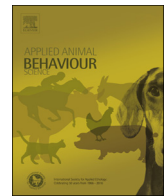




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## Hormonal correlates of behavioural profiles and coping strategies in captive capuchin monkeys (*Sapajus libidinosus*)

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## ABSTRACT

In this study, we tested the hypothesis that individual differences in behavioural profiles correlate to differences in stress-related behaviours and hormonal levels in captive brown capuchin monkeys (*Sapajus libidinosus*). Based on a sample of 25 animals, 143 h of behavioural data collection and 518 faecal samples, principal component analyses indicated the existence of four components that characterize the individuals' Genus Normative Behaviour (GNB) ( $KMO = 0.531$ ,  $X^2 = 127.672$ ,  $p < 0.001$ ): 'Feeding', 'Sociability', 'Exploration', and 'Activity'. Other four components are related to stress coping styles (based on Behaviour Potentially Indicative of Stress – BPIS) ( $KMO = 0.550$ ,  $X^2 = 329.303$ ,  $p < 0.001$ ): 'Self-directed', 'Restless', 'Ingestion/Self-Scratching', and 'Stereotyped'. More active individuals exhibit rapid stress-related behaviours ( $r = 0.443$ ;  $p = 0.044$ ) while less active individuals exhibit more stationary stress-related behaviours ( $r = -0.519$ ;  $p = 0.013$ ). Akaike information criteria indicated that the best linear regression model to predict the physiological profile (Faecal Glucocorticoid Metabolites - FGM) included three GNB and three BPIS components. 'Sociability' ( $p < 0.05$ ), 'Exploration' ( $p < 0.05$ ), and 'Ingestion/Self-scratching' ( $p < 0.05$ ) predicted lower FGM levels. 'Activity' ( $p < 0.05$ ), 'Self-directed' ( $p < 0.05$ ), and 'Stereotyped' ( $p < 0.05$ ) predicted higher FGM levels. 'Feeding' and 'Restless' factors were not included in the models. Our results support previous studies indicating that animals within the same population differ in the way they behave and react to stressful conditions, and these are correlated to different physiological profiles. Mapping inter-individual differences in stress coping strategies may help clarify the long-term reported incongruity between behavioural and physiological indicators of welfare in captive animals, supporting better management practices and assisting translational models of the development of psychopathologies.

### 1. Introduction

The search for non-invasive indicators of welfare in captive animals is fraught with controversial results, particularly regarding a common mismatch between the behavioural and physiological indices of stress in captive groups (Mason and Latham, 2004; Novak et al., 2013). Hormonal levels, for example, seem more appropriate to between-group than to within-group comparisons (Dawkins, 2003). It has been suggested that part of this mismatch could be due to variations in inter-individual temperament and stress coping strategies (Koolhaas et al., 1999; Izzo et al., 2011; Coleman, 2012). For captive populations, inter-individual variation in behaviours potentially indicative of stress (BPIS,

henceforth) and in basal hormonal levels is described for many species, such as leopards (Wielebnowski et al., 2002), polar bears (Shepherdson et al., 2013), giant pandas (Liu et al., 2003), and capuchin monkeys (Pomerantz et al., 2012). Mapping such behavioural and hormonal differences will offer support of better management practices and assist in translational models of the development of psychopathologies.

One approach to investigating the neuroendocrine correlates of individual differences in the stress response is by comparing the variance exhibited when individuals respond to a demanding situation (Carere et al., 2010; Koolhaas et al., 2010). Coping style refers to the way individuals react/adapt to stressful situations (Antoniazzi et al., 1998), and consequently their vulnerability to develop stress-related

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behaviours and illnesses (Cavigelli, 2005). Koolhaas et al. (1999) defined two basic coping styles in laboratory rats based on stable behavioural and physiological responses. In this model, the proactive response is characterized by high mobility, decreased latency for aggression, less sensitivity to changes, and at the physiological level, moderate to high cortisol basal levels, but lower reactivity of the hypothalamic–pituitary–adrenal (HPA) and greater sympathetic reactivity. The reactive response is considered a "self-preservation/withdrawal" response, and it is accompanied by behaviours such as inactivity, a high dependence on environmental signals and less routine formation. Physiologically, there is less adrenocorticotropic hormonal levels, higher reactivity of the HPA axis and less sympathetic reactivity.

Joshi and Pillay (2016) showed that more proactive and bold individuals of the African rodent *Rhabdomys dilectus* exhibited more BPIS than those considered reactive and shy. However, Amazonian parrots (*Amazona amazonica*) scoring higher in the 'Extroversion' dimension were more resilient, developing less BPIS, while those individuals who scored higher in 'Neuroticism' were more likely to develop BPIS, such as damaging their feathers (Cussen and Mench, 2015). In African elephants (*Loxodonta africana*), captive individuals classified as 'fearful' exhibited higher salivary cortisol than those classified as 'sociable' or 'effective' (Grand et al., 2012).

Nonhuman primates are valued biological models for the study of human psychopathologies due to similarities in neurobiology (neural pathways and physiological mechanisms) resulting from shared evolutionary history (Nelson and Winslow, 2009). However, regarding the development of abnormal behaviours, intrinsic factors such as personality are understudied (Coleman, 2012). Vandeleeuw et al. (2011) did not find main effects of temperament on the exhibition of motor stereotypy in rhesus monkeys (*Macaca mulatta*). However, there was an interaction between temperament and early rearing conditions, with individuals considered more 'gentle' or more 'nervous' at a higher risk of developing motor stereotypy when reared indoors, but not when reared outdoors. Maninger et al. (2003) suggest that for rhesus monkeys, physical and social changes can differentially impact the health of individuals, with more sociable animals exhibiting higher immunological responses when compared to less sociable individuals.

Capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) are neotropical primates largely studied in the area of comparative psychology (De Waal, 2000; Visalberghi et al., 1995), neuroscience and cognition (Phillips and Sherwood, 2005; Ottoni and Izar, 2008), due to the genus' high degree of encephalization (Roth and Dicke, 2005) and naturally occurring complex behaviours such as tool use (Ottoni and Izar, 2008), cooperation (Hattori et al., 2005), food sharing (De Waal, 2000), coalitions (Ferreira et al., 2006) and behavioural traditions (Fragaszy et al., 2004). Recent studies describe individual differences in wild (Manson and Perry, 2013) and captive populations (Uher et al., 2013; Morton et al., 2013), with some behavioural traits similar to the five-factor model used to describe personality in humans.

When in captivity, this species exhibits a broad repertoire of BPIS (Boinski et al., 1999). Recently, Ferreira et al. (2016) suggested individual differences in coping styles varying along five different axes, two of them similar to proactive and reactive strategies. Pomerantz et al. (2012) showed that individuals in a captive colony of capuchin monkeys differ in their frequency of stereotyped behaviours (pacing and head twirl) and faecal corticoid levels but that only the head twirl correlated with increased pessimistic judgement bias, a cognitive indicator of stress. In addition, traits associated with personality or coping strategies do not greatly differ between sexes (Uher and Visalberghi, 2016; Uher et al., 2013; Ferreira et al., 2016) in captive *Sapajus* spp.

In this study, we analysed the individual differences in behavioural profiles, stress coping behaviours and faecal glucocorticoid metabolite levels (FGM) in captive capuchin monkeys. We tested two main predictions: (1) individuals differ qualitatively in their stress coping strategy, more active animals, evaluated from their GNB, will exhibit a

**Table 1**  
Group composition, time, and observation period.

Group	Enclosure	Density (animal/m <sup>3</sup> )	Individual	Sex	Observation hours	Month/year of observation
1	CETAS	0.2	Buraco	M	38.97	November/2015 to January/2016
			Maguila	M		
			Sanfona	M		
			Libi	M		
			Gal	F		
			Junior	M		
			Sandy	F		
			Inês	F		
			Claudio	M		
2	CETAS	0.13	Catra	M	12.64	
			Jony	F		
			Ramos	M		
3	QUARANTINE	0.75	Tufo	F	14.49	August-October/2015
			Sivuca	M		
			Acordeom	M		
4	QUARANTINE	0.75	Cabelinho	M	15.99	
			Mi	M		
			Riana <sup>a</sup>	F		
5	CETAS	0.08	Romário	M	40.64	September-December/2013
			Ester	F		
			Hulk	M		
			Lula	M		
6	CETAS	0.11	Soleil	F	20.66	
			Golias	M		
			Queen	F		

<sup>a</sup> Pregnant female: FGM data not included/analyzed.

more proactive coping style (pacing and head twirl), while quieter individuals will exhibit a reactive reaction (self-scratching and crouching); (2) individuals differ quantitatively in their stress reactions, more active individuals will exhibit higher basal activation of HPA axis (i.e., higher levels of FGM excretion), while the opposite will be found in quieter individuals.

## 2. Methods

### 2.1. Animals and location

We observed the behaviour of 25 adult and sub-adult captive capuchin monkeys (*Sapajus libidinosus*), 16 males and 9 females. The animals were distributed in six social groups, ranging in number from three to nine animals, including infants, juveniles, sub-adults and adults of both sexes (Table 1). The data collection occurred in a zoo quarantine and two wildlife rescue centres (CETAS) in Northeast Brazil, between the years of 2013 and 2016. The environment provided to the animals in both institutions was quite similar: non-enriched enclosures, with concrete floor and barred walls allowing an outside view, and low presence of humans (only caretakers and researchers had access to these animals). Individuals were identified by their physical characteristics, such as the colour, size and shape of the head and body. As the exact age, the origin of the animals, and the amount of time each animal was in these environments could not be determined, these parameters were not considered for analyses.

### 2.2. Behavioural data collection

Based on the literature for captive capuchin monkeys (Ferreira et al., 2016; Fragaszy et al., 2004; Boinski et al., 1999), we defined an ethogram with 13 behaviours typically described in wild populations (Genus Normative Behavior *sensu* (Jacobsen et al., 2010) – GNB, henceforth) and 10 BPIS, registered in captive populations. The 13 GNB were: "Forage", "Eat", "Manipulation/Handling of food", "Manipulate environment", "Solitary play", "Grooming", "Social play", "Sexual display", "Scrounge", "Agonism (given/received)", "Scan environment/

Alert”, “Rest/Still”, and “Locomotion”. The BPIS were divided into two types: states (behaviour lasting more than 5 s: “Pacing”, “Self-grooming”, and “Crouching/self-clasp/huddle”) and events (behaviour lasting less than 5 s: “Head twirl”, “Pirouette”, and “Self-scratching”). Four BPIS could be described as either states or events, depending on their duration (“Bouncing/rocking”, “Ingestion/Manipulation of urine, faeces, and sperm”, “Masturbation/auto-erotic”, and “Sexual Display to humans”) (see full ethogram in Tables S1 and S2 in the supplementary material).

Behavioural data were collected through the ‘focal animal’ method (Altmann, 1974), with each animal observed in 10-minute sessions once a day, five days a week, during the afternoon between 12:00 to 17:00. For states, the sampling was instantaneous, with records at 30-second intervals, totalling 20 behavioural records (states) within the 10 min sampling per animal per day. The events were quantified in ‘all occurrences’ (within the 10 min of focal observation), that is, every event of selected behaviours was recorded within the 10 min focal sampling. No inter-activity interval between two events of the same BPIS was required, therefore each event was considered as an independent BPIS bout. For example, if an animal did 10 consecutive head twirls, all head twirls were singly counted, independent of inter-activity interval.

The total time of behavioural collection was 143.39 h over 10 months, and each animal was observed for a mean of 5.73 h. In addition to the behavioural records, data on social proximity (nearest neighbour in the distance of 1 m) and location within the enclosure (both horizontal and vertical) were also recorded every 30 s. All occurrences of agonistic behaviours between focal and/or non-focal individuals, and the identity of initiator and recipient, were recorded in order to calculate the dominance hierarchy for each group.

Data were collected by three researchers (CS, EF and VF) and two assistants. A preliminary period of training to the ethogram and habituation of animals to the presence of observers was allowed before the beginning of this study. By achieving a minimum of 85% agreement between observers on three consecutive sessions, data collection was then started independently.

### 2.3. Faeces collection and glucocorticoid metabolites analyses

To measure HPA axis activity, we used one of the less invasive methods currently available, FGM analysis. Faecal collection was conducted opportunistically at least three times per week, in the morning or afternoon, for all animals observed. The collection occurred within two hours after defecation. The faeces were packed in Eppendorf tubes and the following information was recorded: the name of the animal, time of defecation, time of collection and date. Samples were frozen at  $-5^{\circ}\text{C}$  until analyses. The total number of faecal samples collected and analysed was 561, with a mean of 22.44 samples for each individual.

For the determination of FGMs, we employed immunoenzymatic ELISA assays following the methods of Munro and Stabenfeldt (1984) and Sousa and Ziegler (2000). The samples were analysed in the Laboratory for Hormonal Measurement at Federal University of Rio Grande do Norte UFRN. The laboratory protocols were previously validated for this species based in Mendonça-Furtado et al. (2017).

To extract the steroids, 0.1 g of each faecal sample was weighed and then diluted in 1 ml of methanol 80% (v/v). The dilution was subjected to 30 min of vortex mixing (VWR® Multi-Tube Vortex, VWR Scientific Products, USA) and 10 min of centrifugation at 3000 rpm (Excelsa 4, model 280R, Fanem®, São Paulo, SP, Brazil). The supernatant of the samples was separated and 500 µl of the extracted phase was pipetted into Eppendorf tubes and stored in the freezer at  $-20^{\circ}\text{C}$ . During ELISA procedures, 25 µl of the faecal extracts were pipetted into test tubes and evaporated through a filtered air cascade (Organomation Associates, Inc., Berlin, MA, USA), after which the samples were resuspended in 975 µl EIA buffer (dilution: 1:40). The resuspended extracts (25 µl each sample) were then pipetted into plastic mini-tubes

with 275 µl of HRP-F conjugate enzyme solution (1: 37.500 in EIA). Each sample was assayed in duplicate (100 µl in each well) and the plates were read in an Epoch™ spectrophotometer (BioTek Instruments, Inc., Winooski, VT, USA), using Gen5 software and a 405 filter.

FGM concentrations were measured using a cortisol polyclonal antibody (R4866; Dr. Toni Ziegler, Wisconsin National Primate Research Center, University of Wisconsin, USA), diluted 1: 15 000. The intra-assay coefficients of variation for high and low concentration pools were 2.58% and 1.47%, respectively ( $n = 24$ ). Inter-assay coefficients of variation for high and low concentration pools were 19.09% and 16.76%, respectively ( $n = 24$ ), showing the reliability of the analysis (Chagas, 2016).

We statistically tested the influence of circadian variation in FGM levels through ANOVA (three blocks of hours: from 07:00 to 09:59, from 10:00 to 12:59, from 13:00 to 15:59) and a Pearson correlation (daylight hour x FGM levels). There was no significant difference between the time blocks ( $F(2,515) = 0.053, p = 0.949$ ) or correlation between sampling hour and FGM levels ( $n = 518, r = -0.018, p = 0.690$ ).

### 2.4. Statistical analyses

From the states and events’ samplings, we computed, for each individual, the GNB activity budget, the BPIS activity budget (for states), and BPIS frequency (for events). For the activity budget, we estimated the time allocated (in percentages) to each activity based on the proportion of 30-sec states records. That is, for each individual the number of interval records in a specific behaviour was divided by the total number of records in any behaviour. To calculate frequency, the total number of events exhibited was divided by the total number of hours each individual was observed. The frequency allows us to see the number of events per hour, and the activity budget the overall proportion (or percentage) of each behaviour in the individual routine.

The dyadic events of agonism were used to calculate the dominance index using the SOCPROG 2.4 software (Whitehead, 2008), and the index used was the MDS (Modified David’s Score) (de Vries et al., 2006). From this information, each animal, within its group, was classified from the most dominant to the most subordinate, in order to standardize the dominance hierarchy in the between-groups comparisons.

To obtain a more reliable FGM database, all outliers (values more than three IQRs) were excluded from our analysis ( $n = 43$ ), individually. Our final analyses were composed of 518 faecal samples. To test prediction 1 that individuals differ in their normative and stress coping behavioural profiles, we first defined the behavioural profile axes separately for GNB and BPIS behaviours using Principal Component Analyses (PCA), with direct oblimin rotation due to data dependence. The input of the data occurred as follows: only GNB (states), in order to identify the normative behavioural axes of the species, and only BPIS (states and events, concomitantly), in order to observe the possible coping styles existing between individuals.

Kaiser-Meyer-Olkin values ( $\text{KMO}^{\text{GNB}} = 0.531; \text{KMO}^{\text{BPIS}} = 0.550$ ) and the Bartlett sphericity test (GNB:  $X^2 = 127.672, p < 0.001$ ; BPIS:  $X^2 = 329.303, p < 0.001$ ) show the suitability of our sample ( $n = 25$ ). The number of factors was defined based on eigenvalues greater than 1 and on analysis of the scree plot. Only items that loaded more than 0.5 were considered as part of the factor component. When one behaviour punctuated more than 0.5 in more than one component, it was designated to the component that presented the greatest loading. Then, we performed partial correlations analyses between the regression residuals of each GNB and BPIS component obtained and the z-scores of Total Event and Total State BPIS. Significance levels were defined based on a bootstrap of 1000 samples.

To test prediction 2 that differences in GNB and BPIS correlate to differences in the hormonal milieu, the values obtained in the FGM analyses were compiled into 4 individual indices: median, mean,

maximum, and minimum. We employed an Automatic Linear Regression Modelling function (forward stepwise model selection method) using the z-score of these 4 physiological indices as target variables and the z-score values of the eight components (GNB and BPIS) as predictor (input) variables. We built three types of models: a) including all GNB and BPIS components, dominance, and sex; b) including only GNB, dominance, and sex; and c) including only BPIS components, dominance, and sex. We used Akaike information criterion (AIC) to choose between models.

We used a *t*-test to compare between sexes, based on a free distribution, with significance levels defined on bootstrap of 1000 samples. All analyses were conducted using IBM SPSS 23, with statistical significance being assigned at  $\alpha = 0.05$ .

### 2.5. Ethical consideration

This study was carried out in strict accordance with the recommendations of the Brazilian Agency for Wildlife Protection (ICMBio). The protocol was approved by the SISBIO (Permit Number: 17108, 38855, and 42073).

## 3. Results

### 3.1. Descriptive analyses

When all data for all individuals across the study was grouped, food-related behaviours (eating, foraging, and food manipulation) accounted for one-third of individuals' daily activities (36.83%). 'Scan environment' and 'Locomotion' comprised almost one-fifth of individuals' activity budgets each (20.06% and 17.10%, respectively). One-tenth of individuals' activity budgets was dedicated to BPIS states (10.02%) and to social behaviours (grooming, social play, and sexual display = 9.38%). The remaining behaviours contribute together to less than 10% of the total activity budget.

For BPIS states, the most common behaviour was 'Pacing', occurring in 5.35% of the behavioural samples, followed by 'Self-grooming' and 'Ingestion/Manipulation of urine, faeces, and sperm'. The animals performed, on average, 42.11 BPIS events per hour or 0.70 BPIS events per minute. 'Head twirl' and 'Self-scratching' were responsible for almost all of these events, with an average rate of 0.58 events per minute. The other BPIS events rated approximately 0.12 events per minute.

Males displayed more 'Scan environment/Alert' behaviour than females (23.22% and 14.45%, respectively;  $t = 2.259$ ,  $p = 0.021$ ). We also found that males exhibit self-scratching events at a higher frequency than females (17.76/hour and 12.32/hour, respectively;  $t = 1.837$ ,  $p = 0.043$ ). For detailed description of GNB and BPIS activity budgets, see the supplementary material.

### 3.2. Profiles based on genus normative behaviours and behaviours potentially indicative of stress

For the GNB profile, PCA generated 4 components (Table 2). The first component, labelled 'Feeding' (22.65% of the explained variance), was composed positively of food-related activities such as 'Eat', 'Forage', and 'Handling food'. The second component (21.79% of the variance), labelled 'Sociability', was positively composed of 'Grooming', 'Social play' and 'Sexual display', as well as negatively composed of 'Scan environment/Alert'. The third component (16.81% of the variance) was composed of 'Manipulate environment' and 'Solitary play' and was labelled 'Exploration'. The fourth and last GNB component (12.99% of the variance) scored positively in 'Locomotion' and 'Scrounge' and negatively in 'Rest/Still'. This component was labelled 'Activity'. Sexes differed in 'Sociability', with females presenting more social behaviours than males (Feeding:  $t = -1.470$ ,  $p = 0.188$ ; Sociability:  $t = -2.258$ ,  $p = 0.028$ ; Exploration:  $t = -1.754$ ,  $p = 0.115$ , and Activity:  $t = -0.461$ ,  $p = 0.584$ ).

**Table 2**

PCA of the GNBs, structure matrix by the direct oblimin method, its components and the explained variance.

	Components			
	Feeding	Sociability	Exploratory	Activity
Eat	<b>0.863</b>	0.037	-0.152	0.074
Forage	<b>0.846</b>	0.097	-0.046	-0.246
Handling food	<b>0.703</b>	-0.171	0.303	0.131
Sexual display	0.143	<b>0.753</b>	-0.027	-0.065
Grooming	-0.450	<b>0.747</b>	-0.062	-0.362
Scan environment/Alert	-0.547	<b>-0.722</b>	-0.113	0.028
Social play	-0.261	<b>0.706</b>	0.232	-0.177
Manipulate environment	-0.068	0.122	<b>0.956</b>	-0.056
Solitary play	0.065	0.020	<b>0.953</b>	0.015
Locomotion	-0.181	-0.213	-0.055	<b>0.859</b>
Scrounge	-0.115	-0.249	-0.146	<b>0.736</b>
Rest/Still	-0.322	-0.120	-0.193	<b>-0.676</b>
% of variance explained	22.657	21.797	16.813	12.991

**Table 3**

PCA of the BPIS, structure matrix by the direct Oblimin method, its components and the explained variance.

	Components			
	Self-directed	Restless	Ingestion/ Self-scratching	Stereotyped
Crouching (S)	<b>0.955</b>	-0.084	0.254	-0.065
Bouncing (S)	<b>0.950</b>	-0.037	-0.061	-0.096
Bouncing (E)	<b>0.948</b>	-0.050	-0.049	-0.092
Self-grooming (S)	<b>0.878</b>	0.199	0.284	-0.020
Masturbation (E)	0.071	<b>0.949</b>	-0.013	-0.085
Masturbation (S)	-0.003	<b>0.942</b>	0.008	-0.102
Pacing (S)	-0.135	<b>0.701</b>	-0.302	0.119
Ingestion/Manipulation of urine, feces, sperm (S)	0.084	-0.111	<b>0.920</b>	0.052
Ingestion/Manipulation of urine, feces, sperm (E)	-0.067	-0.057	<b>0.833</b>	0.061
Self-scratching (E)	0.526	-0.141	<b>0.715</b>	-0.066
Pirouette (E)	-0.157	0.014	-0.240	<b>0.717</b>
Sexual display to humans <sup>a</sup>	-0.186	-0.196	-0.297	<b>-0.654</b>
Head twirl (E)	-0.115	-0.253	0.081	<b>0.592</b>
% of variance explained	30.400	19.847	16.147	10.080

S = state, E = event.

<sup>a</sup> 'Sexual display to humans' behavior did not occur as state.

For the BPIS profile, PCA also generated 4 components (Table 3). The first component was labelled 'Self-directed' (accounting for 30.40% of the variance), bringing together the behaviours 'Crouching', 'Bouncing' (state and event) and 'Self-grooming'. The second component, labelled 'Restless' (19.84% of the variance), scored positively for the behaviours 'Pacing' and 'Masturbation' (state and event). The third component (16.14% of the variance) scored positively for 'Ingestion/Manipulation of urine, faeces, and sperm' (state and event) and 'Self-scratching', which we labelled as 'Ingestion/Self-scratching'. The fourth component, 'Stereotyped', explained 10.08% of the variance and displayed positive values for 'Head twirl' and 'Pirouette' and negative value for 'Sexual display to humans'. Similar to the GNB components, there was only one significant difference between males and females for BPIS components, with males exhibiting more self-directed behaviours than females (Self-directed:  $t = 1.937$ ,  $p = 0.036$ ; Restless:  $t = 1.546$ ,  $p = 0.150$ ; Ingestion/Self-scratching:  $t = -0.104$ ,  $p = 0.920$ , and Stereotyped:  $t = 0.475$ ,  $p = 0.638$ ).



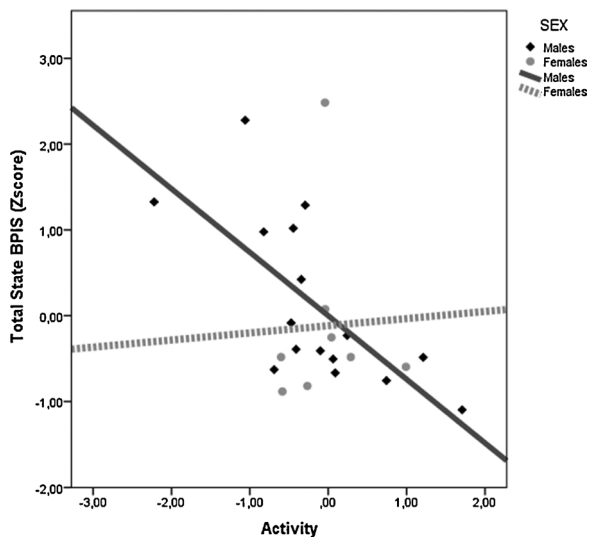


Fig. 1. Relationship between Total State BPIS (Behaviors Potentially Indicative of Stress) and Activity (Genus Normative Behavior component).

### 3.3. Correlations between gnb components and total bpis

We detected a significant negative correlation between the ‘Activity’ GNB and Total State BPIS ( $r = -0.519$ ;  $p = 0.013$ , Fig. 1), and a significant positive correlation between ‘Activity’ and Total Event BPIS, while controlling for sex and dominance ( $r = 0.443$ ;  $p = 0.044$ , Fig. 2).

### 3.4. Predictors of faecal glucocorticoid metabolites

There were no significant differences between males and females for any of the FGM indices considered (median:  $t = 1.369$ ,  $p = 0.201$ , mean:  $t = 1.118$ ,  $p = 0.277$ , maximum:  $t = 0.529$ ,  $p = 0.582$ , and minimum:  $t = 1.301$ ,  $p = 0.176$ ).

The lowest values of AIC showed that the best predictors for FGM indices were generated when including both GNB and BPIS (Table 4). Increased values in GNB ‘Sociability’ predicted lower median, mean and minimum values of FGM. Increased GNB ‘Exploration’ also related to lower mean and minimum FGM values. On the other hand, increased GNB ‘Activity’ related to higher minimum FGM values. Increased values of BPIS ‘Stereotyped’ and ‘Self-directed’ predicted higher median and

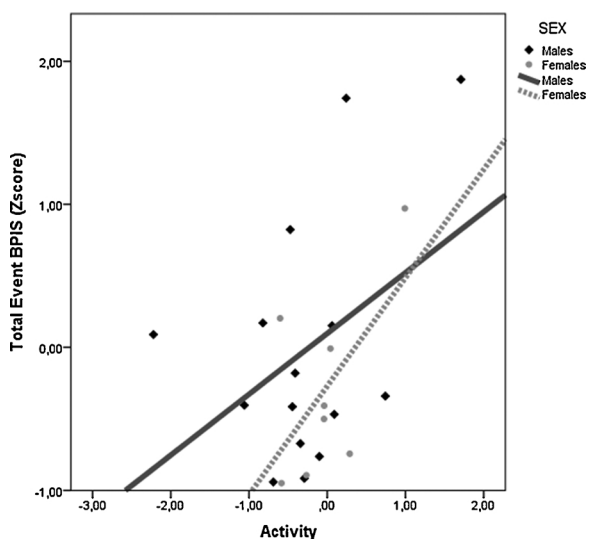


Fig. 2. Relationship between Total Event BPIS (Behaviors Potentially Indicative of Stress) and Activity (Genus Normative Behavior component).

mean FGM values, respectively. Conversely, increased BPIS ‘Ingestion/Self-scratching’ related to lower minimum FGM values.

When including only GNB components in the model, ‘Sociability’ stands as the only significant component predicting lower median, mean and maximum values. For lower FGM minimum values, the only significant predictor was the GNB component ‘Exploration’.

When modelling using only BPIS components, only BPIS ‘Self-directed’ predicted increased FGM mean values.

## 4. Discussion

In this study, we investigated the hypotheses that Genus Normative Behaviours, Behaviours Potentially Indicative of Stress and Faecal Glucocorticoid Metabolite levels are related in adult captive capuchin monkeys.

The activity budget of these 25 monkeys did not vary much when compared to that described for other captive capuchin monkey groups. Approximately 10% of the time was devoted to BPIS, similar to that found by Silva (2015) (11%), lower than that found by Ferreira et al. (2016) (17%) and Mendonça-Furtado (2006) (> 20%) and far below that described by Boinski et al. (1999) for individually housed animals (54%). Some of these differences may occur due to the separation of BPIS into states and events. While Silva (2015) found 5.7 BPIS per hour quantifying only states, we found a mean of 42.11 BPIS events per hour, or 0.7 per minute, highlighting the importance of differentiating between BPIS states and events to better quantify stress-related behaviours that are of a faster and/or shorter duration.

The behavioural profiles of these animals could be parsimoniously described by eight components, four related to genus normative behaviours and four composed of behaviours potentially indicative of stress. Six out of these eight components significantly predicted FGM levels.

The ‘Feeding’ GNB component includes behaviours such as forage, eat and handling of food, suggesting that this axis groups behaviour related to basic needs of living animals. Although it explains almost one-fourth of the inter-individual behavioural variance, this axis did not correlate to FGM levels. As these are captive and provisioned groups, this result indicates that lack of food intake is not a main source of stress for the individuals. That is, animals are not facing an allostatic load type I, characterized by low intake of energy. The hormonal levels of these animals are more related to challenges in restricted social life and lack of opportunities for exploration, suggesting an allostatic load type II (Wingfield, 2013).

The social behaviours composed a second axis, named ‘Sociability’, indicating that this is an independent personality trait. This component is similar to one of the axes of animal personality proposed by Réale et al. (2007). These authors characterize sociable individuals as those who seek contact with other conspecifics, while unsociable individuals avoid it. Morton et al. (2013) also found a ‘Sociability’ axis in captive capuchin monkeys (*Sapajus apella*). These authors showed that animals scoring more in ‘Sociability’ were classified as more social and friendly, as well as less anxious and depressive. Males, in our sample, scored less in the ‘Sociability’ component than females, this difference can be attributed to the role of males in group defence in capuchins and matrilineal organisation of the species (Fragaszy et al., 2004; van Schaik and van Noordwijk, 1989).

In our analyses, the ‘Sociability’ component was included in the model predicting lower median, mean, and maximum levels of faecal glucocorticoid metabolites. At the behavioural level, ‘Sociability’ relates to lower levels of alert behaviour. Some studies show that alarm behaviours, increased orientation and alertness are linked to stress and present physiological correlates (Morgan and Tromborg, 2007; Rimpley and Buchanan-Smith, 2013). As seen in many other species, including humans, our data confirm that individuals with greater social contact have lower physiological stress indicators in chronic stress situation than individuals with lower social contact (DeVries et al., 2003).

The third Genus Normative Behaviour component ‘Exploration’,

**Table 4**  
AIC values for models of Faecal Glicocorticoid Metabolites (FGM).

	Median		Mean			Maximum		Minimum	
<b>GNB + BPIS</b>	AIC: -17.601		AIC: -84.604			AIC: -86.839	AIC: -9.500		
	Sociability	Stereotyped	Sociability	Exploration	Self-directed	Sociability	Exploration	Activity	Ingestion/Self-scratching
	Coefficient: -0.551	Coefficient: 0.363	Coefficient: -0.082	Coefficient: -0.163	Coefficient: 0.275	Coefficient: -0.056	Coefficient: -1.450	Coefficient: 0.512	Coefficient: -0.414
	Significance: 0.001	Significance: 0.008	Significance: 0.004	Significance: 0.032	Significance: 0.020	Significance: 0.036	Significance: 0.012	Significance: 0.035	Significance: 0.044
	Importance: 0.659	Importance: 0.341	Importance: 0.474	Importance: 0.238	Importance: 0.289	Importance: 0.642	Importance: 0.446	Importance: 0.291	Importance: 0.263
<b>GNB</b>	AIC: -12.444		AIC: -86.100			AIC: -97.206	AIC: -2.674		
	Sociability		Sociability			Sociability	Exploration		
	Coefficient: -0.672		Coefficient: -0.113			Coefficient: -0.061	Coefficient: -1.711		
	Significance: 0.000		Significance: 0.001			Significance: 0.013	Significance: 0.011		
Importance: 0.832		Importance: 1.000			Importance: 1.000	Importance: 0.654			
<b>BPIS</b>	NONE		AIC: -78.721			NONE	NONE		
			Self-directed						
			Coefficient: 0.476						
			Significance: 0.002						
			Importance: 1.000						

Only the significant predictors ( $p < 0.05$ ) in each model are showed on the table.

included ‘Manipulate environment’ and ‘Solitary play’, showing similar characteristics to the ‘Openness’ axis from the five-factor model for human personality (Digman, 1990). In humans, men and women who score higher in ‘Openness’ are more able to deal with the psychosocial stress of public speaking (Caramaschi et al., 2013). In analyses of primate personality, more ‘open’ animals were classified as more curious, creative and playful (Morton et al., 2013; Robinson et al., 2016; Manson and Perry, 2013). Byrne and Suomi (2002) also describe that semi-captive capuchin monkeys evaluated as curious show lower cortisol levels. Our data shows that the ‘Exploration’ component predicted negative mean and minimum values of FGM, suggesting that exploration behaviours may have a positive impact on individual physiology, diminishing FGM levels.

The GNB component ‘Activity’ is characterized by increased locomotion and scrounging behaviours, as well as decreased inactivity. This component matches a well-studied axis: the fast-slow or activity-inactivity axis discussed by Réale et al. (2007); Careau et al. (2008), and Biro and Stamps (2010). We found that more active animals engage more frequently in a display of rapid BPIS, exhibiting more BPIS events than BPIS states. Less active individuals, on the other hand, spend more time exhibiting long-duration BPIS. This result corroborates our first hypothesis based on that proposed by Ijichi et al. (2013) that more active animals develop different stress coping strategies and are more prone to the development of more instantaneous and frenetic BPIS (signs of anxiety), while less active individuals develop longer-lasting BPIS (signs of depression).

The ‘Activity’ component was included as a predictor of minimum FGM levels, with more active individuals exhibiting higher levels of FGM. This positive correlation between general activity and FGM levels may be reflecting the normal homeostatic function of glucocorticoids, as a catabolic for glucose for daily activities (Sousa et al., 2015).

Behaviours potentially indicative of stress were grouped into four components: Self-directed, Restless, Ingestion/Self-scratching and Stereotyped. The ‘Self-directed’ component, with a high proportion of ‘Crouching’, ‘Bouncing/Rocking’ and ‘Self-grooming,’ seems to reflect the reactive coping style. Interestingly males exhibited a more reactive (“self-directed”) strategy than females. As the mating system of capuchins is a conservative feature (Izar et al., 2012), it is possible that the biased sex ratio observed in these conditions is more stressful to males than to females, and extra males may use avoidance strategies in

conflicts (Abbott et al., 2003).

The ‘Restless’ component, with a greater display of ‘Pacing’ and ‘Masturbation’ is suggestive of the proactive side of the continuum style. Pacing is a common behavioural indicator of compromised welfare, however, ‘Self-directed’ component, but not ‘Restless’, significantly influenced mean FGM levels. Pomerantz et al. (2012) found that, although pacing did positively correlated to faecal corticoid levels, it did not correlate to pessimistic judgment bias, a cognitive test for welfare. Considering that ‘Activity’ predicts higher levels of FGM, this result indicate that hypoactivity (apathy, inertia) is also a sign of poor welfare being exhibited by individuals through different stress coping strategies, as suggested by Poole (1988). Therefore, those self-directed behaviours should be considered indicators of the emotional state of an individual when evaluating their welfare.

The third component, ‘Ingestion/Self-scratching’, predicted lower minimum FGM levels. Polizzi di Sorrentino et al. (2012) and Maestripieri et al. (1992) suggested that, for primates, displacement behaviours, such as ‘Self-scratching’, become more evident, especially during situations of psychosocial stress. Since our results do not show an increase but rather a decrease in FGM values, this can indicate that exhibition of some BPIS may have a calming effect on individuals, working as a buffer to hormonal levels and stress (Novak et al., 2013). Regarding ingestion behaviours, it has already been suggested that nutritional stress (deficiency) guides the motivation to ingest one’s own fluids and excretions (Prates and Bicca-Marques, 2005). However, more recent studies claim for a reconsideration of this behaviour in captive chimpanzees, as ‘coprophagy’ is grouped into the social factor and not into the abnormal factor after principal component analyses of behaviour (Hopper et al., 2016). Studies in obese humans show that eating large amounts of food (hyperphagia) prevents or decreases negative emotions, such as depression and boredom (Singh, 2014).

The fourth and last component, ‘Stereotyped’, graded positively for ‘Head Twirl’ and ‘Pirouette’, was also found in Ferreira et al. (2016) and was composed of the same behavioural units. As it was the only BPIS component considered a good predictor for median FGM values, this also agrees with what was found by Pomerantz et al. (2012) that capuchin monkeys exhibiting more ‘head twirls’ present with higher faecal corticoid levels and greater pessimistic bias in cognitive tests. Moreover, this indicates that beyond the described proactive-reactive axis expressed by individuals during demanding situations there are

other forms of coping styles found in this species.

## 5. Conclusions

Stable differences (in context and time) in the behavioural profiles of individuals within the same species are reported to different clades (amphibians - Carlson and Langkilde, 2013; birds - Patrick and Weimerskirch, 2014; mammals - King and Figueredo, 1997, and invertebrates - Gherardi et al., 2012; Pinter-Wollman, 2012; Wright et al., 2014). While research on evolution and ecology models in which selective forces maintain the existence of stable alternative behavioural patterns within a population or species (Réale et al., 2010; Dingemans and Réale, 2005; Sih et al., 2004), research on neuroscience (Camus et al., 2013; Pawlak et al., 2008), animal welfare (Watters and Powell, 2012; Powell and Svoke, 2008), and livestock management (Boissy and Erhard, 2014) focus on determining the extent to which these differences have genetic substrates, its neurophysiologic underpinnings, and how these differences relate to fitness and animal production (Quinn et al., 2012; Smith and Blumstein, 2008).

Our results indicate that individual differences in captive capuchin monkeys can be described along four different components of Genus Normative Behaviours. Stress coping behaviours can also be grouped into four strategies. Similar to that described for other species, these behavioural axes and coping strategies are related, with more active individuals presenting faster BPIS and less active individuals exhibiting longer-lasting BPIS. These behavioural differences do present physiological correlates as measured by Faecal Glucocorticoid Metabolites. Animals exhibiting social behaviours, such as grooming and playing, displayed lower median, mean, and maximum levels of physiological arousal. Two components of the behaviours potentially indicative of stress are similar to the two basic axes of the coping styles (Koolhaas et al., 1999, 2010). The 'Restless' component resembles the proactive strategy and the 'Self-directed' is similar to the reactive side of the continuum. However, 'Restless' did not correlate to hormonal concentration, while BPIS 'Self-directed' (crouching, bouncing, self-grooming) significantly predicted higher levels of mean FGM. Analyses confirm previous studies suggesting the existence of another form of stress coping, characterized by high frequencies of 'Head-twirl' and 'Pirouette' with increased median FGM levels. Mapping inter-individual differences in behaviour profiles and its neurophysiological substrate is now a major quest in behavioural, evolution and physiological sciences. It has great impacts on models for evolution and resilience of wild and captive populations. Our results support previous studies indicating that animals within the same population differ in the way they behave and react to stressful conditions, and these are correlated to different physiological profiles. Knowing these differences may help clarify the long-term reported incongruity between behavioural and physiological indicators of welfare in captive animals, offering the support to better management practices and assisting translational models of the development of psychopathologies.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.applanim.2018.07.002>.

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