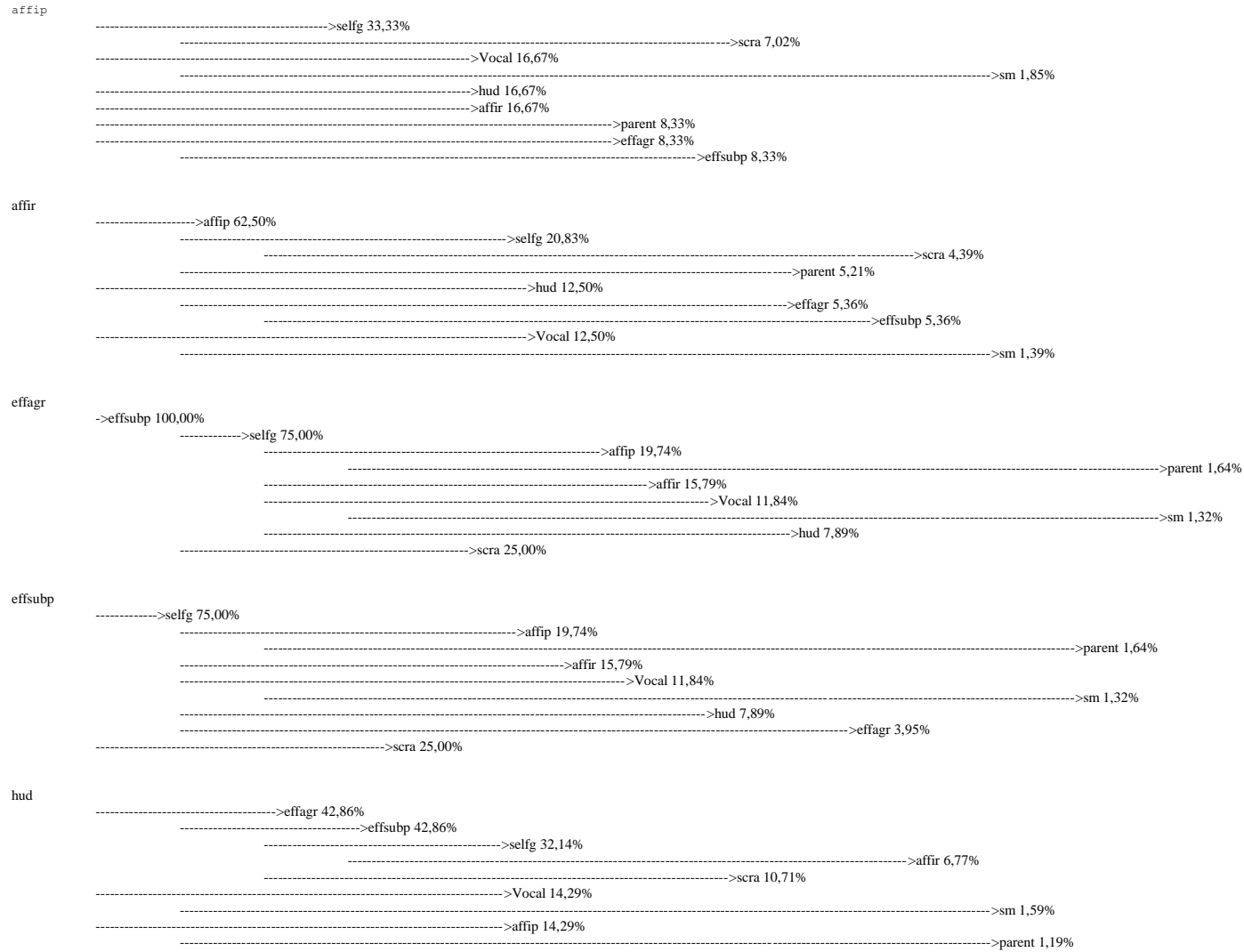
SE30. View of probability behavioral sequences of the behavioral transitions of Den.

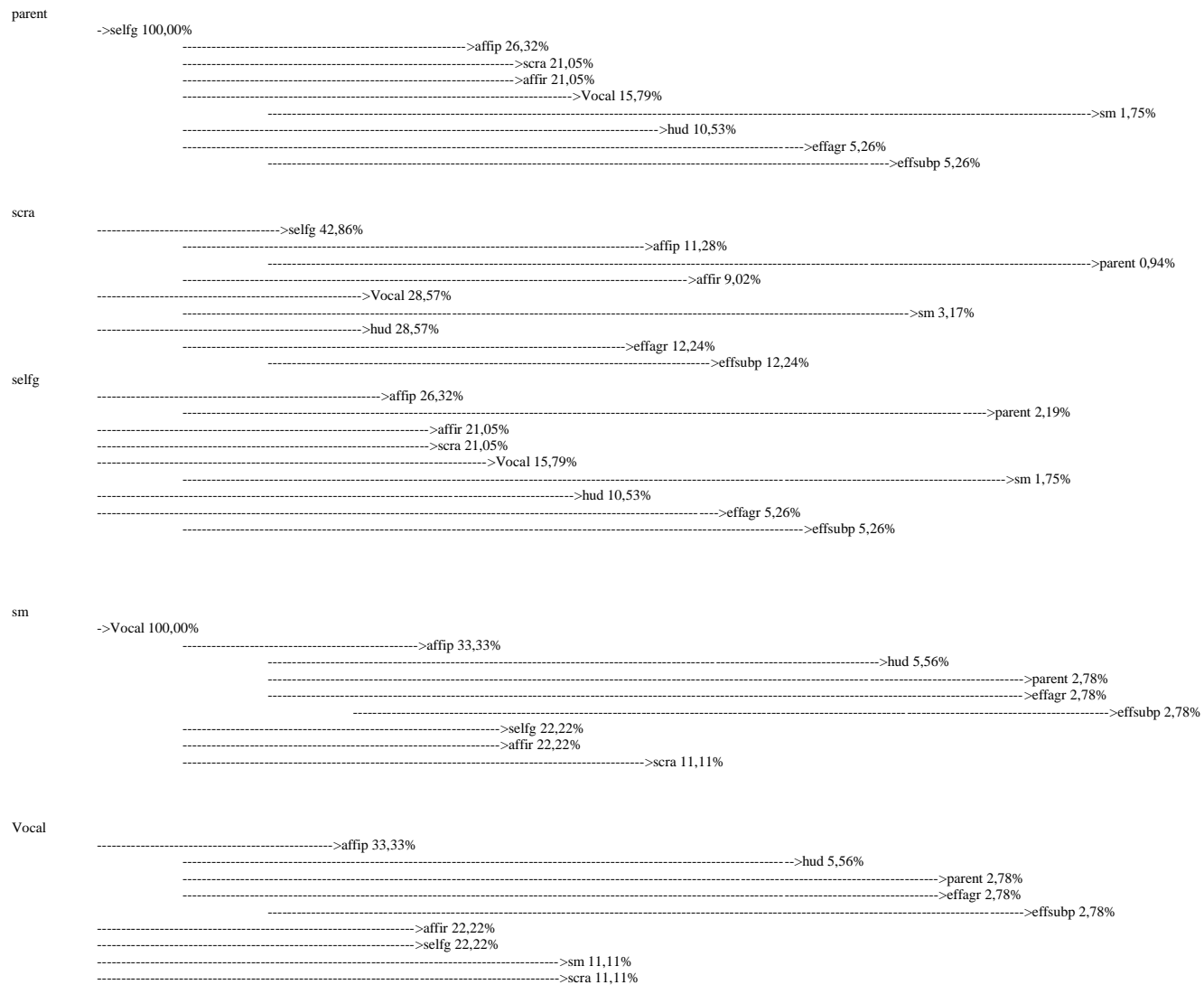






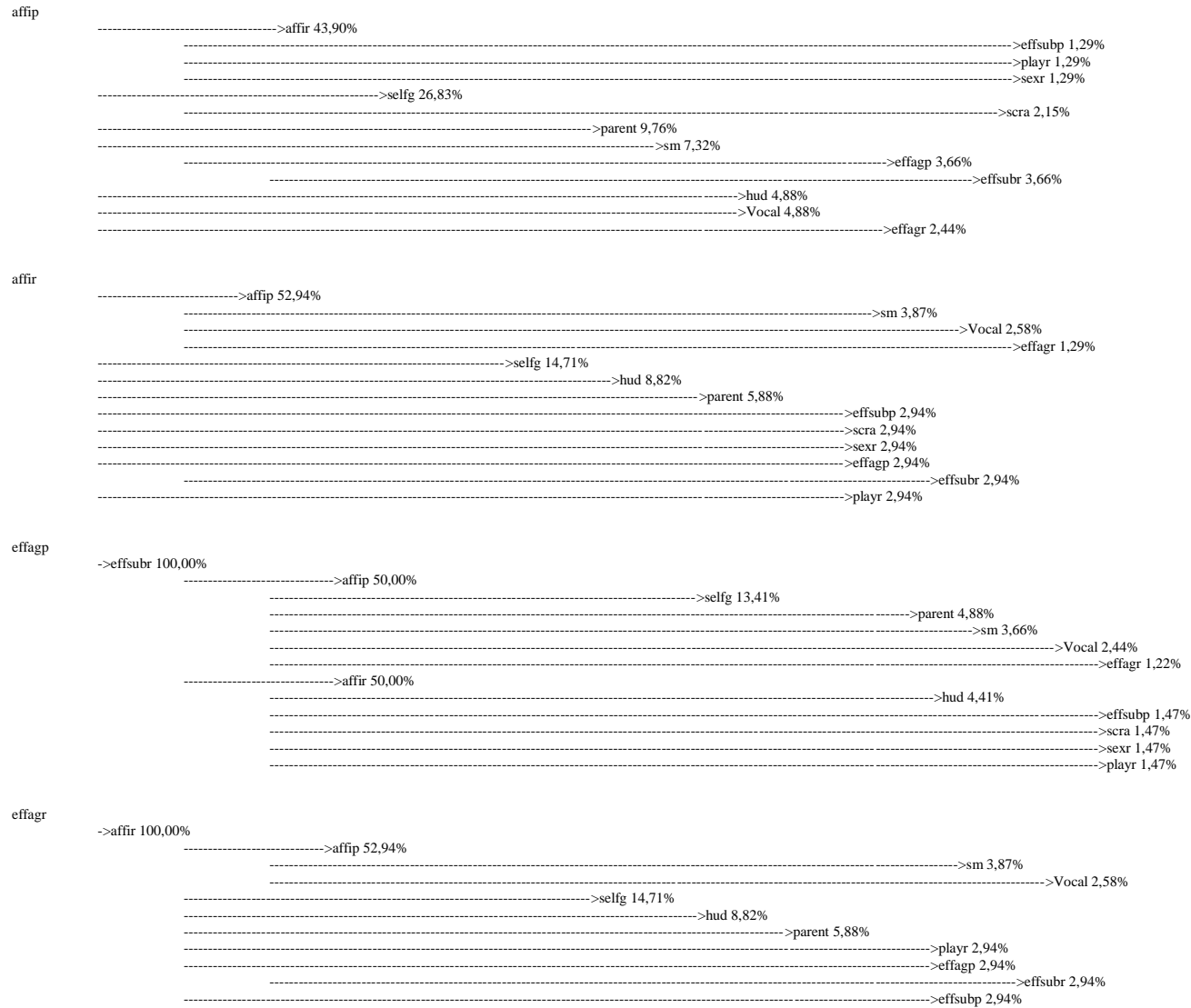
SE31. View of probability behavioral sequences of the behavioral transitions of Jul.

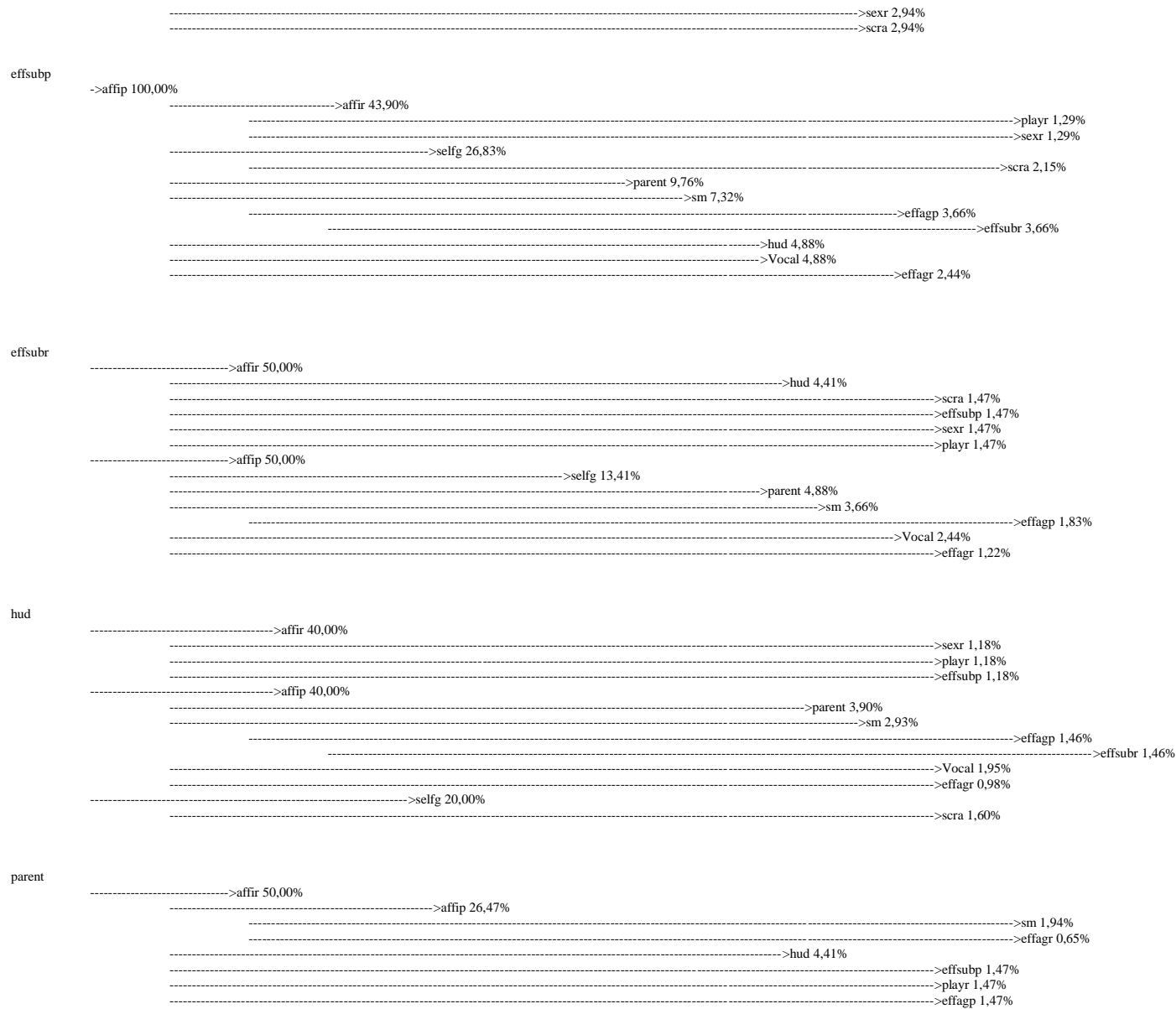


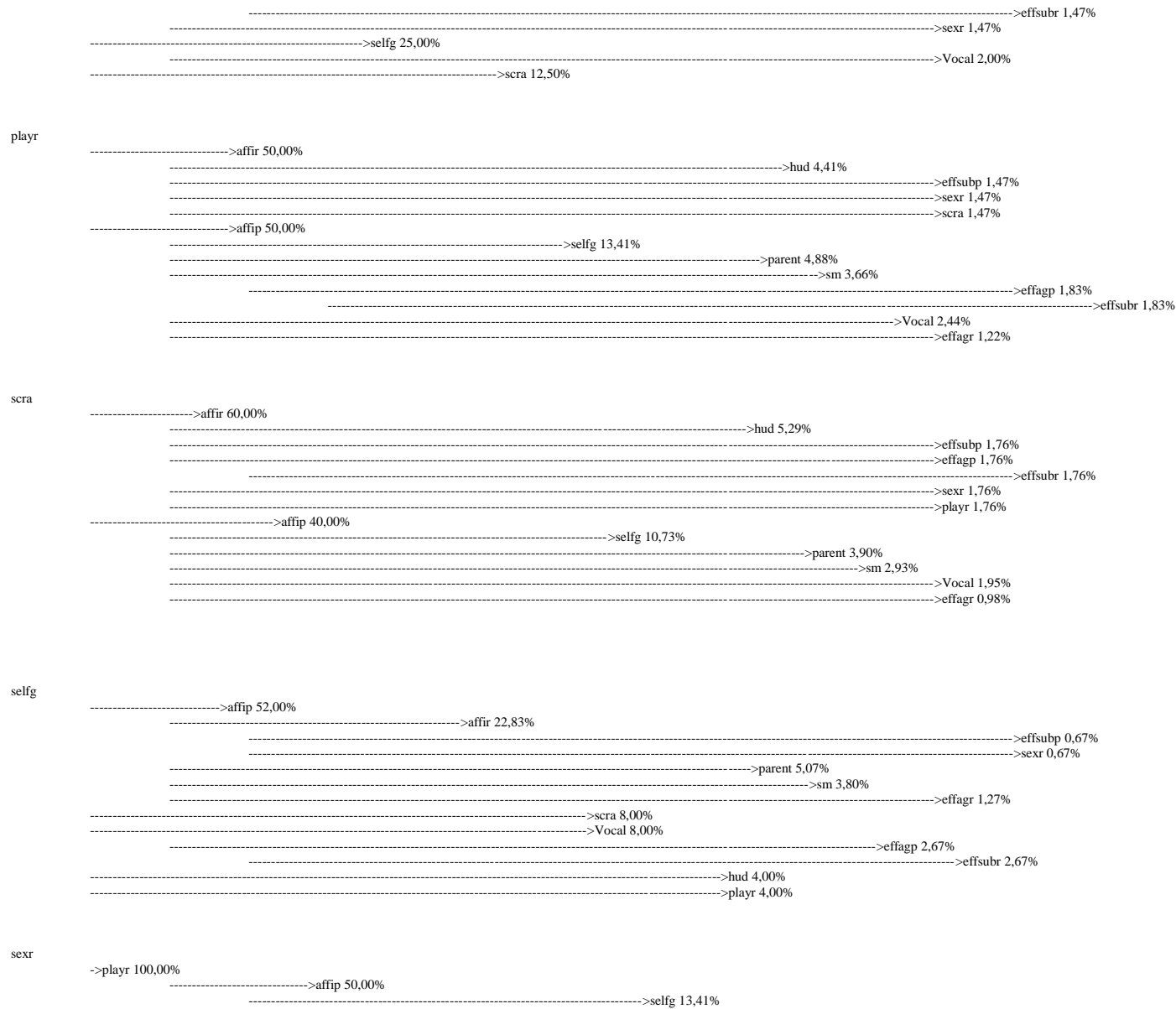


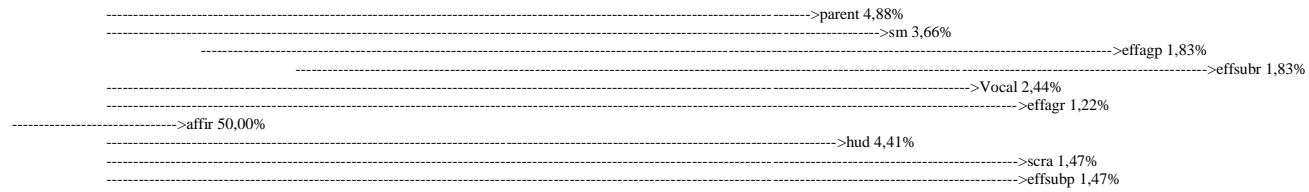


SE32. View of probability behavioral sequences of the behavioral transitions of Maz.

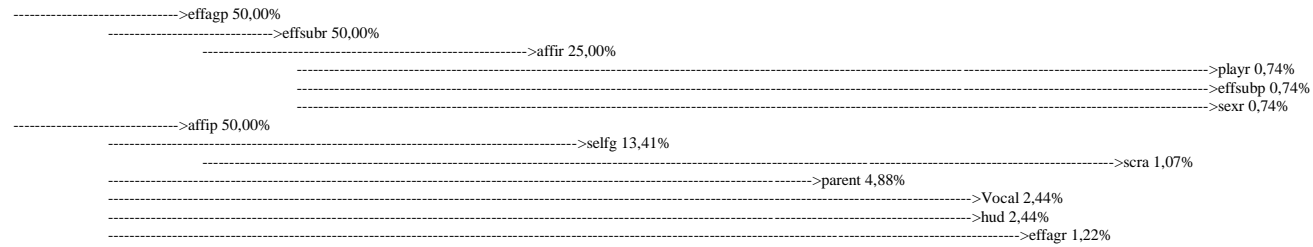




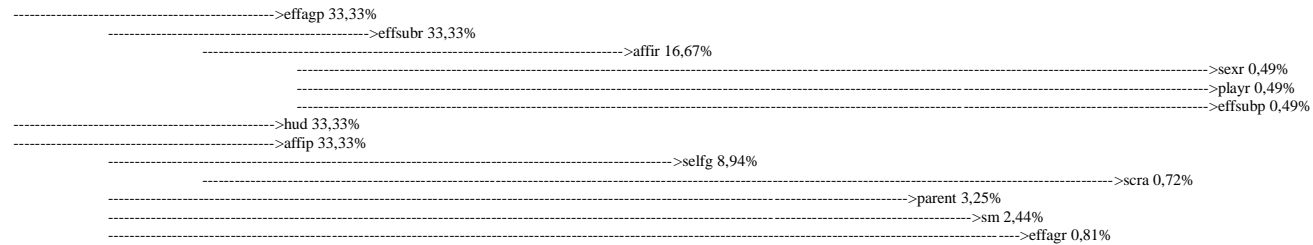




sm

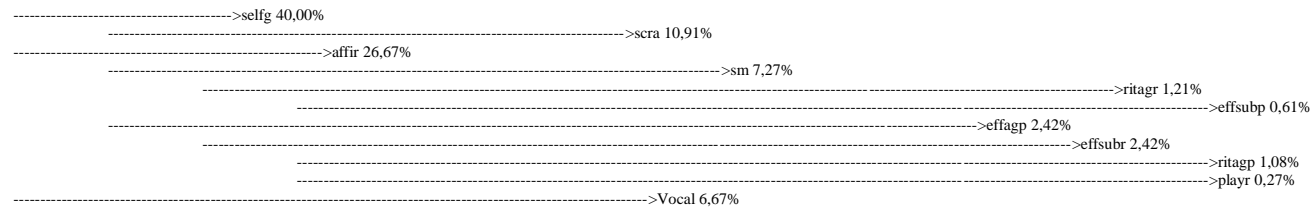


Vocal



### SE33. View of probability behavioral sequences of the behavioral transitions of Min.

affip



----->parent 6,67%  
 ----->hud 6,67%  
 ----->effagr 6,67%

affir

----->affip 45,45%  
 ----->selfg 18,18%  
 ----->scra 4,96%  
 ----->effagr 3,03%  
 ----->hud 3,03%  
 ----->Vocal 3,03%  
 ----->parent 3,03%  
 ----->sm 27,27%  
 ----->ritagr 4,55%  
 ----->effsubp 2,27%  
 ----->effagp 9,09%  
 ----->effsubr 9,09%  
 ----->ritagp 4,04%  
 ----->playr 1,01%

effagp

->effsubr 100,00%  
 ----->ritagp 44,44%  
 ----->ritagr 8,89%  
 ----->effsubp 4,44%  
 ----->affip 11,11%  
 ----->affir 2,96%  
 ----->Vocal 0,74%  
 ----->parent 0,74%  
 ----->effagr 0,74%  
 ----->hud 0,74%  
 ----->playr 11,11%  
 ----->sm 11,11%  
 ----->selfg 11,11%  
 ----->scra 3,03%

effagr

->affir 100,00%  
 ----->affip 45,45%  
 ----->selfg 18,18%  
 ----->scra 4,96%  
 ----->hud 3,03%  
 ----->Vocal 3,03%  
 ----->parent 3,03%  
 ----->sm 27,27%  
 ----->ritagr 4,55%  
 ----->effsubp 2,27%  
 ----->effagp 9,09%  
 ----->effsubr 9,09%  
 ----->ritagp 4,04%  
 ----->playr 1,01%

effsubp

->ritagp 100,00%  
 ----->effsubr 60,00%  
 ----->effagp 6,67%

```

----->sm 6,67%
----->playr 6,67%
----->affip 6,67%
----->effagr 0,44%
----->parent 0,44%
----->ritagr 20,00%
----->selfg 20,00%
----->scra 5,45%
----->affir 4,55%
----->Vocal 0,91%
----->hud 0,91%

```

effsubr

```

----->ritagp 44,44%
----->ritagr 8,89%
----->effsubp 4,44%
----->affip 11,11%
----->affir 2,96%
----->Vocal 0,74%
----->hud 0,74%
----->effagr 0,74%
----->parent 0,74%
----->selfg 11,11%
----->scra 3,03%
----->sm 11,11%
----->playr 11,11%
----->effagp 11,11%

```

hud

```

----->selfg 80,00%
----->scra 21,82%
----->sm 5,45%
----->ritagr 0,91%
----->effsubp 0,45%
----->affip 21,82%
----->effagr 1,45%
----->parent 1,45%
----->affir 18,18%
----->effagp 3,64%
----->Vocal 3,64%
----->effsubr 3,64%
----->ritagp 1,62%
----->playr 0,40%

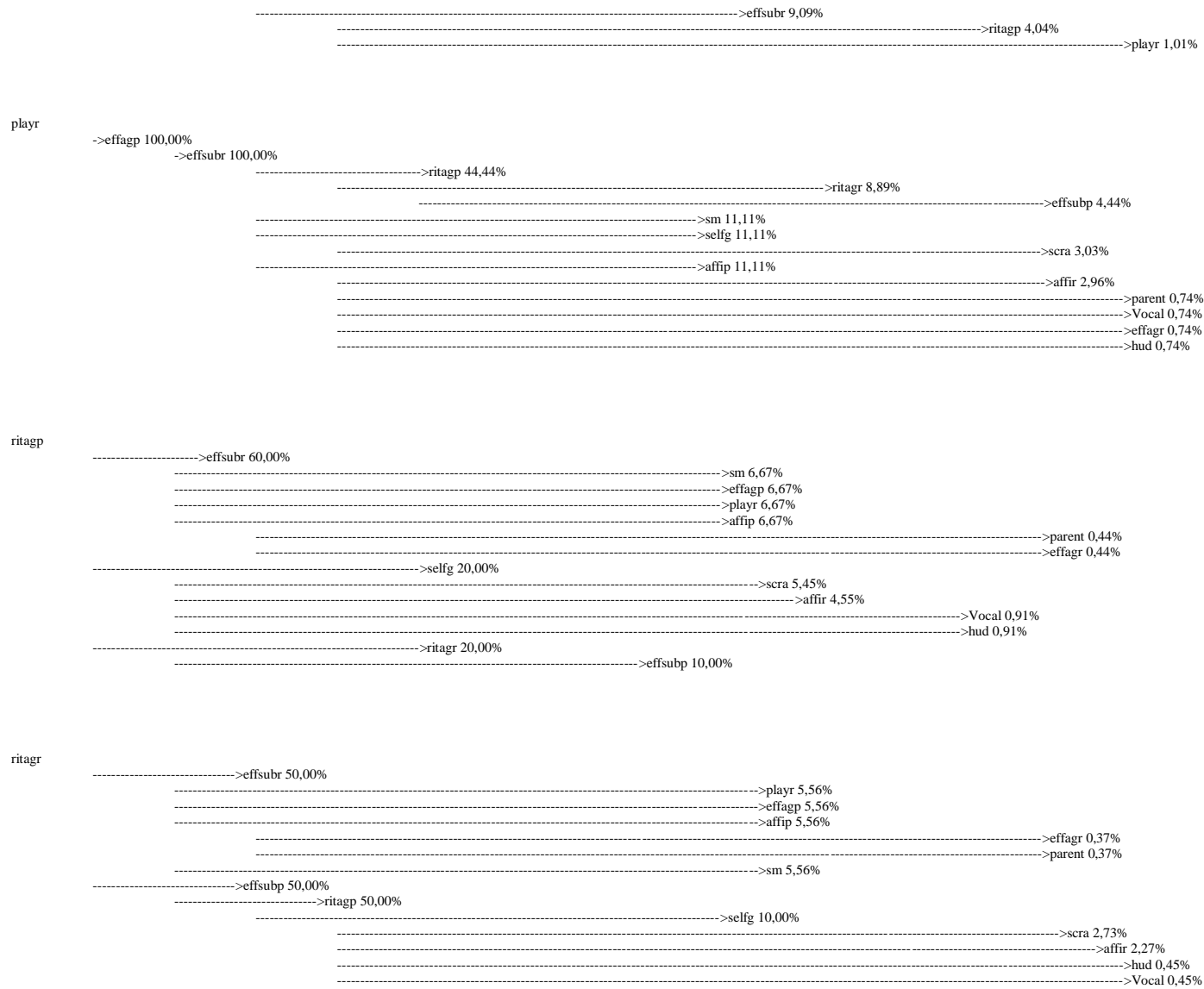
```

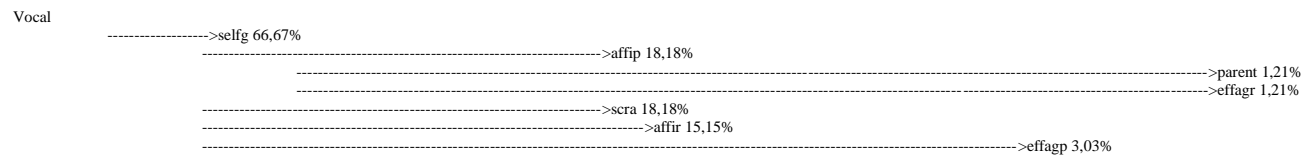
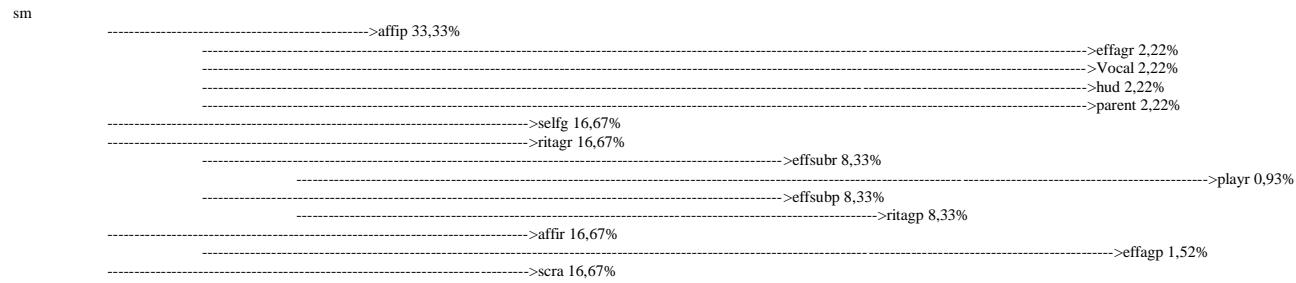
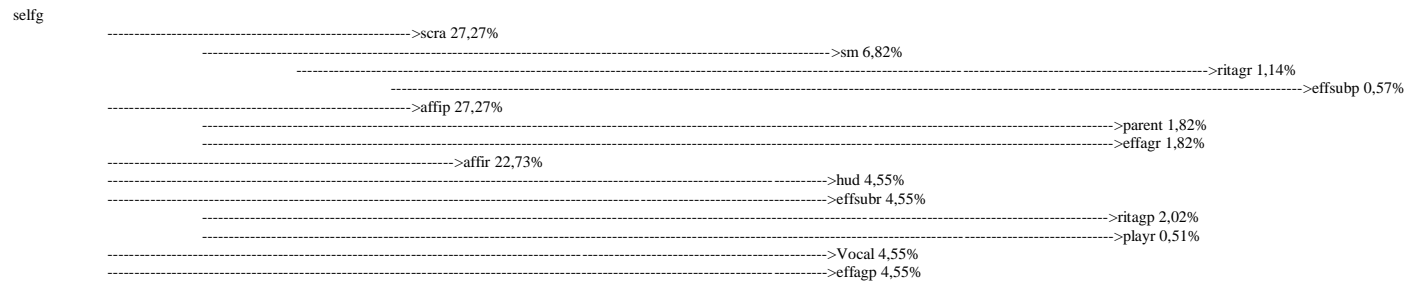
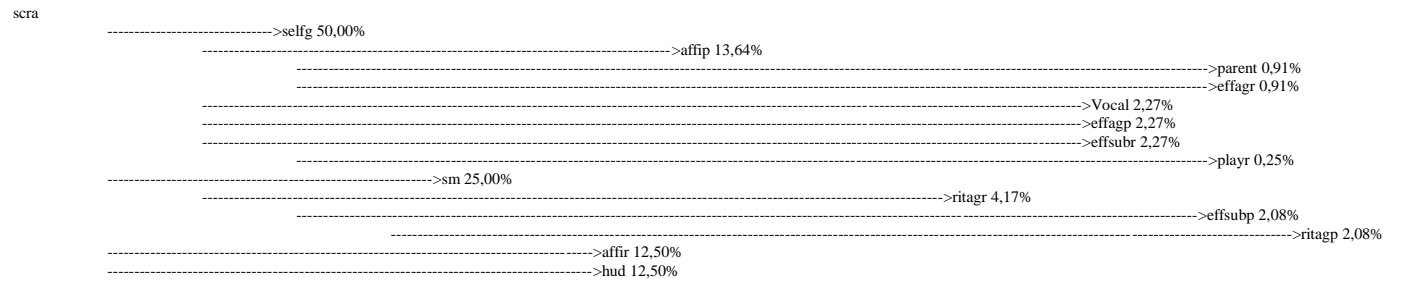
parent

```

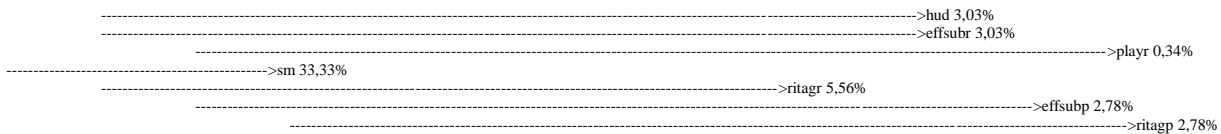
->affir 100,00%
----->affip 45,45%
----->selfg 18,18%
----->scra 4,96%
----->Vocal 3,03%
----->effagr 3,03%
----->hud 3,03%
----->sm 27,27%
----->ritagr 4,55%
----->effsubp 2,27%
----->effagp 9,09%

```

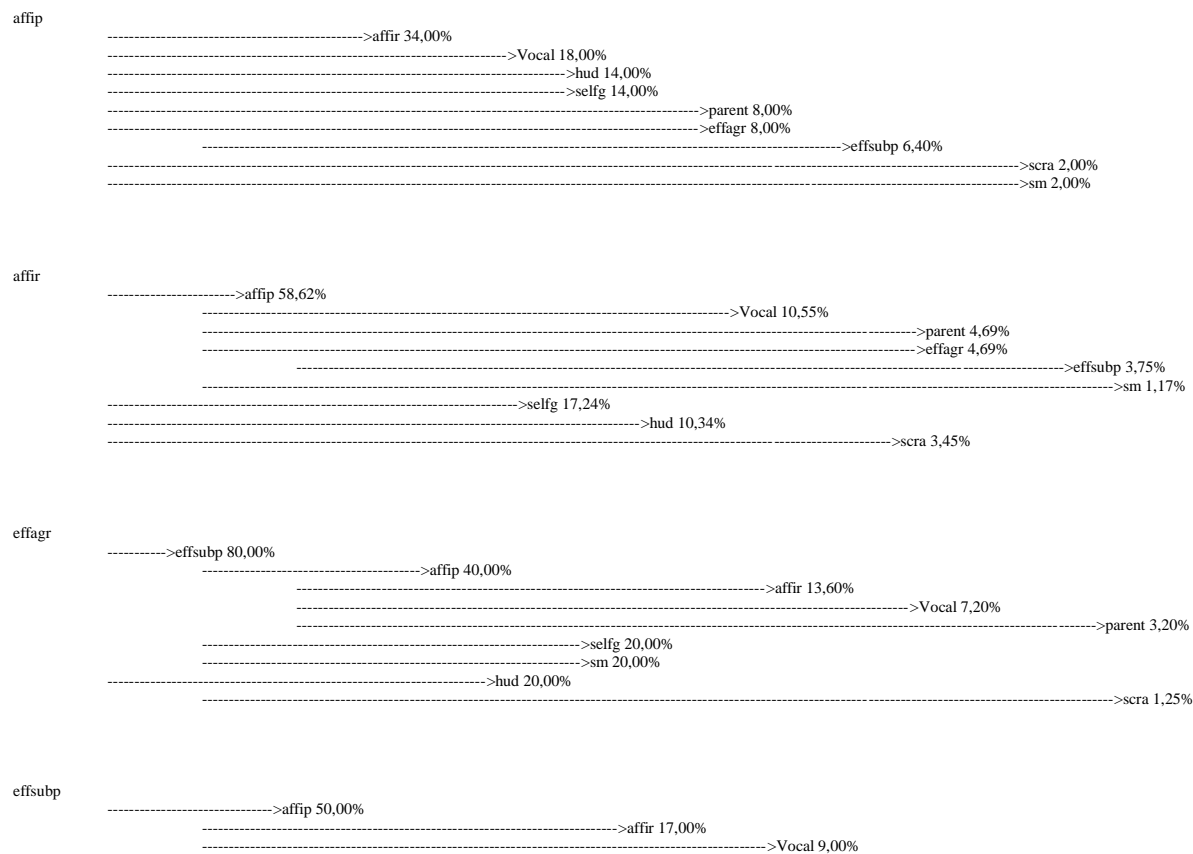








SE34. View of probability behavioral sequences of the behavioral transitions of Ore.



```

----->effagr 4,00%
----->parent 4,00%
----->scra 1,00%
----->sm 25,00%
----->hud 12,50%
----->selfg 25,00%

```

```

hud
----->affip 56,25%
----->affir 19,13%
----->Vocal 10,12%
----->parent 4,50%
----->selfg 12,50%
----->scra 6,25%
----->effagr 6,25%
----->effsubp 5,00%
----->sm 1,25%

```

```

parent
----->selfg 33,33%
----->Vocal 8,33%
----->affip 33,33%
----->hud 4,67%
----->effagr 2,67%
----->effsubp 2,13%
----->sm 0,67%
----->affir 33,33%
----->scra 1,15%

```

```

scra
----->affip 80,00%
----->affir 27,20%
----->Vocal 14,40%
----->hud 11,20%
----->parent 6,40%
----->effagr 6,40%
----->effsubp 5,12%
----->sm 1,60%
----->selfg 20,00%

```

```

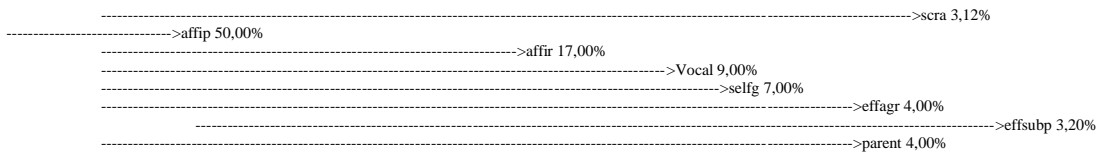
selfg
----->affip 55,00%
----->affir 18,70%
----->parent 4,40%
----->effagr 4,40%
----->effsubp 3,52%
----->sm 1,10%
----->Vocal 25,00%
----->scra 1,39%
----->hud 10,00%

```

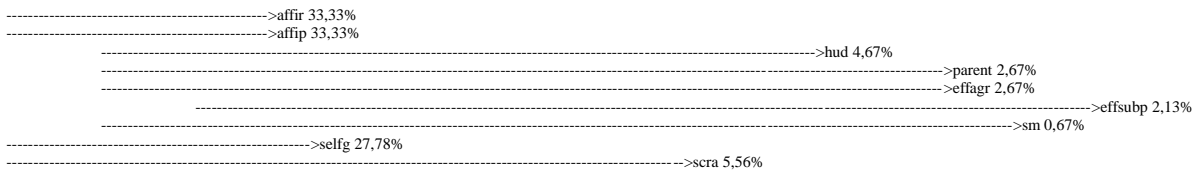
```

sm
----->hud 50,00%

```

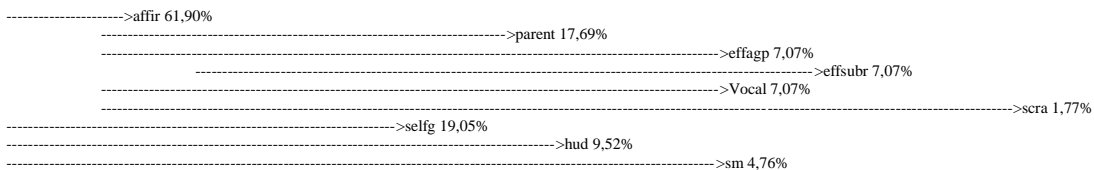


Vocal

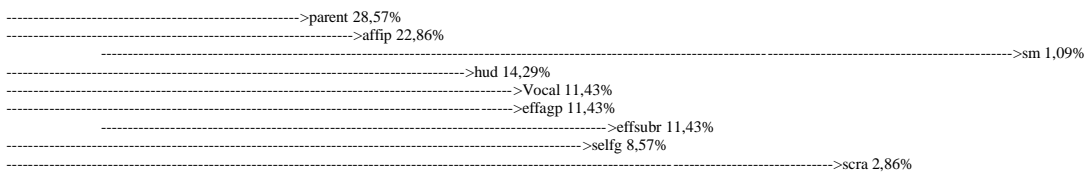


### SE35. View of probability behavioral sequences of the behavioral transitions of Pul.

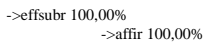
affip



affir



effagp



```

----->parent 28,57%
----->affip 22,86%
----->sm 1,09%
----->hud 14,29%
----->Vocal 11,43%
----->selfg 8,57%
----->scra 2,86%

```

effsubr

```

->affir 100,00%
----->parent 28,57%
----->affip 22,86%
----->sm 1,09%
----->hud 14,29%
----->Vocal 11,43%
----->effagp 11,43%
----->selfg 8,57%
----->scra 2,86%

```

hud

```

----->affir 40,00%
----->parent 11,43%
----->effagp 4,57%
----->effsubr 4,57%
----->scra 1,14%
----->affip 40,00%
----->selfg 7,62%
----->sm 1,90%
----->Vocal 10,00%

```

parent

```

----->affir 47,50%
----->effagp 5,43%
----->effsubr 5,43%
----->Vocal 5,43%
----->selfg 4,07%
----->hud 27,50%
----->affip 20,00%
----->sm 0,95%
----->scra 2,50%

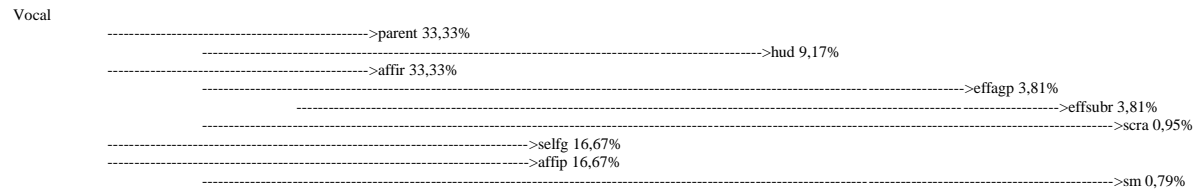
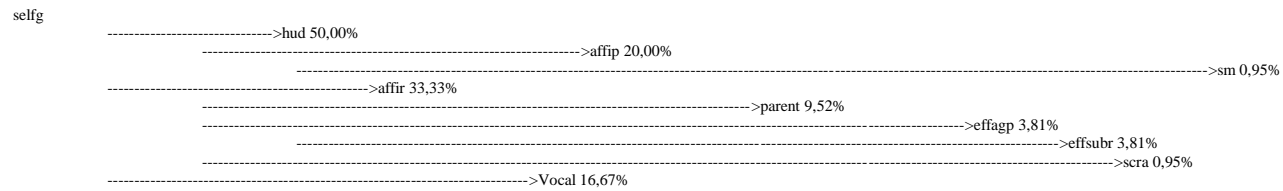
```

scra

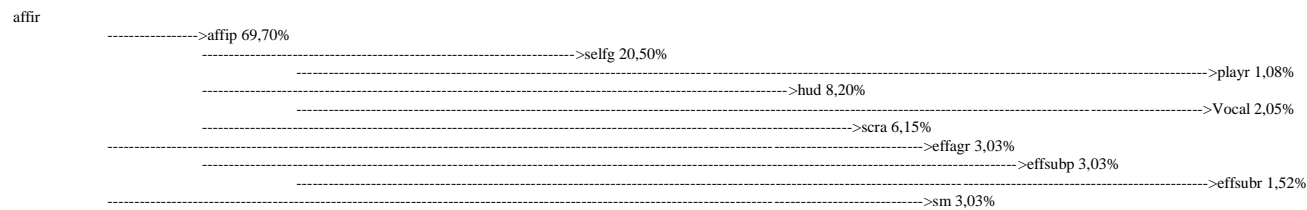
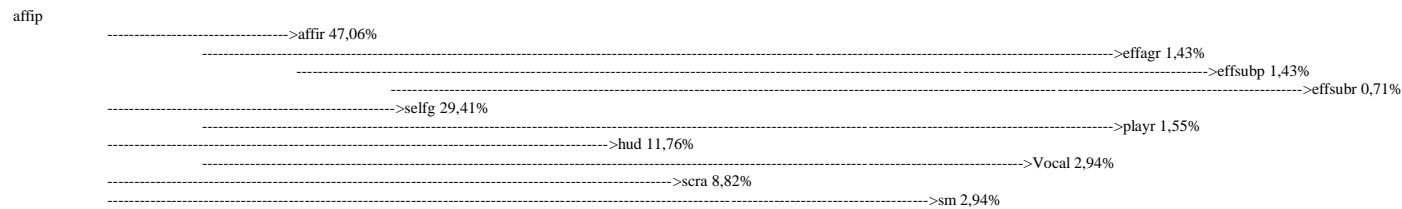
```

----->Vocal 50,00%
----->parent 16,67%
----->affip 8,33%
----->sm 0,40%
----->affir 25,00%
----->effagp 2,86%
----->effsubr 2,86%
----->selfg 25,00%
----->hud 12,50%

```



SE36. View of probability behavioral sequences of the behavioral transitions of Ron.



effagr

```

->effsubp 100,00%
----->effsubr 50,00%
----->affir 50,00%
----->affip 34,85%
----->selfg 10,25%
----->playr 0,54%
----->hud 4,10%
----->Vocal 1,02%
----->scra 3,07%
----->sm 1,52%

```

effsubp

```

----->effsubr 50,00%
----->affir 50,00%
----->affip 34,85%
----->selfg 10,25%
----->playr 0,54%
----->hud 4,10%
----->Vocal 1,02%
----->scra 3,07%
----->effagr 1,52%
----->sm 1,52%

```

effsubr

```

->effsubp 100,00%
----->affir 50,00%
----->affip 34,85%
----->selfg 10,25%
----->playr 0,54%
----->hud 4,10%
----->Vocal 1,02%
----->scra 3,07%
----->effagr 1,52%
----->sm 1,52%

```

hud

```

----->Vocal 25,00%
----->affip 25,00%
----->affir 25,00%
----->effagr 0,76%
----->selfg 16,67%
----->playr 0,88%
----->sm 0,88%
----->scra 8,33%
----->effsubp 1,04%
----->effsubr 0,52%

```

parent

```

->hud 100,00%
----->Vocal 25,00%
----->affir 25,00%
----->effagr 0,76%

```

```

----->affip 25,00%
----->selfg 16,67%
----->playr 0,88%
----->sm 0,88%
----->scra 8,33%
----->effsubp 1,04%
----->effsubr 0,52%

```

playr

```

->affir 100,00%
----->affip 69,70%
----->selfg 20,50%
----->hud 8,20%
----->Vocal 2,05%
----->scra 6,15%
----->sm 3,03%
----->effagr 3,03%
----->effsubp 3,03%
----->effsubr 1,52%

```

scra

```

----->affip 37,50%
----->affir 17,65%
----->effagr 0,53%
----->sm 1,10%
----->selfg 12,50%
----->playr 0,66%
----->hud 12,50%
----->Vocal 12,50%
----->effsubp 12,50%
----->effsubr 6,25%

```

selfg

```

----->affip 42,11%
----->affir 19,81%
----->effagr 0,60%
----->hud 31,58%
----->Vocal 7,89%
----->playr 5,26%
----->scra 5,26%
----->effsubp 0,66%
----->effsubr 0,33%
----->sm 5,26%

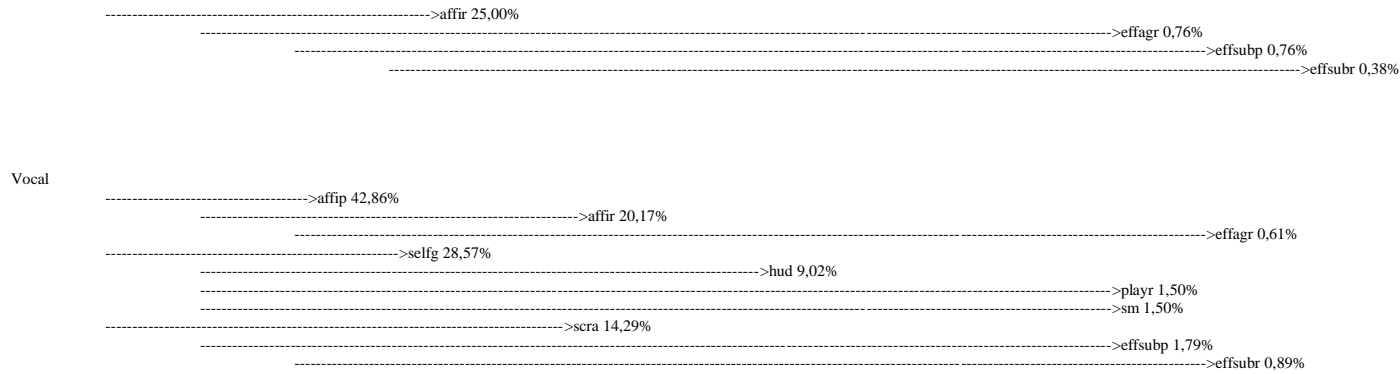
```

sm

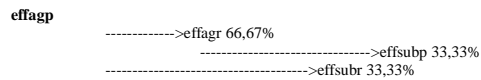
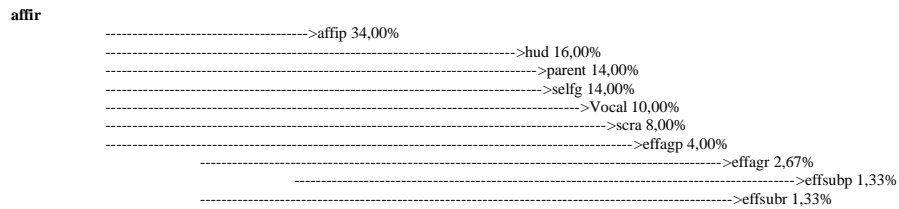
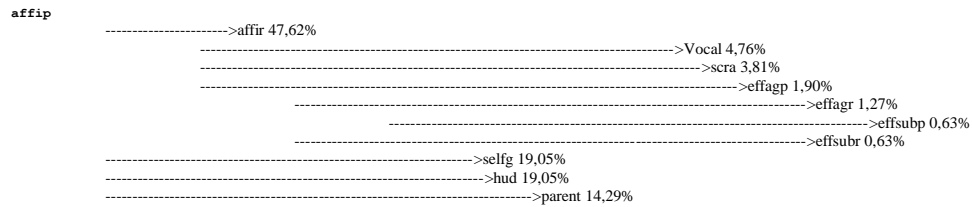
```

----->hud 25,00%
----->affip 25,00%
----->selfg 7,35%
----->playr 0,39%
----->Vocal 25,00%
----->scra 3,57%

```



SE37. View of probability behavioral sequences of the behavioral transitions of Vel.





```

----->affir 33,33%
----->affip 11,33%
----->hud 5,33%
----->selfg 4,67%
----->parent 4,67%
----->Vocal 3,33%
----->scra 2,67%

```

**effagr**

```

----->effsubp 50,00%
----->affir 50,00%
----->affip 17,00%
----->hud 8,00%
----->parent 7,00%
----->selfg 7,00%
----->Vocal 5,00%
----->scra 4,00%
----->effagp 2,00%
----->effsubr 50,00%

```

**effsubp**

```

->affir 100,00%
----->affip 34,00%
----->hud 16,00%
----->parent 14,00%
----->selfg 14,00%
----->Vocal 10,00%
----->scra 8,00%
----->effagp 4,00%
----->effagr 2,67%
----->effsubr 1,33%

```

**effsubr**

```

->affir 100,00%
----->affip 34,00%
----->hud 16,00%
----->parent 14,00%
----->selfg 14,00%
----->Vocal 10,00%
----->scra 8,00%
----->effagp 4,00%
----->effagr 2,67%
----->effsubp 1,33%

```

**hud**

```

----->affir 66,67%
----->affip 22,67%
----->selfg 9,33%
----->Vocal 6,67%
----->scra 5,33%
----->effagp 2,67%
----->effagr 1,78%
----->effsubp 0,89%
----->effsubr 0,89%
----->parent 22,22%

```

**parent**

----->affir 56,76%  
----->affip 19,30%  
----->scra 4,54%  
----->effagp 2,27%  
----->effagr 1,51%  
----->effsubp 0,76%  
----->effsubr 0,76%  
----->hud 13,51%  
----->Vocal 10,81%  
----->selfg 8,11%

**scra**

----->affir 40,00%  
----->affip 13,60%  
----->hud 6,40%  
----->Vocal 4,00%  
----->effagp 1,60%  
----->effagr 1,07%  
----->effsubp 0,53%  
----->effsubr 0,53%  
----->parent 30,00%  
----->selfg 20,00%

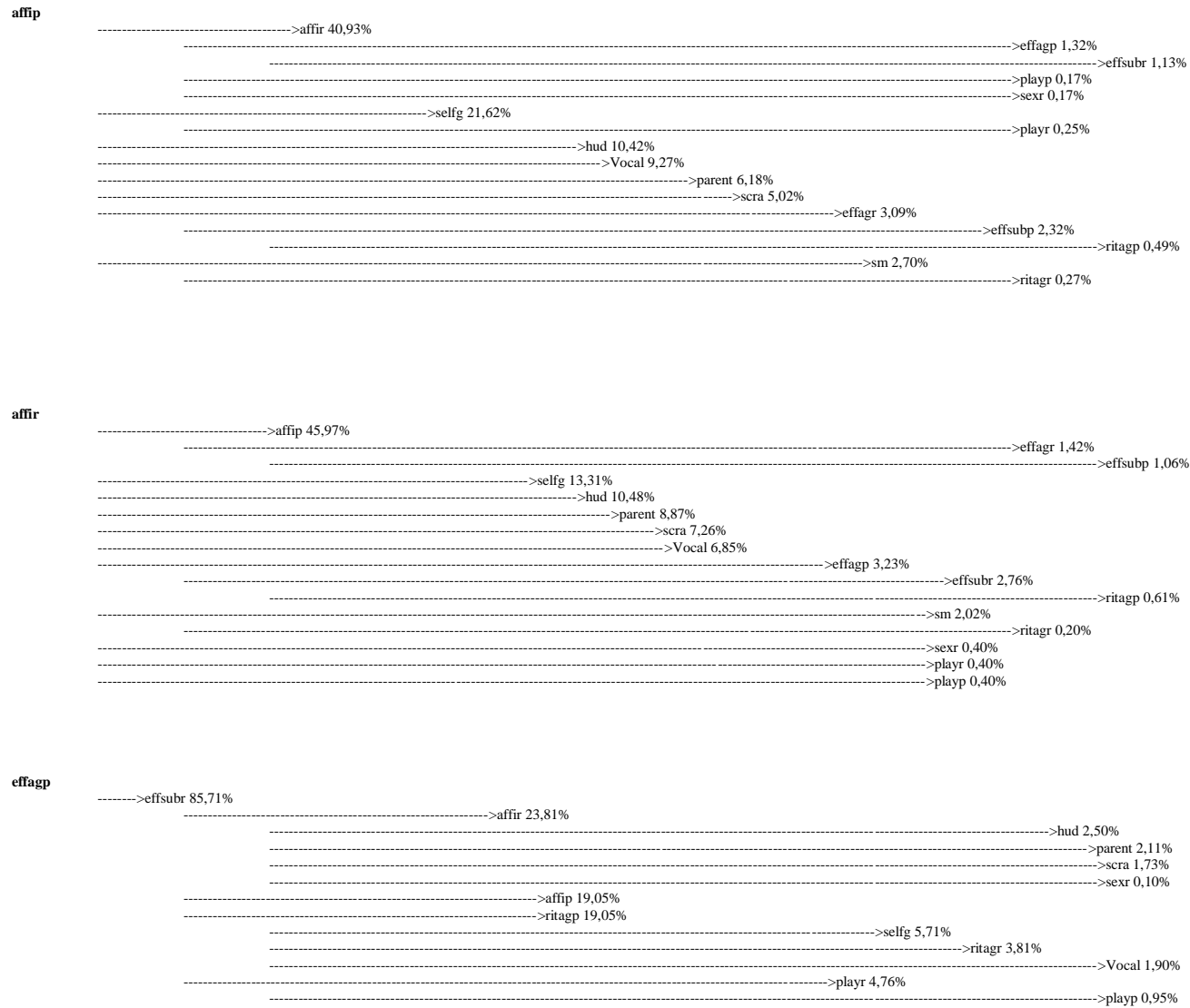
**selfg**

----->affir 64,71%  
----->affip 22,00%  
----->hud 10,35%  
----->parent 9,06%  
----->Vocal 6,47%  
----->scra 17,65%  
----->effagp 5,88%  
----->effagr 3,92%  
----->effsubp 1,96%  
----->effsubr 1,96%

**Vocal**

----->affir 44,44%  
----->affip 15,11%  
----->parent 6,22%  
----->effagp 1,78%  
----->effagr 1,19%  
----->effsubp 0,59%  
----->effsubr 0,59%  
----->selfg 22,22%  
----->scra 11,11%  
----->hud 11,11%

SE38 View of probability behavioral sequences of the behavioral transitions of the ring-tailed lemurs' group.



----->sm 4,76%  
 ----->effagr 14,29%  
 ----->effsubp 10,71%

**effagr**

----->effsubp 75,00%  
 ----->ritagp 15,79%  
 ----->ritagr 3,16%  
 ----->selfg 15,79%  
 ----->Vocal 1,76%  
 ----->playp 0,09%  
 ----->affip 11,84%  
 ----->sm 11,84%  
 ----->effagp 0,59%  
 ----->scra 7,89%  
 ----->affir 12,50%  
 ----->parent 1,11%  
 ----->sexr 0,05%  
 ----->effsubr 6,25%  
 ----->playr 0,35%  
 ----->hud 6,25%

**effsubp**

----->ritagp 21,05%  
 ----->effsubr 6,32%  
 ----->playr 0,35%  
 ----->ritagr 4,21%  
 ----->selfg 21,05%  
 ----->Vocal 2,35%  
 ----->hud 2,23%  
 ----->playp 0,12%  
 ----->affip 15,79%  
 ----->parent 0,98%  
 ----->effagr 0,49%  
 ----->sm 15,79%  
 ----->effagp 0,79%  
 ----->affir 10,53%  
 ----->sexr 0,04%  
 ----->scra 10,53%

**effsubr**

----->affir 27,78%  
 ----->hud 2,91%  
 ----->parent 2,46%  
 ----->scra 2,02%  
 ----->sexr 0,11%  
 ----->affip 22,22%  
 ----->ritagp 22,22%  
 ----->selfg 6,67%  
 ----->ritagr 4,44%  
 ----->Vocal 2,22%

```

----->playr 5,56%
----->playp 1,11%
----->effsubp 5,56%
----->sm 5,56%
----->effagp 5,56%
----->effagr 0,79%

```

**hud**

```

----->affip 31,58%
----->affir 22,37%
----->effagp 0,72%
----->effsubr 0,62%
----->sexr 0,09%
----->selfg 18,42%
----->Vocal 9,21%
----->parent 5,26%
----->effagr 5,26%
----->effsubp 3,95%
----->ritagp 0,83%
----->scra 3,95%
----->playr 1,32%
----->playp 0,26%
----->sm 1,32%
----->ritagr 1,32%

```

**parent**

```

----->affir 49,49%
----->affip 22,75%
----->effagp 1,60%
----->effsubr 1,37%
----->ritagp 0,30%
----->sexr 0,20%
----->playp 0,20%
----->hud 17,17%
----->effagp 0,90%
----->effsubp 0,68%
----->ritagr 0,23%
----->playr 0,23%
----->selfg 7,07%
----->Vocal 6,06%
----->scra 4,04%
----->sm 1,01%

```

**playp**

```

->parent 100,00%
----->affir 49,49%
----->affip 22,75%
----->effagp 1,60%
----->effsubr 1,37%
----->ritagp 0,30%
----->sexr 0,20%

```

```

----->hud 17,17%
----->effagr 0,90%
----->effsubp 0,68%
----->ritagr 0,23%
----->playr 0,23%
----->selfg 7,07%
----->Vocal 6,06%
----->scra 4,04%
----->sm 1,01%

```

**playr**

```

----->affir 40,00%
----->selfg 5,32%
----->hud 4,19%
----->scra 2,90%
----->Vocal 2,74%
----->sexr 0,16%
----->affip 20,00%
----->playp 20,00%
----->parent 20,00%
----->effagp 20,00%
----->effsubr 17,14%
----->ritagp 3,81%
----->ritagr 0,76%
----->sm 0,95%
----->effagr 2,86%
----->effsubp 2,14%

```

**ritagp**

```

----->selfg 30,00%
----->affip 9,71%
----->effagr 0,30%
----->scra 4,41%
----->hud 3,18%
----->effsubr 30,00%
----->affir 8,33%
----->parent 0,74%
----->sexr 0,03%
----->playr 1,67%
----->playp 0,33%
----->effagp 1,67%
----->ritagr 20,00%
----->effsubp 10,00%
----->sm 3,33%
----->Vocal 10,00%

```

**ritagr**

```

----->effsubp 50,00%
----->ritagp 10,53%
----->selfg 10,53%

```

```

----->affip 7,89%
----->effagr 0,24%
----->affir 5,26%
----->sexr 0,02%
----->scra 5,26%
----->sm 16,67%
----->hud 1,67%
----->parent 0,83%
----->Vocal 16,67%
----->effsubr 16,67%
----->playr 0,93%
----->playp 0,19%
----->effagp 0,93%

```

**scra**

```

----->selfg 29,11%
----->playr 0,34%
----->playp 0,17%
----->affip 22,78%
----->affir 16,46%
----->effagp 0,53%
----->effsubr 0,45%
----->sexr 0,07%
----->Vocal 12,66%
----->hud 7,59%
----->parent 5,06%
----->sm 2,53%
----->ritagr 0,25%
----->effagr 2,53%
----->effsubp 1,90%
----->ritagp 0,40%

```

**selfg**

```

----->affip 32,35%
----->parent 2,00%
----->effagr 1,00%
----->affir 21,76%
----->sexr 0,09%
----->scra 14,71%
----->Vocal 11,18%
----->hud 10,59%
----->sm 1,76%
----->effagp 1,18%
----->effsubr 1,01%
----->ritagp 1,18%
----->ritagr 0,24%
----->effsubp 1,18%
----->playr 1,18%
----->playp 0,59%

```

**sexr**

```

->playr 100,00%

```

```

----->affir 40,00%
----->selfg 5,32%
----->hud 4,19%
----->scra 2,90%
----->Vocal 2,74%
----->playp 20,00%
----->parent 20,00%
----->affip 20,00%
----->effagp 20,00%
----->effsubr 17,14%
----->ritagp 3,81%
----->ritagr 0,76%
----->sm 0,95%
----->effagr 2,86%
----->effsubp 2,14%

```

**sm**

```

----->affip 30,00%
----->affir 12,28%
----->sexr 0,05%
----->effagr 0,93%
----->hud 10,00%
----->Vocal 10,00%
----->selfg 10,00%
----->playp 0,06%
----->ritagr 10,00%
----->effsubp 5,00%
----->ritagp 1,05%
----->scra 5,00%
----->effagp 5,00%
----->effsubr 4,29%
----->playr 0,24%
----->parent 5,00%

```

**Vocal**

```

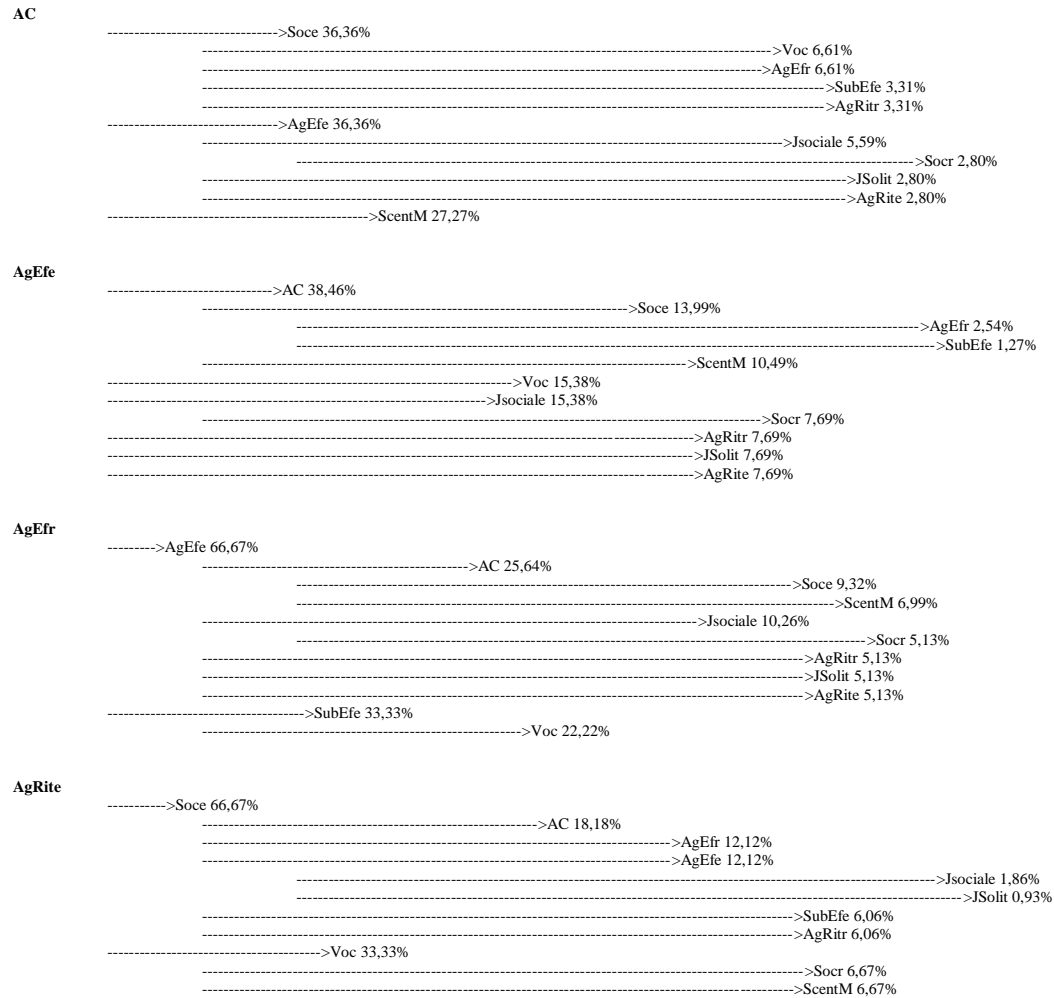
----->affip 32,14%
----->effagr 0,99%
----->effsubp 0,74%
----->selfg 27,38%
----->playr 0,32%
----->ritagp 0,32%
----->playp 0,16%
----->affir 19,05%
----->sexr 0,08%
----->scra 9,52%
----->hud 3,57%
----->sm 3,57%
----->parent 2,38%
----->effagp 1,19%
----->effsubr 1,02%
----->ritagr 1,19%

```



## Red-ruffed lemurs

SE39. View of probability behavioral sequences of the behavioral transitions of Ft.



**AgRitr**

----->AC 50,00%  
----->ScentM 13,64%  
----->AgEfe 25,00%  
----->Jsociale 3,85%  
----->Socr 1,92%  
----->JSolit 1,92%  
----->AgRite 1,92%  
----->Soce 25,00%  
----->Voc 4,55%  
----->AgEfr 4,55%  
----->SubEfe 2,27%

**Jsociale**

----->Socr 50,00%  
----->ScentM 25,00%  
----->Soce 8,33%  
----->AgEfr 1,52%  
----->SubEfe 0,76%  
----->AgEfe 50,00%  
----->AC 19,23%  
----->Voc 7,69%  
----->JSolit 3,85%  
----->AgRitr 3,85%  
----->AgRite 3,85%

**ScentM**

----->Soce 33,33%  
----->AgEfr 6,06%  
----->AgRitr 3,03%  
----->SubEfe 3,03%  
----->AgEfe 16,67%  
----->JSolit 1,28%  
----->Voc 16,67%  
----->AgRite 3,33%  
----->AC 16,67%  
----->Jsociale 16,67%  
----->Socr 8,33%

**Soce**

----->AC 27,27%  
----->ScentM 7,44%  
----->AgEfe 18,18%  
----->Jsociale 2,80%  
----->JSolit 1,40%  
----->Voc 18,18%  
----->Socr 3,64%  
----->AgRite 3,64%  
----->AgEfr 18,18%  
----->SubEfe 9,09%  
----->AgRitr 9,09%

**Socr**

----->ScentM 50,00%  
----->Soce 16,67%  
----->AgEfr 3,03%  
----->SubEfe 1,52%  
----->Voc 8,33%  
----->Jsociale 8,33%  
----->AgEfe 50,00%

----->AC 19,23%  
 ----->JSolit 3,85%  
 ----->AgRitr 3,85%  
 ----->AgRite 3,85%

**SubEfe**

----->Voc 66,67%  
 ----->ScentM 13,33%  
 ----->Jsociale 2,22%  
 ----->Soce 13,33%  
 ----->AgEfr 2,42%  
 ----->AgRitr 1,21%  
 ----->AgRite 13,33%  
 ----->AgEfe 13,33%  
 ----->JSolit 1,03%  
 ----->Socr 13,33%  
 ----->AC 33,33%

**Voc**

----->AgRite 20,00%  
 ----->AgEfe 20,00%  
 ----->AC 7,69%  
 ----->JSolit 1,54%  
 ----->ScentM 20,00%  
 ----->Jsociale 3,33%  
 ----->Socr 20,00%  
 ----->Soce 20,00%  
 ----->AgEfr 3,64%  
 ----->SubEfe 1,82%  
 ----->AgRitr 1,82%

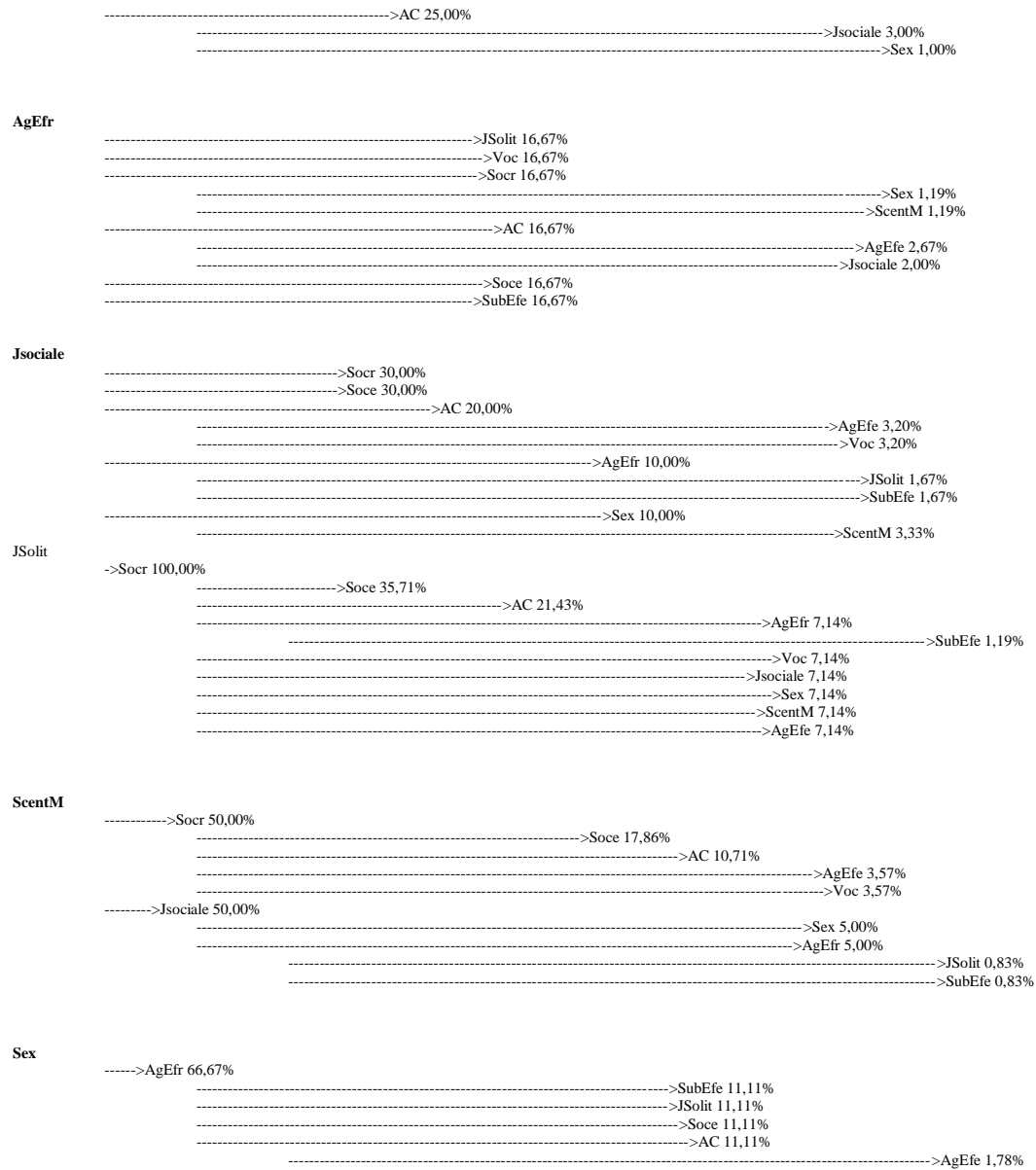
**SE40. View of probability behavioral sequences of the behavioral transitions of Sf.**

**AC**

----->Soce 32,00%  
 ----->Voc 16,00%  
 ----->Socr 16,00%  
 ----->AgEfe 16,00%  
 ----->AgEfr 4,00%  
 ----->JSolit 0,67%  
 ----->Jsociale 12,00%  
 ----->SubEfe 4,00%  
 ----->Sex 4,00%  
 ----->ScentM 1,33%

**AgEfe**

----->Voc 25,00%  
 ----->AgEfr 25,00%  
 ----->JSolit 4,17%  
 ----->SubEfe 4,17%  
 ----->Soce 25,00%  
 ----->Socr 9,62%  
 ----->ScentM 0,69%



----->Voc 11,11%  
 ----->ScentM 33,33%  
 ----->Soer 16,67%  
 ----->Jsociale 16,67%

**Soce**

----->Soer 38,46%  
 ----->Sex 2,75%  
 ----->ScentM 2,75%  
 ----->AC 34,62%  
 ----->AgEfe 5,54%  
 ----->SubEfe 1,38%  
 ----->Jsociale 11,54%  
 ----->Voc 7,69%  
 ----->AgEfr 3,85%  
 ----->JSolit 0,64%  
**Softail**

**Soer**

----->Soce 35,71%  
 ----->AC 21,43%  
 ----->ScentM 7,14%  
 ----->AgEfr 7,14%  
 ----->JSolit 1,19%  
 ----->SubEfe 1,19%  
 ----->Sex 7,14%  
 ----->AgEfe 7,14%  
 ----->Voc 7,14%  
 ----->Jsociale 7,14%

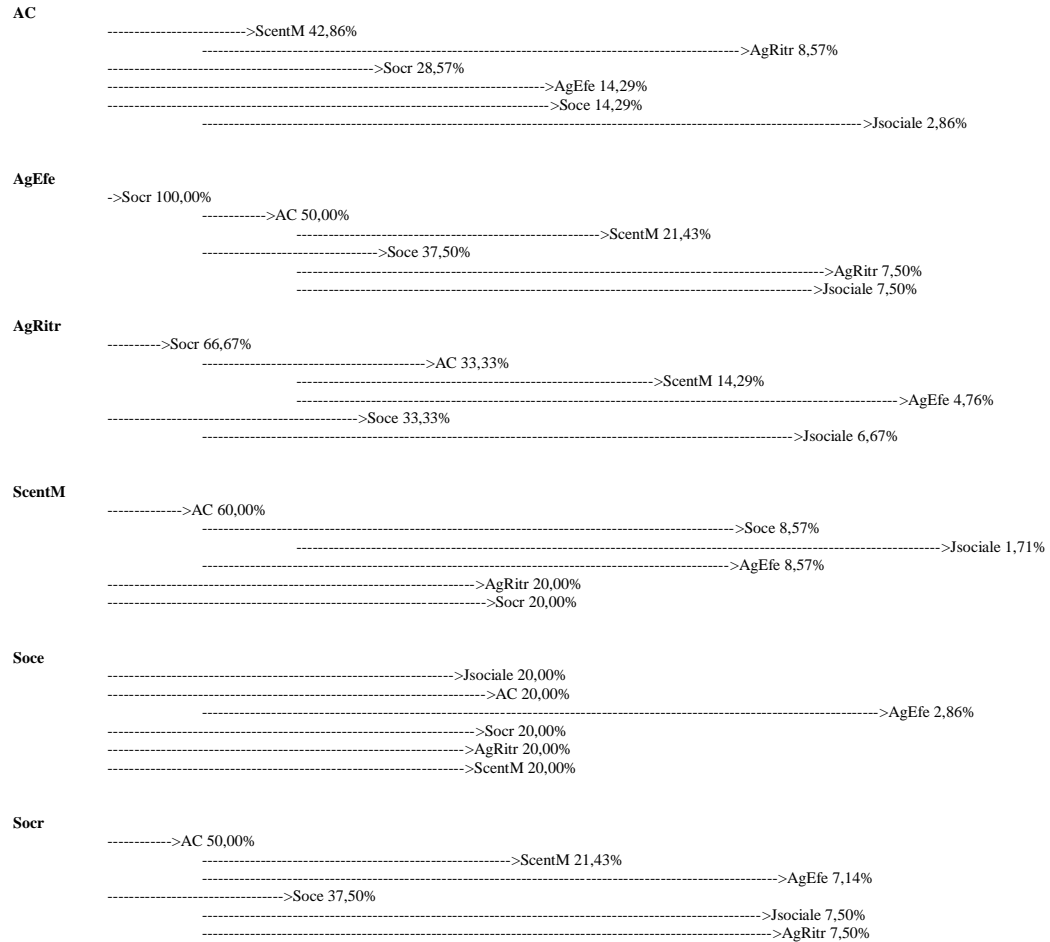
**SubEfe**

->AC 100,00%  
 ----->Soce 32,00%  
 ----->Voc 16,00%  
 ----->Soer 16,00%  
 ----->AgEfe 16,00%  
 ----->AgEfr 4,00%  
 ----->JSolit 0,67%  
 ----->Jsociale 12,00%  
 ----->Sex 4,00%  
 ----->ScentM 1,33%

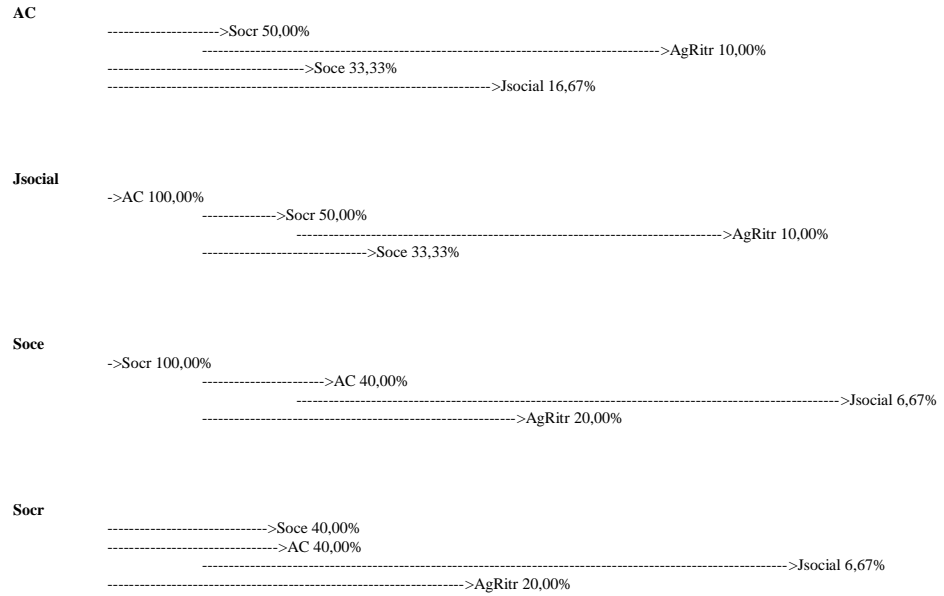
**Voc**

----->AC 62,50%  
 ----->Soer 10,00%  
 ----->AgEfe 10,00%  
 ----->Jsociale 7,50%  
 ----->SubEfe 2,50%  
 ----->Sex 2,50%  
 ----->ScentM 0,83%  
 ----->Soce 25,00%  
 ----->AgEfr 12,50%  
 ----->JSolit 2,08%

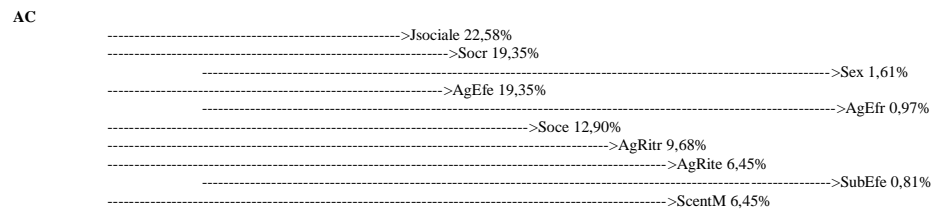
SE41. View of probability behavioral sequences of the behavioral transitions of Ma.



SE42. View of probability behavioral sequences of the behavioral transitions of Pn.



SE43. View of probability behavioral sequences of the behavioral transitions of Sh.



----->Voc 3,23%

**AgEfe**

----->AC 40,00%

----->Jsociale 9,03%

----->Socr 7,74%

----->Sex 0,65%

----->Soce 5,16%

----->ScentM 20,00%

----->AgRitr 10,00%

----->AgRite 10,00%

----->SubEfe 1,25%

----->Voc 5,00%

----->AgEfr 5,00%

**AgEfr**

->AC 100,00%

----->Jsociale 22,58%

----->Socr 19,35%

----->Sex 1,61%

----->AgEfe 19,35%

----->Soce 12,90%

----->AgRitr 9,68%

----->ScentM 6,45%

----->AgRite 6,45%

----->SubEfe 0,81%

----->Voc 3,23%

**AgRite**

----->AC 37,50%

----->Jsociale 8,47%

----->AgRitr 3,63%

----->Voc 25,00%

----->Soce 8,33%

----->ScentM 4,17%

----->Socr 12,50%

----->Sex 1,04%

----->AgEfe 12,50%

----->AgEfr 0,62%

----->SubEfe 12,50%

**AgRitr**

----->AC 42,86%

----->Jsociale 9,68%

----->AgEfe 28,57%

----->ScentM 5,71%

----->AgRite 2,86%

----->SubEfe 0,36%

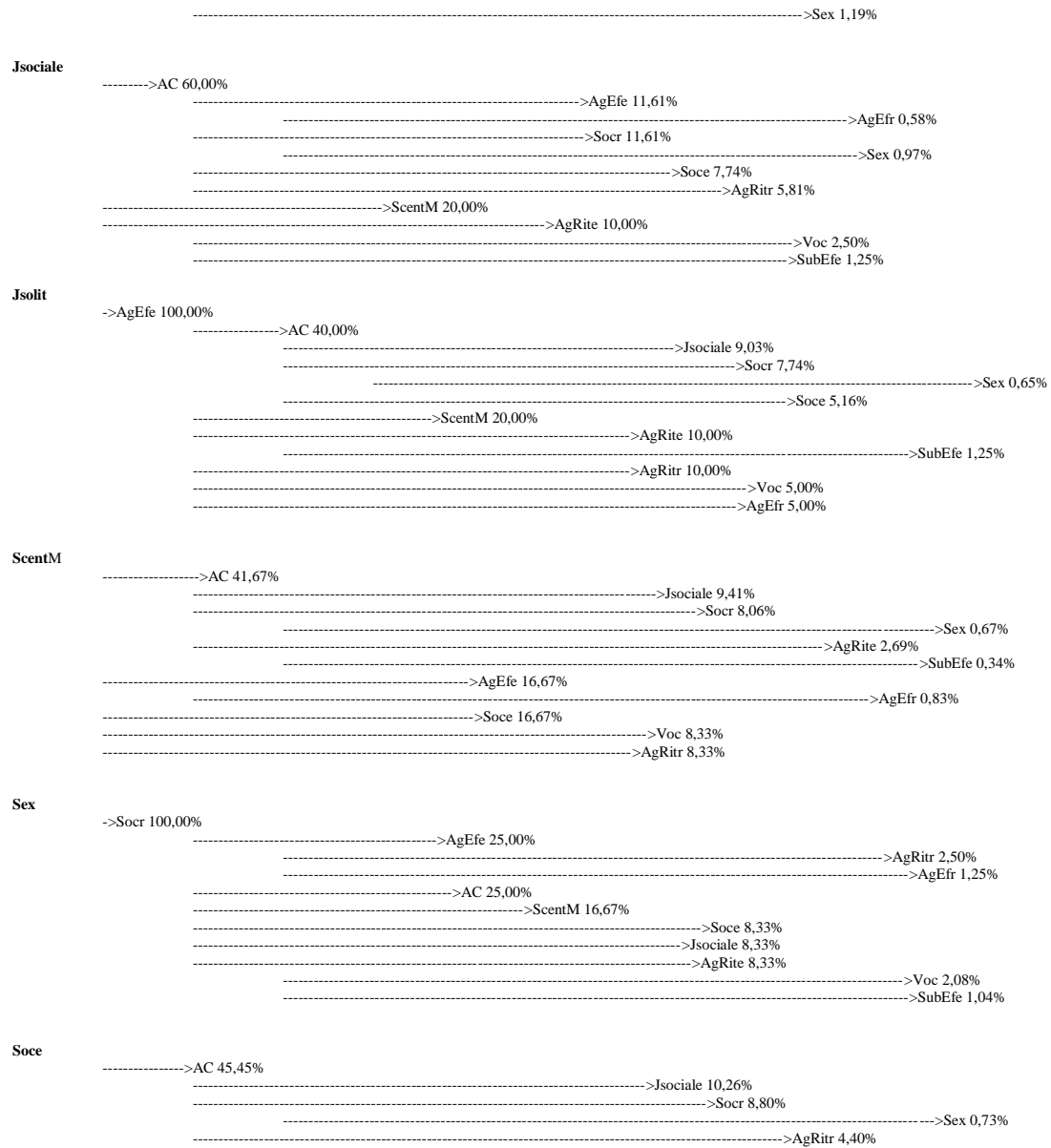
----->Voc 1,43%

----->AgEfr 1,43%

----->Soce 14,29%

----->Socr 14,29%





----->ScentM 18,18%  
----->AgEfe 9,09%  
----->AgEfr 0,45%  
----->Voc 9,09%  
----->AgRite 9,09%  
----->SubEfe 1,14%

**Socr**

----->AgEfe 25,00%  
----->AgRitr 2,50%  
----->AgEfr 1,25%  
----->AC 25,00%  
----->ScentM 16,67%  
----->Jsociale 8,33%  
----->Soce 8,33%  
----->AgRite 8,33%  
----->Voc 2,08%  
----->SubEfe 1,04%  
----->Sex 8,33%

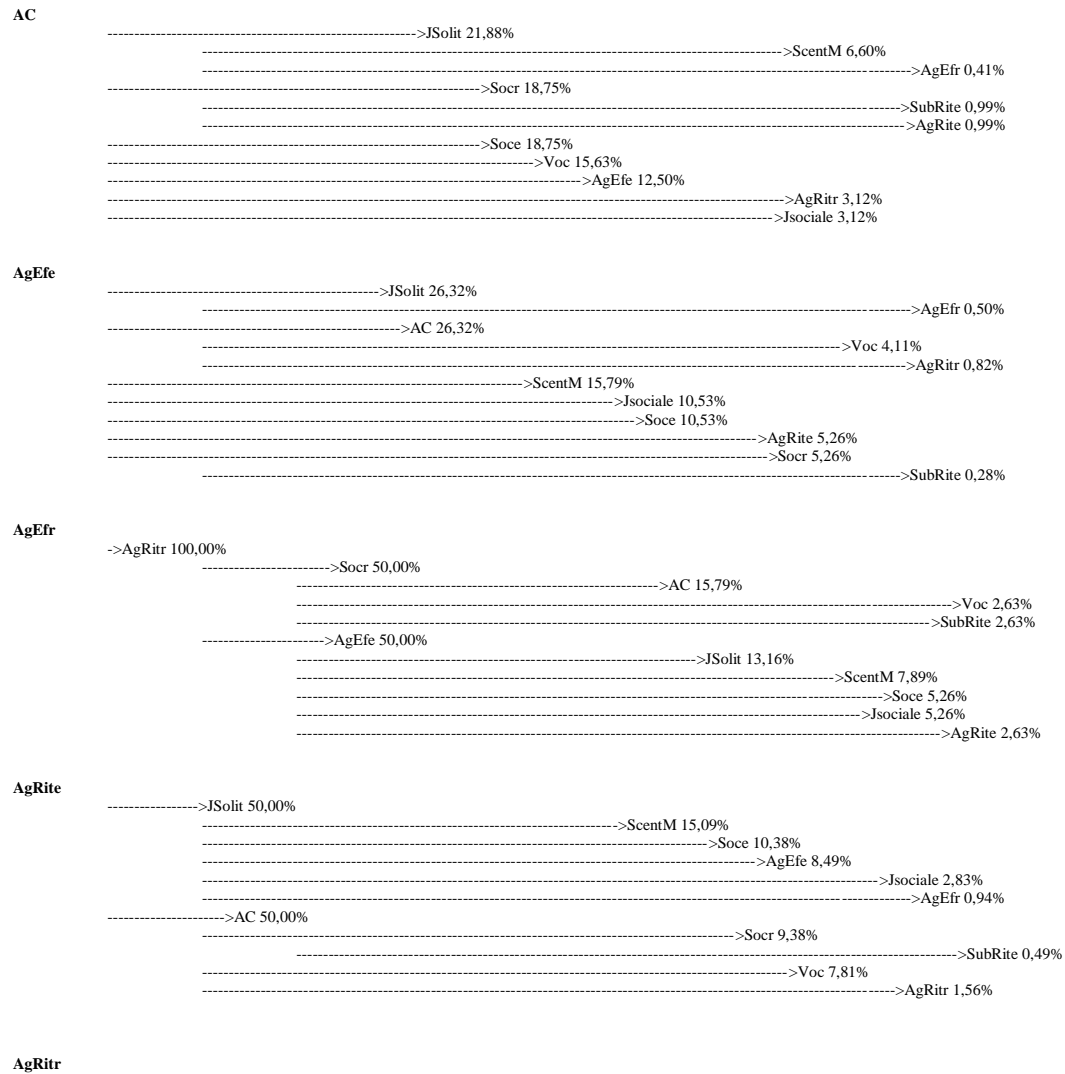
**SubEfe**

->Socr 100,00%  
----->AC 25,00%  
----->AgEfe 25,00%  
----->AgRitr 2,50%  
----->AgEfr 1,25%  
----->ScentM 16,67%  
----->Sex 8,33%  
----->Soce 8,33%  
----->AgRite 8,33%  
----->Voc 2,08%  
----->Jsociale 8,33%

**Voc**

----->Soce 33,33%  
----->AgRite 3,03%  
----->SubEfe 0,38%  
----->AC 33,33%  
----->Jsociale 7,53%  
----->Socr 6,45%  
----->Sex 0,54%  
----->AgRitr 3,23%  
----->ScentM 16,67%  
----->AgEfe 16,67%  
----->AgEfr 0,83%

SE44. View of probability behavioral sequences of the behavioral transitions of CI.



----->Socr 50,00%  
----->AC 15,79%  
----->SubRite 2,63%  
----->Voc 2,63%  
----->AgEfe 50,00%  
----->JSolit 13,16%  
----->AgEfr 0,25%  
----->ScentM 7,89%  
----->Soce 5,26%  
----->Jsociale 5,26%  
----->AgRite 2,63%

**Jsociale**

----->AgEfe 33,33%  
----->AgRite 1,75%  
----->Soce 16,67%  
----->Socr 5,56%  
----->SubRite 0,29%  
----->ScentM 16,67%  
----->AC 16,67%  
----->Voc 2,60%  
----->AgRitr 0,52%  
----->JSolit 16,67%  
----->AgEfr 0,31%

**JSolit**

----->ScentM 30,19%  
----->Soce 20,75%  
----->AgEfe 16,98%  
----->AC 11,32%  
----->Socr 7,55%  
----->SubRite 0,40%  
----->Jsociale 5,66%  
----->Voc 3,77%  
----->AgRite 1,89%  
----->AgEfr 1,89%  
----->AgRitr 1,89%

**ScentM**

----->JSolit 90,91%  
----->Soce 18,87%  
----->AgEfe 15,44%  
----->AC 10,29%  
----->Socr 6,86%  
----->SubRite 0,36%  
----->Jsociale 5,15%  
----->Voc 3,43%  
----->AgRite 1,72%  
----->AgEfr 1,72%  
----->AgRitr 1,72%

**Clarinha**

**Soce**

----->JSolit 33,33%  
----->ScentM 10,06%  
----->AgEfe 5,66%  
----->AgEfr 0,63%  
----->Socr 33,33%  
----->AgRite 1,75%  
----->SubRite 1,75%  
----->AC 20,83%

----->Voc 3,26%  
 ----->AgRitr 0,65%  
 ----->Jsociale 4,17%

**Socr**

----->AC 31,58%  
 ----->JSolit 15,79%  
 ----->Soce 10,53%  
 ----->AgEfe 10,53%  
 ----->ScentM 10,53%  
 ----->AgRite 5,26%  
 ----->SubRite 5,26%  
 ----->Jsociale 5,26%  
 ----->Voc 5,26%  
 ----->AgRitr 0,99%  
 ----->AgEfr 0,30%

**SubRite**

->AC 100,00%  
 ----->JSolit 21,88%  
 ----->ScentM 6,60%  
 ----->Soce 18,75%  
 ----->Socr 18,75%  
 ----->Voc 15,63%  
 ----->AgEfe 12,50%  
 ----->Jsociale 3,12%  
 ----->AgRitr 3,12%  
 ----->AgEfr 0,41%  
 ----->AgRite 0,99%

**Voc**

----->AC 40,00%  
 ----->AgEfe 5,00%  
 ----->AgRitr 1,25%  
 ----->Jsociale 1,25%  
 ----->Socr 20,00%  
 ----->SubRite 1,05%  
 ----->AgRite 1,05%  
 ----->Soce 20,00%  
 ----->JSolit 20,00%  
 ----->ScentM 6,04%  
 ----->AgEfr 0,38%

SE45View of probability behavioral sequences of the behavioral transitions of Rs.

**AC**

----->Soce 37,93%  
 ----->AgEfr 5,58%  
 ----->SubEfr 1,12%  
 ----->Jsociale 27,59%  
 ----->Sox 1,53%  
 ----->Socr 13,79%

```

----->SubEfe 0.99%
----->SubRitr 0.99%
----->Voc 10.34%
----->AgEfe 6.90%
----->ScenFM 1.38%
----->Jsolit 1.38%
----->AgRite 3.45%

```

**AgEfe**

```

----->Jsolit 20.00%
----->Jsociale 20.00%
----->Soce 12.22%
----->SubEfr 0.36%
----->Sex 20.00%
----->Soer 5.00%
----->SubEfe 0.36%
----->SubRitr 0.36%
----->AgEfr 5.00%
----->Ac 20.00%
----->Voc 2.07%
----->AgRite 0.69%
----->ScenFM 20.00%

```

**AgEfr**

```

----->Soce 33.33%
----->Soer 7.84%
----->SubRitr 0.56%
----->SubEfe 0.56%
----->ScenFM 0.98%
----->SubEfr 0.98%
----->Jsolit 0.98%
----->Ac 33.33%
----->Voc 3.45%
----->AgEfe 2.30%
----->AgRite 1.15%
----->Sex 16.67%
----->Jsociale 16.67%

```

**AgRite**

```

->AgEfe 100.00%
----->Ac 20.00%
----->Voc 2.07%
----->Jsolit 20.00%
----->Sex 20.00%
----->Soer 5.00%
----->SubEfe 0.36%
----->SubRitr 0.36%
----->AgEfr 5.00%
----->ScenFM 20.00%

```

----->Jsociale 20.00%  
 ----->Soce 12.22%  
 ----->SubEfr 0.36%

**Jsociale**

----->Soce 61.11%  
 ----->Soct 14.38%  
 ----->SubEfe 1.03%  
 ----->SubRitr 1.03%  
 ----->AgEfr 8.99%  
 ----->Voc 3.59%  
 ----->AgEfe 3.59%  
 ----->ScentM 1.80%  
 ----->SubEfr 1.80%  
 ----->Jsolit 1.80%  
 ----->Ac 16.67%  
 ----->AgRite 0.57%  
 ----->Sex 5.56%

**Jsolit**

----->Sex 50.00%  
 ----->Jsociale 25.00%  
 ----->Soct 12.50%  
 ----->SubEfe 0.89%  
 ----->SubRitr 0.89%  
 ----->AgEfr 12.50%  
 ----->Soce 50.00%  
 ----->Ac 13.24%  
 ----->AgRite 0.46%  
 ----->Voc 2.94%  
 ----->AgEfe 2.94%  
 ----->ScentM 1.47%  
 ----->SubEfr 1.47%

**ScentM**

----->Jsolit 33.33%  
 ----->Sex 16.67%  
 ----->Ac 33.33%  
 ----->Jsociale 9.20%  
 ----->Voc 3.45%  
 ----->AgEfe 2.30%  
 ----->AgRite 1.15%  
 ----->Soce 33.33%  
 ----->Soct 7.84%  
 ----->SubEfe 0.56%  
 ----->SubRitr 0.56%

----->>AgtEfr 2.90%  
 ----->>SubEfr 0.98%

**Sex**

----->>Jsocial 50.00%  
 ----->>Soce 30.56%  
 ----->>Voc 1.80%  
 ----->>AgtEfe 1.80%  
 ----->>Jsolit 0.90%  
 ----->>SubEfr 0.90%  
 ----->>SceptM 0.90%  
 ----->>AgtEfr 25.00%  
 ----->>AC 8.33%  
 ----->>AgtRite 0.29%  
 ----->>Soer 25.00%  
 ----->>SubRitr 1.79%  
 ----->>SubEfe 1.79%

**Soce**

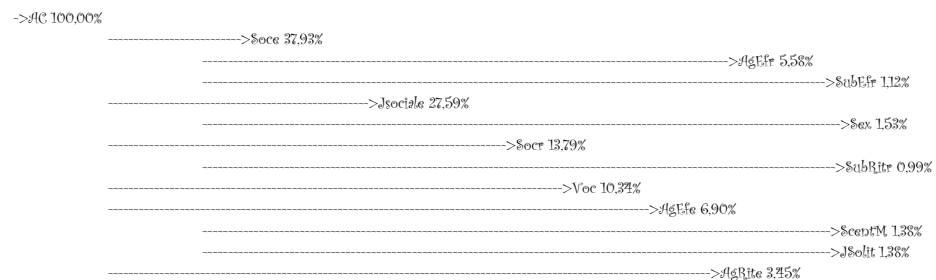
----->>AC 26.27%  
 ----->>AgtRite 0.91%  
 ----->>Soer 23.53%  
 ----->>SubEfe 1.68%  
 ----->>SubRitr 1.68%  
 ----->>AgtEfr 12.71%  
 ----->>Jsocial 11.76%  
 ----->>AgtEfe 5.88%  
 ----->>Voc 5.88%  
 ----->>SubEfr 2.92%  
 ----->>SceptM 2.92%  
 ----->>Sex 2.92%  
 ----->>Jsolit 2.92%

**Soer**

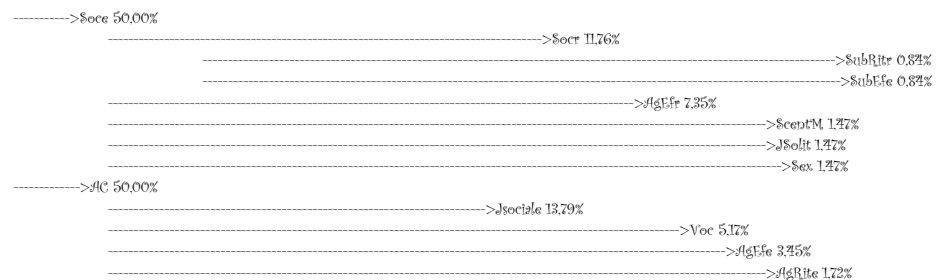
----->>Soce 22.86%  
 ----->>AgtEfr 6.30%  
 ----->>SubEfr 1.26%  
 ----->>AC 12.29%  
 ----->>AgtRite 0.29%  
 ----->>Jsocial 12.29%  
 ----->>AgtEfe 7.12%  
 ----->>SceptM 1.23%  
 ----->>Jsolit 1.23%  
 ----->>Sex 1.23%  
 ----->>Voc 7.12%  
 ----->>SubRitr 7.12%  
 ----->>SubEfe 7.12%



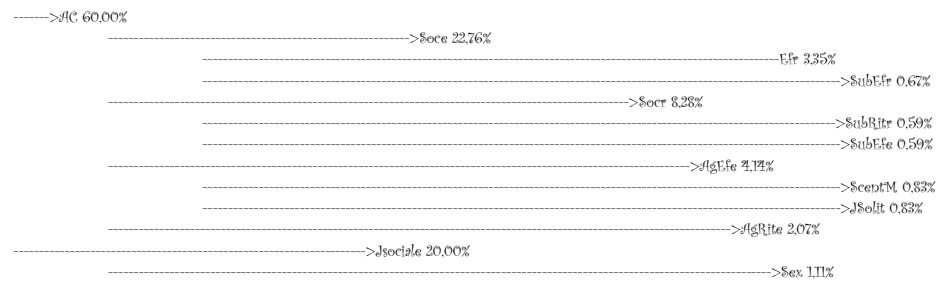
**SubEte**



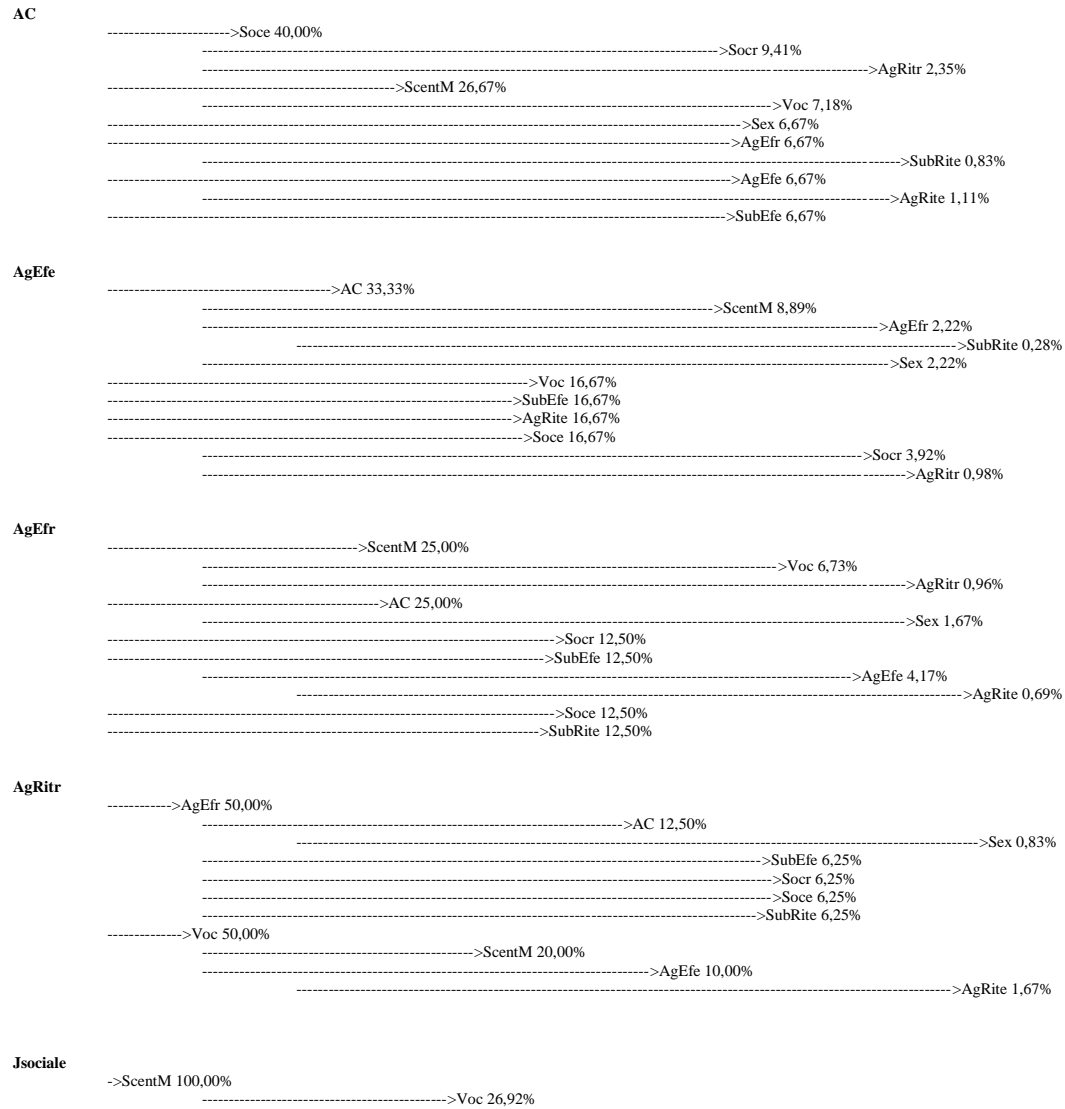
**SubEte**



**Voc**



SE46. View of probability behavioral sequences of the behavioral transitions of Tx.



```

----->AgEfe 5,38%
----->AgRite 0,90%
----->Soce 26,92%
----->Socr 6,33%
----->AgEfr 15,38%
----->SubRite 1,92%
----->AC 15,38%
----->AgRitr 3,85%
----->SubEfe 3,85%
----->Sex 3,85%

```

**ScentM**

```

----->Voc 26,92%
----->AgEfe 5,38%
----->AgRite 0,90%
----->Soce 26,92%
----->Socr 6,33%
----->AgEfr 15,38%
----->SubRite 1,92%
----->AC 15,38%
----->SubEfe 3,85%
----->Sex 3,85%
----->AgRitr 3,85%

```

**Sex**

```

->ScentM 100,00%
----->Voc 26,92%
----->AgEfe 5,38%
----->AgRite 0,90%
----->Soce 26,92%
----->Socr 6,33%
----->AgEfr 15,38%
----->SubRite 1,92%
----->AC 15,38%
----->AgRitr 3,85%
----->SubEfe 3,85%

```

**Soce**

```

----->ScentM 47,06%
----->Voc 12,67%
----->AgEfr 7,24%
----->SubRite 0,90%
----->Sex 1,81%
----->SubEfe 1,81%
----->Socr 23,53%
----->AC 17,65%
----->AgRitr 5,88%
----->AgEfe 5,88%
----->AgRite 0,98%

```

**Socr**

```

----->AC 75,00%
----->Soce 30,00%
----->AgRitr 1,76%
----->ScentM 20,00%
----->Voc 5,38%
----->AgEfe 5,00%
----->AgRite 0,83%
----->SubEfe 5,00%
----->Sex 5,00%
----->AgEfr 12,50%

```

----->SubRite 1,56%

**SubEfe**

----->Soce 33,33%

----->Socr 7,84%

----->AgRitr 1,96%

----->ScentM 33,33%

----->Voc 8,97%

----->AgEfr 5,13%

----->SubRite 0,64%

----->Sex 1,28%

----->AgEfe 33,33%

----->AC 11,11%

----->AgRite 5,56%

**SubRite**

->AgEfr 100,00%

----->ScentM 25,00%

----->Voc 6,73%

----->AgRitr 0,96%

----->AC 25,00%

----->Sex 1,67%

----->Soce 12,50%

----->Socr 12,50%

----->SubEfe 12,50%

----->AgEfe 4,17%

----->AgRite 0,69%

**Voc**

----->ScentM 40,00%

----->Soce 10,77%

----->Socr 2,53%

----->AgRitr 1,54%

----->Sex 1,54%

----->AC 20,00%

----->AgEfe 20,00%

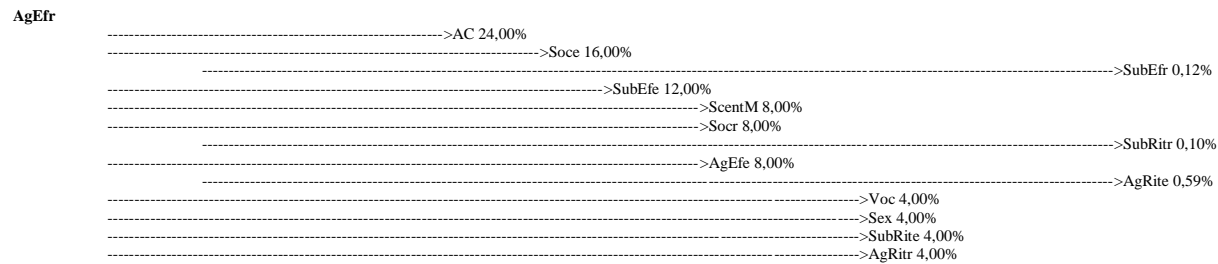
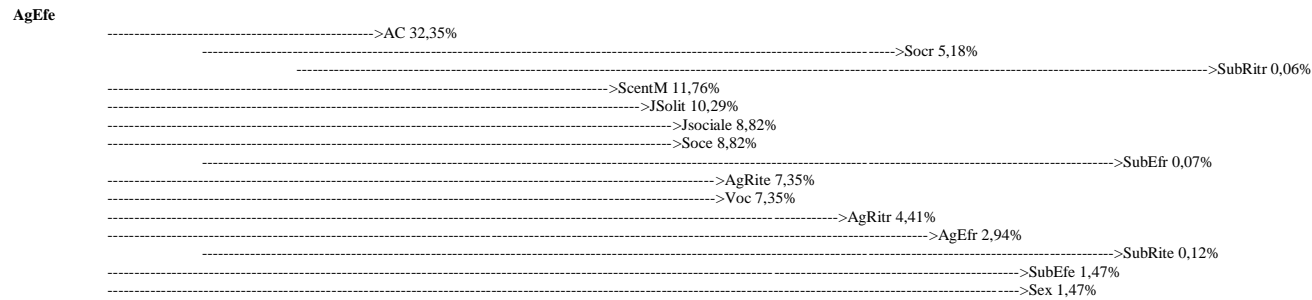
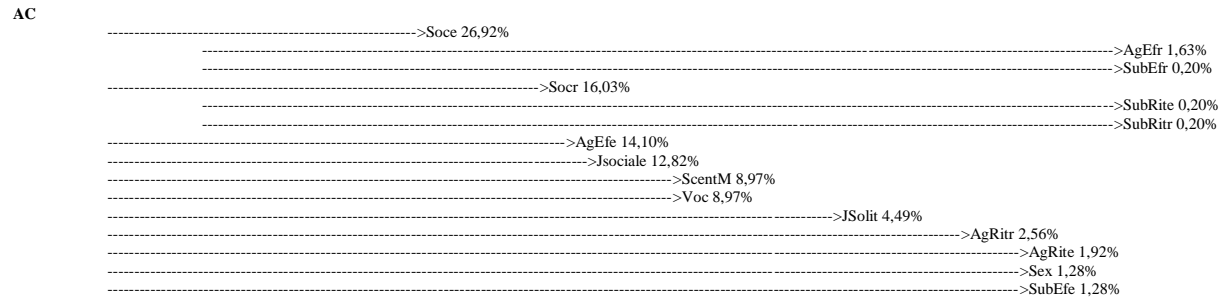
----->SubEfe 3,33%

----->AgRite 3,33%

----->AgEfr 10,00%

----->SubRite 1,25%

SE47. View of probability behavioral sequences of the behavioral transitions of the red-ruffed lemurs' group.



----->Jsociale 4,00%  
 ----->JSolit 4,00%

**AgRite**

----->AC 28,57%  
 ----->Jsociale 3,66%  
 ----->AgRitr 0,73%  
 ----->Sex 0,37%  
 ----->Voc 21,43%  
 ----->ScentM 3,30%  
 ----->AgEfr 1,10%  
 ----->Soce 14,29%  
 ----->SubEfr 0,11%  
 ----->AgEfe 14,29%  
 ----->SubEfe 7,14%  
 ----->Socr 7,14%  
 ----->SubRitr 0,09%  
 ----->SubRite 0,09%  
 ----->JSolit 7,14%

**AgRitr**

----->AC 27,78%  
 ----->Jsociale 3,56%  
 ----->AgEfe 22,22%  
 ----->ScentM 2,61%  
 ----->JSolit 2,29%  
 ----->AgRite 1,63%  
 ----->Socr 22,22%  
 ----->Sex 0,54%  
 ----->SubRite 0,27%  
 ----->SubRitr 0,27%  
 ----->Soce 16,67%  
 ----->SubEfr 0,13%  
 ----->AgEfr 5,56%  
 ----->SubEfe 0,67%  
 ----->Voc 5,56%

**Jsociale**

----->Soce 31,25%  
 ----->AgRitr 0,71%  
 ----->SubEfr 0,24%  
 ----->AC 27,08%  
 ----->Voc 2,43%  
 ----->Socr 12,50%  
 ----->SubRitr 0,15%  
 ----->AgEfe 8,33%  
 ----->ScentM 8,33%  
 ----->JSolit 2,30%  
 ----->AgEfr 4,17%  
 ----->SubEfe 0,50%  
 ----->SubRite 0,17%  
 ----->Sex 4,17%  
 ----->AgRite 2,08%

**JSolit**

----->ScentM 28,07%  
----->AgRitr 1,11%  
----->SubEfe 0,37%  
----->Soce 21,05%  
----->SubEfr 0,16%  
----->AgEfe 17,54%  
----->AC 10,53%  
----->Socr 8,77%  
----->SubRite 0,11%  
----->SubRitr 0,11%  
----->Jsociale 5,26%  
----->Voc 3,51%  
----->AgEfr 1,75%  
----->Sex 1,75%  
----->AgRite 1,75%

**ScentM**

----->JSolit 27,63%  
----->AgRite 0,48%  
----->AC 19,74%  
----->Soce 15,79%  
----->Socr 4,19%  
----->SubRitr 0,05%  
----->SubEfr 0,12%  
----->Voc 11,84%  
----->AgEfe 5,26%  
----->AgEfr 5,26%  
----->SubRite 0,21%  
----->Jsociale 3,95%  
----->AgRitr 3,95%  
----->Sex 1,32%  
----->SubEfe 1,32%

**Sex**

----->AgEfr 30,00%  
----->AC 7,20%  
----->SubEfe 3,60%  
----->AgEfe 2,40%  
----->SubRite 1,20%  
----->AgRitr 1,20%  
----->ScentM 30,00%  
----->JSolit 8,29%  
----->Voc 3,55%  
----->Jsociale 20,00%  
----->Soce 6,25%  
----->SubEfr 0,05%  
----->Socr 20,00%  
----->AgRite 0,49%  
----->SubRitr 0,24%

**Soce**

----->Socr 26,52%  
----->SubRite 0,32%  
----->SubRitr 0,32%  
----->AC 26,52%  
----->ScentM 9,85%  
----->Jsociale 7,58%  
----->JSolit 6,82%  
----->AgEfe 6,06%  
----->AgEfr 6,06%  
----->Voc 5,30%  
----->AgRitr 2,27%  
----->AgRite 0,76%  
----->SubEfe 0,76%  
----->Sex 0,76%  
----->SubEfr 0,76%

**Socr**

----->AC 31,71%  
----->Soce 23,17%  
----->SubEfr 0,18%  
----->ScentM 9,76%  
----->AgEfe 9,76%  
----->Jsociale 6,10%  
----->Voc 3,66%  
----->JSolit 3,66%  
----->AgEfr 2,44%  
----->Sex 2,44%  
----->AgRite 2,44%  
----->SubRite 1,22%  
----->SubEfe 1,22%  
----->SubRitr 1,22%  
----->AgRitr 1,22%

**SubEfe**

----->AC 40,00%  
----->Soce 10,77%  
----->SubEfr 0,08%  
----->Jsociale 5,13%  
----->AgRitr 1,03%  
----->AgRite 0,77%  
----->Sex 0,51%  
----->Voc 20,00%  
----->AgEfr 1,03%  
----->AgEfe 10,00%  
----->ScentM 10,00%  
----->JSolit 2,76%  
----->Socr 10,00%  
----->SubRite 0,12%  
----->SubRitr 0,12%



**SubEfr**

----->Soce 50,00%  
----->Socr 13,26%  
----->SubRitr 0,16%  
----->SubRite 0,16%  
----->ScentM 4,92%  
----->JSolit 3,41%  
----->AgEfr 3,03%  
----->AC 50,00%  
----->AgEfe 7,05%  
----->Jsociale 6,41%  
----->Voc 4,49%  
----->AgRitr 1,28%  
----->AgRite 0,96%  
----->Sex 0,64%  
----->SubEfe 0,64%

**SubRite**

----->AgEfr 50,00%  
----->SubEfe 6,00%  
----->AgRitr 2,00%  
----->Sex 2,00%  
----->AC 50,00%  
----->Soce 13,46%  
----->SubEfr 0,10%  
----->Socr 8,01%  
----->SubRitr 0,10%  
----->AgEfe 7,05%  
----->Jsociale 6,41%  
----->Voc 4,49%  
----->ScentM 4,49%  
----->JSolit 2,24%  
----->AgRite 0,96%

**Voc**

----->AC 35,90%  
----->Socr 5,75%  
----->SubRitr 0,07%  
----->Jsociale 4,60%  
----->AgRitr 0,92%  
----->Sex 0,46%  
----->Soce 20,51%  
----->SubEfr 0,16%  
----->ScentM 15,38%  
----->JSolit 4,25%  
----->AgEfe 10,26%  
----->AgEfr 5,13%  
----->SubEfe 0,62%  
----->SubRite 0,21%  
----->AgRite 2,56%

**D. How diverse, flexible and complex are primate personalities? A comparative analysis**

Table S29. Ethogram of the *Hylobate lars*'s behaviors reported in this study. Although Affiliation category is very broad and certainly some behaviors included might show differences due to personality, we decided to maintain all into the same category group to prevent the increase of total number of variables to be observed, under the assumption that the differences in some of the behaviors included would not obscure potential differences in the broad category (Continued on the next page).

	<b>Behavior</b>	<b>Defenition</b>
<b>Individual</b>	Observing	Observing/tracking of specific objects or individuals. The animal must be standing still without doing any other activities at same time.
	Grooming	Using teeth to clean its fur and fingers/toes to massage body or to clean its own fur.
	Vocalizations	Male Solo Call - Follows this structure: the male begins with intermittent low pitched <i>oos</i> and <i>was</i> , soon grouping these into phrases and adding low pitched quaver <i>wa-oos</i> ; phrase structure tightens up until the male is producing low pitched male quaver phrases. These reach normal pitch a few minutes after the start of the bout. The male continues to deliver these phrases at a rate of 2-3/min until the end of the bout. Great Call - Produced only by the female; it has a invariable two-humped shape peaking at 0,8-1,2 KHz and at 1,3-1,6 KHz.
	Solitary Play	Acrobatics- Hanging or swinging from tree branches or chasing around in circles.
<b>Social</b>	Simple vocalisations	Hoo-oo - Quiet figure pitched low and comprising both inhalation and exhalation. Generally given by adult females. Wa - Short, uninflected, steeply rising note. It is the simplest and most common note. Leaning Wa - A more prolonged wa, with a monotonous beginning and finishing abruptly. Wa-oo - Inflected note, which rises steeply and then either more or less holds the peak pitch to produce a horizontal arm of varying length, or descends again to produce a convex, dome-shaped note. Oo - Drawn out on a low, fairly even pitch, though it often rises slightly at first. Ooaa - A wa which is so concave as to be J-shaped.
	Complex vocalisations (phrases)	Male quaver phrase - As the name indicates, it is only given by the male. Although it is very variable, ranging between 5 possible types of vocalisation. Male simple phrase - It has a similar structure of the male quaver phrase but lacks quavers and it is less common. Male trill - Rapid series of was with high initial pitch and spanning a fairly narrow pitch range. Ooaa burst - Rhythmical series of ooaa notes.
	Social Play	Chasing - chase another individual. Mock biting - biting without harming the other individual. Pulling - grab and move an individual towards the effector. Embracing - envelop an individual with its arms. Slaping - hitting smoothly the other individual with the hand or the arm.
	Food sharing	Presenting and giving food to an individual.
	Allogrooming	Using teeth and fingers/toes to clean the fur of another individual
	Vocalisations	Duet call - Structured vocalizations given by the mating-pair.

<b>Behavior</b>	<b>Defenition</b>
Agonistic Ritualized Behaviors	Dropping Objects - Break a dead branch and drop it towards another individual. Body Shake - Rhythmic shaking of the head, hands and arms. Branch Shaking - Vigorously shake a reachable tree branch. Opening/closing mouth - Open and close mouth with tensed lips as if smacking them together. Grimace - Exaggerated mouth opening, exposing the teeth as if smiling.
Aggressive Behaviors	Grappling - Hold the individual in order to cause harm. Biting - Bite strongly the individual. Dropping Objects - Break a dead branch and drop it towards another individual.
Vocalisations	Male dispute call - In most disputes the male(s) of one or both groups deliver vocalisations ranging from quiet, low was to shrill male quaver phrases. These last about an hour and have also a territorial defense basis. Disturbed call - Call with a wide spectrum of structures but which are all identified by their content of oos, wa-oos and sharp wows. They are distinguished from the introductory sequences of duets by the lack of rhythm and by offspring participation.
Parental care	Carrying and Suckling - Transport the infant on the ventral region. The infant sucks the nipples of its mother during the lactation period. Grooming - Using teeth and fingers/toes to clean the infant's fur. Food sharing- Presenting and giving food to the infant. Play - Social playing with the infant.
Sexual behavior	Copulation - Sexual intercourse between individuals. Sexual Display: Male Display - One-arm dangles, locomotion back and forth around a particular pathway, and the breaking of branches. Receptivity-linked behaviours - Female bends forward and lifting her hip and genitals towards the male, grasping and pulling the male towards herself while bent and/or using eye contact during intromission.
Abnormal behavior	Infanticide, Repetitive teeth clenching, Body rocking, Circling and Pacing, Spinning, Coprophagia, Cage biting, Pluck hair, Urine drinking, Excessive grooming.
Others	Not previously mentioned.

Table S30. Ethogram of the *Saimiri boliviensis*'s behaviors reported in this study. Although Affiliation category is very broad and certainly some behaviors included might show differences due to personality, we decided to maintain all into the same category group to prevent the increase of total number of variables to be observed, under the assumption that the differences in some of the behaviors included would not obscure potential differences in the broad category (Continued on the next pages).

	<b>Behavior</b>	<b>Definition</b>
<b>Individual</b>	Visual attention	Vigilance - Monkey standing in a upright position, looking alert and scanning the surrounding area. Facing, Looking at - Orienting toward; looking or staring at.
	Solitary play	Back Rolling - Lying on back and rolling on side to side. Steep leap - Vertical jumps with minimal forward locomotion. Run away - Rapid flight. Darting - Running with quick changes of direction. Swinging - Hanging by feet and swinging.
	Scent mark/release pheromone	Anogenital rub- The anogenital area is rubbed against a perch.
	Self-groom	Manipulation of own fur or skin. Lick- Genital, mouth, hand or wetted perch are licked. Anogenital Inspection (self) - Manual or visual inspection of male's own anogenital region.
	Kick-wash	Rear foot rubbed along chest wall, usually with urine, in males.
	Urine wash	Urine is release onto the hand and rubbed repeatedly against the sole of the ipsilateral foot. This is often repeated on the opposite hand and foot.
<b>Social</b>	AFFILIATION	Allogroom - Manipulation of others fur or skin. Grasp (hold)- Similar to, but more vigorous than, hand-on, since the hand grabs the skin or fur of other individual. Smell - One individual smells the genital, mouth or hands of another individual or perch wetted by it. Pull - One individual may pull the tail or other body parts of other individual. Cling - Clasp arms and legs around other individual. Looking through the legs - Facing other individual while looking between the legs. Bobbing head - Head bobs from side to side. Huddle Together - Huddle posture with body contact with other animal. Hand on (touch) - One individual puts it's hand on a second individual, often touching the head, shoulder, arm, tail, hip, waist, back, hand or genital.
	Sexual behaviour	Anogenital inspection (others) - Visual, manual or olfactory inspection. Mount with Thrust (copulation) - Male mount female making thrust movement. Genital present - male places genital region in face of female and holds position for at last 3 sec. Mount attempt - Mount with short thrust, no apparent intromission. Oral-Oral contact - Close face to face proximity usually involving sniffing or licking of the partner. Pursue - Male follows female rapidly from place to place. Penile Erection - A partial or complete erection of the penis. Posturing before mounting - The female assumes a stable position with leg apart, tail to the side.

<b>Behavior</b>	<b>Definition</b>
Social play	Grasp (hold) - Similar to, but more vigorous, than hand-on, since the hand grabs the skin or fur of other individual. Pull - One individual may pull the tail or other body parts of other individual. Cling - Clasp arms and legs around other individual. Proximity - Maintaining a fixed distance. Approach - General movements toward. Circling around - Moving around other animal in close circles. Distance play - Hooping and running through environment without contact. Wrestling or contact play - Consists of numerous combinations of holding, grasping, pulling, pushing, shambiting, rolling and jumping onto each other. Jump onto - Approach with a jump.
Ritualized agonism	Penile display - Male exhibit his penis associated with spreading legs. Visual display - Visual cues involving expression can be associated with aggression. Branch shaking - (auditory and visual display)- Shaking branches or vines with vigorous movements of all 4 limbs. Scream - High pitched vocalization, ears flattened, usually directed to other animal. Grimace - Uncovering the teeth. Ear wiggle - Both ear pulled back. Lunges - Rapid but short move toward other individual. In close quarters, hips are thrust toward recipient.
Effective agonism	Push - First individual actively increases distance to other individual by pushing with hand (or feet). Grasp (hold) - Similar to, but more vigorous, than hand-on, since the hand grabs the skin or fur of other individual. Pull - One individual may pull the tail or other body parts of other individual. Cling - Clasp arms and legs around other individual. Chase - Rapid approach or following. Thrusting chin against other individual -Jutting movement of head with chin first. Pile-up Display -Adult males climb onto each other's backs, clings and firmly hold each other down. When several males are involved, this produces a pile-up of animals. Food Steal (Taking Object Away) - One individual uses it's hand(s) to take food or objects from another individual. Fighting - Rapid succession of many intense behavioural units such as jumping onto, grasping, pulling or biting, etc (more intense than wrestling). Semichases - Harassing an adult male until he moves away.
Submission	Visual display - Visual cues involving expression can be associated with fear. Submissive Huddling - Crouching while receiving a close penile display or threat. Avoiding - Moving away, turning away.
Parenting	Allomaternal care-Care of an infant in a maternal way by a monkey other than the birth mother. Breast feeding- An infant establish nipple contact with its mother. Infant transport- An individual (mother or another individual) carries an infant from point A to point B, in a fast or slow pace, maintaining dorsal, ventral or lateral contact with the infant. Nursing -Infant hold nipple in the mouth and suck rhythmically. Shoulder present -Mother or aunt pushes down and toward infant (often with purr vocalization). Gathering infant - Picking up a small infant by using hands and arms. Carrying - One individual carries a second individual on its back. Shaking or rubbing the infant off -Carrier shakes it's body or rubs against a branch or object to dislodge a riding infant. Hand massage -Infant rhythmically strokes mother's hand. Solicit grooming -Infant lies down in front of its mother.

	<b>Behavior</b>	<b>Definition</b>
	Abnormal behaviour	Stereotypical movements -Repetitive and unvarying movement apparently functionless. Pacing -Repetitive walking on the same path. Self-hair pulling -Plucking out hair from the body using hand. Self-biting -Individual bites his self making injuries.
	Other	Any behaviour (solitary or social) not described on this catalogue .
	Out of sight	Monkey not visible during observation.

Table S31. Hylobates lar's: Statistics summary.

Behavioral Categories	Random Effect Model			REM control critical value (Benjamini- Hochberg)	Donald		Charruinha		Lagos		Tina		Maya		Ágil	
	variance pop.	F	Sig.		Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean
Self-grooming	0.008	61.778	0.000*	0.001*	0.000	0.019	0.001	0.031	0.001	0.032	0.003	0.031	0.013	0.100	0.019	0.132
Solitary Play	0.002	13.183	0.001*	0.002*	0.000	0.001	0.000	0.006	0.001	0.007			0.001	0.006	0.006	0.047
Simple Vocalization	0.001	4.066	0.053	0.011	0.000	0.004	0.000	0.001	0.000	0.000			0.000	0.002	0.003	0.019
Complex Vocalization	0.000	2.031	0.184	0.014	0.001	0.003	0.000	0.001					0.000	0.002		
Play Initiator	0.000	9.083	0.003*	0.004*			0.001	0.023	0.000	0.004						
Affiliation Initiator	0.000	6.432	0.026	0.008	0.000	0.002	0.000	0.002			0.001	0.008	0.001	0.009	0.000	0.002
Parental Grooming Initiator	0.005	14.196	0.000*	0.001*	0.000	0.004	0.003	0.018	0.001	0.005	0.019	0.094				
Social Vocalization Initiator	0.005	5.304	0.022*	0.007	0.021	0.025	0.006	0.015			0.006	0.018				
Sex Initiator	0.000	0.111	0.744	0.017	0.000	0.001					0.000	0.002				
Ritual agonism	0.000	4.559	0.036*	0.009	0.001	0.011			0.000	0.001						
Play Receiver	0.001	4.258	0.065	0.012			0.000	0.008	0.000	0.004	0.004	0.009				
Affiliation Receiver	0.001	10.055	0.002*	0.003*	0.002	0.008			0.000	0.001			0.001	0.007	0.003	0.018
Social Vocalization Receiver	0.005	3.964	0.047*	0.01	0.020	0.020	0.006	0.015			0.002	0.012				
Sex Receiver	0.000	1.000	0.318	0.015							0.000	0.000				
Ritual Agonism Receiver	0.000	4.841	0.036*	0.009	0.001	0.004			0.000	0.008			0.000	0.000		
Abnormal Behavior	0.000	3.024	0.083	0.013			0.000	0.000					0.000	0.001	0.000	0.001
Abnormal Behavior Event	0.000	1.000	0.318	0.015											0.000	0.000
Arms Reach	0.000	86.394	0.000*	0.001*	0.000	0.007	0.000	0.014	0.0053077	0.000	0.000	0.031	0.000	0.003	0.000	0.002
Arms Reach 1	0.000	81.082	0.000*	0.001*	0.000	0.004	0.000	0.007	0.000	0.003	0.000	0.023	0.000	0.003	0.000	0.002
Arms Reach 2	0.000	38.85	0.000*	0.001*	0.000	0.002	0.000	0.006	0.000	0.002	0.000	0.007				
Arms Reach 3	0.000	10.822	0.004*	0.004*	0.000	0.000	0.000	0.001	0.000	0.001	0.000	0.001				

Table S32. *Saimiri boliviensis*'s: Statistics summary

Behavioral Categories	Random Effect Model				Tordo	Veríssimo		Vera		Aurélio		Vina		Vanessa		
	variance pop.	F	Sig.	REM control critical value (Benjamini-Hochberg)	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean	Individual Flexibility	Mean
Solitary Play	0.000	5.729	0.052	0.008							0.000	0.004				
Sent Marking	0.000	1.000	0.318	0.022	0.000	0.000										
Self-grooming	0.000	7.12	0.008*	0.004	0.000	0.002	0.000	0.001	0.000	0.000	0.000	0.002	0.000	0.000		
Affiliation Initiator	0.000	2.031	0.164	0.013	0.000	0.002	0.000	0.006	0.000	0.000	0.000	0.000				
Sex Initiator	0.000	0.004	0.953	0.024							0.000	0.001				
Ritual Agonism Initiator	0.000	0.969	0.335	0.021	0.002	0.009	0.000	0.001			0.000	0.002				
Aggression Initiator	0.000	5.188	0.046*	0.007	0.005	0.019	0.000	0.005			0.000	0.000			0.000	0.000
Aggression Initiator Event	0.000	1.726	0.19	0.017							0.000	0.000				
Submission Initiator	0.000	3.581	0.059	0.010	0.000	0.002										
Affiliative Receiver	0.000	3.381	0.067	0.011			0.001	0.005			0.000	0.002			0.000	0.000
Play Receiver	0.000	1.861	0.174	0.014		0.002					0.000	0.001				
Aggression Receiver	0.000	1.834	0.177	0.015	0.000	0.001	0.000	0.000			0.000	0.001				
Aggression Receiver Event	0.000	1.000	0.318	0.019	0.000	0.000										
Arms Reach	0.000	48.655	0.000*	0.001*	0.000	0.004	0.000	0.004	0.000	0.000	0.000	0.003	0.000	0.001	0.000	0.002
Arms Reach 1	0.000	56.339	0.000*	0.001*	0.000	0.003	0.000	0.004	0.000	0.000	0.000	0.002	0.000	0.001	0.000	0.001
Arms Reach 2	0.000	7.582	0.006*	0.003	0.000	0.000	0.000	0.000			0.000	0.000	0.000	0.000	0.000	0.000
Arms Reach 3	0.000	1.541	0.215	0.018	0.000	0.000					0.000	0.000			0.000	0.001
Arms Reach 4	0.000	3.992	0.047*	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000				



Table S33. The table presents the abbreviations of the behavioral categories analyzed using the EthoSeq Software to analyze the behavioral transitions and sequences.

<b>BEHAVIOR CATEGORY</b>	<b>BEHAVIOR</b>	<b>ABBREVIATION</b>	
<b>NON SOCIAL BEHAVIORS</b>	Self-grooming	Selfg	
	Scent Marking	Scent	
	Solitary Play	Solplay	
	Huddling	Hudd	
	Vocalizations	Voc	
<b>SOCIAL BEHAVIOR</b>	Affiliation Initiator	Affi	
	Sex Initiator	Sexi	
	Play Initiator	Playi	
	Parental Behaviour	Parent	
	Ritual Agonism Initiator	Ritagi	
	Aggression Initiator	Effagi	
	Ritual Submission Initiator	Ritsubi	
	Effective Submission Initiator	Effsubi	
	Affiliative Receiver	Affir	
	Infant Affiliation Receiver	Affrinfant	
	Sex Receiver	Sexr	
	Play Receiver	Playr	
	Ritual Agonism Receiver	Ritagr	
	Aggression Receiver	Effagr	
	Ritual Submission Received	Ritsubr	
	Effective Submission Received	Effsubr	
	<b>RARE</b>	Abnormal Behavior	Abnorm

Table S34. *Hylobates lar*. First transitions of behavioral categories. Labels of behavioral categories can be found in supplementary materials (Table S29). In the first column are the behavioral categories that started a sequence. The remaining columns represent the second behavior of the behavioral sequence. In the second column are the behaviors that represent the first transition calculated by EthoSeq program for the capuchin monkeys as a group; all behaviors represent at least 15% of the existed transitions. Each animal has one column where the second behavior that follows the initial one is registered (only if that transition happened 25% or more of the times). In each line, the typical transition for each animal can be consulted; in bold are the unusual transitions when compared with the transitions calculated for the group (Continued on the next pages).

	<b>Group</b>		<b>Ágil</b>		<b>Maya</b>		<b>Donald</b>		<b>Tina</b>		<b>Lagos</b>		<b>Charruinha</b>	
	<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>		<b>1st trans.</b>	
<b>Selfgrooming*</b>	pare	29.38	solip	52.27	affi	66.67	ritagi	50,00	pare	91.07	rita	53.57	playi	35.29
	nt	%	lay	%	lay	%	nt	%	nt	%	gi	%	ni	%
	solip	17.53	vocsi	29.55	solipl	16.67								
(sg)	lay	%	mp	%	ay	%								
<b>Solitary Play*</b>		38.16	vocsi	54.55		50,00	vocsi	100.0				57.14	playi	52.38
	sg	%	mp	%	sg	%	mp	0%			sg	%	ni	%
	vocsi	35.53		40.91		50,00								28.57
(soliplay)	mp	%	sg	%	affir	%							sg	%
<b>Simple Vocalization</b>	solip	32.18	solip	51.43	vocco	33.33		50,00			play	66.67	playi	28.57
	lay	%	lay	%	mp	%	ritagi	%			ini	%	ni	%
		29.68		42.86		33.33					rita	33.33		
(voc simp)	sg	%	sg	%	affi	%				gr	%			
					vocso	33.33								
					ci	%								
<b>Complex Vocalization</b>	vocs	50,00	vocs	100.0			vocso	57.14						50,00
	oci	%	oci	0%			ci	%					sg	%
		20,00						28.57					vocsi	50,00
(voc comp)	ritagi	%					ritagi	%				mp	%	
		20,00												
	sg	%												
<b>Play Initiator*</b>		32.65						100,0	pare	100.0	rita	41.67		35.29
	sg	%					sexi	0%	nt	0%	gr	%	sg	%
												33.33		
(play ini)										sg	%			
<b>Affiliation Initiator</b>		38.1		50,00		70,00	paren	100,0	pare	66.67			playi	40,00
	sg	%	sg	%	sg	%	t	0%	nt	%			ni	%
		28.57		50,00						33.33				40,00
(Affi ini)	affir	%	affir	%					affir	%			affir	%
	pare	19.05												
	nt	%												
<b>Parental Behavior</b>		63.37						66.67		68.29		50,00	playi	
	sg	%					sg	%	sg	%	affir	%	ni	50%
								33.33				25,00		41.67
(parent)							playr	%			sg	%	sg	%
											rita	25,00		
											gr	%		
<b>Social Vocalization Initiator</b>	vocs	78.57	vocsi	100.0			vocco	80,00	vocs	100.0			vocs	100.0
	ocr	%	mp	0%			mp	%	ocr	0%			ocr	0%
(voc soc ini)														
<b>Sex Initiator</b>		100.0								100.0				
	affi	0%							affi	0%				
(sex ini)														
<b>Effective Agonism Initiator</b>		50,00		100.0			vocsi	50,00		100.0				
	sg	%	sg	0%			mp	%	sg	0%				
		25,00						50,00						
(effe ag ini)	ritagi	%					ritagi	%						
	vocsi	25,00												
	mp	%												
<b>Ritual Agonism</b>		26.67						26.92			rita	100.0		
	ritagr	%					sg	%			gr	0%		

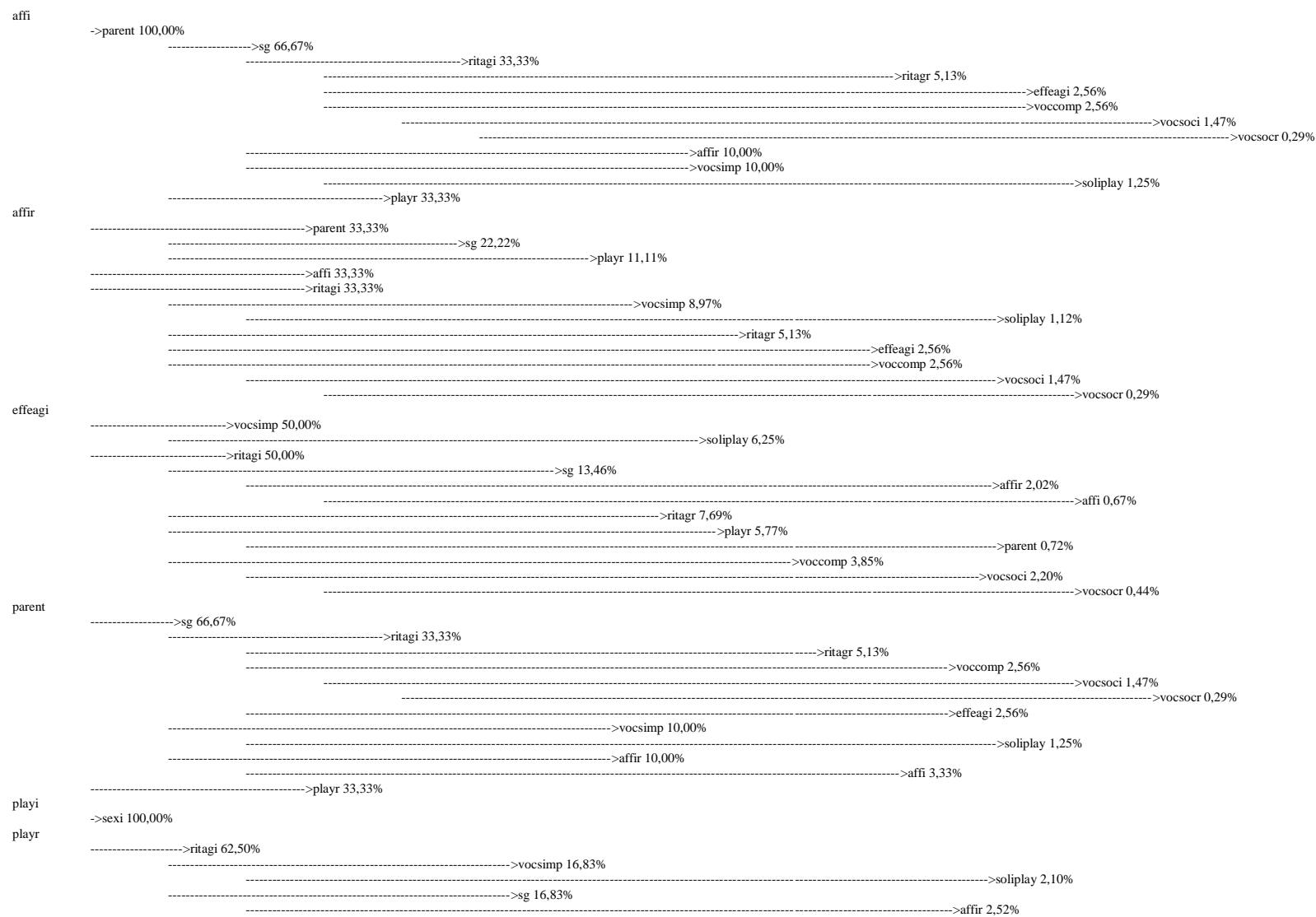
	Group	Ágil	Maya	Donald	Tina	Lagos	Charruinha
	1st trans.	1st trans.	1st trans.	1st trans.	1st trans.	1st trans.	1st trans.
	sg	23.33		vocsi	26.92		
	vocsi	%		mp	%		
(rit ag ini)	mp	23.33					
		21.47			62.5	pare	77.78
<b>Play Receiver*</b>	sg	%		ritagi	%	nt	%
(play rec)	pare	17.39				gr	33.33
	nt	%				rita	33.33
<b>Affiliation Receiver*</b>	pare	25.64	80,00	100,0	33.33	pare	80,00
(affi rec)	nt	%	sg	%	sg	0%	affi
		25.64			33.33	pare	80,00
	sg	%			33.33	nt	%
		20.51			33.33	play	66.67
	playr	%			ritagi	%	37.5
<b>Social Vocalization Receiver</b>	vocs	72.22				vocs	70,00
(voc soc rec)	oci	%				oci	%
	pare	16.67				pare	30,00
	nt	%				nt	%
<b>Sex Receiver</b>	pare	100.0				pare	100.0
(sex rec)	nt	0%				nt	0%
<b>Effective Agonism Receiver</b>	sg	100.0					100,0
(effe ag rec)		0%				sg	0%
<b>Ritual Agonism Receiver</b>	sg	41.18		100.0	vocsi	60,00	39.29
(rit ag rec)		%		sg	0%	mp	%
						40,00	
						sg	%
<b>Abnormal Behavior*</b>	sg	66.67	50,00	100.0	100.0		100.0
(abn)	solip	16.67	vocsi	25,00	sg	0%	sg
	lay	%	mp	%			0%
	vocsi	16.67					
	mp	%					

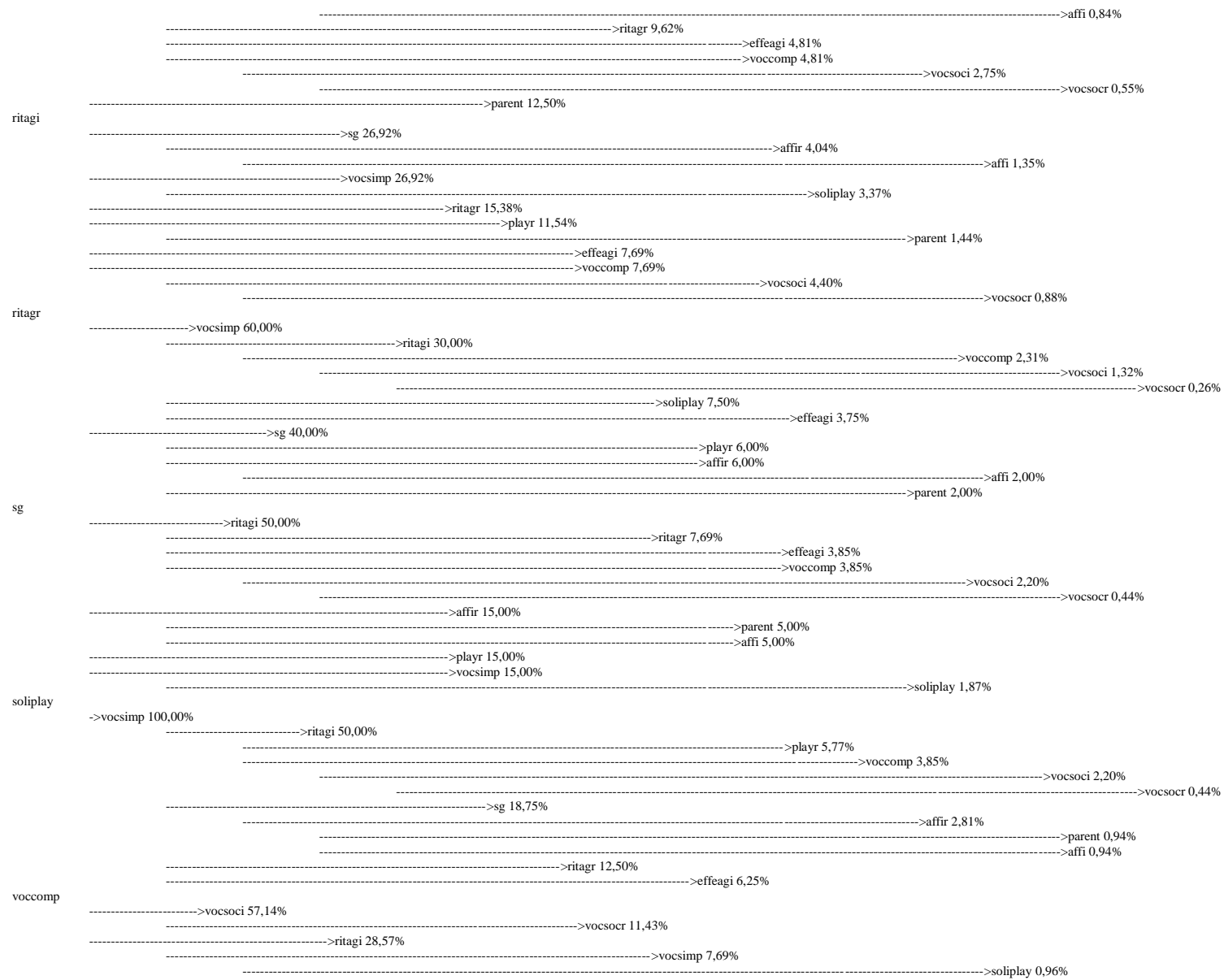
Table S35. EthoSeq Schematic Matrices.

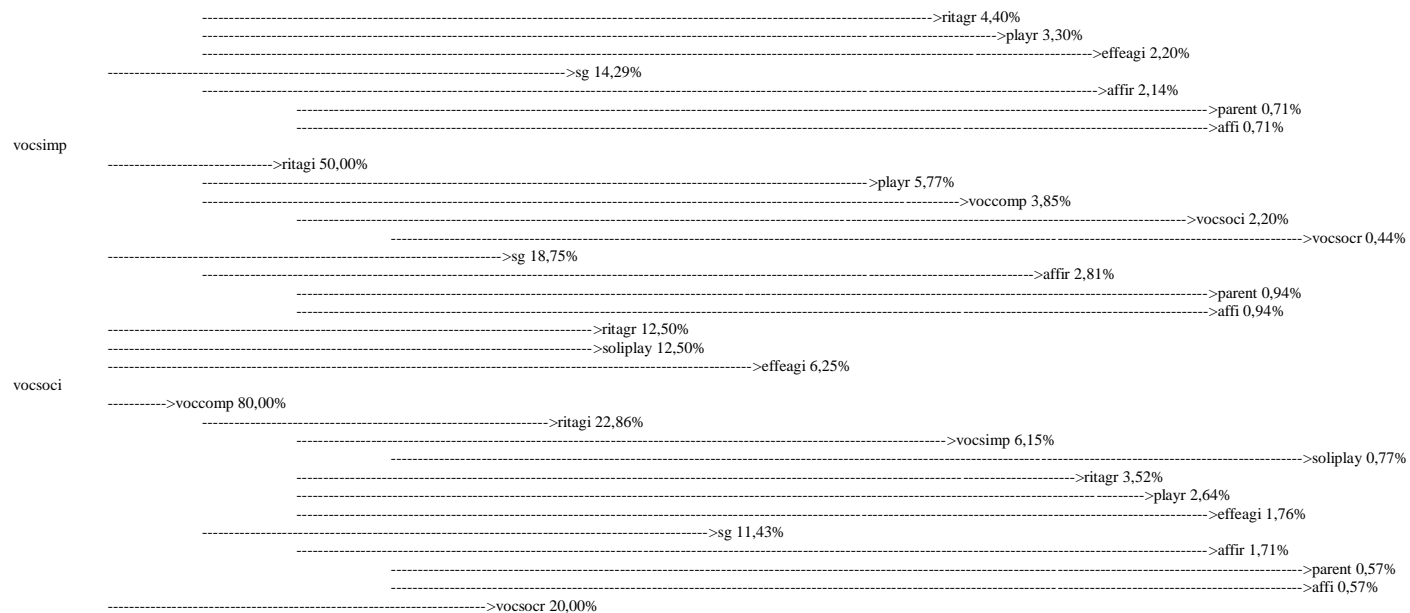
	abn	af	af	effe	effe	par	pl	pl	rit	rit	se	se	s	sol	vocc	vocs	voc	voc
	orm	fi	fir	agi	agr	ent	ay	ay	agi	ag	xi	xr	g	play	omp	imp	soci	socr
abno																		
rm																		
affi																		
affir																		
effea																		
gi																		
effea																		
gr																		
pare																		
nt																		

playi																		
playr																		
ritagi																		
ritag r																		
sexi																		
sexr																		
sg																		
solip lay																		
voc omp																		
vocsi mp																		
vocs oci																		
vocs ocr																		

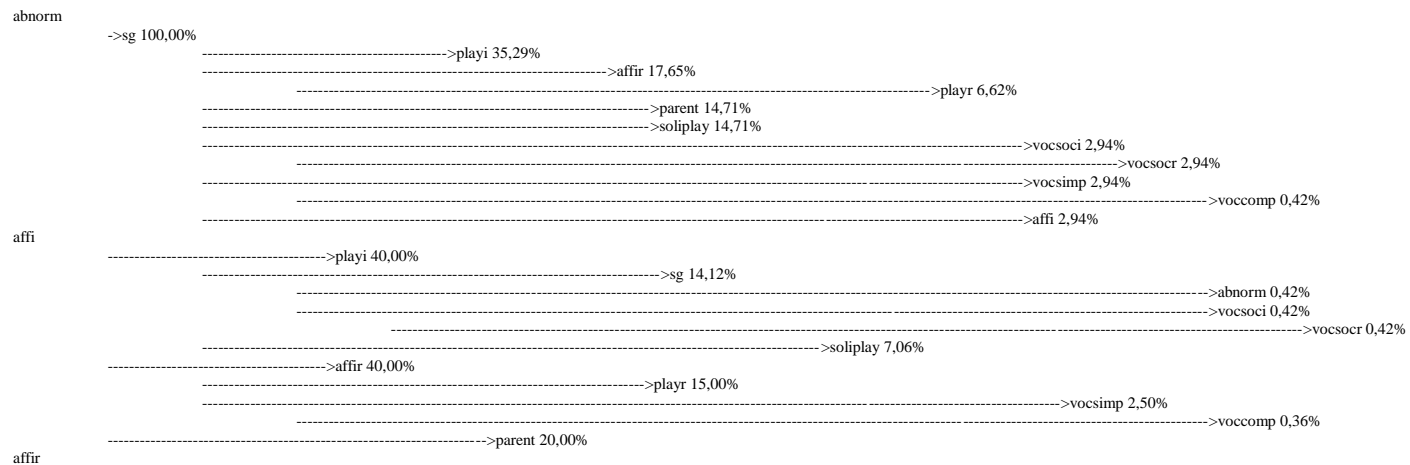
## SE48. View of probability behavioral sequences of the behavioral transitions of Donald







SE49. View of probability behavioral sequences of the behavioral transitions of Charruíña.

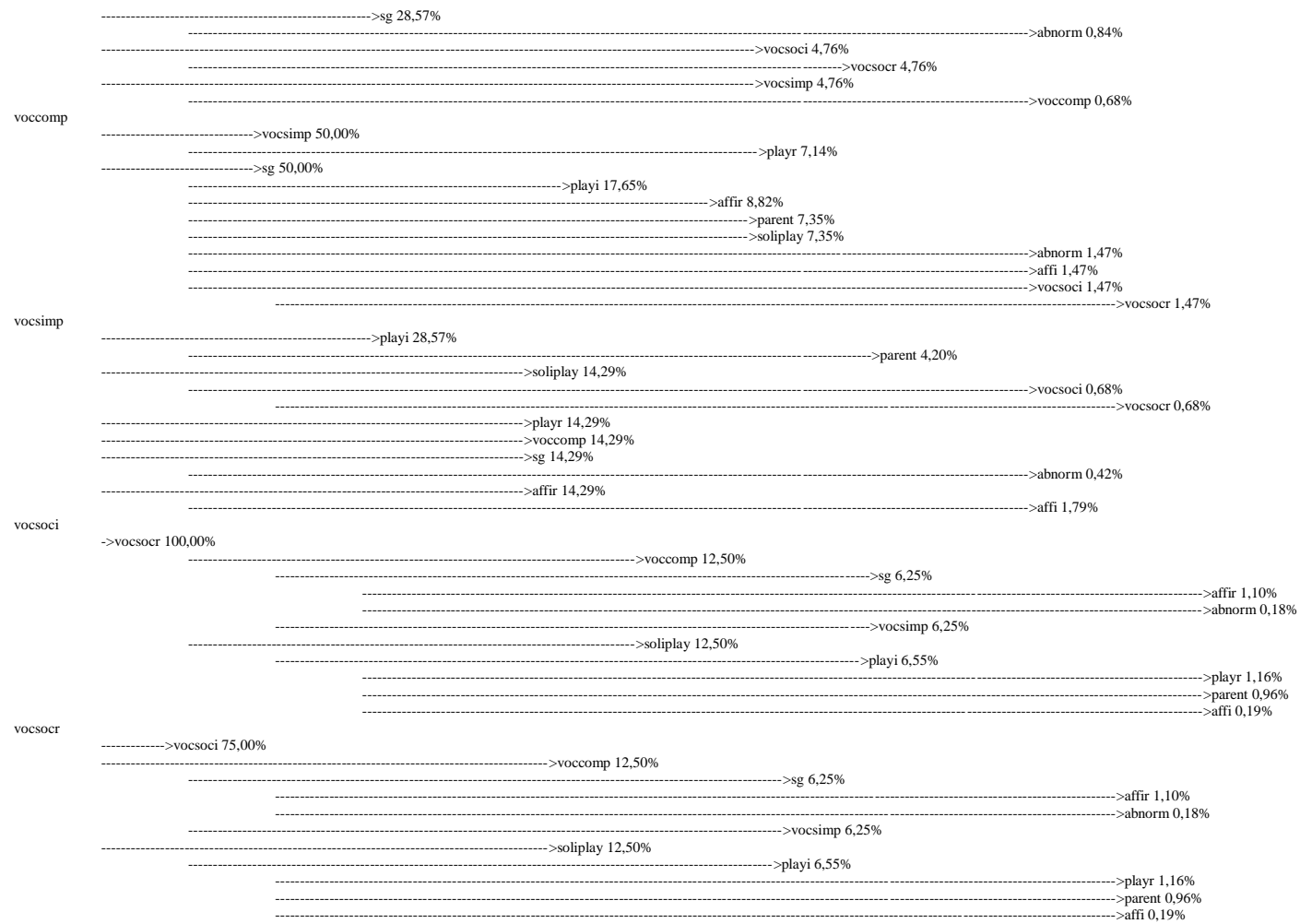


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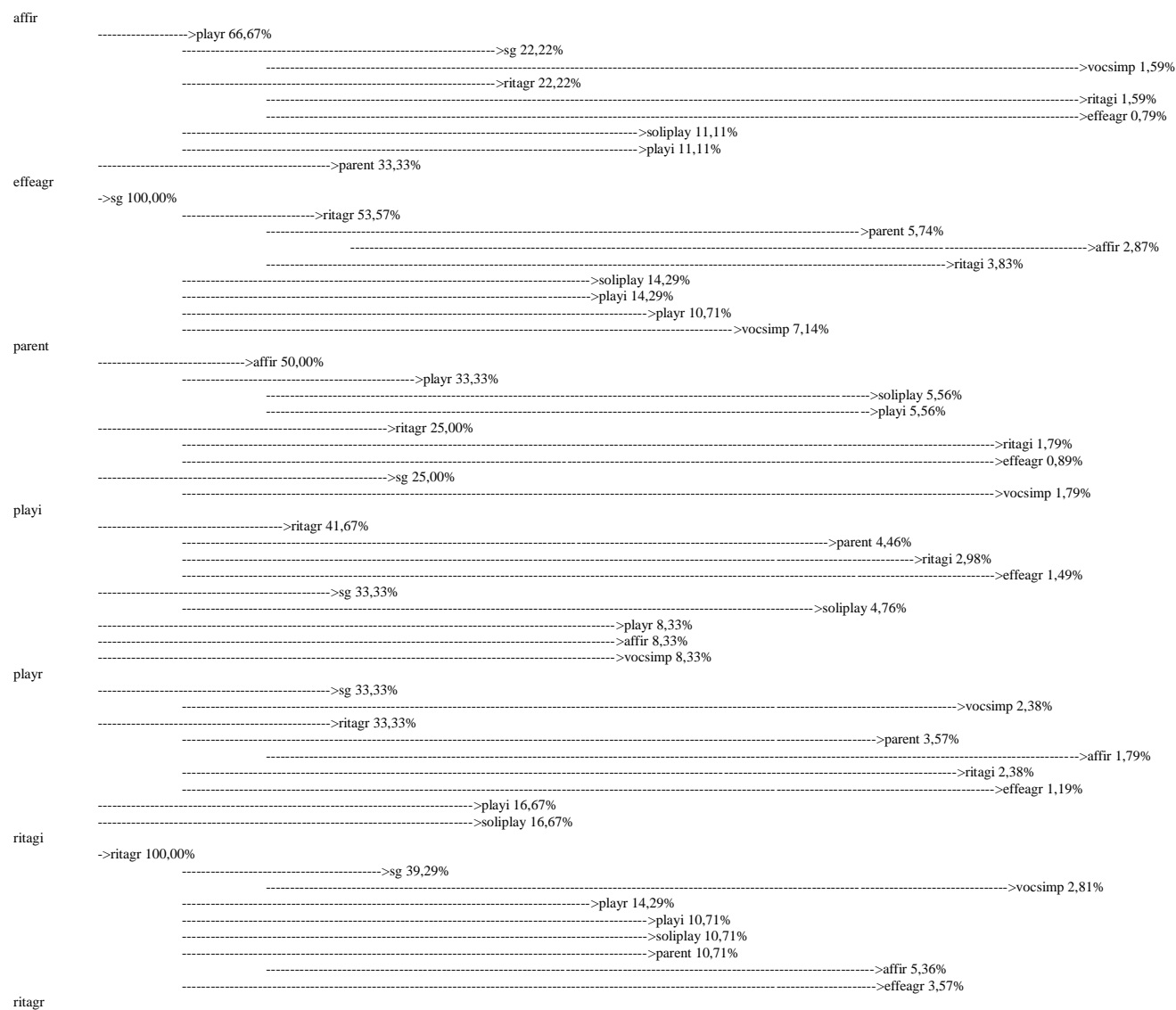
----->playr 37,50%
----->soliplay 8,82%
----->vocsoci 0,42%
----->vocsoer 0,42%
----->playi 25,00%
----->parent 3,68%
----->sg 12,50%
----->abnorm 0,37%
----->affi 12,50%
----->vocsimp 6,25%
----->voccomp 0,89%
parent
----->playi 50,00%
----->soliplay 8,82%
----->playr 8,82%
----->affi 1,47%
----->sg 41,67%
----->affir 7,35%
----->vocsimp 1,23%
----->voccomp 0,18%
----->abnorm 1,23%
----->vocsoci 1,23%
----->vocsoer 1,23%
playi
----->sg 35,29%
----->vocsoci 1,04%
----->vocsoer 1,04%
----->abnorm 1,04%
----->vocsimp 1,04%
----->voccomp 0,15%
----->soliplay 17,65%
----->playr 17,65%
----->parent 14,71%
----->affir 11,76%
----->affi 2,94%
playr
----->sg 29,41%
----->parent 4,33%
----->abnorm 0,87%
----->soliplay 23,53%
----->vocsoci 1,12%
----->vocsoer 1,12%
----->playi 23,53%
----->affir 23,53%
----->affi 2,94%
----->vocsimp 1,47%
----->voccomp 0,21%
sg
----->playi 35,29%
----->affir 17,65%
----->playr 6,62%
----->soliplay 14,71%
----->parent 14,71%
----->affi 2,94%
----->vocsimp 2,94%
----->voccomp 0,42%
----->abnorm 2,94%
----->vocsoci 2,94%
----->vocsoer 2,94%
soliplay
----->playi 52,38%
----->playr 9,24%
----->parent 7,70%
----->affir 6,16%
----->affi 1,54%

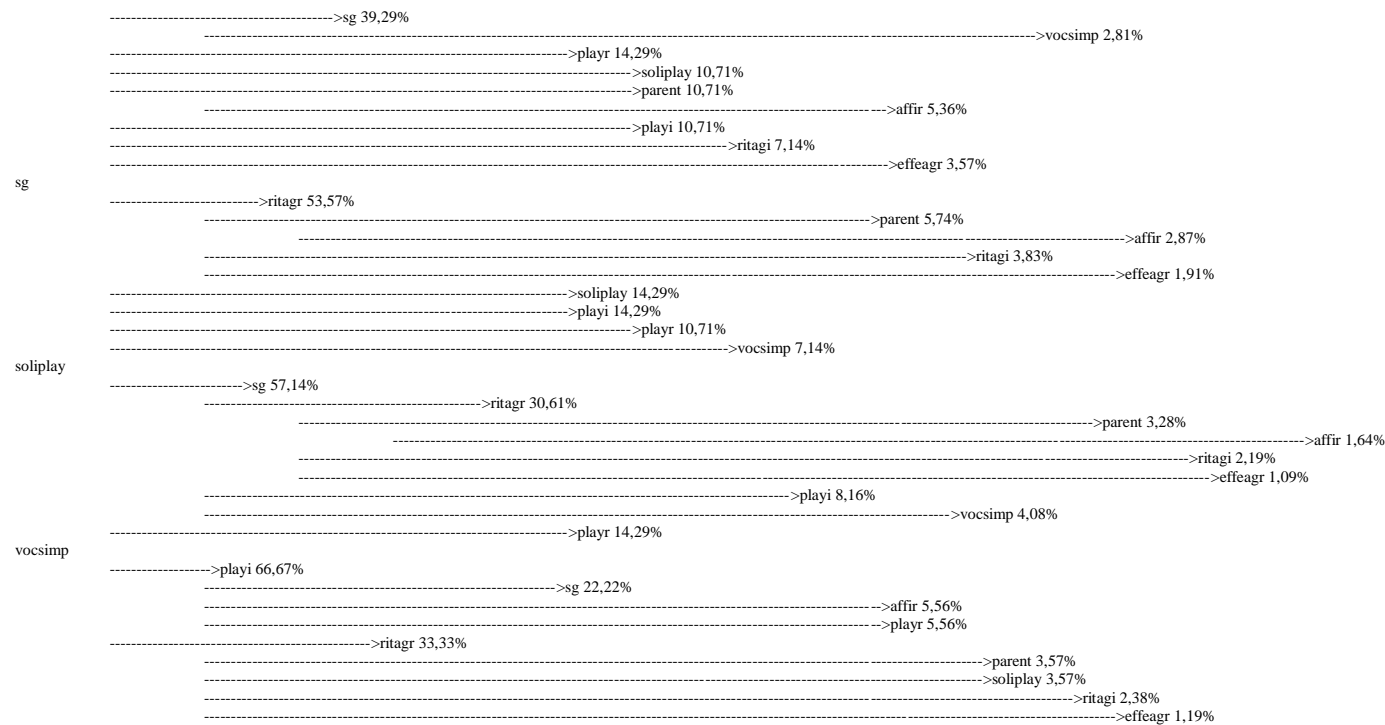
```



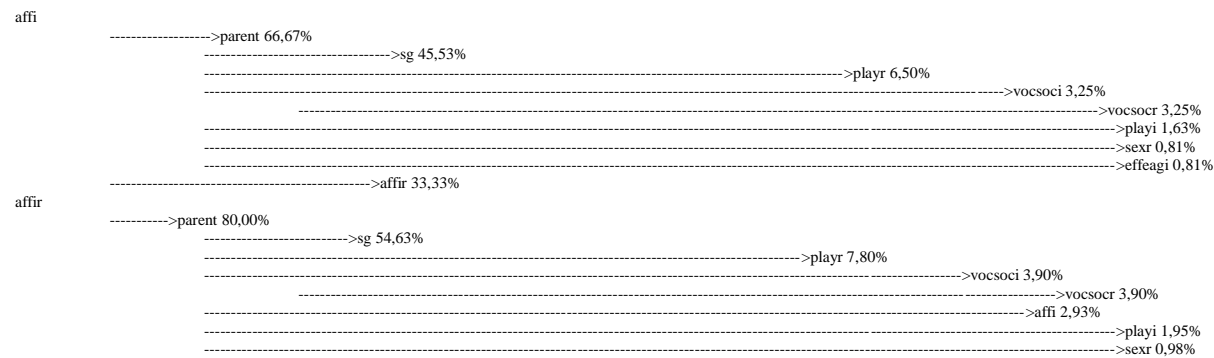


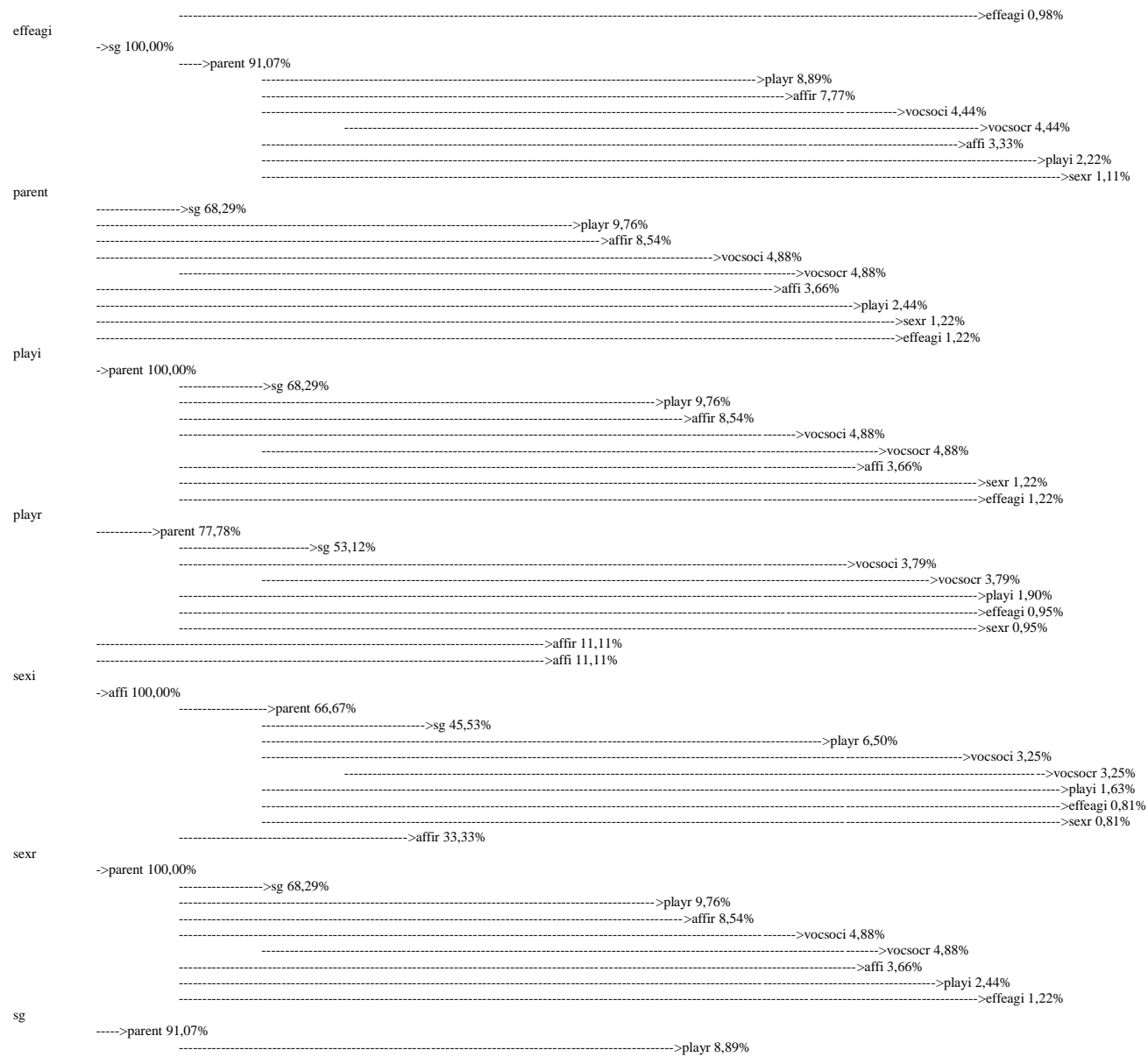
## SE50. View of probability behavioral sequences of the behavioral transitions of Lagos.

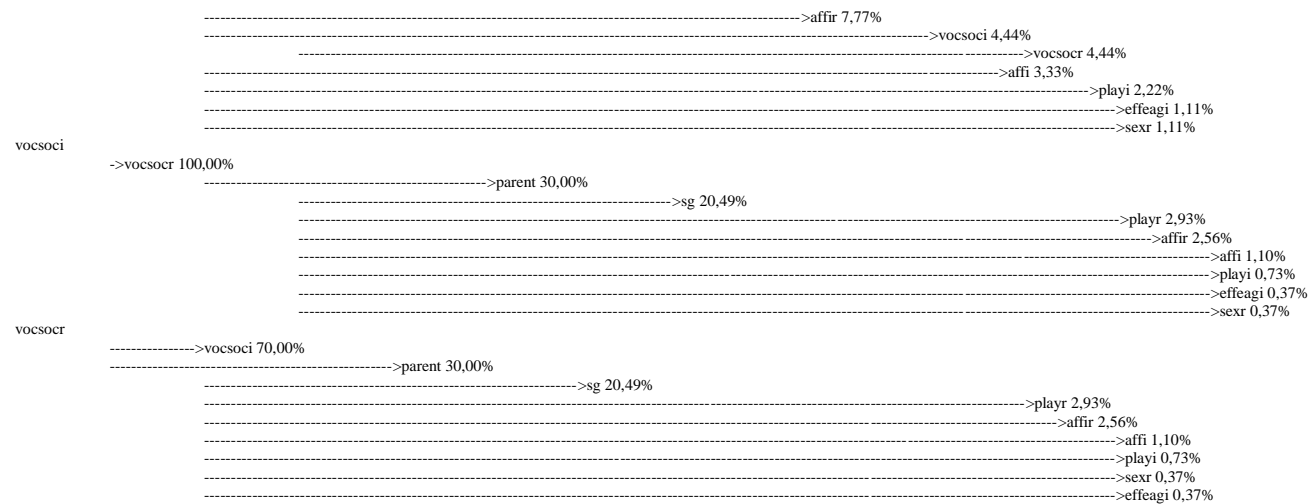




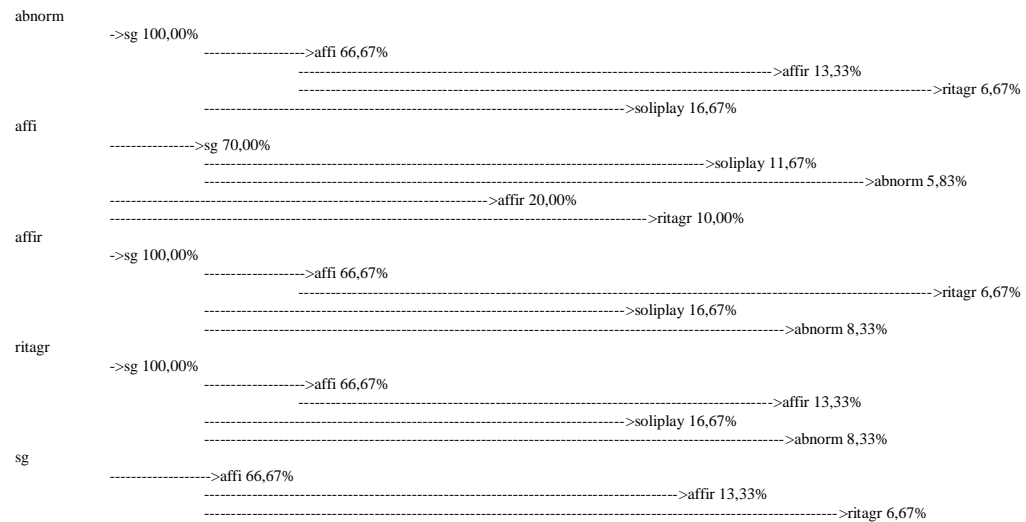
SE51. View of probability behavioral sequences of the behavioral transitions of Tina.

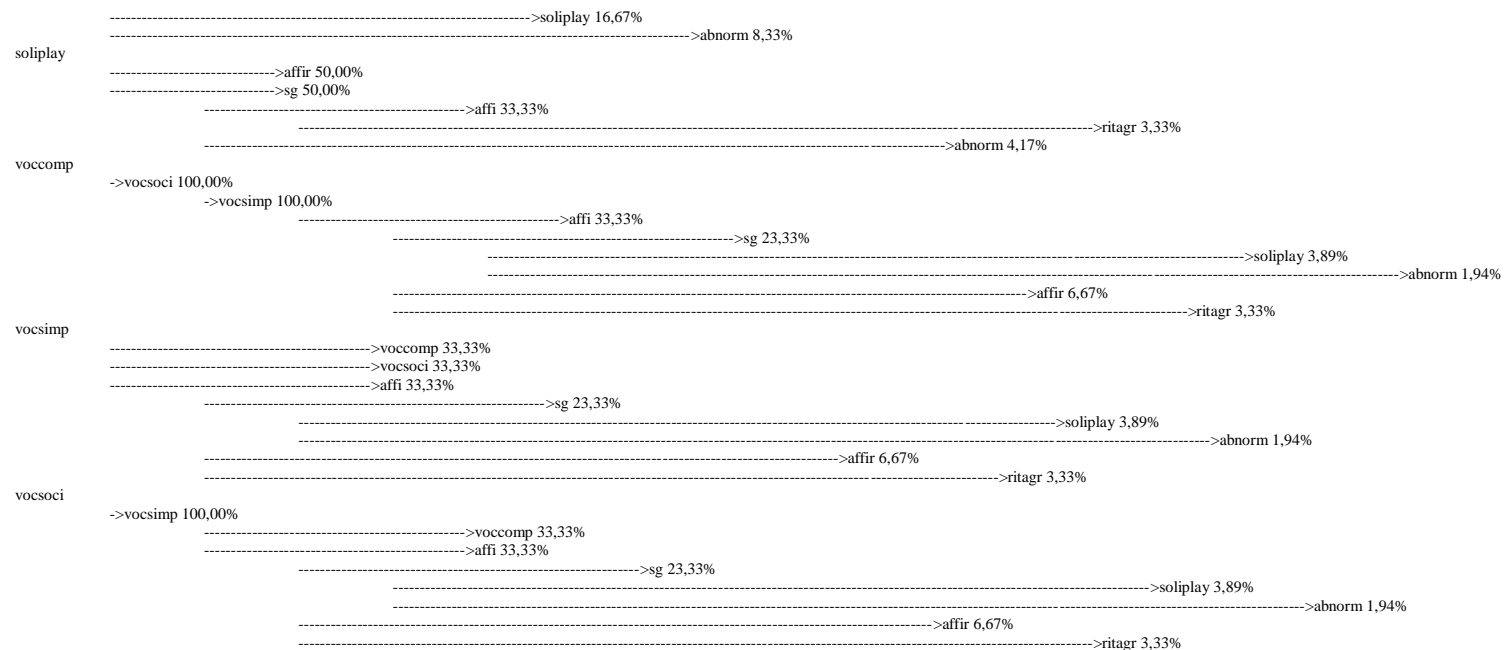




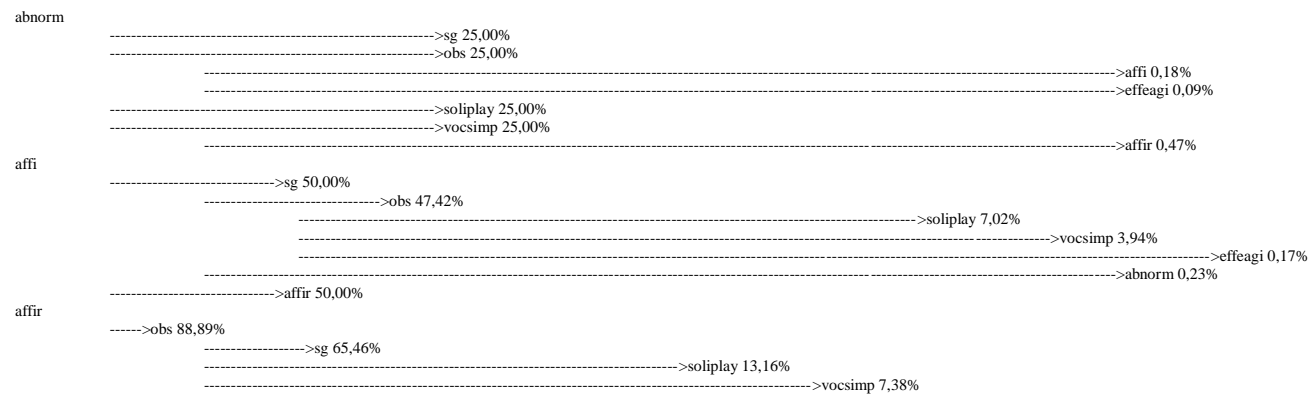


SE52. View of probability behavioral sequences of the behavioral transitions of Maia.





### SE53. View of probability behavioral sequences of the behavioral transitions of Ágil

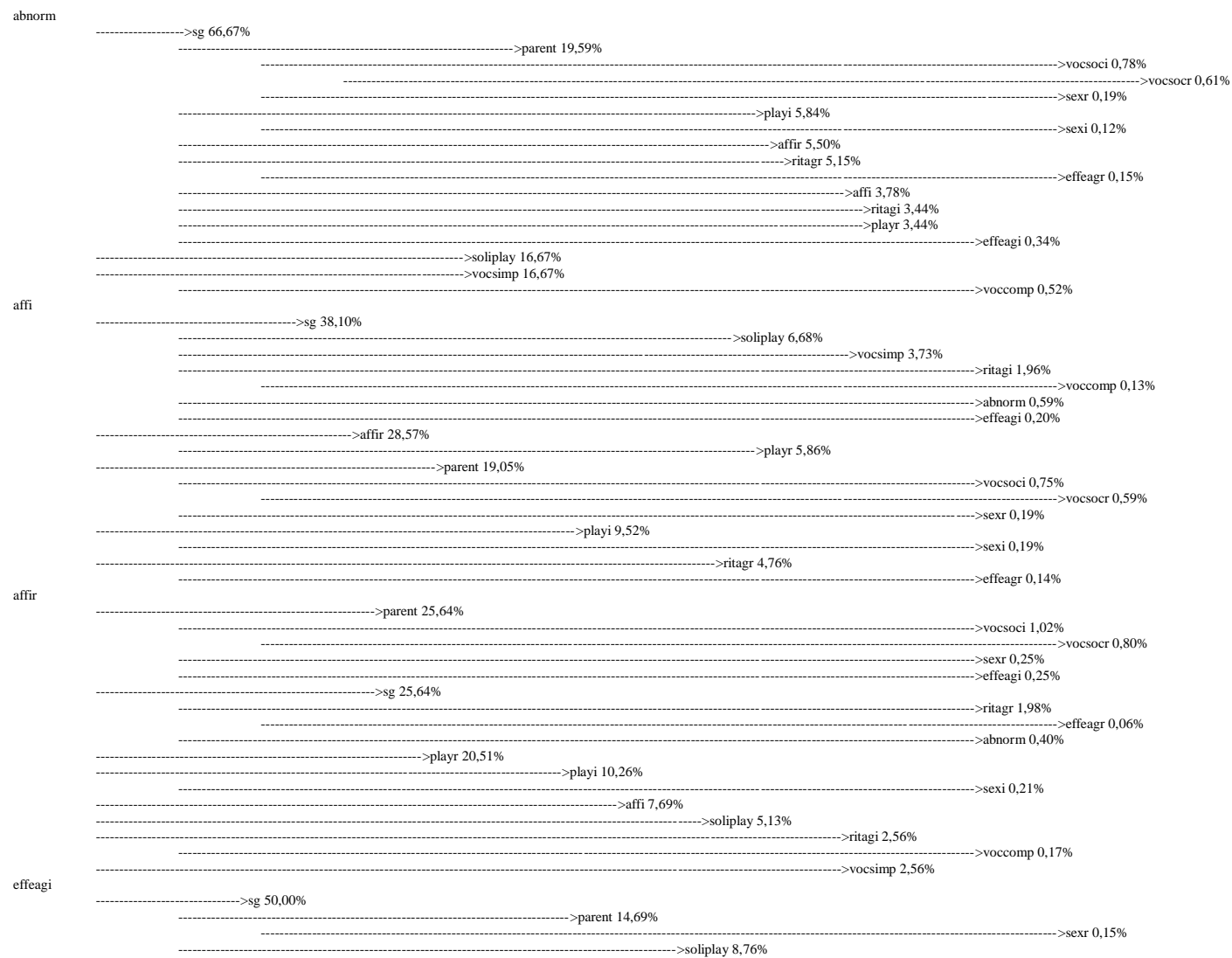


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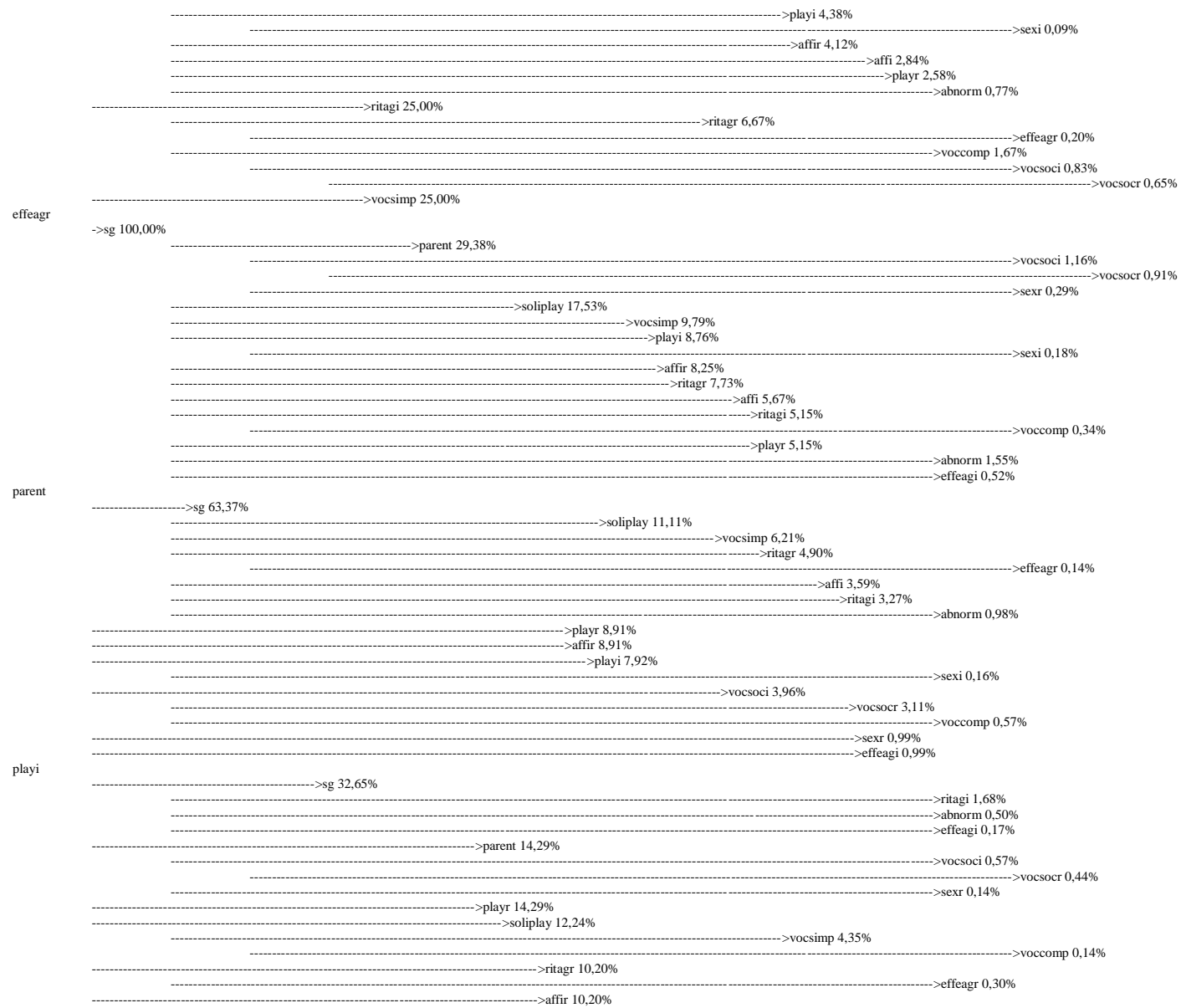
----->affi 0,64%
----->abnorm 0,32%
----->effeagi 0,32%
effeagi
-->sg 100,00%
--->obs 94,84%
----->soliplay 14,04%
----->vocsimp 7,87%
----->affir 1,71%
----->affi 0,68%
----->abnorm 0,47%
obs
----->sg 73,65%
----->soliplay 14,80%
----->vocsimp 8,30%
----->affir 1,81%
----->affi 0,72%
----->effeagi 0,36%
----->abnorm 0,36%
sg
--->obs 94,84%
----->soliplay 14,04%
----->vocsimp 7,87%
----->affir 1,71%
----->affi 0,68%
----->effeagi 0,34%
----->abnorm 0,47%
soliplay
----->obs 59,65%
----->sg 43,93%
----->affir 1,08%
----->affi 0,43%
----->effeagi 0,22%
----->vocsimp 36,84%
----->abnorm 1,39%
vocsimp
----->obs 52,83%
----->sg 38,91%
----->affi 0,38%
----->effeagi 0,19%
----->soliplay 33,96%
----->abnorm 3,77%
----->affir 1,89%

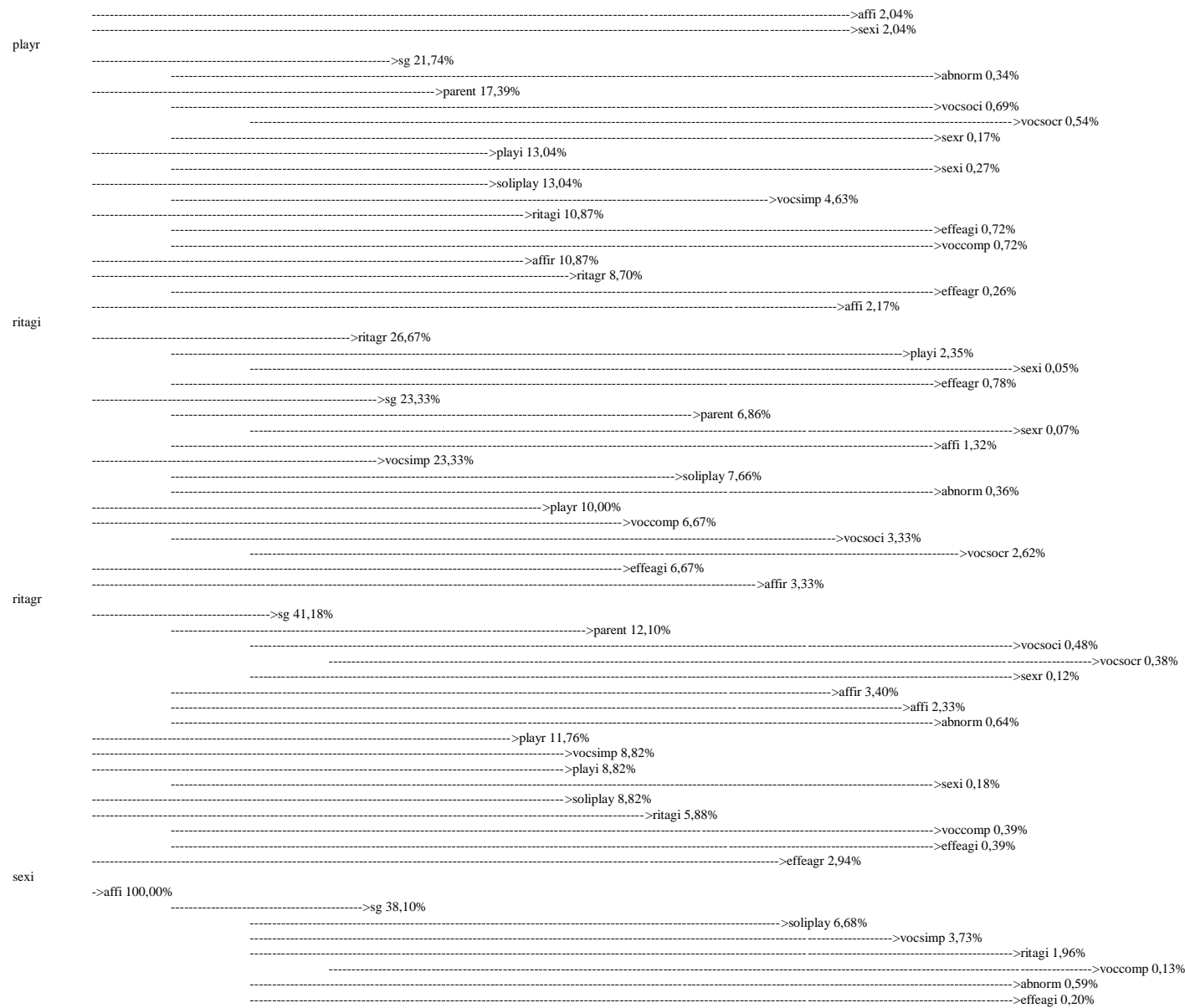
```

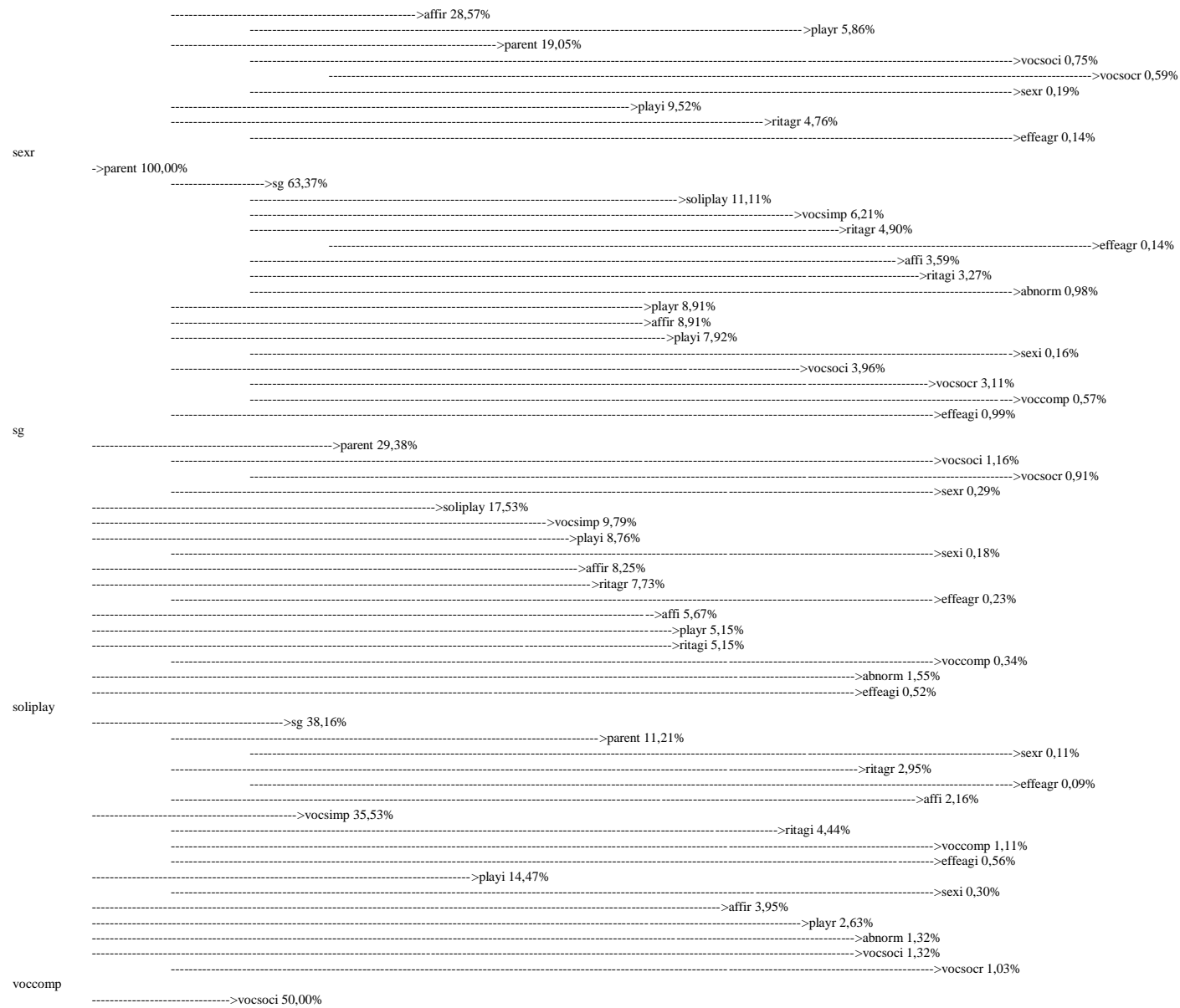
SE54. View of probability behavioral sequences of the behavioral transitions of the *Hylobates lar*'s group.

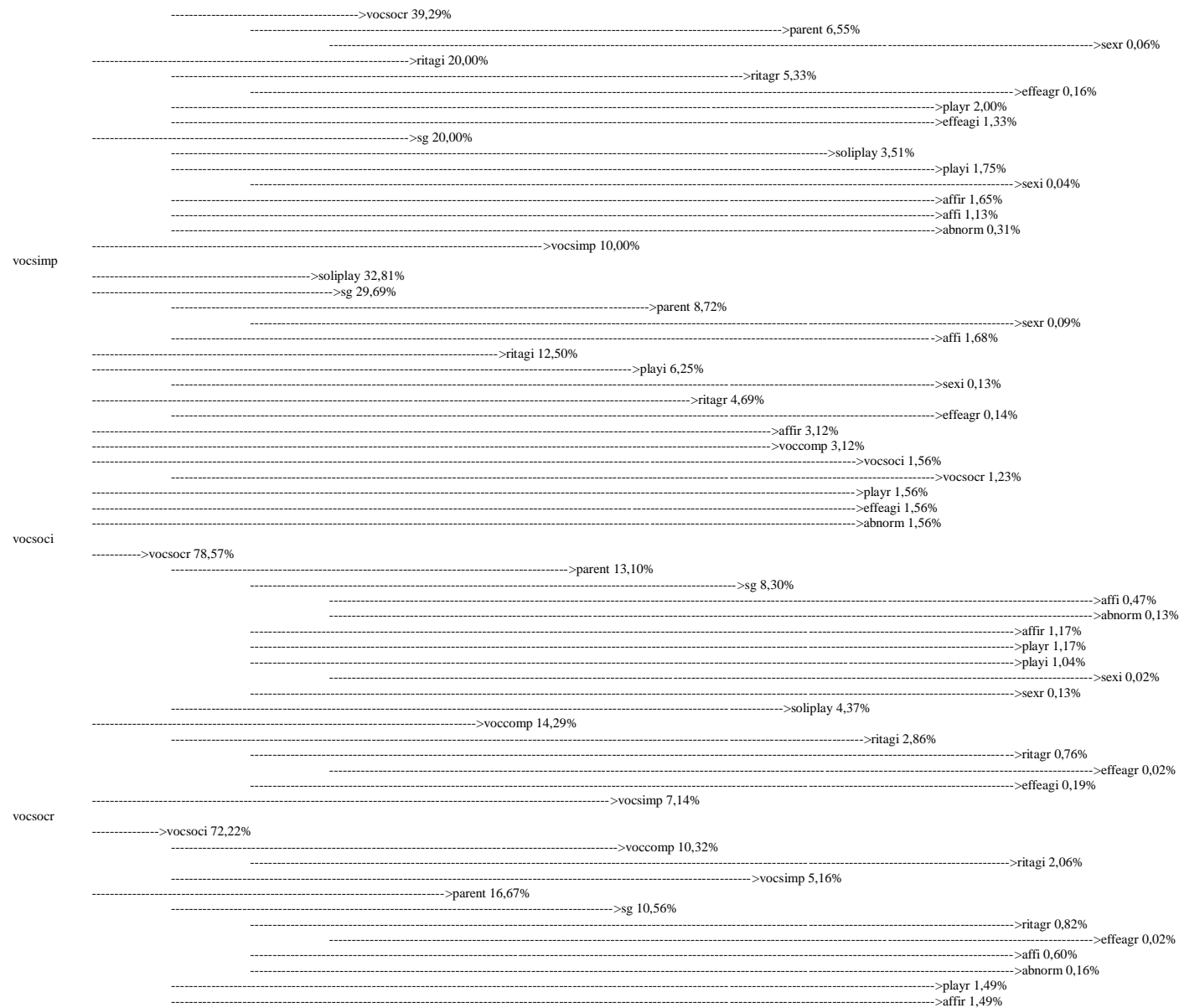












----->playi 1,32%  
----->sexr 0,17%  
----->effeagi 0,17%  
----->soliplay 5,56%