Universidade Federal do Rio Grande do Norte
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Carolina Pereira Cadório da Silva

Behavioural Profiles of Captive Capuchin Monkeys (*Sapajus* spp.): analyses at group and individual levels

Dissertação apresentada à
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"Minha vida é andar por este país
Pra ver se um dia descanso feliz
Guardando recordações
Das terras onde passei
Andando pelos sertões e dos amigos que lá deixei"

em *A vida do viajante*, por Luiz Gonzaga

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Resumo

O uso de indicadores comportamentais de sofrimento e bem-estar de animais em cativeiro tem produzido resultados ambíguos. Em comparações entre grupos, aqueles em piores condições tendem a apresentar um aumento generalizado em todas as taxas de Comportamentos Potencialmente Indicativos de Estresse (BPIS), mas em comparações dentro de grupos, os indivíduos diferem nas suas estratégias de enfrentamento ao estresse. Esta dissertação apresenta análises para revelar o perfil comportamental de uma amostral de 26 macacos prego em cativeiro, de três espécies diferentes (*Sapajus libidinosus, S. flavius* e *S. xanthosternos*), mantidos em diferentes tipos de recinto. No total foram coletadas 147,17 horas de registros comportamentais. Explorámos quatro tipos de análises: Orçamento de Atividades, índices de Diversidade, cadeia de Markov e análise de Sequência, e Análise de Rede Social, resultando em nove índices de ocorrência e de organização comportamental. No capítulo Um exploramos diferenças entre grupos. Os resultados apoiam as predições de que existem diferenças mínimas entre sexo e espécie e são observadas diferenças maiores no perfil comportamental devido ao tipo de recinto: *i.* indivíduos em recintos com menos enriquecimento ambiental apresentaram um repertório de BPIS mais diverso e uma menor probabilidade de sequências de seis passos de Comportamentos Normativos de Género (GNB); *ii.* o número de transições comportamentais que incluíam pelo menos um BPIS foi superior em recintos menos enriquecidos; *iii.* índices de proeminência de BPIS indicam que estes funcionam como pontos fim de sequências comportamentais, e que a proeminência de três BPIS (locomoção aberrante, auto-direccionadas e activas I) foram maiores em recintos menores. No geral, estes dados não corroboram a ideia de que os BPIS têm um padrão repetitivo, com um efeito relaxante, tipo "mantra". Pelo contrário, a imagem que surge é de que os BPIS são atividades que interrompem a organização dos comportamentos, introduzindo "ruido" que compromete o orçamento de atividades ótimo. No capítulo Dois exploramos diferenças individuais em seis eixos de comportamento exploratório. Estes mostraram-se pouco correlacionados, o que indicam baixa correlação entre indicadores comportamentais de síndromes. No entanto, os resultados sugerem duas estratégias de enfrentamento ao estresse abrangentes, semelhantes ao padrão audaz/proactivo e tímido/reativo: macacos prego mais exploratórios apresentaram maior proeminência em locomoção aberrante, exibição sexual aberrante e ativas I, enquanto que animais menos ativos apresentaram uma maior probabilidade de sequencias com pelo menos um BPIS, e maior proeminência em estereotipia-própria. Macacos prego são conhecidos pelas suas capacidades cognitivas e flexibilidade comportamental, portanto, a procura de um conjunto de indicadores comportamentais de bem-estar consistente requer mais estudos e conjuntos de dados mais amplos. Com este trabalho, pretendemos contribuir para a criação de protocolos, com embasamento científico e estatisticamente corretos, para amostragem de dados comportamentais que permitam a comparabilidade de resultados e meta-análises, de qualquer que seja a interpretação teórica que possa receber.

Palavras-chave: Bem-estar, estratégias de enfrentamento ao estresse, sequências comportamentais, Rede Social, diferenças individuais, plasticidade comportamental**.**

Abstract

The use of behavioural indicators of suffering and welfare in captive animals has produced ambiguous results. In comparisons between groups, those in worse condition tend to exhibit increased overall rate of Behaviours Potentially Indicative of Stress (BPIS), but when comparing within groups, individuals differ in their stress coping strategies. This dissertation presents analyses to unravel the Behavioural Profile of a sample of 26 captive capuchin monkeys, of three different species (*Sapajus libidinosus, S. flavius* and *S. xanthosternos*), kept in different enclosure types. In total, 147,17 hours of data were collected. We explored four type of analysis: Activity Budgets, Diversity indexes, Markov chains and Sequence analyses, and Social Network Analyses, resulting in nine indexes of behavioural occurrence and organization. In chapter One we explore group differences. Results support predictions of minor sex and species differences and major differences in behavioural profile due to enclosure type: *i*. individuals in less enriched enclosures exhibited a more diverse BPIS repertoire and a decreased probability of a sequence with six Genus Normative Behaviour; *ii.* number of most probable behavioural transitions including at least one BPIS was higher in less enriched enclosures; *iii*. proeminence indexes indicate that BPIS function as dead ends of behavioural sequences, and proeminence of three BPIS (pacing, self-direct, active I) were higher in less enriched enclosures. Overall, these data are not supportive of BPIS as a repetitive pattern, with a mantra-like calming effect. Rather, the picture that emerges is more supportive of BPIS as activities that disrupt organization of behaviours, introducing “noise” that compromises optimal activity budget. In chapter Two we explored individual differences in stress coping strategies. We classified individuals along six axes of exploratory behaviour. These were only weakly correlated indicating low correlation among behavioural indicators of syndromes. Nevertheless, the results are suggestive of two broad stress coping strategies, similar to the bold/proactive and shy/reactive pattern: more exploratory capuchin monkeys exhibited increased values of proeminence in Pacing, aberrant sexual display and Active 1 BPIS, while less active animals exhibited increased probability in significant sequences involving at least one BPIS, and increased prominence in own stereotypy. Capuchin monkeys are known for their cognitive capacities and behavioural flexibility, therefore, the search for a consistent set of behavioural indictors of welfare and individual differences requires further studies and larger data sets. With this work we aim contributing to design scientifically grounded and statistically correct protocols for collection of behavioural data that permits comparability of results and meta-analyses, from whatever theoretical perspective interpretation it may receive.

Key words: Welfare, stress coping strategies, behavioural sequence, Social Network, individual differences, behavioural plasticity

Foreword

To behavioural biology the presence of patterns in diversity, and variation within the patterns, is neither a surprise nor a mystery. Darwin (1859) dedicated two chapters of his book “On the Origins of Species” by means of Natural Selection to exemplify variation in animals. A traditional interpretation of the theory is that variation is the raw material for evolution, that is, among the naturally occurring variation those best fitted will survive and reproduce, resulting in varied forms, each adapted to a particular environmental condition. This approach accounted for variation between species, or between populations, but had problems in explaining variations within the same population. According to Sober (1980) this view shares the Aristotelean perspective of *natura state*, that is, “the existence of hidden structures which unite diverse individuals into natural kinds”. The real is invariant, and any variability is an anomaly resulting from interfering forces on the conditions that ensures the continuity of the natural state.

One hundred years later, Mayr (1994) argues that this approach is not at all in accordance to Darwin’s theory, and that one of the greatest insights from Darwin’s ideas is replacing a typological by a populational thinking. Mayr calls racist the search for types that are separated from the representatives of other types by a distinct gap. While both the populational and the typological thinking acknowledges the existence of patterns and variations, the way of looking is radically different: “For the typologist the type (*eidos*) is real and the variation is an illusion, while for the populationist, the type (average) is an abstraction and only variation is real.” (Mayr, 1994, pp. 158).

Phenotypic plasticity refers to the range of phenotypes that can be observed in the same species, population or individual (Foster, 2013). Different morphologies in non-reproductive traits of males and females of the same species (e.g. plumage in birds or body size in primates), or between individuals of the same sex in a population (e.g.. three different morphs of male lizards), or still during the lifetime of the same individual (e.g. caterpillars and butterflies) are all examples of phenotypic plasticity (Foster, 2013). Consistent differences between individuals in different environments reveal different exchanges (trade-offs) between levels of predation and resource acquisition. On a larger scale, differences in reaction norms could explain the choice of habitats or sexual partners by different individuals and, therefore, have important implications for the geographical distribution and evolution of species.

What about behaviours? Biological approaches to behaviour vary depending on the time frame used. At a proximal level, behaviours are considered the most flexible traits of individuals, and are by definition a reactive response to stimuli from the environment (external or internal environment). Behaviours make the fine scale adjustment of animals to environment improving the chances of survival and reproduction (Krebs e Davies, 1997). The study of behavioural profiles has implications in two major areas, and offers practical and theoretical developments. On a more theoretical level, the existence of individual differences in behavioural profiles (or reaction norms do stimuli) calls into debate characterizing average, optimal or species-typical behaviour. Models in behavioural ecology accepts the existence of alternative behavioural strategies, such as frequency dependent or fluctuating selection in models of competitive economy, or skill pool sets in models of cooperative economy (Giraldeau & Caraco, 2000). One recent volume of Animal Behaviour Journal (v. 85, issue 5, 2013) is dedicated to discuss the functional and evolutionary origins of behavioural plasticity in behaviour patterns, as well as the developmental processes and the implications of the occurrence of these differences. Curiously, in order to study behavioural plasticity and flexibility one must first develop methods to identify behavioural patterns. Therefore constant refinement of methods of analyses are required.

On a practical level, studies on welfare and management of animals in captivity have shown that individuals exhibit behavioural patterns rarely seen in wild groups (called stereotypies or abnormal behaviours). These are interpreted as behavioural expressions of the animal trying to cope with the stress of highly altered environment. This suggestion is supported by studies showing that in comparisons between groups, those in worse condition tend to exhibit increased overall rate of Behaviours Potentially Indicative of Stress. However, intra-group the picture is not that clear. Individuals differ in susceptibility to pathologies, resilience and disease progression (e.g. Cavigelli, 2005). These differences are attributed to different cognitive appraisal of environmental stimuli, which, in turn, are attributed to differences in physiological profiles (with genetic and epigenetic bases), that is, these differences result from different norms of reaction to environmental stimuli and different ways of coping with stressors (coping styles). The focus turns to the understanding of different patterns of individual behaviours (e.g. proactive x reactive, not explorer x explorer), and in which environment / context different strategies would be most effective.

This dissertation presents analyses to unravel the Behavioural Profile of captive capuchin monkeys. Statistical analyses assuming independency of data sampling and computational methods to identify transitions of behaviours were used to test hypotheses of differences at group and individual levels. This study is part of a larger research project entitled “Reintroduction of blond capuchin monkeys (*Sapajus flavius*): criteria for selecting individuals and receptor areas”, which aims to develop protocols to accompany the behaviour of capuchin monkeys found in environments highly altered by human actions – captivity or forest fragments - in northeast Brazil.

The analyses are presented in two chapters. In the first chapter we explore four different methods to analyse occurrences of Genus Normative Behaviour (GNB) and Behaviours Potentially Indicative of stress (BPIS) and we compare the indexes obtained by group, specifically we compare differences in sex, species and enclosure size. In the second chapter the same indices of GNB and BPIS are analysed at individual level. Specifically we aim to explore whether we can distinguish individual differences in stress coping strategies. Literature review, hypothesis, methods, results and discussions are presented in the corresponding chapter. The dissertation is finalized with highlights of the findings.

Chapter 1: Behaviour Potentially Indicative of Stress in Captive Capuchin Monkeys (*Sapajus* spp.): an exploration of methods for data analyses

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Abstract: The use of behaviour as potentially indicator of stress (BPIS) of captive animals is equivocal. However, behavioural indicators of suffering and welfare in captive animals, has produced ambiguous results. Face validity predicts that BPIS will be more frequent and diverse in poorer environments. We studied a sample of 26 captive capuchin monkeys, of three different species (*Sapajus libidinosus, S. flavius* and *S. xanthosternos*), kept in three different enclosure types. In total, 147,17 hours of data were collected using focal animal sampling, with registers at every 10 sec, during 10 min. Behaviours were registered according to an ethogram of 9 macro-behavioural categories and 10 BPIS. We explored four type of analysis: Activity Budgets, Diversity indexes, Markov chains and Sequence analyses, and Social Network Analyses, resulting in nine indexes of behavioural occurrence and organization, and those index were compered across groups: enclosure type, sex and species. Results support predictions of minor sex and species differences and major differences in behavioural profile due to enclosure type: *i*. individuals in less enriched enclosures exhibited a more diverse BPIS repertoire and a decreased probability of a sequence with six Genus Normative Behaviour; *ii.* number of most probable behavioural transitions including at least one BPIS was higher in less enriched enclosures; *iii*. proeminence indexes indicate that BPIS function as dead ends of behavioural sequences, and proeminence of three BPIS (pacing, self-direct, active I) were higher in less enriched enclosures. Overall, these data are not supportive of BPIS as a repetitive pattern, with a mantra-like calming effect. Rather, the picture that emerges is more supportive of BPIS as activities that disrupt organization of behaviours, introducing "noise" that compromises optimal activity budget.

Key-words: stress, welfare, behavioural index, Markov chains, Social Network Analyses

Introduction

According to Mason & Latham, by 2004, an (under)estimative of 85 million animals may be suffering in farms, laboratory and zoos worldwide. Although the interest in animal welfare has increased over the last 20 years, the authors argue that there is still need for more studies on reliable and fast tracking indicators of welfare and suffering. In her long series of work, Dawkins (1990, 2003, 2004, 2006, 2008) argues that while health is the foundation of any welfare measure, when we move beyond basic physiological needs and start to ask whether animals have good "psychological" health, new indicators must be defined and tested. Behaviour, she argues, is an important adjunct index as an early warning of physical health problems, and in its own right as external signs of fearfulness, frustration, contention and of what animals want.

While there is agreement that multiple behavioural measures must be taken, and that these must be correlated to other physical measures (e.g. heart rate, cortisol, cytokines), there are plenty disagreement on what measures, and which combination of indexes, should be taken. When reviewing the data on use of behaviour as welfare index, Mason & Latham (2004) says that a confusing picture emerges. One first source of confusion is on what constitutes a species-normative behaviours (SNB) (Jacobsen, Mikkelsen, & Hau, 2010) and how should one expect this to be expressed under captive conditions. Wild animals show flexible behavioural patterns adjusting their activities according to seasonal changes in daylight, food availability, predation pressures and, even, social organisation of each group (Hosey, 2005; Jack et al., 2008; Meehan & Mench, 2007; Novak, Hamel, Kelly, Dettmer, & Meyer, 2013). So which baseline expect from captivity, and whether some species with more behavioural flexibility would fare better in human altered environments (fragments or captivity or city borders) are open questions (Mason et al., 2013; Wingfield, 2013). Nevertheless, a rough pattern emerges that species with larger home ranges, omnivorous diet and larger group sizes would do worse in captivity (Abbott et al., 2003; Clubb & Mason, 2003; Pomerantz, Meiri, & Terkel, 2013a).

Another source of confusion regards the use of abnormal or stereotyped behaviours as indicators of welfare. Stereotypies have been described as repetitive behavioural patterns, invariant and without any apparent motive or goal (Dantzer & Mormede, 1983; Mason, 1991a). This definition has been used in several of studies, from wellbeing to animal cognition (Dantzer & Mormede, 1983; Dantzer, 1986, 1991; Garner, 2005; G. Mason, Clubb, Latham, & Vickery, 2007; G. J. Mason, 1991a, 1991b; Pomerantz, Terkel, Suomi, & Paukner, 2012). Stereotypies are often considered to be abnormal behaviours, because they differ in form, frequency or context, from behaviours displayed by free-living animals (Brilot, Asher, Feenders, & Bateson, 2009; Garner, 2005; Meehan & Mench, 2007). At the same time, stereotypies are “endemic” of captive animal populations (Birkett & Newton-Fisher, 2011) thence they are taken as signal of potential suffering. This definition led to a concept that animal’s housing facilities should allow the animals to perform the most “natural” behaviour as possible (Fraser, Weary, Pajor, & Milligan, 1997).

Garner (1999) proposes that stereotypies are symptoms of alterations in the behavioural organisation, mediated by malfunctions at the *corpus striatum*, hence the similarity of repetitive movements to that of autistic or schizophrenic individuals. The link between stereotypies and welfare is not straightforward. When comparing between groups, those in worse condition do exhibit increased overall stereotyped rate, but when comparing within groups, those individuals in better conditions tend to exhibit increased rates of stereotypy (Dawkins, 2003). While agreeing that stereotypies should be taken seriously, Mason & Latham (2004) lists four reasons why repetitive behaviours may not indicate decreased welfare: i. stereotypies as “do-it-yourself enrichment”, in which the animal itself creates activity and cognitive distraction from impoverished environment; ii. “mantra effects”, in which animals would get calmer through repetition of movements; iii. “Habit”, in this case repetition of behaviour would shift to an automatic process, named central control, that enables animals to perform regular and fast movements with minimal cognitive processing or sensory input, and finally; iv. “Perseveration”, which is the continuation or recurrence of an activity without the appropriate stimulus. It would be an autistic-like disconnection to novel stimuli and maintenance of previously learned patterns. In the first two cases the performance of stereotypies would have beneficial consequences *per se*, and in the latter two cases, the stereotypy appears as a scars from past stress but that do not reflect the current welfare state (G. J. Mason & Latham, 2004). Therefore, different stereotypies may indicate different underlying phenomenon. Large sample sizes are needed – but not always achieved- to disentangle these phenomena.

As for any behavioural study (see Altmann, 1974 cornstone manuscript), one final source of confusion on interpretation of behavioural indices regards the different protocols of data entry, such as definition of what is a state or an event , sampling procedures (continuous or at intervals, at which intervals), normalisation procedures and methods of analyses for indexes calculation. These discrepancies arise as data collection procedures fit proximal factors such as number of animals, time and resources available for data collection, and specific questions for each study. Nevertheless, comparability of data is an aim in science for it allows meta-analyses of the greater pattern.

While time allocation in activity budget analyses, frequency and diversity indices of GNB and BPIS are easy to calculate, it is long argued that blunt proportions of behaviours are too much coarse grained analyses, for it does not offer a picture of how the sequence of actions occurs over time (Escós, Alados, & Emlen, 1995; Rutherford, Haskell, Glasbey, Jones, & Lawrence, 2003). Asher et al., 2009 use the term behavioural organization to refer to the arrangement of behavioural states relative to each other in time and space, and in relation to other individuals or behaviours. Reznikova (2012), says that we need to read ethological texts distinguishing between “regular” and “chaotic” behavioural patterns, for this is important for understanding the role of behavioural mechanisms both in individual development and speciation. These authors, for example, found that for both wild and naive ants key elements are the same (R-A-C-K-P, running, attack capture, kicking and prey transport), but they appear in different order in wild and naive ants. Successful hunting sequences of wild ants were less complex (had less noise) than unsuccessful sequences, that is, successful sequences contained more key elements, had less redundancy, were more predictable and less complex. Egge et al. 2010 use analysis of sequence to investigate ritualized aggressive encounters in stalked eyed fly (*Teleopis dalmanni*). Authors found that flies that lose conflicts make use of more ritualized low-intensity displays during contests, while the frequency of these ritualized sequences are less common in winner flies.

In their review on recent methods for analyses of behaviour, Asher and collaborators (2009) list four promising methods to analyse organization of behaviour: Fractal analyses; Temporal analyses (here including Markov and Monte Carlo chain), Social Network analyses, and Agent-based modelling and simulation. Despite such improved analytical tools, results are still ambiguous. For example, in two studies cited by Asher et al. (2009), one found that self-similarity of the fractal dimension of vigilance behaviour in hens decreased under stress conditions (which is in accordance with the idea that stereotypies disorganize and compromises normal pattern behaviour). However, in another study, the fractal dimension of the locomotor behaviour in hens increased (that is, became more self-similar) in worse conditions (which is in accordance with the idea of stereotypies as repetitive patterns).

Lusseau et al. (2003, 2004, 2009) published a series of papers on the impact of boats on the behaviour of dolphins. The authors found that the behaviours exhibited a first order Markov chain dependency, that is, the current behaviour was dependent of the previous behaviour (which in the Lusseau case was registered at 15 min intervals). Besides, the transition probabilities differed in situations with and without boats, with the transitions involving socializing and resting decreasing and the ones involving diving increasing in the presence of boats.

Asher et al (2009) presents the social network analyses (SNA) and agent-based models as tools for understanding social interactions and how that affects the behavioural pattern. Social Network Analysis was developed to analyse social interactions and social organization. It examines and quantifies the patterns of interactions among entities, and it has been applied to the study of primate societies since 1930s (Brent, Lehmann, & Ramos-Fernández, 2011). It is useful in identifying central individuals (or hubs) that can be important as nodes for disease transmission (for example), or cut points (e.g., by removing one individual, a group may fragment in two). The advantage of this technique is that it offers individual and group level indices that can be used to compare among social organization of different groups (populations or species). Makagon and collegues (2012) list four uses for SNA to applied ethology: *i*. evaluate the spread of disease, information on abnormal behaviour; *ii*. regrouping or separation of animals; *iii*. evaluate the impact of social environmental on health, and *iv*. evaluate differences in resource and environment use according to social interactions.

The genus *Sapajus*, robust capuchin monkeys, is the second primate species with higher occurrence in northeast wildlife rescue centres (28,1%) according to Levacov et al (2011). The Wildlife rescue centres (Centro de Triagem de Animais Silvestres - CETAS) are supposedly housing for animals during a short period of time, until there is a better solution for their future. Unfortunately, this rarely happens, and animals are kept, most of the times, in small and overcrowded enclosures, for an undetermined period (do Nascimento, Schiavetti, & Montaño, 2013). If animals are not kept at CETAS, they are often sent to public governmental zoos (Vidolin, Mangini, Moura-Britto, & Muchailh, 2004).

Capuchin monkeys are medium size (4.5 kg) New World primates. The clade was recently divided in two genus, the gracile forms (*Cebus*) occurring in Central America and north of Amazon forest, and the robust form (*Sapajus*) occurring in all biomes in South America from caatinga dry areas to swamps and Atlantic forest (Alfaro, Izar, & Ferreira, 2014). The genus *Sapajus* contains eight species, two of them listed as endangered by the IUCN: *Sapajus flavius* and *S. xanthosternos*, both with occurrence in northeast Brazil.

Throughout their range capuchin monkeys display an omnivorous diet and they are known for their behavioural diversity and cognitive capabilities, which include coalitions (Izar, Ferreira, & Sato, 2006) and the use of stones to crack open nuts and dig roots and sticks to probe on holes (Ottoni & Izar, 2008). Although there is one clear *alfa* male and female, they are also known for their tolerant social hierarchy, with harems of one male to three or four females found in different robust species, regardless of biome (Izar et al., 2012). Because of these characteristics capuchin monkeys are seen as good models for comparative analyses on the evolution of cognition and behavioural plasticity (Fragaszy et al, 2004).

Activity budget of wild animals is composed by 20% to 30% of foraging for fruits and insects (mostly), another 20-30% is employed in eating and further 20-30% employed in Locomotion. Social interaction composes less than 10% of individual's activity budget. These proportions change depending on environmental conditions, for example, black-horned capuchins (*Sapajus nigritus*) spent 26% of time in locomotion and 38% of their time eating at Atlantic forest, while bearded capuchin monkeys (*S. libidinosus*) spent 41% of time in locomotion and 16% of time eating at the dryer biome of Cerrado (source: table 8 in Verderane, 2010).

This activity budget differs from that of captive groups in which higher proportions of Vigilance and exhibitions of BPIS are reported. For example, Ferreira et al. (2016) describes analyses of the GNB and BPIS of a sample of 123 bearded capuchin monkeys (*S. libidinosus*) all kept in same sized enclosures (25 m^3). The authors found

Energy gain related behaviours accounted for 27%, vigilance for 25%, while BPIS composed a mean of 17% of activity budget.

In this manuscript we offer two ethograms for registering captive capuchin's (*Sapajus spp.*) behaviour: one for Genus Normative Behaviour (GNB) (Jacobsen et al., 2010) and one for Behaviour Potentially Indicative of Stress (BPIS). The ethogram for GNB was adapted from the book Complete Capuchin, authored by Fragaszy, Visalberghi, & Fedigan, therefore, we refer to this book for readers to willing access the original sources. At least half of the BPIS are already listed at Boinski et al., 1999 seminal papers on behavioural and physiological indicators of welfare in single housed capuchin (*Sapajus apella*) monkeys. Overall these ethograms synthesize the descriptions of GNB and BPIS found in manuscripts published in scientific journals, scientific books and PhD thesis (see references in the tables). But descriptions are also based on personal observations and practice, and informal conversations with experts.

We explore four type of analysis: Activity Budgets, Diversity indexes, Markov chains and sequence analyses, and Social Network Analyses for GNB and BPIS macro-categories, in three different capuchin species (*Sapajus libidinosus, S. flavius* and *S. xanthosternos*), kept in three different enclosures. We test the following predictions:

- Previous studies indicate lack or very small sexual differences in BPIS exhibition in capuchin (Mendonça-Furtado, 2006; Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012), hence we expect small sexual differences.
- Due to great behavioural flexibility of Genus, we expect small species differences in BPIS.

- Enclosure type is reported as one important dimension for welfare (Beisner & Isbell, 2009a, 2009b; Vandeleest, McCowan, & Capitanio, 2011), therefore we expect that:
    - The amount of time committed to BPIS from individual’s activity will be higher in smaller enclosures
    - BPIS will be more diverse and frequent in non-enriched and smaller enclosures;
    - If repetitive behaviour is indicative of stress then Markov chain order and probability of sequences ending in one BPIS should be higher in smaller enclosures
    - If BPIS disrupts GNB pattern then centrality indexes of BPIS should be higher in smaller than in larger enclosures.

Methods

Subjects

In this research we focused on three species of tufted capuchins: bearded capuchin (*Sapajus libidinosus*), blond capuchin (*S. flavius* Schreber, 1774 - endangered) and yellow-breasted capuchin (*S. xanthosternos* Wied-Neuwied, 1826 - endangered), adding 26 individuals (table 1).

Data collection was made at a governmental wildlife’s rescue centre (CETAS) in the city of Natal (Rio Grande do Norte) and at Salvador’s Zoo (Bahia), both in Brazil. At Natal’s rescue centre, the six *S. libidinosus* were kept in closed enclosures, of 23 m^3 (fig. 4 and 9). These were non-enriched enclosures, with a half-fenced wall that allowed outside view. At Salvador's Zoo we observed two species, *S. flavius* and *S. xanthosternos*. The 7 individuals from *S. flavius* were maintained in two enclosures of similar sizes (124 m^3) (fig. 5 and 6). The enclosures at Salvador's Zoo are multi-cage complexes, of indoor and outdoor compartments, with environmental enrichment (e.g. branches and ropes). Similar to *S. flavius*, one *S. xanthosternos* group with 5 adult individuals is kept in a closed enclosure of approximately the same size (fig. 7), while the other group, with 8 adult animals, is kept in an island of 100 m^2 (fig. 8). This habitat had more environmental enrichment than the closed enclosures.

Each observed group, except one, had juveniles in their composition (table 1). However, only adults and sub-adults were considered for this study.

Both Zoo's and CETAS's animals were fed during the morning period and had water *ad libitum*. At CETAS animals were fed fresh vegetables, fruits, boiled eggs, dried dog food and, occasionally, a vitamin supplement. At the zoo, animals were fed fresh fruits and vegetables, boiled eggs, raw meat and primate dried food.

Most individuals came from apprehensions made by the governmental organ IBAMA. Unfortunately, the origin or amount of time that the animals have been at CETAS or zoo is unknown. Each animal was identified by physical characteristics such as coat coloration, body and head shape, tuft and face.

Table 1. Group composition and enclosure distribution.

Group	Enclosure	Species	Number of females	Number of males	Number of juveniles	Total
1	closed CETAS	*S. libidinosus*	1	1	3	5
2	closed CETAS	*S. libidinosus*	2	3	-	4
3	closed Zoo	*S. flavius*	3	1	1	5
4	closed Zoo	*S. flavius*	2	1	3	6
5	closed Zoo	*S. xanthosternos*	3	2	3	8
6	island	*S. xanthosternos*	3	5	3	11

Figure 1, 2 and 3. 1. Female of *S. libidinosus* (Queen) engages in faeces-painting. **2.** Female of *S. flavius* (Ruiva) observes environment. **3.** Male of *S. xanthosternos* (Carlinhos) self-bites his arm. (Photos: Carolina Cadório).

Figure 4, 5 and 6. 4. Closed enclosure (left picture) at CETAS. **5 and 6.** Closed enclosures at Salvador's zoo (right pictures), housing *S. flavius.* (Photos: Carolina Cadório and Mariana Winandy).

Figure 7, 8 and 9: 7 and 8. Closed enclosure at Salvador's zoo and island (left pictures), housing *S. xanthosternos*. **9.** Closed enclosure at CETAS (right picture). (Photos: Carolina Cadório and Mariana Winandy).

Ethograms

Genus Normative Behaviours

Given the known behavioural flexibility exhibited by capuchin monkeys, it is at least risky to make a list of Species Normative Behaviour, or in this case, Genus Normative Behaviour (GNB). Nevertheless, part of the flexibility refers to differential allocation of time to the same basic functional behavioural categories.

In the ethogram, the GNB labels and definitions are adapted from the book Complete Capuchin (Fragaszy et al., 2004) to avoid unnecessary novelties. In total we use 21 GNB categories grouped into 9 GNB macro-categories.

The first column in the Table 2 refers to a possible grouping of these behaviours into macro-categories. We used an *a priori* clustering criteria in order to mimic the four basic categories proposed by Dunbar, 1992, who argues that time act as a hidden constraint to individual fitness, for sometimes there are too many activities (e.g. foraging, patrol territory, search for mates) or much time is employed to one activity (e.g. search for food) that individuals must trade-off between activities. The author then lists four major categories that would summarize the activity cycle of a primate: forage, locomotion, rest, and socialise. The behaviour that would compose these macro-categories varies for each species and situation. The idea of trade-off is implicit in the definition of stereotypies as a functionless behaviour, therefore, verifying correlations between GNB and BPIS can help shed some light in the phenomena.

Behaviours Potentially Indicative of Stress

Most of the BPIS are listed at Boinski et al. (1999a,b) seminal papers on behavioural and physiological indicators of welfare in single housed capuchin (Sapajus apella) monkeys. New BPIS were added to the list as studies on captive capuchins increased (Mendonça-Furtado, 2006; Polizzi di Sorrentino et al., 2012; Pomerantz, Meiri, & Terkel, 2013b; Prates & Bicca-Marques, 2005; Rimpley & Buchanan-Smith, 2013; Ulyan et al., 2006). Special attention will be given to the stereotyped behaviour head-twirl, for a previous study indicates that this BPIS correlates to cortisol levels and pessimistic judgement bias in capuchin monkeys (Pomerantz et al., 2012).

Again, we include a column of macro-categories grouping behaviours into *a prior* constructs. These macro-categories aimed to capture the active *vs* passive coping strategies suggested by some authors (see chapter 2 for a discussion on coping strategies) and are based on a previous work of our groups (Ferreira et al., 2016). In total we use 17 categories and 10 BPIS macro-categories.

Table 2. Genus Normative Behaviour's ethogram (GNB). Behaviours are compiled in macro categories.

Macro-category	**Behaviour**	**Definition**	**Adapted from**
Energy Gain (EG)	Foraging	The individual moves around searching for food, but without ingestion at the moment of registration.	1, 2, 3
	Eating	The animal is stationary and takes food into his mouth, chews and ingests.	1, 2, 3
	Drinking	Animal is stationary next to a water source taking water into is mouth followed by ingestion.	1, 2, 3
Exploratory (EX)	Food manipulation	Food is manipulated with apparent aim to ease the ingestion (soften, crack), but without necessary ingestion afterwards.	1, 2
	Manipulation of environment	The individual touches, moves, licks, rubs or bites objects or part of the environment.	1, 2
	Play alone	The individual interacts with objects (manipulation of the surrounding environment with no apparent motive). Pushes and pulls ropes, branches, twigs and wires. Swings itself with inferior or superior limbs.	1, 3
Social positive activities (SP)	Grooming	The act of manipulate hair from others with hands or mouth.	
	Social play	Two or more animals interact physically and/or chase each other without aggression involved. There may occur manipulation of the environment	1, 4
	Sexual behaviours	The individual opens the eyes widely and repeatedly, together with contortion body movements (this behaviour occurs directed to another individual), body rocking from side to side. This usually happens during female oestrous.	1, 5
	Scrounge	The animal approaches another and feeds on scraps that fall from this one's mouth.	
	Mount	Individual mount each other and it may occur contact between genitalia. This usually happens during female oestrous.	
Social negative	Incite aggression	One individual incites another to attack a third member.	
	Aggression	The individual threats, hits, bites or attacks other individuals.	

activities (SN)	Approach/retreat	One individual retracts by the approaching of another. The identity of who approached and who retreated is noted.	
Vigilance (VI)	Alert	The individual turns the eyes and head slowly, looking at least at two different directions. The animal alternates between looking at inside and out of the enclosure, without performing any other behaviour.	1, 2, 3
	Threat to the observer	The animal threats the observer. (e.g.: shows the teeth, aggressive vocalization)	1, 2, 3
Inactivity (IN)	Inactivity	The individual stays in rest and static. The eyes may be open or closed.	1, 2, 3
Locomotion (LO)	Locomotion	Vertical or horizontal locomotion on the enclosure, without manipulation or search for food.	1, 2
Vocalization (VO)	Vocalization	Makes sounds and calls with different meanings. Sounds are made with mouth generally open. Sound can be high or low pitched.	1, 3
Others (O)	Others	Other behaviours that are not contemplated in the ethogram. These behaviours do not occur so often.	
	Urine wash	Urination on hands and/or feet, followed by rubbing urine on members or neck.	6

Table 3. Behaviour Potentially Indicative of Stress' (BPIS) ethogram. Behaviours are compiled in macro-categories.

Macro-category	**Behaviour**	**Definition**	**Adapted from**
Pacing (PA)	Pacing	Walks or runs repeatedly, without aim, around the same path.	4, 5
Body-Rocking (BR)	Body-Rocking	Repeated movements of body rocking, backward and forward or side to side.	2, 4
Active I (AC I)	Head twirl	Turns the head looking up and side to side.	7
	Pirouette	Turns on itself without leaving the same spot.	
Active II (AC II)	Shiver	Shakes body like a shiver, from head to tail.	
	Jumper	Jumps up and down on the same spot.	
Self-directed (SD)	Scratching	The animal scratches a body part, with his hands or feet, during a brief moment.	8
	Self- grooming	Grooming with hands or mouth, compulsively.	2
	Self-biting	Bites itself in any body part.	2, 3, 4
Crouching (CR)	Crouching / self clasp / huddle	Individual holds itself with arms, legs and the tail. Eyes are opened but tend to look to floor or to itself. It does not move or bounce nor is it scanning the environment. It differs from resting in that animal is not in a relaxed position and slow changes its position just to crouch again few centimetres away.	2, 3, 4
Ingestion (IG)	Manipulation/ingestion of faeces, urine or sperm	Licks or touches urine or sperm. Eating of own or other's faeces, urine or sperm.	3, 4
	Vomit followed by eating	Vomits and eats its own vomit, or ingestion of another's vomit.	
Screaming (SC)	Screaming	Seating starts screaming with no apparent motive.	9

Sexual-display (SX)	Sexual-display	Individual opens the eyes widely and repeatedly, together with body rocking from side to side. Hands usually located near the armpit. Legs open displaying genitalia. This behaviour is directed at humans.	4
	Masturbation	Manipulation with hands, or tail, of the genital and anal regions of the body.	2, 4
Own-stereotypy (OS)	Finger-sucking	Sucking one or more fingers.	4
	Food/Faeces painting	Smears or rubs faeces, scraps of food and other materials (e.g. pieces of wood, grass) together across the floor.	10

1. Fragaszy et al., 2004; 2. Boinski, Swing, Gross, & Davis, 1999; 3. Tárano & López, 2015 4.Ferreira, Almeida, & Martinez, 2013; 5. Carosi, Linn, & Visalberghi, 2005; 6. Miller Buckholz, Laszlo, & Suomi, 2008; 7. Pomerantz et al., 2012; 8. Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012 9. Boinski, Gross, et al., 1999 10. Gottlieb, Connor, & Coleman, 2014

Data collection

One of the basic differences in studies of behaviour is that between state and events. States are longer lasting behavioural patterns (e.g. eating), while events as instantaneous occurrences (e.g. sneeze). Of course this distinction is not simple (e.g. one can eat a peanut in an “instantaneous” bite). This distinction is not much a matter when one is conducting a focal continuous sample of behaviour, for any behaviour listed in the ethogram, of any length will be recorded. Although the best, this method is not always feasible, and one would need a voice recorder (and later, time to transcribe the recordings), or a help person (one to keep the focal continuously and say the behaviour to a helper, that is typing the code into a palmtop with some software for behavioural analyses, such as Observer).

Recording the behaviour at sampling intervals has the advantage that one person can record the behaviour, either in paper or directly in palmtops, which decreases the time and team demands. Such form of registering behaviour offers a table similar to excel sheet that is didactical to calculate simple descriptive statistics, such as mean, minimum and maximum values. However, in this case the difference between state and event can be an issue. Sampling will always be biased toward the behaviour that the animal spends most time in. And that’s the statistical logicale and advantage of this sampling method. However, the greater the interval between two registers tothe greater the bias toward not registering fast behaviours.

Here we used a focal animal sampling length of 10 min, registering the behaviours cited at ethograms 1 and 2 at every 10 sec. (see appendix A). Note that this register interval is shorter than that used by Ferreira et al. (2016), who used the same ethograms but registered behaviours at every 30 sec. This short interval was chosen because: *i.* it decreases the bias towards longer lasting behaviours; *ii.* it was feasible; *iii*. The sampling interval can be extended *a posteriori* by filtering the registers at longer intervals in the excel table.

Furthermore, this method allow a more direct comparability to other studies for this is the method used by many research of wild (Janson, 1990; Lynch, Ziegler, & Strier, 2002; Perry, 1997) and captive animals (Boinski, Swing, et al., 1999; Jacobsen et al., 2010).

Animals were observed sequentially in a random order, and five minute interval was imposed between focals of different individuals, in order to avoid time dependency and correlations between behaviours of individuals (De Queiroz & Ferreira, 2009).

At CETAS there were three observers and at the zoo two of the three observers. Inter-observer agreement trials were conducted and independent collection started when observers reached 85% agreement (that is only 9 out of 60 register per animal focal sampling could differ between observers). Observations were made from public viewing areas at the zoo, at a distance of about 1,5 m at the close enclosures and 7 m at the island. At CETAS observations were made at a distance of 1 m, in the enclosures access corridor. Data was collected in the afternoon, during week days, between September 2013 and May and June 2014. Sampling effort yield a total of 147,17 hours of data collected, with an average of 6 hours behavioural sampling per individual.

Data Analyses

Activity Budget

This is an estimative of the time allocated to each activity based on the proportion of registers. It is calculated by the following formula:

$$T_i = \frac{R_i}{R_t} x\ 100$$

With T_i is the proportion of time employed by each animal in behaviour i; R_i is the number of register in which the individual was in activity i; and R_t is the total number of registers of that individual, in any behaviour.

Although we recorded the behaviour at every 10 sec., for activity budget analyses we used the behavioural state registered at every 30 sec., in order to allow better comparability to Ferreira et al., (2016).

Frequency

The sum of behaviour registered at every 10 sec. divided by the total amount of hours each individual was observed (number of bouts per hour). Although correlated to the previous one, this index offers another perspective on the analyses of behaviour. While activity budget depicts the overall “investment” of individuals’ time, the frequency gives the number of behaviour bouts per hour.

Diversity Indices

Prevalence: proportion of individuals that perform each one of the macro-categories of BPIS (number of individuals per category). It was calculated by the following formula:

$$P_i = \frac{N_i}{N_t}$$

Where, P_i is the prevalence of BPIS; N_i is the number of individuals that performed that behaviour (regardless of how much); and N_t is the total number of individuals in the sample.

Diversity: from the 17 BPIS categories, it indicates how many of them each individual performs (number of BPIS per individual). It was calculated by the following formula:

$$D_i = \frac{B_i}{B_t}$$

Where, D_i is the diversity of BPIS; B_i is the number of different BPIS each individual exhibited (regardless of how much); and B_t is the total number of BPIS, in this case, B_t = 17.

Markov Chain and Sequence analyses

Markov chain analyses the dependency of one event from previous events (Dans, Degrati, Pedraza, & Crespo, 2012; Egge et al., 2011; Lusseau, 2003). When two events are independent from each other they are said to have a zero-order dependency. When one event at *t+1* depends on which event occurred at t_0, then the sequence exhibits first-order. If the event at time *t* is dependent on the two previous events then the sequence exhibits second-order dependency (Lusseau, 2003; Venegas-Barrera, Morales-Bojórquez, & Arnaud, 2008). Based on the order of dependency one may calculate the probability of sequences (in this case, behavioural sequences).

In order to select which order the sequence exhibits we used the *Bayesian Information Criterion* (BIC) (Sobral & Barreto, 2011). This is a method to calculate the goodness-of-fit of data to a model, the larger the value, the greater the residuals between real values and model predicted values. The BIC imposes a correction in model selection by imposing a penalisation in values that is dependent on number of possible states the sequence may exhibit. BIC was calculated by the following formula:

$$\text{BIC}\,(k) = -2\,\log\widehat{L}(k) + k\,\log n$$

In which, k is the order to be tested, $\hat{L}(k)$ is the function of maximum goodness-of-fit, and *n* is the number of observations (transitions).

Once defined the dependency order, a transition matrix is built in which each "behavioural unit" is present at rows and columns, and the cells are filled with the probability of transitions between units. As we used 19 behavioural categories, the transition matrix was:

$$P_{\text{ij}}=\begin{bmatrix} p_{1\,1} & \cdots & p_{1\,19} \\ \vdots & \ddots & \vdots \\ p_{19\,1} & \cdots & p_{19\,19} \end{bmatrix}$$

The most probable sequence is calculated from this matrix. So if we want a probability of six different behaviours P_{abcdef} and, if Markov ‘s order is confirmed to be zero, we multiply the probability of occurrence of each behaviour: $P_a \text{ x } P_b \text{ x } P_c \text{ x } P_d \text{ x } P_e \text{ x } P_f$.

Given the order-dependency between transitions found we calculated the probabilities of the following sequences: *i*. six consecutive GNB (regardless of which macro-category), with higher probability; *ii.* six consecutives BPIS (regardless of the macro-category), with higher probability; *iii*. the probability of five GNB and one BPIS (regardless of macro-category), with higher probability. These Markov chain’s analyses, were conducted using a script written in R (appendix B) by us.

We employed also the program Ethoseq to extract the significant probabilistic behavioural sequences (Japyassú, Alberts, Izar, & Sato, 2006). This method is based on Graph Theory and, from the matrix of behavioural transitions, it calculates the most probable sequence based on Brown’s chi-square. The program outputs Direct Trees, a hierarchical diagram summarizing the information about the sequence of acts. For each individual we calculated the number of significant behavioural sequences that contained at least one BPIS, and the probability of occurrences of sequences containing at least one BPIS.

Social Network Analyses

In its original form Social Network Analysis (SNA) is a methodological approach to study the structure of societies. It depicts a sociogram in which nodes are individuals, connected by ties (edges) that represent the interactions between individuals. It is not a statistical method, but rather an analytical method, also grounded on Graph Theory. Several indexes can be calculated based on proportions of ties that link nodes (see review in Makagon et al., 2012, Whithead, 2008). Makagon et al. (2012) distinguish some dimensions that can be analysed: *Prominence*, *Cohesion*, *Range* and *Brokerage.* Definitions and formulas to calculate these indexes vary from one author to another depending on penalization and power indices chosen to calculate the index, and we refer to the above cited sources for formulas. SNA can be used to analyse undirected or symmetrical interactions (e.g. proximity) or asymmetrical interactions (e.g. grooming, aggression). Indexes can be calculated per individual (e.g. the centrality of one node) or for the group (e.g. the centralization of the network as a whole).

Although traditionally used to analyse societies, SNA also has been used to unravel other types of interactions such as molecules and words in a text (Asher et al., 2009). Here we use SNA to analyse interactions between behaviours. So, nodes are behaviours, and ties between behaviours represent the transitions between them. We calculated the Prominence indexes for each BPIS, to measures the importance or key nodes. That is, we run a total of 26 SNA, in which the input was the transition matrix of the behaviours exhibited by each individual. The SNA outputs the *indegree*, *outdegree* and *betweeness* of each node (behaviours in our analyses). We focused only on the prominence indexes of the 10 BPIS macro-categories. Degree refers to the number of direct connections a focal node has to other nodes in the network, regardless of the strength of the interaction. *Indegree* refers to the number of direct connections a node receives (in asymmetrical interactions), regardless of the strength of that interaction. So in the present analyses, indegree of a BPIS represents the number of other behavioural categories that at least once were followed by a BPIS. *Outdegree* is the opposite, it refers to the number of direct connections a node makes to other nodes (in asymmetrical interactions). So in the present analyses, outdegree of a BPIS represents the number of other behavioural categories that at least once followed a BPIS. Betweeness is the proportion of shortest paths between any two nodes in the network that pass through the focal node. So, contrary to the other two indices, betweeness considers the strength of the interactions, and it is calculated by the following formula:

$$g(v) = \sum_{s \neq v \neq t} \frac{\sigma_{st}(v)}{\sigma_{st}}$$

Where σ_{st} is the total number of shortest paths from *s* node to *t* node and $\sigma_{st}(v)$ is the number of those paths that pass through v. In the present analyses, increased betweenness indicated that a BPIS is included in more behavioural sequences of that animal. SNA analyses were run on SOCPROG and NETDRAW free software packages.

Statistical Analyses

These indices (Activity Budget, Frequency, Diversity indexes, Markov Chain's order, number of significant sequences, Indegree, Outdegree, and Betweeness) were used as response variables.

Allocation type, sex and species were entered as factors, and analysed with a multivariate General Linear Model (GLM), with a bootstrap with 1000 samples. For GLM analyses, we considered the total number of registers in our sample. Since we didn’t have all species across enclosures, GLM was made for interactions between sex and enclosure, and sex and species, and those results that were significant both in species and enclosures will be interpreted as an enclosure difference. We performed a post-hoc Tukey two-sided test. Error I was set at α = 0,05 and tendency considered α up to 0,1. Spearman correlation was used to verify associations between GNB and BPIS. All data were analysed with IBM SPSS Statistics 21.

Results

Activity Budgets: GNB and BPIS

Energy gain related behaviours composed an average of 30% of individual’s activity budget, less 20% then the average established for wild groups. Vigilance composed 18%, and Locomotion, Social Positive and Exploratory composed, each, about 10% of individual’s allocated time. Inactivity was represented in less than 5% of scans, and two small parcels dedicated to Social Negative and Vocalization behaviours. BPIS were registered in 11% of scans (see fig. 10). From all the BPIS the most common were self-directed (scratching, self-grooming and self-biting) and pacing occurring 4,5% and 4% of registers respectively (see fig. 11). Ingestion was the third BPIS most common occurring in 1% of registers and AC I BPIS (head-twirl and pirouette) was registered at an average of 0,66% of animals time.

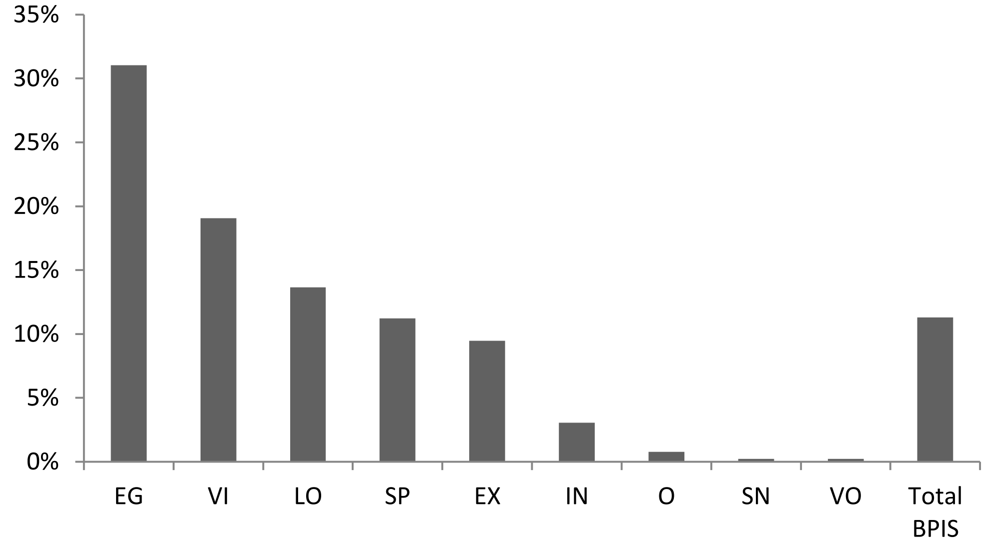

Figure 10. Activity budget with macro-categories of GNB and total BPIS. Results are presented in average percentage per total sample size (n = 26). EG: energy gain; VI: vigilance; LO: locomotion; SP: social positive activities; EX: exploratory; IN: inactivity; O: others; SN: social negative activities; VO: vocalization.

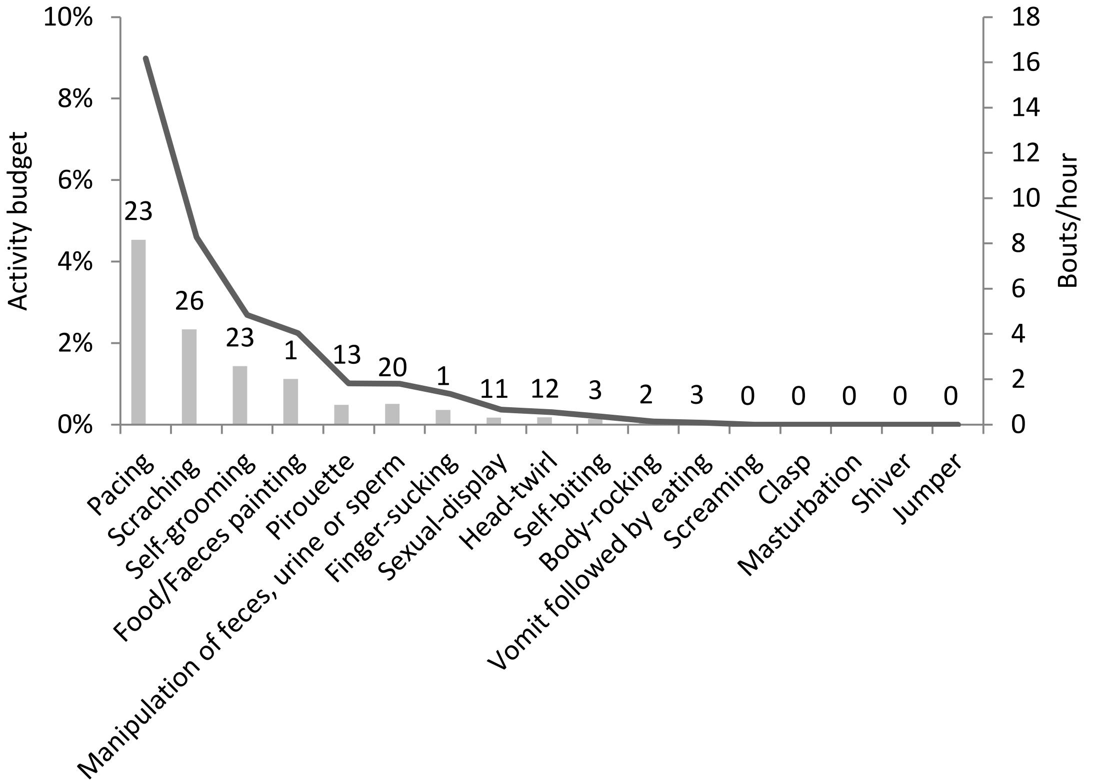

Figure 11. Activity budget and frequency for BPIS. Exact number of individuals that displayed that behaviour is represented on top of each column. Activity budget is presented in mean percentage (columns, light grey) and frequency in mean bouts per hour (line, dark grey).

Frequency, Prevalence and Diversity of BPIS

BPIS represented a total of 11,30 % of the activity budget and all animals displayed an mean of 40,03 bouts per hour of BPIS, in a total of 360 bouts/hour. Pacing occurred with a mean frequency of 16,17 bouts per hour, followed by self-directed ($\bar{x}$= 13,46 bouts/hour) and own-stereotypy ($\bar{x}$ = 5,38 bouts/hour). Animals engaged in AC I (pirouette and head-twirl) with a mean frequency of 2,36 bouts/hour. Ingestion, sexual-display and body-rocking occur less frequently (mean frequency: 1,88 bouts/hour, 0,65 bouts/hour and 0,13 bouts/hour, respectively, see fig 11).

All 26 individuals engaged in at least one of the BPIS macro-categories. The most common macro category of BPIS was self-directed, with 100% of the individuals exhibiting scratching at least once (figure 11), followed by pacing (23 individuals) and ingestion (21 individuals). Manipulation of faeces, urine and sperm was the fourth most common BPIS in the sample, however only three individuals did bouts of vomit followed by eating, all three from the same enclosure at CETAS. Active I macro-category, composed by pirouette and head-twirl, was engaged by 14 individuals. Own-stereotypy was only displayed by two individuals, a female *S. libidinosus* named Queen and a male *S. xanthosternos*, Carlinhos, both living in closed enclosures. It is noteworthy that, for these two individuals, the behavioural category Own-stereotypy is also the one most represented in the activity budget of each animal.

Individuals displayed at least 2 BPIS, with a mean of 5 BPIS for total sample size (minimum 2; maximum 8) (table 4).

Two macro-categories were never seen in this research, active II and screaming, even though they are referred to and described in literature (Boinski, Gross, et al., 1999).

Table 4. Diversity of BPIS across variables sex, enclosures and species. Frequency (bouts per hour) of BPIS (macro-categories) across sex, enclosures and species. PA: pacing; BR: body-rocking; SD: self-directed; OS: own-stereotypy; SX: sexual-display; IG: Ingestion; ACI: active I.

		Diversity	**Frequency**						
		Mean	PA	BR	SD	OS	SX	IG	AC I
Sex	Female	0,33	12,70	0,24	14,17	7,49	0,87	2,03	3,15
	Male	0,29	20,23	0,00	12,63	2,92	0,40	1,70	1,44
Enclosure	CETAS	0,38	21,57	0,00	12,74	17,47	0,10	0,69	6,41
	Closed Zoo	0,35	13,18	0,29	15,94	2,92	1,17	2,90	1,91
	Island	0,20	16,63	0,00	10,27	0,00	0,30	1,23	0,00
Species	*S. libidinosus*	0,38	21,57	0,00	12,74	17,47	0,10	0,68	6,41
	S. flavius	0,40	16,14	0,49	17,82	0,00	0,77	1,37	3,24
	S. xanthosternos	0,23	13,70	0,00	11,44	2,70	0,85	2,70	0,02

Analyses by Sex, Species and Allocation type

We found sex differences for one GNB, with males being more exploratory (F = 0,08 %, M = 0,11%), and one BPIS, active I (head twirl and pirouette), with females exhibiting more ACI than males (F = 0,9%, M = 0,4%). There was also a tendency for females to be involved in more social negative behaviours (0,3% vs 0,2%) and to exhibit more body-rocking than males (0,06%).

We found three statistical significant species differences in GNB, and three in BPIS. Blonde capuchins (*S. flavius*) exhibited more GNB exploration and more diversity in BPIS. *S. xanthosternos* were more GNB vigilant, inactive, and exhibited more BPIS ingestion and sexual display.

Enclosure size affected four GNB categories, and three BPIS indices (fig. 12). Animals kept in the island exhibited more energy gain, while animals in closed zoos exhibited more exploration, vigilance, locomotion, and the BPIS sexual display and ingestion. Animals kept either in closed CETAS or in Zoos exhibited more diversity of BPIS than animals kept in the island.

Sex and enclosure had significant joint interaction in GNB, with males exhibiting more energy gain and less vigilance than females, both in closed enclosures, while females exhibited more energy gain and less vigilance at the island.

Sex and species had significant joint interaction in GNB exploratory, inactivity, locomotion, and in BPIS pacing and self-directed. Female blonde capuchins explored, paced and self-directed more, and locomoted less, while male yellow breasted capuchins showed this pattern (males explored, paced and self-directed more and locomoted less).

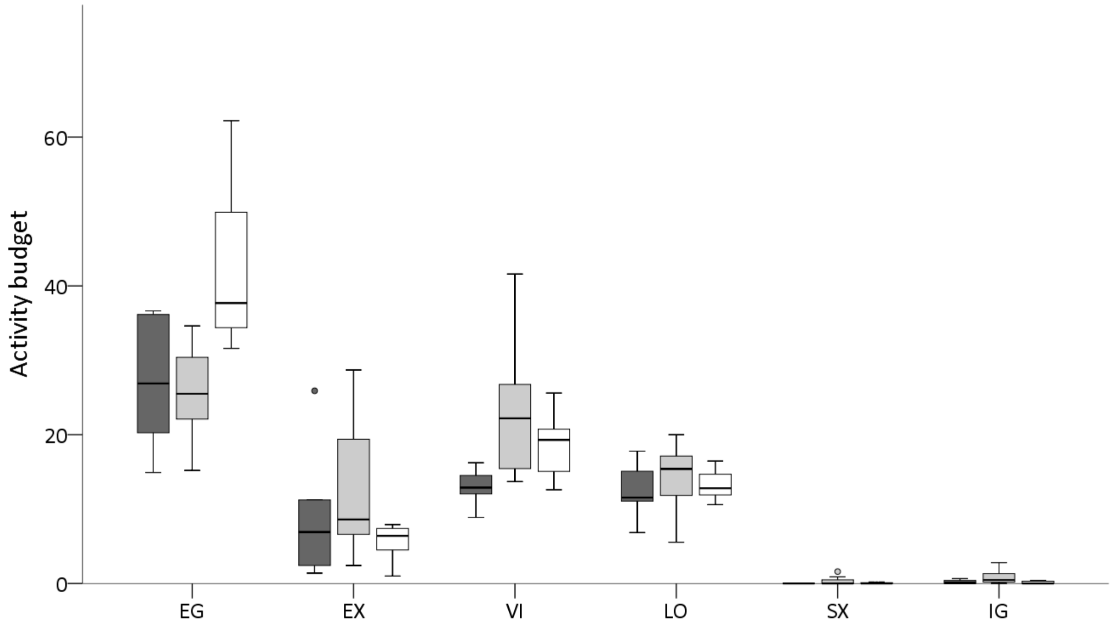

Figure 12. Differences in GNB and BPIS' activity budget, across enclosures (dark grey: CETAS; light grey: closed enclosures at zoo; white: island). EG: energy gain; EX: exploratory; VI: vigilance; LO: locomotion; SX: sexual-display; IG: ingestion.

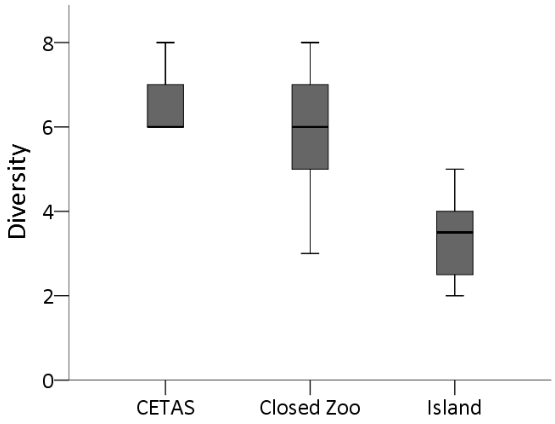

Figure 13. Differences in BPIS diversity across enclosures.

Correlations GNB and BPIS

Our analyses showed that GNB energy gain is negatively correlated with total BPIS; Active 1 (pirouette and head-twirl) and Own-stereotypy. There was a tendency for negative correlation to Self-Directed, Sexual display (see σ and p values at table 5)

BPIS Pacing correlated negatively to GNB Exploratory and Locomotion. Self-directed correlated negatively to Energy Gain.

BPIS Active 1 (pirouette and head-twirl) correlated negatively to GNB energy gain, and tendency for negative correlate to Social positive, Inactivity and Vocalization.

BPIS Sexual display correlated positively to Vigilance and Inactivity.

BPIS screaming, ingestion and active II did not correlate to any GNB.

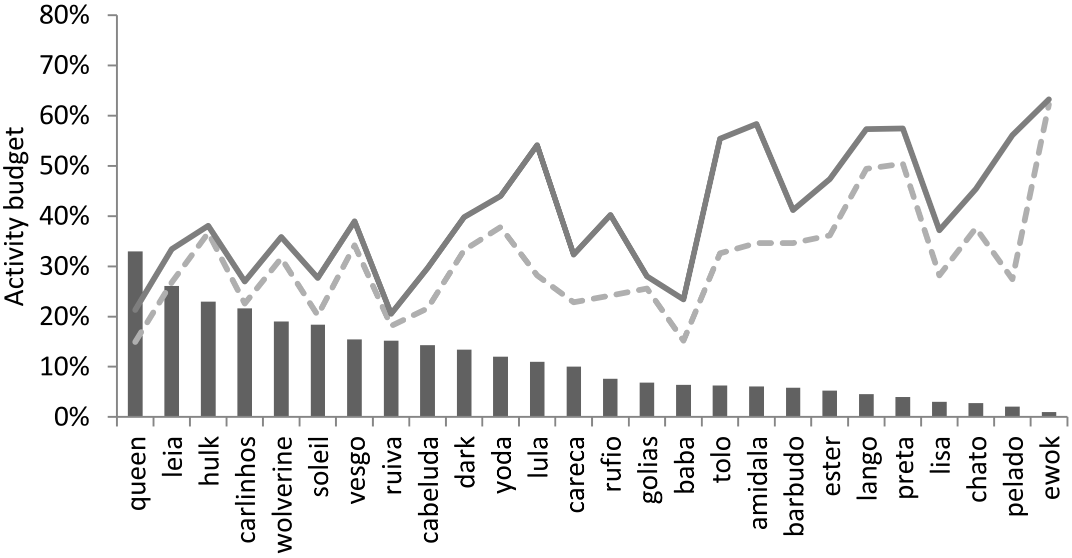

Figure 14. Negative correlation between total BPIS (bars) and exploratory behaviours (line) and energy gain behaviours (dots). Values are presented per individual.

Table 5. Summary of all significant results across analyses (Yes: significant results; Ŧ: tendency; numbers in potency: F, χ2, ρ and p values under the tabel).

	Sex	**Species #**	**Enclosure**	**Interactions**	**Correlations**
Energy gain			Yes[15]	Sex-encl.[22]	Negative AC I, OS[33] Negative SD, SX[34] Ŧ
Exploratory	Yes[1]	Yes[7]	Yes[16]	Sex-sp.[23]	Negative PA[35]
Social positive					Negative AC I[36] Ŧ
Social negative	Ŧ [2]			Sex-sp.[24] Ŧ	
Vigilance		Yes[8]	Yes[17]	Sex-encl.[25]	Positive SX[37] Positive BR[38] Ŧ
Inactivity		Yes[9]		Sex-sp.[26]	Positive SX[39] Negative AC I[40] Ŧ
Locomotion			Yes[18]	Sex-sp.[27] Sex-encl.[28] Ŧ	Negative PA[41]
Vocalization					Positive AC I[42]
Others	Yes[3]	Yes[10]		Sex-encl.[29]	Negative AC I[43]
% BPIS					
Frequency					
Prevalence					
Diversity		Yes[11]	Yes[19]		
Pacing				Sex-sp.[30]	Negative EX, LO
Body-rocking	Ŧ [4]	Ŧ [12]		Sex-sp.[31] Ŧ	Positive VI Ŧ
Self-directed				Sex-sp.[32]	Negative EG Ŧ
Own-stereotypy	Yes[5]				Negative EG

Screaming				
Sexual display		Yes[13]	Yes[20]	Positive VI, IN
Ingestion		Yes[14]	Yes[21]	
Screaming				
Active I	Yes[6]			Negative EG, O Negative SP, IN Ŧ Positive VO
Active II				
Markov Chain			GNB prob.[52] GNB seq.[53] GNB and BPIS seq.[54]	
Ethoseq		Total behaviours[44] BPIS[45]	N seq.[55] BPIS[56]	
Social Network Analyses		AC_{in}[46],AC_{out}[47], AC_{bet}[48] PA_{in}[49] Ŧ, PA_{out}[50], PA_{bet}[51] Ŧ	AC_{in}[57],AC_{out}[58], AC_{bet}[59] Pa_{in}[60] Ŧ, PA_{out}[61] Ŧ IG_{in}[62] Ŧ SD_{out}[63] Ŧ	

given that our sample does not contain all combinations of sex/species/enclosure, whenever a statistical difference is found in both species and enclosure type, we will give priority to enclosure type. Only significant differences found exclusively at species will be discussed as such.

1. F = 32,673, df = 1, p = 0,000; **2.** F = 3,022, df = 1, p = 0,082; **3.** F = 16,257, df = 1, p = 0,000; **4.** F = 2,894, df = 1, p = 0,089 (only females of *S.flavius*); **5.** F = 11,178, df = 1, p = 0,001 (only two individuals); **6.** F = 5,116, df = 1, p = 0,024; **7.** F = 31,072, df = 1, p = 0,000; **8.** F = 16,569, df = 1, p = 0,000; **9.** F = 6,276, df = 1, p = 0,012; **10.** F = 7,446, df = 1, p = 0,006; **11.** χ^2 = 16,058, df = 2, p = 0,000; **12.** F = 2,850, df = 1, p = 0,092; **13.** F = 4,772, df = 1, p = 0,029; **14.** F = 13,435, df = 1, p = 0,000; **15.** F = 59,311, df = 1, p = 0,000; **16.** F = 5,189, df = 1, p = 0,023;**17.** F = 22,687, df = 1, p = 0,000; **18.** F = 6,043, df = 1, p = 0,014; **19.** χ^2 = 13,142, df = 2, p = 0,001; **20.** F = 6,625, df = 1, p = 0,010; **21.** F = 17,640, df = 1, p = 0,000; **22.** F = 10,267, df = 1, p = 0,001; **23.** F = 18,196, df = 1, p = 0,000; **24.** F = 3,544, df = 1, p = 0,060; **25.** F = 14,487, df = 1, p = 0,000; **26.** F = 12,268, df = 1, p = 0,000; **27.** F = 12,481, df = 1, p = 0,000; **28.** F = 3,174, df = 1, p =

0,075; **29.** F = 5,378, df = 1, p = 0,021; **30.** F = 4,837, df = 1, p = 0,028; **31.** F = 2,850, df = 1, p = 0,092;**32.** F = 6,719, df = 1, p = 0,010; **33.** AC I: ρ = -0,394, p = 0,047; OS: ρ = -0,388, p = 0,050; **34.** SD: ρ = -0,384, p = 0,053; SX: ρ = -0,376, p = 0,058; **35.** PA: ρ = -0,427, p = 0,030; **36.** AC I: ρ = -0,358, p = 0,073; **37.** SX: ρ = 0,553, p = 0,003; **38.** BR: ρ = 0,348, p = 0,081; **39.** SX: ρ = 0,407, p = 0,039; **40.** AC I: ρ = -0,386, p = 0,052; **41.** PA: ρ = -0,423, p = 0,031; **42.** AC I: ρ = 0,412, p = 0,037; **43.** AC I: ρ = -0,530, p = 0,005. **44.** χ^2 = 6,328, df = 2, p = 0,042; **45.** χ^2 = 8,797, df = 2, p = 0,012; **46.** χ^2 = 17,006, df = 2, p = 0,000; **47.** χ^2 = 16,983, df = 2, p = 0,000; **48.** χ^2 = 7,326, df = 2, p = 0,026; **49.** χ^2 = 4,953, df = 2, p = 0,084; **50.** χ^2 = 6,312, df = 2, p = 0,043; **51.** χ^2 = 5,371, df = 2, p = 0,068; **52.** χ^2 = 9,069, df = 2, p = 0,011; **53.** χ^2 = 9,115, df = 2, p = 0,010; **54.** χ^2 = 7,970, df = 2, p = 0,019; **55.** χ^2 = 6,610, df = 2, p = 0,037; **56.** χ^2 = 7,538, df = 2, p = 0,023; **57.** χ^2 = 10,819, df = 2, p = 0,004; **58.** χ^2 = 10,699, df = 2, p = 0,005; **59.** χ^2 = 6,856, df = 2, p = 0,032; **60.** χ^2 = 4,849, df = 2, p = 0,082; **61.** χ^2 = 5,711, df = 2, p = 0,058; **62.** χ^2 = 5,218, df = 2, p = 0,074; **63.** χ^2 = 4,875 df = 2, p = 0,087.

Markov Chains and Sequence Analyses

No sex, species or allocation type differences were found in the Markov Chain's order analyses, for all individuals exhibited zero-order data dependency (see table 6) that is, the behaviour exhibited at time t+1 is not dependent on the behaviour exhibited at time t (which in our case is 10 sec). Therefore, the transition matrix can be calculated directly from absolute number of transitions observed, and the sequences of n steps can be calculated simply by multiplying the probability of occurrence n times.

There were no sex or species differences in none of the three sequence probabilities calculated. No significant differences in the probability of six consecutive BPIS or five GNB and one BPIS was detected, but the probability of an animal staying six consecutive registers in a GNB was significantly higher at Island than at CETAS or Zoo enclosures (fig. 15 and 16).

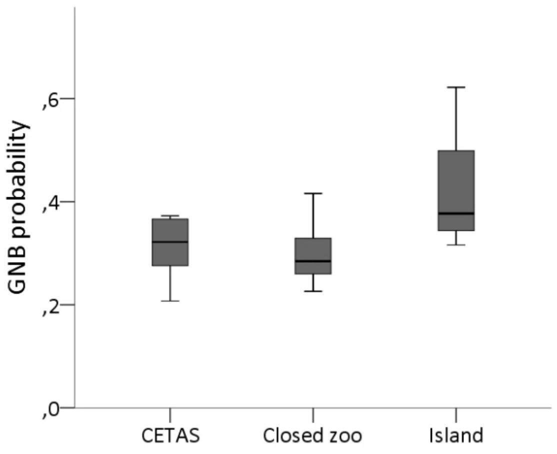

Figure 15. Differences in GNB occurrence probability across enclosures.

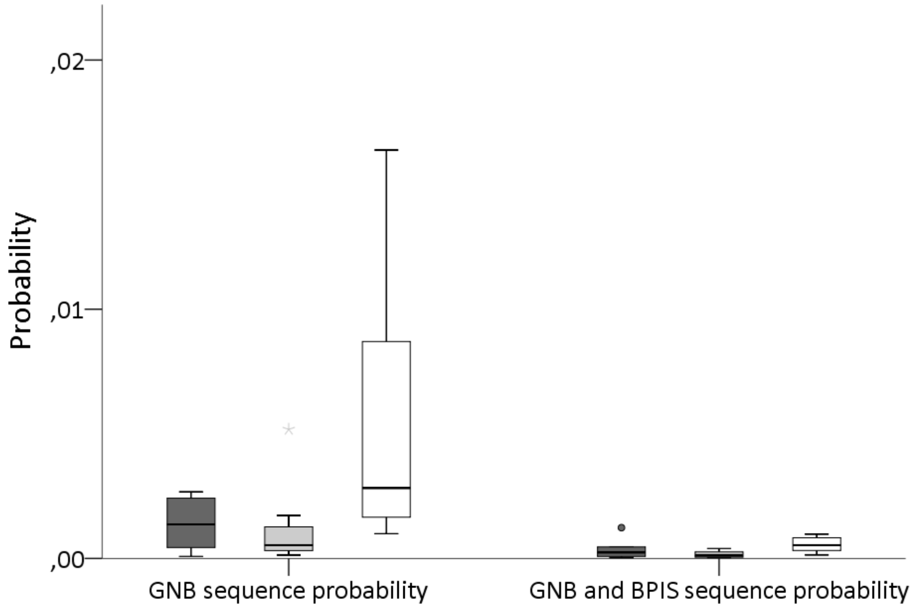

Figure 16. Differences in the probability of six step sequences of GNB and in the probability of sequences of five steps of GNB plus one BPIS, across enclosures.

Table 6. Markov chain's order (0, 1 and 2), per individual. Order is given by the BIC value calculated in R.

	Markov chain's order		
Individuals	**Order 0**	**Order 1**	**Order 2**
Amidala	1883,64	5515,34	48464,41
Baba	1737,26	4411,77	33019,59
Barbudo	1799,20	3503,75	21816,79
Cabeluda	2210,12	5503,30	48358,81
Careca	2231,72	8301,36	95299,02
Carlinhos	2140,97	4461,89	32960,94
Chato	1749,24	4289,12	32999,75
Dark	1965,63	3669,61	21853,58
Ester	4407,86	7480,89	50126,94
Ewok	1231,57	2436,34	13644,62
Golias	4164,20	5122,45	23236,69
Hulk	4277,99	8319,45	70156,42
Lango	1580,47	3258,41	21632,37
Leia	2206,86	10128,74	129214,06
Lisa	1790,03	4446,05	33128,30
Lula	4594,06	7719,15	50318,63
Pelado	1775,29	2405,33	8679,39
Preta	1843,28	3504,16	21822,95
Queen	4277,99	8319,45	70156,42
Rufio	1936,45	5516,58	48369,39
Ruiva	2113,95	6690,39	68695,93
Soleil	5010,78	7885,08	50401,51
Tolo	1862,10	2845,11	13970,05
Vesgo	1700,80	3495,88	21805,57
Wolverine	1921,38	4383,80	33033,24
Yoda	1883,64	5515,34	48464,41

Individuals exhibited a mean of 10 significative behavioural transitions, three of them including at least one BPIS. There were no sex differences either in number or in probability of significant transitions. Species and enclosure type presented similar patterns with animals in less enriched enclosures (CETAS and Zoo) presenting more significant transitions involving at least one BPIS than capuchin monkeys in island (U= 8.7, p = 0.012; U= 7.5, p = 0.023, respectively) (fig. 17).

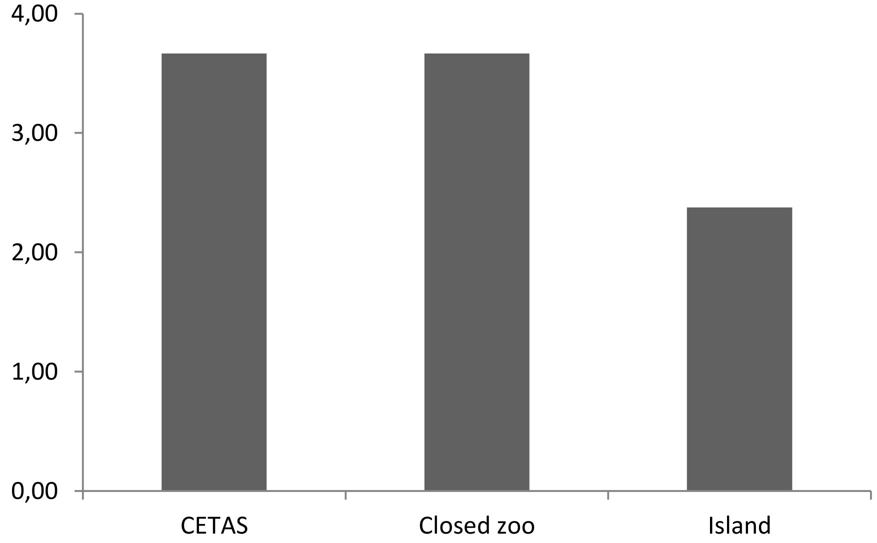

Figure17. N significant transitions involving at least one BPIS

Social Network Analyses

Figure 19 summarises the network of all behaviours after analysing the matrix of behavioural transitions of all individuals summed. It is possible to see that the more frequent behavioural transitions are among the GNBs VI-LO-EG-EX. Also involved in frequent behavioural transitions are the GNBs SP and IN and the BPIS SD and PA. As expected, the most frequent GNB also exhibit great centrality, and BPIS tend to be peripheral, relative to GNB given its low occurrence.

In table 7 it is possible to see that 14 other behaviours reaches and 13 other behaviours departs from Self-direct node. Similar values are found to Pacing node. These two nodes exhibit high betweenness. This indicates that they are embededed in more behavioural sequences than the other BPIS. Active stereotypies and Ingestion although reached and followed by large number of nodes do no exhibit great centrality, indicating that not many behavioural sequences pass through these behaviours. Crouching and Sexual displays appear as ending or starting points of sequences, but are not central or included in many sequences.

Table 7. Indegree, outdegree and betweenness per BPIS.

BPIS	**Indegree**	**Outdegree**	**betweeness**
Body Rocking	3	4	0
Sexual Display	6	6	0
Active I	7	9	1.778
Ingestion	9	10	1.151
Own-stereotypy	10	9	1.071
Pacing	13	13	8.225
Self-directed	14	13	7.615

No sex differences were found for proeminence indexes of BPIS (tabel 5). Both species and enclosure type had significant influence, with species differing in PA_{in}, PA_{out}, PA_{bet}, AC_{out} and AC_{bet}. Enclosure size influenced PA_{in}, IG_{in}, PA_{out}, AC_{in}, AC_{out}, AC_{bet}, and SD_{bet}. These measures of proeminence of BPIS were higher in less enriched enclosures, with especially higher values in CETAS’ enclosures (see fig 18). It is noteworthy that although Active BPIS are not much proeminent in general (see table above), they become significantly more proeminent in poor environmental conditions.

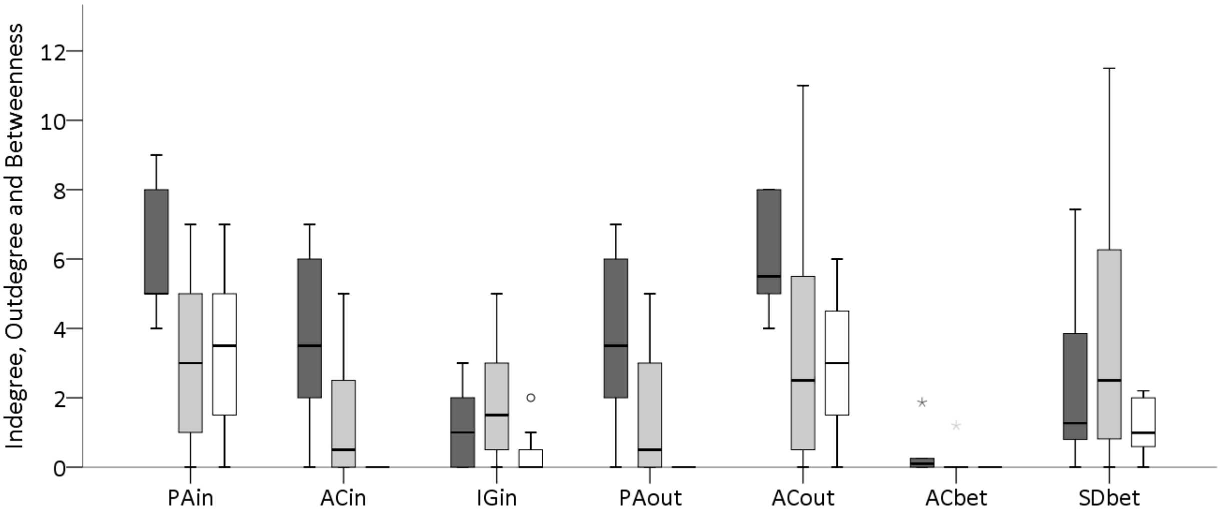

Figure 18. Significant BPIS that presented differences in indegree, outdegree and betweeness. PA: pacing; AC: active I; IG: ingestion; SD: self-directed. In, out and bet: indegree, outdegree and betweeness, respectively.

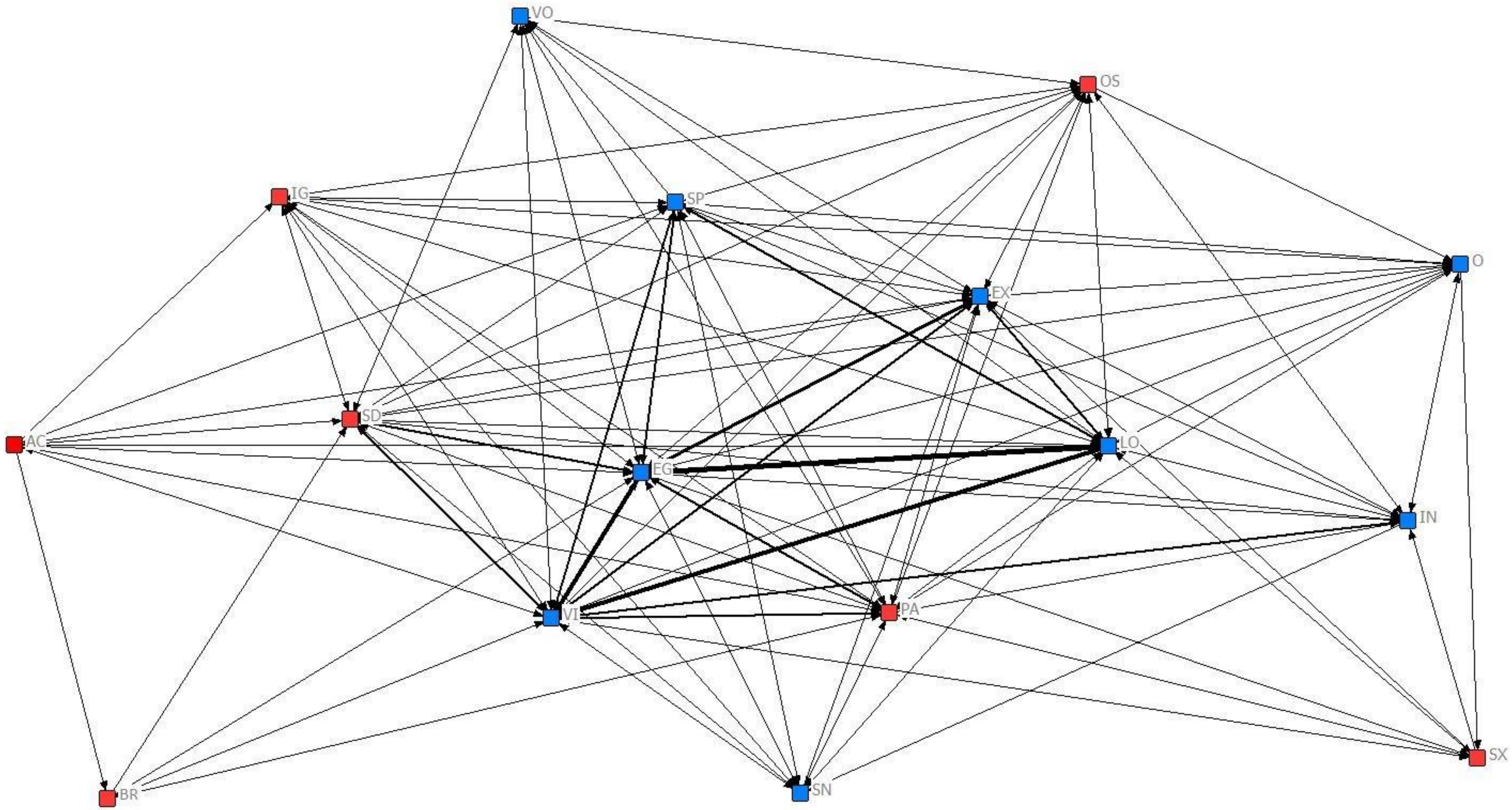

Figure 19. Social network analyses for total transitional matrix (n = 26). Blue nodes: GNB; red nodes: BPIS. Arrows point to the direction of the connection between behaviours. Blue nodes: EG: energy gain; EX: exploratory; LO: locomotion; SP: social positive activities; SN; social negative activities; VI: vigilance; IN: inactivity; VO: vocalization; O: others. Red nodes: PA: pacing; SD: self-directed; OS: own-stereotypy; IG: ingestion; AC I: active I; SX: sexual-display; BR: body rocking.

Discussion

In this manuscript we employed a battery of methods to analyse the behavioural pattern of 26 capuchin monkeys kept captive in social groups at rescue centres and at a Zoo. We: *i.* calculated basic Activity Budget proportions and frequency rates, diversity and prevalence indexes; *ii.* modelled order-dependency and probabilities of transitions in Markov chain analyses, using a script written in R (appendix B); *iii.* counted the number and probability of significant transitions offered by the Ethoseq Software; *iv.* analysed the network formed by the transitions between behaviours. It is important to remember that all these indices tend to be intercorrelated, for they come from the same data base. Thus, one behaviour that occurs at higher rates, will also tend to be more probable and central. The comparison, therefore, is on whether these analyses do offer a congruent and more detailed picture of the phenomena in focus (i.e. the behaviour profile of adult captive capuchin monkeys). Based on current literature we expected minor sex or species differences and major discrepancies in BPIS indexes between enclosures.

Similar to descriptions of other captive capuchin groups and different from wild groups vigilance composed large proportion of the individuals' activity budget (20%). Locomotion (15%) and exploration (10%) times were also lower than that exhibited by wild groups (see table 8 in Verderane, 2010). That is, animals are trading locomotion and exploration time to vigilance.

More than one tenth (10%) of individuals' activity budget was composed by BPIS. This is the same percentage of that described to zoo captive *S. apella* groups (Mendonça-Furtado, 2006). It is lower than that described by Boinsky (1999a) to single housed capuchins (54%) and lower than the described by Ferreira et al. (2016) for CETAS captive capuchins (17%).

BPIS occurred at a frequency of 5,7 events per hour, and individuals exhibited a mean of 5 different BPIS. These values are different from that found by Ferreira et al (2016) that found a frequency of 27 events per hour, but a mean diversity of 3 BPIS. Although the data collection on *S. libidinosus* group was conducted in the same CETAS as that studied by Ferreira et al. (2016), the group studied in this research was in a new area, without visual or vocal contact to other capuchin groups in adjacent cages.

Pacing and self-directed were the two most common BPIS occurring about 5% of time each, and at a frequency of 16 and 13 bouts per hour, respectively. They were followed by Ingestion of urine, faeces and sperm, and active I (head-twirl and pirouette), occurring at 2% and 1% of registers and at a frequency of 1.88 and 2,36 bouts per minute respectively.

In accordance to our predictions we found no major sex differences, but females tend to exhibit active I stereotypies (head-twirl and pirouette) at higher proportions than males.

Testing species differences was hindered by the fact that we did not have all species *vs* enclosures combinations possible. After removing those indexes explained by both enclosure and species, species alone differ in time inactive (higher *S. xanthosternos*), and body-rocking was observed only in *S. flavius*.

Analyses of Activity budget reveal that enclosure size impacts on time spent in 4 out of 9 GNB macro-categories, and 2 out of 10 BPIS macro-categories, with animals kept in an island exhibiting more energy gain, and animals caged at the zoo and CETAS exhibiting more exploration, vigilance, locomotion, sexual-display to humans and Ingestion.

The activity budget or frequency analyses could not detect differences in the two most frequent BPIS. One possibility is that Pacing and Self-direct are such two basic modes to cope with stress that are exhibited by all individuals of any species (and this could include species from other taxa) that the scale differences in enclosure sizes (from larger $100m^3$ to smaller $25m^3$) are not big enough to relief some animals and hence produce an detectable difference. López & Tárano, 2008, studying three *Cebus olivaceous* groups, found no exhibition of BPIS in the groups occupying larger areas (the smallest area had 7 ha).

Another possibility is that activity budget and frequency analyses, although easy to conduct at large scale, are not refined enough to detect differences in individuals behavioural profile. The fact that pacing correlated negatively to exploration and locomotion, self-directed correlated negatively to energy gain, while active I correlated negatively to energy gain, social positive, inactivity and vocalization indicated the existence of a trade-off between some BPIS and some GNB that need to be further explored.

GLM analyses could detect differences in diversity index in accordance with our predictions. That is, the diversity of BPIS did not differ between sexes or species, however, animals kept in smaller-less enriched areas exhibited a more diverse repertoire of BPIS.

Contrary to our predictions, Markov Chain analyses offered zero-order dependency as the most parsimonious model (based on BIC values) for all individuals, except one. This result stands against the definition of stereotypy as a repetitive behaviour. One possible explanation is that the input sample size (number of observations per animal) relative to number of categories (behaviours) analysed is small. It is known that Markov Chains analyses as a data-mining procedure is time consuming and that it requires large input size (i.e. many sequences- Asher et al 2009). The algorithm we designed to calculate order adjustment imposes the Bayesian Information Criterion, that powers the probable sequences by the number of categories used. Lusseau (2003) inputed 1297 registers of 5 macro-categories of dolphin behaviour and could detect a first-order dependency between behaviours sparsed by 15 min long. We used a total of 16 macro-categories for the Markov chain analyses (9 GNB and 7 BPIS), inputting 833 transitions of behaviours registered at 30 sec interval. While this number is more than enough for statistics of activity budget analyses, this may not be sufficient for Markov detecting higher order dependency. Nevertheless, Markov chain analyses did detect first order dependency in the behaviour of one animal, the female Queen, a bearded capuchin (*S. libidinosus*) kept at CETAS. The predominant behaviour of this female was an own stereotypy of faeces painting. In this sense, the Markov chain analyses could offer an index (the order of dependency) for an animal with repetitive behaviour and, therefore, can be a useful tool for analysing BPIS.

We found no significant differences in the probability of six consecutive BPIS between sex, species or enclosures. This lack of difference speaks against the model of stereotypies as mantra, in which individuals would use BPIS repetition as a calming effect. However, as for Markov Chain analyses, it is possible that repetition occurs at intervals shorter than 10 sec. Further analyses can be conducted by filtering the input matrix to test such possibility. Concurrently, the probability of a capuchin monkey to remain for six consecutive registers in a Genus Normative Behaviour was significantly higher for animals in islands than for animals in other enclosure types. This result agrees with our predictions and calls attention for the importance to study positive signs of welfare

Analyses of the most probable transitions are also in accordance to predictions, with results indicating lack of sex and species differences. Although not more probable, there was a significant increase in number of behavioural transitions involving BPIS, tat was exhibited by animals in worse enclosure conditions. This corroborates the models indicting that stress creates "noise" in the inner coordination and regularity of species-specific repertoire (Escós et al., 1995; Reznikova et al., 2012).

The graph offered by the social network analyses, show that the organization of behaviours of captive capuchins runs along the Energy Gain, Vigilance, Locomotion key elements, with less transitions to SP and IN. BPIS had low betweenness and moderate in and out degree. In conjunct these indexes pictures BPIS as dead ends of sequences, not as hubs or key elements.

No significant sex differences were found for the proeminence indexes of the behaviours. Five species differences and six enclosure type differences in proeminence indexes were detected. After excluding sobrepositions, pacing was more proeminent for the blonde capuchin monkeys than for other species. Significant differences in prominence values of BPIS, according to enclosure type, were found for Active I, Pacing and Self-directed. For individuals kept in CETAS these behaviours were more proeminent in the network of behavioural transitions. That is they were preceded as well as followed by a larger number of different behaviours, and they become more embedded in the behavioural transitions of animals. This agrees with the previous finding of more noise being embedded in the behavioural transitions of animals in worse environmental conditions. This impact of BPIS in the organization of behaviour pattern was not detected. The activity budget or frequency analyses did not find differences in enclosure type for these BPIS.

At a distal level, welfare means fitness or number of decedents. At proximal level, it is to keep the allostatic load at minimum (McEwen & Wingfield, 2010; Wingfield, 2005, 2013). At behavioural level, measuring welfare has some difficulties for data collection of large data sample and proper analyses methods. In a scientific scenario in which flexibility and plasticity of behaviour comes to the focus of interest (Sih, Bell, & Johnson, 2004), speak of a Genus Typical Behaviour of a known flexible species, such as capuchin monkeys, is risky, let alone speak of “abnormal” behaviours.

We offered a list of Behaviour Potentially Indicative of Stress and we scrutinize the data using four different types of analyses. Our results show that: *i.* individuals in islands spend more time in Energy gain, while capuchin monkeys in smaller enclosures spend more time in exploration, vigilance and locomotion; *ii.* BPIS was more diverse in the repertoire of animals kept in smaller enclosures; *iii.* The three most common BPIS (pacing self-direct and Head-twirl/pirouette) negatively correlated to energy gain, social positive, exploration, locomotion and inactivity patterns; *iv.* we could not find increased dependency in the transitions between behaviours at 30 sec intervals (zero-order in Markov chain analyses), which stands against the idea of stereotypies as repetition with mantra effects. However, this method could detect a higher order (first-order) in the most stereotyped individual, offering an index to measure the repeatability of behavioural categories; *iv.* probability of staying six registers in a GNB sequence was higher in animals in islands; *v.* number of most probable behavioural transitions including at least one BPIS was higher in smaller enclosures; *vi.* proeminence indexes of three BPIS (pacing, self-direct, active I) were higher in smaller enclosures. Overall this supports the list presented at table 3 as a list of Behaviour employed by capuchin monkeys as strategies to cope with the stress in captivity. These data are also more supportive of BPIS as activities that disrupts organization of behaviours and compromise optimal activity budget.

As well pointed by Tárano et al. 2015 in their study on BPIS of captive *Cebus capucinus*, due to hypothesis-testing research interest, behavioural catalogues and basic data collection protocols tend not to be published. However, they are crucial to further test behavioural and evolutionary hypothesis. Scientifically grounded and statistically correct protocol permits comparability of results and meta-analyses from whatever theoretical perspective interpretation it may receive.

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Chapter 2: Individual Differences in Stress Coping Strategies in Captive Capuchin Monkeys (*Sapajus* spp.)

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Abstract: In the study of animal behaviour analyses are revealing multimodal distributions, in which different behavioural strategies can be distinguished within the same species or population. Studies on welfare and management of captive animals are showing that individuals differ in susceptibility to pathologies, resilience and disease progression. The term coping styles refers to the way individuals react and adapt to stressful environment and two major strategies are described: proactive and reactive. In this work we explore individual differences in the exhibition of Behaviours Potentially Indicative of Stress (BPIS) (e.g. pacing, head-twirl) of captive capuchin monkeys (*Sapajus* spp.). We studied 26 individuals: 6 *Sapajus libidinosus*, maintained in 24 m3 non-enriched enclosures (CETAS, Natal – RN- Brazil), 7 *S. flavius*, maintained in enriched enclosures of approximately 120 m3 (Zoo of Salvador – BA) and 13 *S. xanthosternos*, held in an enriched enclosure of approximately 120 m3 and on an island of approximately 100 m2 (Salvador Zoo). Every 10 sec, during 10 min of focal animal sampling, we registered the behaviours according to an ethogram of 9 macro-behavioural categories and 10 BPIS. We explored four type of analysis: Activity Budget, Diversity indexes, Markov chains and Sequence analyses. We classified individuals as bold/shy according to their standardized z-score and group them through a Hierarchical Cluster Analysis, in three axes of exploratory related behaviours. The exploratory analyses were then compared across classifications and groups. Classification and group analyses pointed to the differences: Bold/group3 presented higher levels of pacing, self-directed and active I BPIS while Shy/group1 individuals presented higher diversity of BPIS and a high probability of sequences containing BPIS. Overall, the results are suggestive of two broad stress coping strategies, similar to the bold/proactive in which some individual react by trying to change or scape from environment and other by hiding.

Key-words: coping strategies, individual differences, welfare, behavioural sequence

Introduction

In the study of animal behaviour is it shown that, beyond a Gaussian distribution, where the mean reflects a supposed optimal behavioural pattern, analyses are revealing multimodal distributions, in which different behavioural strategies can be distinguished within the same species or population. Bell (2007) and Sih et al., (2004) define behavioural types as differences in the behaviour pattern between individuals of a population that are kept in different contexts and/or time. Behavioural syndromes are defined as correlations between behaviours that are presented in different contexts. Thus, for example, an individual classified as explorer/proactive presents a low latency to leave the refuge, to get closer to an object, or to explore a new environment or social partner. This explorative behaviour will be part of a syndrome if it is detected that explorers also tend to be more aggressive in different contexts. A behavioural syndrome consisting of low-latency to explore, high aggression, low parental care, low reactivity to environmental stimuli and formation of behavioural routines seems evident in different species (Sloan Wilson, Clark, Coleman, & Dearstyne, 1994; Wolf, van Doorn, & Weissing, 2008)

In a proximal level the different behavioural types are attributed to different causes: different genetic makeup, parasite load, immune system, metabolic rate, ontogenetic or developmental plasticity during environment change (Snell-Rood, 2013), and different social context (Biro & Stamps, 2010; Careau, Thomas, Humphries, & Réale, 2008). At a functional level, these different behavioural syndromes are maintained by frequency-dependent selection (in environments ruled by economies of dispersion) and/or by efficiency in cooperative groups with complementary skills ("skill pool" in environments ruled by economies of aggregation - Giraldeau & Caraco, 2000). For example, the literature indicates that a syndrome of high exploiration/aggression can be most effective in situations of high environmental stability, while animals with the reverse syndrome, low exploration/aggression, can be more effective in situations of migration or formation of new groups, due to being individuals less prone to conflict. There occurs an evolutionary feed-back loop, in which spatial and temporal fluctuations in the environment occupied by the population would explain the maintenance of different behavioural syndromes, and this variability would maintain population protected from environmental fluctuations (Dall, Houston, & McNamara, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

Studies on welfare and management of animals in captivity are showing that individuals differ in susceptibility to pathologies, resilience and disease progression (e.g. Cavigelli, 2005). The concept of coping style has been widely discussed by Koolhaas et al., (1999). Coping styles refers to the way individuals react and adapt to stressful environment and hence its vulnerability to stress-related illnesses. According to the authors a coping style could be defined as "*a coherent set of behavioural and physiological stress responses that would be consistent over time and that would be characteristic of certain groups of individuals*" (p. 925). This paper cites several studies with different species (poultry, pigs and rats) suggesting that proactive individuals (or explorers) when subjected to stress has lower activation on the hypothalamus-pituitary-adrenal (HPA) axis (low cortisol response) but high in sympathetic response (high levels of catecholamine). The animals reactive (non-exploitative) has a way of dealing with stress by increasing the activity of the HPA axis and high parasympathetic reactivity. Different styles of coping with stress result in different responses to acute stress and to different pathologies when under chronic stress. The pro-active animals seem to be more susceptible to developing hypertension, arteriosclerosis, tachyarrhythmia, ulcer formation and presentation of stereotypic behaviours when in stress situation. The more reactive animals react by freezing, and are more susceptible to depression and bradycardia.

The theoretical framework defines that an individual is in stress (or its welfare is under threat) when the behavioural or physiological mechanisms to deal with environmental stimuli to maintain homeostasis are not effective or are being demanded with high frequency (Honess & Marin, 2006; McEwen & Wingfield, 2010). Koohlaas et al (1999) point out that "*it is not the physical characteristics of a certain aversive stimulus but rather the cognitive evaluation of stimuli that determine their character of aversive and if a state termed as stress is induced*" (p.927). Coleman (2012), for example, argues that environmental enrichment, seen as an important factor to improve the welfare of captive animals, is actually perceived as aversive by less explorers/reactive individuals. Considering this, Novak & Suomi (1988) argue that it its improbable that one general diagnostic for welfare and general descriptions to improve welfare can be applicable to all individuals of a species, let alone to all species. This is because individual differences in coping strategies results in different exhibitions of behaviours potentially indicative of stress (BPIS). That is, the behaviour would not indicate the same inner state for different individuals.

Despite the difficulties mentioned above, it is widely documented that stereotyped behaviours represent a cost to the animal, and that these behaviours are related to poor environmental condition, frustration, relate to low immunity and reproduction, and that frequency of stereotypies is diminished when the environmental condition of the animal is improved (Broom, 1991; Dawkins, 1990; G. J. Mason, 1991). In general, the more different the number of stereotypies, the worst the condition of the animal's welfare (Barnett & Hemsworth, 1990). Uher, 2011 points out that a major challenge in behavioural studies is to explore systematically and empirically whether, how and under what conditions, individual differences are indeed significant. The author argues that it is necessary to measure and compare the variance within and between individuals. In both cases (validation of different indicators, and comparing the intra and inter-individual) a high *n* sample needs to be available, preferably under the same environmental conditions. In this context, it is noteworthy that in a review of the published work on behavioural syndromes in animals, Gosling & John (1999) detected only 19 articles with a sample presenting more than 20 individuals. Throughout this decade, studies with a sample greater than 20 are still scarce, mainly in primates.

For primates, studies are showing that individual differences co-vary in behavioural and physiological indexes. Reimers, Schwarzenberger, & Preuschoft, (2007 found that less exploratory chimps (as measured by novel object tests) reacted to the acute stress of moving to novel environments (social and physical) with increased immobility than more exploratory chimps. Capitanio (2011) found that low socially (LS) motivated rhesus monkeys have a more passive strategy for coping with social stress in unstable social conditions, by presenting more submissive displays and sit-stare reactions than high socially (HS) motivated animals, which react by moving-out movements and grimaces. Sapolsky and Rey (1989) showed three dominance and subordinate styles in wild male baboons that translate into different coping strategies in socially derived stressful situations: animals that buffer stress by having friendship to females, those that form friendship to males, and those that react aggressively (Abbott et al., 2003; Sapolsky & Ray, 1989; Virgin & Sapolsky, 1997). For New World monkeys Galvão-Coelho, Silva, Leão, & de Sousa (2008) identified three strategies to cope with induced social separation in captive common marmosets (*Callithrix jacchus*): scent marking (made via genital rubbing in surfaces), pacing and piloerection. Taylor, Mustoe, & French (2014) showed that, in marmosets (*Callithrix geoffroy*), different behaviours relate to moderate acute stressors during development, with alarm calls relating to increased cortisol in young animals, while in adults motor activity and cage manipulations were associated to poorer cortisol regulation.

Presenting high neocortical ratio and exhibiting behaviours considered complex (such as use of instruments, coalitions, inequality aversion, behavioural traditions and prosociality) these 4,5kg neotropical primates are the focus of several studies in the areas of Cognition, Psychology and Comparative Evolutionary Anthropology. The socio-ecological characteristics of the clade, such as manipulative foraging, large home range, and large and complex social groups, prone these animals to increased stereotypies (Gosling, 2001; Abbott et al., 2003, Pomerantz et al. 2013).

Previous studies show that capuchin monkeys exhibit varied behaviours potentially indicative of stress (BPIS), ranging from 54% of activity budget in single housed animals, to 10%-17% in group housed animals (Olivia-Mendonça, 2006, Rimpley & Buchannan-Smith, 2012; Pomerantz et al 2012). Studies indicate lack or very small sexual differences in BPIS exhibition in capuchins (Mendonça-Furtado, 2006; Polizzi di Sorrentino et al., 2012).

Three recent studies indicate the existence of individual differences in wild (Manson & Perry, 2013) and captive capuchins (Morton et al., 2013; Uher, 2011). Two studies (Mason & Perry, 2013, Morton et al, 2013) used Principal Component Analyses of observers rates in questionnaires constructs, while the third study (Uher et al, 2013) used rates of behaviour to infer and distinguish the capuchins individual differences. Of the over 20 constructs measured, sex differences were found, with males being more aggressive, dominant, and neurotic while females were more social.

In a recent study Ferreira et al. (2016) explored the occurrence Behaviour Potentially Indicative of Stress (BPIS) in a sample of 123 bearded capuchin monkeys kept at wildlife rescue centres. The Principal Component Analyses indicates the existence of five different factors: Pacing, Self-direct, Active (head-twirl and pirouette); Masturbation-scream, and Sexual display to humans. The authors highlight that the two most common factors (Pacing and Self-direct) resemble the two basic coping strategies described for several animals (proactive and reactive).

In this work we explore individual differences in the exhibition of BPIS of 26 captive capuchin monkeys (*Sapajus spp*). Specifically we will test whether differences in Genus Normative Behaviours (GNB) explain differences in nine indexes of BPIS: 1. time allocation, 2. frequency, 3. diversity, 4. probability of behavioural transitions involving a BPIS, 5. number of significant transitions involving a BPIS, 6. probability of significant transitions involving a BPIS, 7. indegree, 8. outdegree and 9. betweeness values of BPIS.

Methods

The study animals, site, methods for data collection and analyses are described in the previous chapter.

Individual Differences Scores

In order to identify individual differences in Genus Normative Behaviours we used the framework suggested by Réale et al. (2007). The author proposed five axes to evaluate individual differences: 1- shy/bold correspond to the pattern of reaction in front of risky situations/stimuli; 2- exploration/avoidance, refers to the pattern of reaction to new situations, including objects, food and habitats; 3- general level of activity; 4- aggression towards conspecifics; 5- sociability.

Here we will use the axis 3, general level of activity, based on their exhibition of Exploration, Locomotion and Inactivity pattern. We calculated the Z-score for each individual using the following formula

$$Z = \frac{x - \mu}{\sigma}$$

Where Z is the standardized score for an individual; x is the proportion of registers that individual exhibited a behaviour (locomotion, exploration, or inactivity); μ is the mean value of the proportions of registers exhibited by all animals in the sample; and σ is the standard deviation of the values in the sample.

So a z-score indicates how many standard deviations an individual is above or below the mean of the population.

We employed two different methods to classify animals. Firstly we simply attributed a code to individuals based on z-score values: Bold1 to those individuals values ranging from 0 to 1 at exploration and locomotion axis; Shy1 to those individuals values ranging from 0 to -1 at exploration and locomotion axis; Bold2 and Shy2 to those individuals exhibiting z-score values above +1 or below -1, respectively. We reversed the z-values for the Inactivity axis. Thus, Bold 1 are those that have z-scores values ranging from 0 and -1 at the inactivity axis; Shy 1 are those that have z-scores values ranging from 0 and +1 at the inactivity axis; Bold 2 and Shy 2 to those individuals exhibiting z-score values above -1 or below +1, respectively.

The second method of classification was through a Hierarchical Cluster Analysis asking to group individuals by the squared Euclidean distance to centroid along each of the axes (exploration, locomotion and inactivity). Thus, in total, each individual received six tags: three derived from z-scores and three derived from cluster analyses.

From these classifications we conducted non-parametric Kruskall-Wallis and Mann-Whitney analyses to test differences in the exhibition of the 9 indexes of occurrence of BPIS. Significance values was set to $\alpha \leq 0,05$ and a tendency was accepted at $\alpha \leq 0,1$. Analyses were run using SPSS 21, SocProg, Netdraw, Ethoseq softwares and an algorithm in R to detect Markov Chain analyses.

Results

Individual Differences Based on a priori Classification

As expected from a normal distribution, Bold 1 and Shy 1 type individuals composed the bulk of our sample (see table 1). However, there was no correlation between the classification scores among the three axis (EX-LO: $\rho = 0.258$, p= 0.203; EX-IN: $\rho = 0.215$, p= 0.291; LO-IN: $\rho = 0.121$, p= 0.557). One example of perfect concordance is Rufio that was classified as Bold1 along the three axes. An example of complete disagreement is Soleil, that was classified as Shy1 via exploration, Bold2 via Locomotion, and Bold1 via Inactivity axis.

Table 1. Individual's distribution (n = 26) across Bold/Shy type and Exploration, Locomotion and Inactivity axis.

	Axis		
	Exploration	**Locomotion**	**Inactivity**
Bold 2	4	4	0
Bold1	2	9	18
Shy1	18	11	6
Shy2	2	2	2

GLM analyses using the classification based on exploration axis indicates 4 significant differences, with Bold1 individuals exhibiting higher values of Sexual Display indegree and outdegree, and higher betweeness in body-rocking, while Shy2 individuals show higher probability of a sequence of six steps contain at least one BPIS (see table 2).

A similar pattern was found for the analyses of the Locomotion axis, with Shy2 individuals having higher probability of a six steps BPIS sequence, and an increased frequency of own-stereotypy.

Comparisons using the classification based on the Inactivity axis offered the largest number of significant differences (13 in total). Bold1 capuchins had higher values frequency of Active I BPIS, as well as indegree, outdegree, and betweeness, Shy1 capuchins had more significant transitions involving one BPIS, and Shy2 capuchins had increased number of significant transitions involving one BPIS, more diverse BPIS, higher indegree in Ingestion BPIS, and increased frequency, indegree, outdegree and betweeness of own-stereotypy.

Table 2. Differences between Bold/Shy types across Exploratory, Locomotion and Inactivity axis. Higher values are marked with *. SX: sexual-display; OS: own-stereotypy; AC: active I; IG: ingestion; in, out and bet: indegree, outdegree and betweeness, respectively.

		Bold 2	Bold 1	Shy 1	Shy 2	Statistics (χ2 and p values)
BOLD EX	SX$_{\text{in}}$	0	5^{*}	0,556	0	7,668; p =0,053
	SX$_{\text{out}}$	0	5^{*}	0,556	0	8,695; p = 0,034
	BR$_{\text{bet}}$	0	$0{,}2^{*}$	0	0	12,00; p = 0,007
	GNB and BPIS sequence probabilities	0,0001	0,0001	$0{,}0003^{*}$	0,001	7,692; p = 0,053
BOLD LO	BPIS prob.	0,039	0,051	0,076	$0{,}243^{*}$	7,00; p = 0,072
	BPIS sequences	0	0	0	$0{,}0003^{*}$	7,00; p = 0,072
	OS frequency	0	0	13,27	541^{*}	6,34; p = 0,096
SHY IN	Nº transitions to BPIS (Ethoseq)	0	3,39	2,5	$4{,}5^{*}$	5,56; p = 0,062
	Transitions to BPIS prob. (Ethoseq)	0	0,055	$0{,}06^{*}$	0	4,80; p = 0,90
	AC$_{\text{in}}$	0	$1{,}944^{*}$	0	1,5	5,025; p = 0,081
	IG$_{\text{in}}$	0	1,128	0,5	$3{,}5^{*}$	4,839, p = 0,089
	OS$_{\text{in}}$	0	0,389	0	$4{,}5^{*}$	5,90; p = 0,052
	AC$_{\text{out}}$	0	$1{,}944^{*}$	0	1,5	5,05; p = 0,80
	OS$_{\text{out}}$	0	0,389	0	$4{,}5^{*}$	5,90; p = 0,052
	OS$_{\text{bet}}$	0	0,2	0	$4{,}359^{*}$	5,90; p = 0,052
	OS activity budget	0	0,016	0	$0{,}046^{*}$	4,98; p = 0,083
	AC activity budget	0	$0{,}009^{*}$	0	0,007	4,99; p = 0,082
	Diversity	0	0,337	0,206	$0{,}412^{*}$	8,783; p = 0012
	OS frequency	0	60,167	0	73^{*}	4,98; p = 0,083
	AC frequency	0	$26{,}5^{*}$	0	10	7,48; p = 0,24

Individual Differences Based on Hierarchical Cluster

Clustering of individuals using the Exploration axis offered three clear groups and three individuals without clear cluster membership (Ester, Pelado and Rufio at fig. 1). The more active group with a mean rank of 24 is composed by three individuals

(Amidala, Tolo, Lula - see bottom cluster at fig. 1), the less explorative group with a mean rank of 4 is composed by seven individuals (cluster between Carlinhos and Hulk), and the medium explorative group composed by the top cluster presented at figure 1. For clarity we will name the most explorative animals as group 3, the medium as group 2 and the less explorative group as 1.

The clustering of individuals according to axis Locomotion offered three groups. The less active, with a mean rank of 1.5, formed by two individuals (Leia and Queen); The most active group, with a mean rank of 20, composed by 13 individuals, and a medium active group, formed by 11 animals (see fig. 2).

Again, the clustering along the inactivity axis offered three groups. One large group composed by 18 more active (or less inactive) individuals (mean rank = 9,5), and two other groups composed by less active (or more inactive) individuals (see fig. 3).

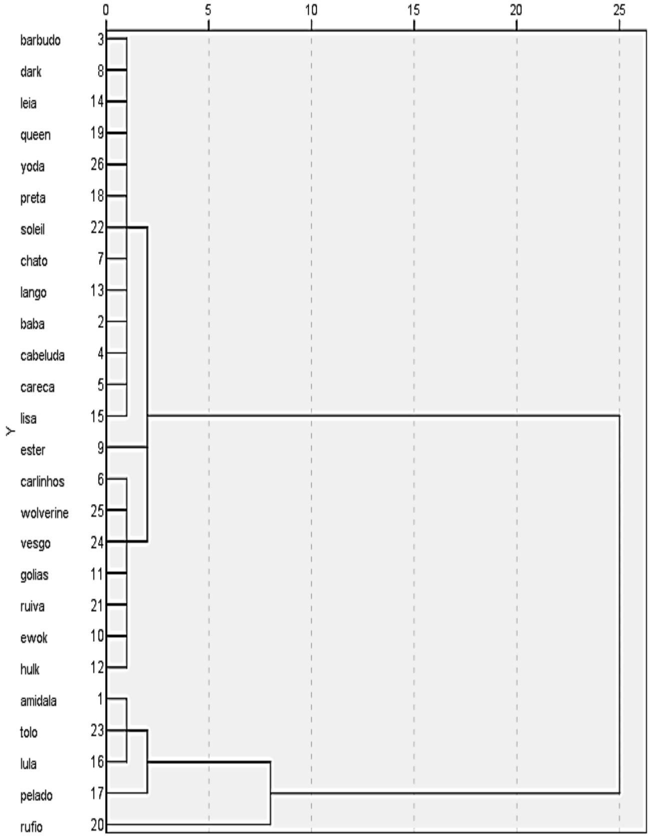

Figure 1. Dendrogram showing the clustering of individuals across Exploration axis.

Table 3. Mean rank of Exploration allocation time.

	boldcluster	N	Mean Rank
EX	1,00	7	4,00
	2,00	13	14,00
	3,00	3	24,00
	9,00	3	23,00
	Total	26	

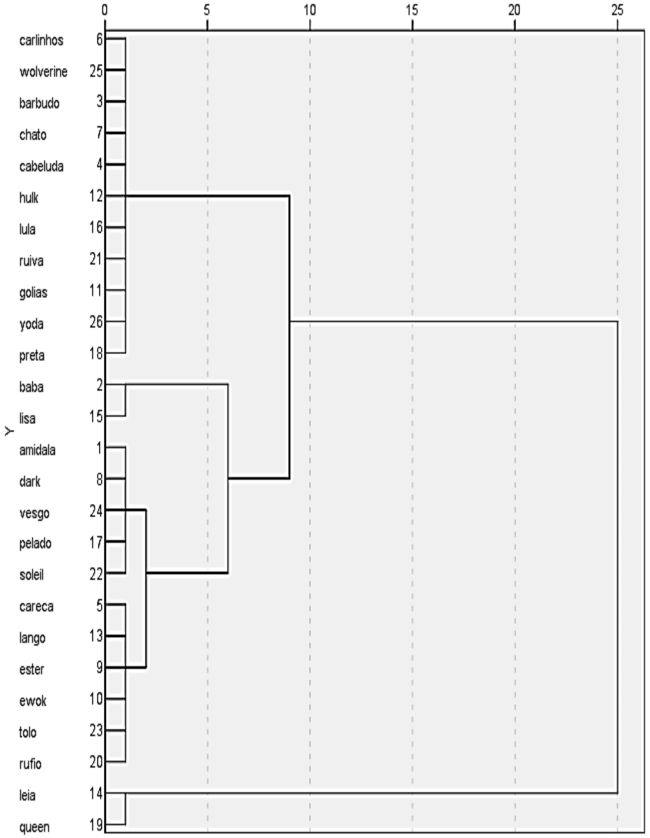

Figure 2. Dendrogram showing the clustering of individuals across Locomotion axis.

Table 4. Mean rank of Locomotion allocation time.

	boldcluster	N	Mean Rank
LO	1,00	2	1,50
	2,00	11	8,00
	3,00	13	20,00
	Total	26	

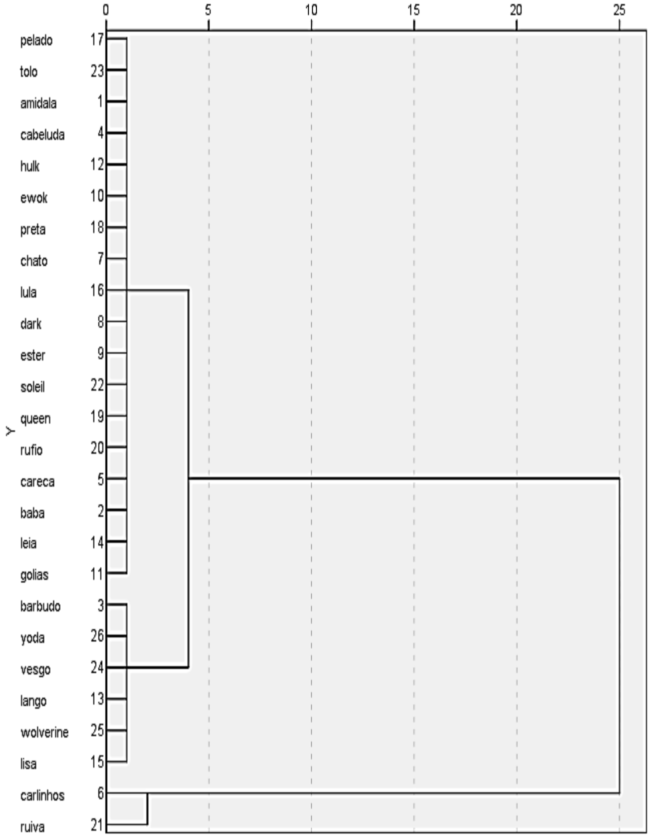

Figure 3. Dendrogram showing the clustering of individuals across Inactivity axis.

Table 5. Mean rank of Inactivity allocation time

	boldcluster	N	Mean Rank
IN	3,00	18	9,50
	2,00	6	21,50
	1,00	2	25,50
	Total	26	

There was a significant positive correlation between the classification of individuals along the axis Explorations and Inactivity (EX-IN: $\rho = 0.432$, $p= 0.018$), and a tendency for positive correlation between the classifications along the axis exploration and Locomotion (EX-LO: $\rho = 0{,}307$, $p = 0{,}090$). There was no significant correlation between Locomotion and Inactivity axis classifications (LO-IN: $\rho = 0{,}127$, $p = 0{,}50$). One example of disparity is the case of animal Golias, an adult *S. libidinosus* male kept at CETAS. He was classified as 1 along the exploration axis, as 2 along the locomotion axis and as 3 along the inactivity axis. An example of perfect concordance is Barbudo, *S. xanthosternos* adult male in island, that was classified as 2 along the three axis.

Comparing the three clusters formed by the Exploration axis, we found a tendency for differences in the time spent in BPIS active I (head twirl and pirouette) with most active individuals (group 3) allocating more time to this behaviour than other groups. Also a tendency for outdegree of this behaviour (AC_{out}) to be higher in group 3 (see table 6).

Comparing the three clusters formed by the Locomotion axis we found significant differences for probability of a sequence with six consecutive BPIS and Betweeness of pacing both higher in group 1. Tendencies to significance were found for frequency of sexual-display, pacing indegree and outdegree and own-sterotypy in and out degree, always group of animals with less locomotion showing lower values of sexual display but higher values of pacing and own-stereotypy proeminence values.

Comparing the three clusters formed by the Inactivity axis we found significant differences for the own-stereotypy indegree, outdegree and betweenness, with the group 1 that exhibit increased inactivity showing higher values in these indexes. There were also tendencies to significances to the following in the number and probability of significant transitions involving a BPIS in this group. Active I, indegree and outdegre, and Ingestion, indegree, values were higher for the group that exhibited lower levels of inactivity (group 3).

Table 6. Differences between groups based on hierarchical cluster analyses. PA. pacing; OS: own-stereotypy; SX: sexual-display; IG: ingestion. in, out and bet: indegree, outdegree and betweeness, respectively.

	1	**Statistics (χ2 and p values)**	**2**	**3**	**Statistics (χ2 and p values)**
EX				ACI activity budget	5,405; p = 0,067
				$\mathrm{AC}_{\mathrm{out}}$	4,77; p = 0,092
LO	BPIS sequences	6,539; p = 0,038		SX frequency	5,56; p = 0,062
	$\mathrm{PA}_{\mathrm{bet}}$	6,14; p = 0,046		$\mathrm{PA}_{\mathrm{in}}$	4,62; p = 0,099
	$\mathrm{OS}_{\mathrm{in}}$	5,49; p = 0,064		$\mathrm{PA}_{\mathrm{out}}$	4,90; p = 0,086
	$\mathrm{OS}_{\mathrm{out}}$	5,49; p = 0,064			
IN	Nº transitions to BPIS (Ethoseq)	5,49; p = 0,064		$\mathrm{AC}_{\mathrm{in}}$	5,02; p = 0,081
	Transitions to BPIS prob. (Ethoseq)	5,56; p = 0,062		$\mathrm{AC}_{\mathrm{out}}$	5,05; p =0,08
	$\mathrm{OS}_{\mathrm{in}}$	5,90; p = 0,052		$\mathrm{IG}_{\mathrm{in}}$	4,83; p= 0,089
	$\mathrm{OS}_{\mathrm{out}}$	5,90; p = 0,052			
	$\mathrm{OS}_{\mathrm{bet}}$	5,90; p = 0,052			

Discussion

In this manuscript we explored whether differences between individuals in the exhibition of Genus Normative Behaviour would match differences between individuals in the exhibitions of Behaviours Potentially Indicative of Stress. We grouped individuals according to differences in z-scores values along the Exploration, Locomotion and Inactivity axes, which we assume as representative of the General Level of Activity suggested by Réale et al (2007). Two grouping procedures were employed: an *a priori* classification into an ordinal scale of Bold 2, Bold 1, Shy 1, Shy 2; and a classification based on a hierarchical cluster analysis. As response variables we used nine indexes of BPIS: 1. time allocation, 2. frequency, 3. diversity, 4. probability of behavioural transitions involving a BPIS, 5. number of significant transitions involving a BPIS, 6. probability of significant transitions involving a BPIS, 7. indegree, 8. outdegree and 9. betweeness values of BPIS.

The *a priori* classification showed no inter-variable consistency, exhibiting non-significant correlations between the indexes values among the three axis. Classification via cluster analyses, on the other hand, exhibited correlation between the axis Exploration and Inactivity, but not with Locomotion. These discrepancies are similar to that found in other studies in behavioural syndromes. Gosling (2001) highlights two difficulties of using behavioural indicators to measure personality and psychopathology: reliability and validity. Validity is an index of how well the instrument is measuring what it proposes to measure. It refers to the correlations between indexes. Digman, (1990) , for example, showed that the correlation index of traits in male rat was r = 0.47, while in females was r = 0.27. Stamps & Groothuis (2010) note that scores that measure the same dimension (e.g. latency to explore the new environment or new object) are not always correlated, and that measures of reaction norms and behavioural response to stress are influenced by context of measurement. Uher et al (2013) in their study of personality in captive capuchins found low internal consistency (i.e non-significative correlations) between the behavioural indicators used to infer the same construct (although the authors found moderate to high test-retest reliability – see Uher et al, 2013 – table 3). Still, Stamps and Groothius (2010) suggest that individuals with median values have greater variance in measures of values than individuals who have had extreme values, and this is due to ceiling statistical effects.

Nevertheless, classifications were able to detect some differences between groups and patterns that are concordant. Bolder individuals tend to exhibit more proeminence in the BPIS sexual display and active I (head twirl and pirouette), while shier individuals had more diverse BPIS repertoire, tend to exhibit higher probability of staying six consecutive registers in a BPIS sequence, and show more own-stereotypy. This agrees with the pattern outlined by the cluster analyses with more exploratory capuchins (group 3) exhibiting increased values of proeminence in Pacing and Active I BPIS, and animals less active exhibiting increased probability in significant sequences involving at least one BPIS, and increased prominence in own stereotypy.

This picture, however, does not totally agree with descriptions of coping strategies Proactive and Reactive. The formation of behavioural routines is normally related to proactive animals. According to Ijichi and collaboratores (2013), in their attempt to cope with the stressor, proactive animals would become fixed in a behavioural sequence that would be self-rewarding in itself. Dutton (2008) cites that hipersexuality and inappropriate sexual behaviours (copulating attempts with objects) are observed in captive capuchin monkeys, however, the author does not offer rates of occurrence of this behaviour. The higher probability of sexual display/masturbation on the other hand agrees with descriptions that bolder animals are more sexually active The increased diversity of BPIS in shyer individuals is also in accordance with descriptions that for being reactive these individuals develop more diverse behavioural sequences (Koolhaas et al., 2008).

Pomerantz et al. (2012) defends that head twirl is a good indicator of welfare in capuchins for it correlated to cortisol level and pessimistic judgment in cognitive bias tests. As bolder and more exploratory individuals also tend to have higher levels of cortisol (Koolhaas et al., 1999 and 2008) the higher proeminence this behaviour in bolder/more exploratory individuals found in this work is suggestive that this is a stress coping strategy typical of some individuals.

In their discussion on use of behavioural indicators to infer personality in capuchin monkeys, Uher et al. (2013) reminds that captive settings may be so constraining that behavioural profiles converge to a mean where all individuals are demanded the most. This could be one possible explanation to the lack of significant differences between individuals in the two most common BPIS (pacing and self-directed). Hence, individual differences are noted only in secondary BPIS.

The measurement of any trait involves debates, and this is no different for personality, welfare and behavioural disorders (Uher, 2011). Koolhaas et al (1999) argue that a major difficulty for the study of behavioural syndromes is the choice of indicators for the assessment of behavioural traits of a syndrome. Cavigelli (2005) also argues that a difficulty for defining coping styles is to find a consistent set of answers. Nevertheless, the study of individual differences in stress coping strategies is of much theoretical and practical importance, At theoretical level these analyses help uncover the evolutionary origins of patterns of cope and resilience to environmental challenges (Sih, 2013). At practical level, it helps design management protocols. For example, according to McDougall, Réale, Sol, & Reader (2006) most active and exploring animals can be worse for maintenance in captivity but are better for re-introduction programs. Conversely, individuals less reactive and exploring individuals may be best to maintain in captivity and for reintroduction in areas that are already occupied, because these animals are more easily accepted in established groups.

Capuchin monkeys occupy diverse biomes, and they are known for their increased cognitive capacities and behavioural flexibility, with animals adjusting their dietary and social behaviour according to proximate factors. Gosling (2001, p 74) argues that more differentiated behavioural types and syndromes are expected to be found in species with greater diversity of social organization and that occupy a greater diversity of environments than those species that are less social and occupying less diverse environment. Mason et al (2013) suggest that species with increased behavioural plasticity would also fare better in human altered environments, here included captive settings. The analyses conducted in this work are suggestive, although not exhaustive, of a pattern similar to the bold/proactive and shy/reactive pattern. Whether these differences in behavioural coping strategies will protect animals from impacts of the rapid changes are conducting in the environment are open questions.

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Highlights

The analyses conducted in this study indicate that:

- Minor sex and species, and major enclosure type differences in total occurrence, frequency, diversity, probability and proeminence of BPIS in the behavioural profile of captive capuchin monkeys.
- The zero-order dependency between behavioural transitions and the lack of differences in the probability of six consecutive BPIS behaviours are not supportive of the definition of stereotypy as repetitive patterns.
- The increased number of transitions including at least one BPIS, and increased proeminence of BPIS in the behavioural network of individuals in less enriched environments conditions is supportive of the models of BPIS as “noise” elements that disrupts optimal behavioural sequences.
- results are suggestive of two broad stress coping strategies, a pattern similar to the bold/proactive and shy/reactive pattern: more exploratory capuchins exhibited increased values of proeminence in pacing, aberrant sexual-display and active I BPIS, while less active animals exhibited increased probability in significant sequences involving at least one BPIS, and increased prominence in own stereotypy.

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Appendix A: Exemple of behavioural data registry sheet.

		Individual 1	**Neighbour**	**Individual 2**	**Neighbour**	**Individual 3**	**Neighbour**
Date: ___/___/___ Time: Enclosure number: Observer:	**Name**						
	10''						
	20''						
	30''						
	40''						
	50''						
	1'						
	1' 10''						
	1' 20''						
	1' 30''						
	1' 40''						
	1' 50''						
	2'						
	2' 10''						
	2' 20''						
	2' 30''						
	2' 40''						
	2' 50''						
	3'						
	3' 10''						
	3' 20''						
	3' 30''						
	3' 40''						
	3' 50''						
	4'						
	4' 10''						
	4' 20''						
	4' 30''						
	4' 40''						
	4' 50''						
	5'						
	...						
	9'						
	9' 10''						
	9' 20''						
	9' 30''						
	9' 40''						
	9' 50''						
	10'						

Labels		**Code**	**Individual**
*****	Interaction	**E**	Estér
()	Interaction over 1 meter	**S**	Soleil
<	Grooming direction	**Q**	Queen
>	Grooming direction	**H**	Hulk
sol	Grooming solicitation	**L**	Lula

Appendix B: R input script for Markov Chain analyses

```
teste <- read.csv('ruiva.csv',header=T,sep=';')
teste2 <- na.omit( teste )
teste2$Sequencia <- as.character(teste2$Sequencia)
teste2$sequencia[teste2$Sequencia=="CO"]=1
teste2$sequencia[teste2$Sequencia=="BE"]=1
teste2$sequencia[teste2$Sequencia=="FO"]=1
teste2$sequencia[teste2$Sequencia=="MC"]=2
teste2$sequencia[teste2$Sequencia=="BS"]=2
teste2$sequencia[teste2$Sequencia=="MA"]=2
teste2$sequencia[teste2$Sequencia=="AG"]=3
teste2$sequencia[teste2$Sequencia=="AF"]=3
teste2$sequencia[teste2$Sequencia=="IA"]=3
teste2$sequencia[teste2$Sequencia=="OA"]=4
teste2$sequencia[teste2$Sequencia=="AH"]=4
teste2$sequencia[teste2$Sequencia=="CA"]=5
teste2$sequencia[teste2$Sequencia=="BO"]=5
teste2$sequencia[teste2$Sequencia=="CS"]=5
teste2$sequencia[teste2$Sequencia=="S"]=5
teste2$sequencia[teste2$Sequencia=="MN"]=5
teste2$sequencia[teste2$Sequencia=="IN"]=6
teste2$sequencia[teste2$Sequencia=="LO"]=7
teste2$sequencia[teste2$Sequencia=="VO"]=8
teste2$sequencia[teste2$Sequencia=="O"]=9
```

```
teste2$sequencia[teste2$Sequencia=="UE"]=9

teste2$sequencia[teste2$Sequencia=="LA"]=10

teste2$sequencia[teste2$Sequencia=="MP"]=11

teste2$sequencia[teste2$Sequencia=="ACA"]=12

teste2$sequencia[teste2$Sequencia=="CC"]=12

teste2$sequencia[teste2$Sequencia=="MO"]=12

teste2$sequencia[teste2$Sequencia=="EP"]=13

teste2$sequencia[teste2$Sequencia=="DS"]=14

teste2$sequencia[teste2$Sequencia=="MUR"]=15

teste2$sequencia[teste2$Sequencia=="MFE"]=15

teste2$sequencia[teste2$Sequencia=="MESP"]=15

teste2$sequencia[teste2$Sequencia=="REI"]=15

teste2$sequencia[teste2$Sequencia=="GC"]=16

teste2$sequencia[teste2$Sequencia=="PI"]=16
```

```
teste2$sequencia <- as.double(teste2$sequencia)

andre <- list()

a<-unique(teste2$Dia)

for(i in 1:length(a)) andre[[i]]<-(teste2$sequencia[teste2$Dia==a[i]])
```

```
aic<-c(0,0,0,0,0)
bic<-c(0,0,0,0,0)


ngrupos<-length(a)
N<-c(rep(0,16))


for(rep in 1:ngrupos){
    dimamostra<-length(andre[[rep]])
for (i in 1:16){
for (a in 1:(dimamostra)){
                        if (andre[[rep]][a]==i)
N[i]<-N[i]+1
                        }
                        }
                        }


#Este proximo procedimento retira os estados que não apareceram na amostra, pois teoricamente é como se eles não fizessem parte do espaço de estados da cadeia de Markov
vetor1<-c(NA)
j<-1
for(i in 1:16){
if (N[i]==0){
vetor1[j]<-i
```

```
j<-j+1

}

}

x<-1:16

x<-x[-vetor1]


nestados<-length(x)


save(x,nestados,file="estadosruiva.RData")


# Próximo passo cria matrizes de ordens superiores e transição para posteriormente
        calcular sequências de x passos


N<-c(rep(0,nestados))

n<-matrix(rep(0,(nestados*nestados)), nrow=nestados, byrow=TRUE)

h<-array(rep(0,(nestados*nestados*nestados)),dim=c(nestados,nestados,nestados))

P<-array(rep(0,(nestados^4)),dim=c(nestados,nestados,nestados,nestados))

U<-array(rep(0,(nestados^5)),dim=c(nestados,nestados,nestados,nestados,nestados))

dimamostra<-0

for(rep in 1:ngrupos){

        dimamostra<-length(andre[[rep]])

        A<-matrix(c(andre[[rep]]),ncol=1)

        a<-b<-c(0)

        a<-andre[[rep]][-dimamostra]

        b<-andre[[rep]][-1]
```

```
        B<-matrix(c(a,b),ncol=2)

        a<-b<-c<-c(0)

        a<-andre[[rep]][-c(dimamostra-1,dimamostra)]

        b<-andre[[rep]][-c(1,dimamostra)]

        c<-andre[[rep]][-c(1,2)]

        C<-matrix(c(a,b,c),ncol=3)

        a<-b<-c<-d<-c(0)

        a<-andre[[rep]][-c(dimamostra-2,dimamostra-1,dimamostra)]

        b<-andre[[rep]][-c(1,dimamostra-1,dimamostra)]

        c<-andre[[rep]][-c(1,2,dimamostra)]

        d<-andre[[rep]][-c(1,2,3)]

        D<-matrix(c(a,b,c,d),ncol=4)

        a<-b<-c<-d<-e<-c(0)

        a<-andre[[rep]][-c(dimamostra-3,dimamostra-2,dimamostra-1,dimamostra)]

        b<-andre[[rep]][-c(1,dimamostra-2,dimamostra-1,dimamostra)]

        c<-andre[[rep]][-c(1,2,dimamostra-1,dimamostra)]

        d<-andre[[rep]][-c(1,2,3,dimamostra)]

        e<-andre[[rep]][-c(1,2,3,4)]

        E<-matrix(c(a,b,c,d,e),ncol=5)

for (i in 1:nestados){

        A1<-matrix(c(rep(x[i],dimamostra)))

        result1<-apply(abs(A-A1),1,sum)

        N[i]<-N[i]+length(which(result1==0))

for (j in 1:nestados){
```

```
        B1<-matrix(c(rep(x[i],(dimamostra-1)),rep(x[j],(dimamostra-1))),ncol=2)

        result2<-apply(abs(B-B1),1,sum)

        n[i,j]<-n[i,j]+length(which(result2==0))

for (k in 1:nestados){

        C1<-matrix(c(rep(x[i],(dimamostra-2)),rep(x[j],(dimamostra-
        2)),rep(x[k],(dimamostra-2))),ncol=3)

        result3<-apply(abs(C-C1),1,sum)

        h[i,j,k]<-h[i,j,k]+length(which(result3==0))

for (p in 1:nestados){

        D1<-matrix(c(rep(x[i],(dimamostra-3)),rep(x[j],(dimamostra-
        3)),rep(x[k],(dimamostra-3)),rep(x[p],(dimamostra-3))),ncol=4)

        result4<-apply(abs(D-D1),1,sum)

        P[i,j,k,p]<-P[i,j,k,p]+length(which(result4==0))

        for (q in 1:nestados){

        E1<-matrix(c(rep(x[i],(dimamostra-4)),rep(x[j],(dimamostra-
        4)),rep(x[k],(dimamostra-4)),rep(x[p],(dimamostra-4)),rep(x[q],(dimamostra-
        4))),ncol=5)

        result5<-apply(abs(E-E1),1,sum)

        U[i,j,k,p,q]<-U[i,j,k,p,q]+length(which(result5==0))

}}}}}}


gamma<-function(n,nestados)

{

return((nestados-1)*nestados^n)

}
```

```
aic[1]<-0
for(i in 1:nestados){
        if(N[i]!=0){
aic[1]<- aic[1]+N[i]*log(N[i]/sum(N))
}
}
bic[1]<--2*aic[1]+gamma(0,nestados)*log(nestados)
aic[1]<--2*aic[1]+2*gamma(0,nestados)

aic[2]<-0
for(i in 1:nestados){
        for(j in 1:nestados){
            if(n[i,j]!=0){
aic[2]<-aic[2]+n[i,j]*log(n[i,j]/N[i])
            }
        }
}
bic[2]<--2*aic[2]+gamma(2,nestados)*log(nestados)
aic[2]<--2*aic[2]+2*gamma(2,nestados)

aic[3]<-0
for(i in 1:nestados){
        for(j in 1:nestados){
```

```
            for (k in 1:nestados){
                        if(h[i,j,k]!=0){
aic[3]<-aic[3]+h[i,j,k]*log(h[i,j,k]/n[i,j])
                        }
            }
        }
}
bic[3]<--2*aic[3]+gamma(3,nestados)*log(nestados)
aic[3]<--2*aic[3]+2*gamma(3,nestados)
aic[4]<-0
for(i in 1:nestados){
        for(j in 1:nestados){
            for (k in 1:nestados){
                                    for (p in 1:nestados){
                                                if(P[i,j,k,p]!=0){
aic[4]<-aic[4]+P[i,j,k,p]*log(P[i,j,k,p]/h[i,j,k])
                                                }
                                    }

            }
        }
}
bic[4]<--2*aic[4]+gamma(4,nestados)*log(nestados)
aic[4]<--2*aic[4]+2*gamma(4,nestados)
```

```
aic[5]<-0
for(i in 1:nestados){
        for(j in 1:nestados){
            for (k in 1:nestados){
                                    for (p in 1:nestados){
                                                for(q in 1:nestados){
                                                if(U[i,j,k,p,q]!=0){
aic[5]<-aic[5]+U[i,j,k,p,q]*log(U[i,j,k,p,q]/P[i,j,k,p])
                                                }
                                    }
                                    }


            }
        }
}
bic[5]<--2*aic[5]+gamma(5,nestados)*log(nestados)
aic[5]<--2*aic[5]+2*gamma(5,nestados)


save(N,n,h,P,U,file="matrizesruiva.RData")
save(aic,bic,file="aicbicruiva.RData")
```