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Coping strategies in captive capuchin monkeys (*Sapajus* spp.)

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ABSTRACT

Studies on diverse species indicate the existence of individual differences in stress coping strategies labelled as 'proactive' and 'reactive'. Identifying taxonomic distribution of such coping strategies is fundamental to evolutionary models and to management of captive animals. Capuchin monkeys (*Sapajus* spp.) are neotropical primates noted for their cognitive skills and behavioural plasticity. The capuchin clade faces increasing threats from Human Induced Rapid Environment Change, and a growing number of animals are kept in rescue centers and zoos. Based on an ethogram with 28 behavioural categories, we employed Principal Component Analysis to explore differences in behaviour potentially indicative of stress (BPIS) in a sample of 123 captive brown capuchins. We identified five principal components summarising BPIS and labelled as: Restless, Self-narcotizing/fear, Self-protection, Stereotyped, and Help-seek. Multivariate GLM and regression analyses indicated no sex differences. It was not possible to map the five components onto the five personality dimensions recently described for capuchins. However, two of the patterns (Restless and Self-protection) parallel the two coping strategies described in several other species (Proactive and Reactive), and may reflect stress-reactivity that is conserved across species.

1. Introduction

Research on individual differences in animal behaviour is now a prominent focus of behavioural ecology (Dingemanse et al., 2009; Foster and Sih, 2013). At a theoretical level, identifying the types of behavioural variation that exist and how conserved these appear to be across species is fundamental to our understanding of the evolutionary forces that shape behavioural traits and biodiversity (e.g., Gosling, 2001). At a practical level, studies of the health and welfare of captive animals show that individuals differ in strategies that they adopt to cope with stressful events (acute and chronic stressors), and thus differ in their resilience to disease, psychopathy (Cavigelli, 2005; Capitanio, 2011), and plasticity in responses to Human Induced Rapid Environmental Changes—HIREC (Sih et al., 2011; Winfield, 2013).

The concept of coping style or coping strategy refers to the way individuals react and adapt to stressful situations or environments (Koolhaas et al., 1999, 2010). One prominent approach to studying coping styles has been to search for the existence of two distinct clusters of characteristics labelled as 'proactive' and 'reactive' coping, often regarded as two ends of a continuum. Studies on a variety of different species (e.g., birds, mice, rats, pigs) suggest that proactive individuals are characterised by high levels of locomotor activity, rapid attack behaviours and a tendency to form routine-like behaviors with low sensitivity to changes in the environment. Reactive animals are characterized by low levels of aggression, a tendency to freeze or show low activity in response to challenges, and a propensity for more flexible behaviour that is sensitive to environmental change (Koolhaas et al., 2010). Proactive animals tend to be more susceptible to developing hypertension, arteriosclerosis, tachyarrhythmia, and ulcer formation. Reactive animals tend to be susceptible to depression, various changes in immune system function and bradycardia (Cavigelli, 2005; Honess and Marin, 2006; Capitanio, 2011).

Although this proactive/reactive axis has proved to be an important heuristic and methodological approach, and seems to capture two basic forms of reaction to stress, it is not an exhaustive charac-

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terisation of the stress reaction behaviours exhibited by animals, particularly for more plastic species that inhabit variable environments (Bell, 2007; Wolf et al., 2008). For primates, besides the evidence for proactive/reactive differences, more complex and diverse responses to challenge are also found. Reamer et al. (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 colleagues 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 with females, those that form friendship with males, and those that react aggressively (Ray and Sapolsky, 1992; Virgin and Sapolsky, 1997). For new world monkeys Galvão-Coelho et al. (2008) identified three types of response to induced social separation in captive common marmosets (*Callithrix jacchus*): scent marking (made via genital rubbing in surfaces), pacing, and piloerection. Taylor et al. (2014) showed that in marmosets (*Callithrix geoffroy*) different behaviours relate to moderate acute stressors during development, with alarm call relating to increased cortisol in young animals, while in adults motor activity and cage manipulations were associated with poorer cortisol regulation.

Capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) are receiving increased attention in primatological, psychological and anthropological literature due to their striking cognitive capacities such as: combinatorial tool use skills, cooperative and pro-social propensities in food sharing, triadic awareness with increased social learning in tolerant social organisation, and exhibition of behavioural traditions (see review in Fragaszy et al., 2004). Ranging over large areas (from 80 to 900 ha), capuchins show flexibility of foraging behaviour and social organisation (Emidio and Ferreira, 2012; Izar et al., 2012). Two recent studies indicate that capuchins (wild—*C. capucinus* and captive—*S. apella*) show stable inter-individual differences along behavioural axes that resemble the Big Five dimensions of personality found in humans and chimpanzees (Manson and Perry, 2013; Morton et al., 2013a,b). In wild but not in captivity, females ranked higher in Agreeableness while males were more Open, Neurotic, Extroverted and Eccentric. In a third study, employing detailed behavioural tests, as many as 20 personality constructs could be distinguished in 24 captive *S. apella* (Uher et al., 2013). Between-individual variation in probability of behaviour was stable over a short-period time, but no age-sex differences were found in 17 out of 20 constructs. Furthermore, capuchins with different personalities vary in their boldness to novel stimuli, as measured by their willingness to voluntarily participate in cognitive experimental sessions (Morton et al., 2014). Physiological underpinnings of these differences are hitherto unknown, but the aetiology of behavioural styles do have developmental components: Byrne and Suomi (2002) describe that juvenile capuchin monkeys with secure attachment to their mothers were more playful and explorative (from 6 months to 4 years old), more aggressive and presented lower cortisol increases in response to separation from mothers, while insecure juveniles were more fearful and presented higher increases in cortisol facing similar challenging situations.

Composed of 11 species, two listed by the IUCN—2014 as critically endangered (*Sapajus flavius* and *S. xanthosternus*), the clade Cebus faces increased Human Induced Rapid Environment Changes (HIREC—Sih et al., 2011; Winfield, 2013) due to loss of habitat, hunting pressures, and capture and use as pets by local and traditional populations. As a consequence, a growing number of animals are kept in rescue centers and zoos where they remain for years before re-introduction to nature, if that happens at all (Lynch-Alfaro et al., 2014). Captivity can be considered an extreme form of HIREC and it has been suggested that species (or individuals) that thrive well in captivity may also thrive well in wild but altered environments (Mason et al., 2013). In a review social factors affecting welfare in captive animals Abbott et al. (2003) suggest that species that form larger and despotic groups would be more prone to development of stress in captivity due to increased social tension in crowded conditions. Similarly, Pomerantz et al. (2013) suggest that species with larger home and day ranges would be more susceptible to stress in captivity. Thus capuchin monkeys socio-ecological characteristics (large home size, manipulative foraging and tolerant but complex social system) may make capuchins prone to the development of psychopathologies when kept in captivity. Considering the increased need to manage these animals in captivity, and the growing interest in capuchin monkeys as an independent model for comparison of the evolution of cognitive capacities in humans, it is surprising that relatively few studies have been conducted on psychopathologies and coping strategies in captive capuchin monkeys.

In this paper we investigate whether distinctive ways of responding to chronic captive conditions could be detected in a sample of 123 capuchin monkeys kept at rescue centres in northeast Brazil. If so, we predicted that we would find at least two clusters of behaviours, one indicating a more proactive strategy (more pacing) and another indicting a more reactive strategy, characterised by more avoidance and withdrawal. We also predicted no sex differences in stress reactions, as was found in other studies with captive *S. apella* (see references in Table 1).

2. Methods

2.1. Study animals and site

We collected data on 123 capuchins, 63 males and 60 females, distributed in 14 social groups (see Table 3). We classify these capuchins as *Sapajus* spp. although all are possibly *S. libidinosus*, since all animals were rescued from conflict areas at Caatinga (savannah-like) biome, where city growth is encroaching animals on hill tops (Ferreira et al., 2009). All animals were wild-born, and veterinary analyses of dental patterns indicate all animals were adults. However, exact age, as well as time in captivity prior to rescue, was impossible to determine because capuchins' previous owners are normally afraid to reveal such information to environmental agencies. Therefore, we did not include age, previous experience and time in captivity as variables in our analyses.

Our observations were conducted at wildlife rescue centres run by the Brazilian Federal Agency for Environment (CETAS—IBAMA) in the states of Rio Grande do Norte and Paraiba, from March 2008 until May 2012. In these centres capuchin monkeys were kept in groups occupying similar space (5 m length × 3 m high × 3 m wide), and fed twice a day at 0900 and 1400 (although exact feeding times may vary).

2.2. Data collection

Based on the published literature on wild and captive capuchins, we defined a list of 18 genus normative behavioural patterns (GNB—Jacobsen et al., 2010) and 10 behaviours potentially indicative of stress (BPIS—Mendonça-Furtado, 2006) that we recorded throughout data collection (see Table 1). Four of these 10 BPIS are observed in wild animals and they are linked to stressful events. For example, self-groom may occur as a response to biting of ants,

Table 1
Ethogram used for data collection.

Macro-category	Behaviour	Description	Reference
Genus normative behaviours			
Feeding	Forage	Animal moves on the area searching for food, but without handling or eating during the sampling interval	Review in Fragaszy et al. (2004)
	Manipulation/handling of food	Handling of food with apparent goal of making more efficient intake (soften, open, break . . .), but without intake during the sampling interval	
	Eat	Animal brings food to the mouth, followed by ingestion	
	Drink	Ingestion of water	
Locomotion	Locomotion	Vertical or horizontal mobility in the environment, without manipulation or foraging. There is an end point to the locomotion (animal moves from A to B) and the same path is not followed twice (cf pacing below)	
Social positive	Social groom	Animal slowly manipulates the fur of another individual with the hand or mouth	
	Social play	Two or more individuals interact by holding, grasping, chasing or biting without aggression	
	Sexual display	Animal opens eyes wide in repetitive partial opening and closing, writhing body movement, swaying from one side to the other (the behavior is always carried toward another individual). The arms are folded across its chest, its hands placed in the armpits. Usually presented by females in estrous, but may also occur out of estrus and by males. There may occur manipulation of one own or partner genitals or nipples	
	Mount	Individuals of the opposite sex or same sex ride one over the other and there may be contact between the genital regions	
	Scrounge	One animal approaches another and feeds the food scraps that fall from the mouth/hands of the possessor	
Social Negative[a]	Agonism given	Individual threatens (by lunging, screaming and showing teeth), hits, bites or attacks another individual	
	Agonism received	Individual is threatened, hit, bitten or attacked by other individual	
Inactivity	Rest/still	The individual is relatively static in a relaxed position. Animal may be lying, sitting or hanging in mesh, and normally arms and legs are wide spread or hanging from a surface. The eyes may be open or closed	
Vigilance	Scan environment/alert	Animal rotates its head, looking at or staring at to least two different spatial positions, but without performing any other behaviour. Individual is alert, not in a resting position, normally sitting on the floor or hanging at wire of cages	
	Scan others	Animal rotates its head, looking at or staring at group mates, but without performing any other behaviour. Individual is alert, not in a resting position, normally sitting on the floor or hanging at wire of cages	
Manipulate environment		Animal touches, moves, licks, bites or rubs objects or part of the environment	
Solitary play		Pushing and hanging on a rope, twig, branch, wires	
Others		Urinate, defecate	
Behaviour potentially indicative of stress			
Active	Pacing	Walk or run repeatedly covering the same routine-like circuit inside the enclosure without an obvious goal. This behaviour is commonly described for captive animals, especially carnivores and primates	1,6,7
	Bouncing/rocking	Sitting, the individual shakes his whole body back and forth or sideways, repeatedly, at least twice in sequence, but normally many body shakes that last over 10 sec. In wild tend to occurs after and animal received intense aggression, and is followed by receipt of groom by group mates. In captivity, it may occur without prior aggression. Scream may occur	1,7,8
	Head twirl	The subject turns his head looking sideways and upwards repeatedly (the animal may be stationary or locomotion)	4,6,7,8
	Pirouette	Individual revolves around himself performing a complete 360° rotation, animal may stay in same position or a pirouette may occur during locomotion or pacing	6,7
Self-directed	Self grooming	Animal repetitively manipulates its own fur with the hand or mouth. Includes self-scratching and hair pulling	1,3, 4,5,67,8,9
	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	1,4,5,7

Table 1 (*Continued*)

Macro-category	Behaviour	Description	Reference
Other directed	Ingestion of urine, faeces, sperm	Lick and eating/drinking of urine, faeces and sperm	3, 6, 7
	Masturbation/auto-erotic	The stimulation or manipulation of one's own genitals	1,6
	Salute[b]	Poking or touching a finger into the eye	1
	Self-suckle[b]	Sucking or licking a body part	1
	Self-bite[b]	Biting or chewing a body part	1,2,6,7
	Scream	Animal starts to vocalise loudly without any aggression received or any alarming event in the environment. No bouncing occurs	2,6,7
	Sexual display to humans[c]	Similar to sexual display (see above) but directed towards humans	2,

1: Boinsky et al. (1999a); 2: Boinsky et al. (1999b); 3: Prates and Bicca-Marques (2005); 4: Pomerantz et al. (2012); 5: Sorrentino et al. (2012); 6: Mendonça-Furtado (2006); 7: Uylan et al. (2006); 8 Rimpley and Buchannan-Smith (2013); 9: Van Wolkenten et al. (2006).

[a] Agonism was also registered on an all occurrence basis. States of agonism were used to calculate total proportion of behaviours, events of agonism were used to compute rank of individuals.

[b] Self-suckle and self-bite were rare and could not be easily distinguished from strenuous repetitive self-grooming with mouth, so instances of these behaviours were summed to self-grooming category. Salute was observed only once, and was removed from the analyses.

[c] Sexual displays during females' estrus period were not included in this category.

termites or cleaning of detritus during foraging, but several papers report increased and long bouts of self-grooming or scratching after challenging events, such as after a fight or prior to food distribution (e.g., Dellinger-Ness and Handler, 2006; Sorrentino et al., 2012). Bouncing, crouch and scream tend to be exhibited when an animal loses a conflict (Fragaszy et al., 2004). The other BPIS (pacing, head-twirl, pirouette, repetitive ingestion of urine, faeces or sperm, masturbation and sexual display to humans) are rarely described in wild situations but are behaviour patterns described in captive primates associated with poor welfare, lack of adequate space or cognitive stimulation or imprinting on humans (e.g., Mestripieri et al., 1992; Lutz et al., 2003; Tomsen and Solstis, 2004; Mantuefel et al., 2004; Troisi 2005; Reamer et al., 2007; Birkett and Newton-Fischer, 2011).

We used 10-min blocks of instantaneous sampling for each focal animal, registering at every 30 s the behavioural state of the focal animal (Altmann, 1974). This method offers an estimate of the time allocated to each behaviour but not the exact duration of each bout. This data collection method was employed to allow comparison with other behavioural studies of capuchins (see references in Table 1). Within each group, individuals were observed in random order and a five min interval between observations was imposed to decrease inter-individual dependency in behaviour. All observations were conducted from 10 h to 17 h, circa 30 min after food was distributed to animals to avoid increased sampling of long feeding bouts. Sampling blocks were distributed across a minimum of 4 weeks, and a maximum of two focal animal record blocks per day (one during the morning and one during the afternoon) was imposed to avoid biasing sampling to a limited set of events or momentary states. The mean observation time was 4.2 h per individual, ranging from 1.6 to 8 h. We recorded a total of 39,783 instantaneous samplings of behavioural states, of which 8131 were of BPIS.

A total of 13 observers were trained in filling a protocol for registering activity patterns of animals. Only after reaching an index of inter-observer agreement of 85% with an experienced observer (RGF) could a student proceed to data collection by him/herself (i.e. in a block of 20 instantaneous samples, only 3 samples could be scored differently. This agreement had to be reached for 3 consecutive 10 min blocks, on two consecutive days, during training phase). Animals were allowed two weeks to habituate to the presence of observers before data collection.

2.3. Data analyses

From the instantaneous sampling data we computed the proportion of BPIS states within the overall activity budget of each individual. We also calculated the richness and frequency of BPIS. Richness refers to the number of different BPIS behaviours presented by each individual (hence this value varied from 0 [no BPIS exhibited] to 10 [all BPIS exhibited]). Frequency refers to the total amount of BPIS states presented divided by the total time each individual was observed (Birkett and Newton-Fischer, 2011). These three indices are not necessarily correlated and offer different information. While frequency tells us how often one individual exhibits a BPIS, proportion tells us how much of the activity budget is occupied by BPIS, and richness tell us if the animal exhibits only one type of BPIS or several.

A single value of each index (proportion, richness and frequency) was calculated for each individual over the whole observation period. Sex composition of each group was measured in ordinal scale with three levels depending on whether the group had proportionally more males, more females, or a more equal ratio of sex (see Table 3).

We used Multivariate General Linear Models to test if sex and group sex-ratio influenced the total proportion, richness and frequency of BPIS. As our sample was composed of animals from different areas, with varied rearing conditions, we opted to use resampling procedures to define significance limits, setting bootstrap to 1000 permutations. The identity of animal, group and group size were inserted as random variables. Analyses on social fac-

Table 2
Activity budget of individual states and statistics for effects of sex.

	Feeding	Vigilance	BPIS	Locomotion	Social (+)	Inactivity	Manipulate environment	Solitary play	Others	Social (−)
Mean[a] ($n = 113$)	27.32	25.12	17.72	11.41	10.34	6.18	1.50	0.67	0.19	0.15
SE mean	0.014	0.015	0.015	0.010	0.010	0.09	0.003	0.001	0.00	0.000
Males[a]($n = 59$)	27.43	23.89	17.87	13.74	9.66	5.11	1.44	0.78	0.12	0.23
SE mean	0.020	0.020	0.023	0.017	0.014	0.011	0.004	.001	0.000	0.001
Females[a] ($n = 54$)	27.21	26.41	17.55	8.96	11.04	7.30	1.57	0.55	0.26	0.07
SE mean	0.021	0.021	0.021	0.010	0.015	0.015	0.004	0.002	0.000	0.000

[a] Values are mean proportions of total instantaneous samplings taken per individual. SE = standard error of mean.

Table 3
Group Composition, Observation time, richness and frequency of BPIS per group.

Group	*N*	Male	Female	Sex composition score[c]	Total observation time (h)	Richness	Frequency (number/min)	Month/year observation
1[a,b]	10	4	6	1	26.6	6.8	1.40	March/April 2008
2	7	1	6	1	12.6	2.29	0.55	July–September 2008
3	8	8	0	3	16.32	1.37	0.21	
4	7	6	1	3	15.32	3.85	0.73	
5	7	2	5	1	20	4.43	0.53	
6[b]	10	3	7	1	22	2.80	0.87	October–November 2008
7[b]	10	4	6	1	17.32	2.8	0.43	
8[b]	13	8	5	2	86.66	3.23	0.12	June–August 2009
9[b]	16	10	6	2	86.16	4.00	0.42	
10[b]	14	5	9	1	57.98	2.9	0.21	
11	8	4	4	2	15.62	3.00	0.61	October–December 2012
12	4	2	2	2	9.7	2.25	0.44	
13	5	4	1	3	10.54	2.60	0.47	
14	4	2	2	2	9.5	3.00	0.79	
Total	123	63.00	60.00		406	3.06	0.45	

[a] Group 1 outliers were removed from all analyses.
[b] Groups re-introduced after ending of captive observation period.
[c] Sex composition score (SCs) = males/n individuals in each group. Ordinal scale: 1: $0 < SCs \leq 0.4$; 2: $0.40 < SCs \leq 0.65$; 3: $0.7 < SCs \leq 1$.

tors influencing the expression of BPIS are described elsewhere (Authors, in prep).

To investigate whether and how the 10 BPIS co-occurred across individuals we ran Principal Component Analyses with direct oblimin oblique rotations (since proportion of behaviours are not independent from each other) to extract components. The Kaiser criterion of eigenvalue greater than 1 was used to determine the number of components, and items loading more than 0.5 were accepted in components.

We conducted simple linear correlations to access possible associations between genus normative behaviours and behaviours potentially indicative of stress. All analyses were conducted using IBM SPSS statistics 21, significance was set to $\alpha = 0.05$ two-tailed.

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

3. Results

3.1. Overall occurrence of BPIS and sex differences in the expression of BPIS

Overall, BPIS was the third most frequent behavioural category in the activity budget of the individuals, being sampled in a mean of 17% of all records taken (Table 2). Individuals presented a mean of 3.06 different BPIS at a frequency of 0.45 BPIS per minute (Table 3). Frequency and richness were significantly but weakly correlated ($R^2 = 0.229$; $P = 0.015$). No sex difference was found for the total proportion of time presenting BPIS ($F_{1,113} = 0.100$, $p = 0.753$) or for richness ($F_{1,113} = 2.998$; $p = 0.086$), and there was a significant but weak effect of sex on frequency of BPIS ($F_{1,113} = 5.374$; $p = 0.022$, Partial eta squared = 0.049) with females exhibiting BPIS at a frequency of 0.53 BPIS/min and males at 0.37 BPIS/min. Sex composition of the group did not influence either index: proportion ($F_{2,113} = 0.606$, $p = 0.547$); richness ($F_{2,113} = 0.931$; $p = 0.398$) or frequency ($F_{2,113} = 0.270$; $p = 0.764$). However, there was a significant interaction between sex and sex composition of the group for richness ($F_{2,113} = 6.546$; $p = 0.002$, Partial eta squared = 0.110:), with females in groups with more males exhibiting a richer BPIS repertoire than females in more balanced groups or in groups with more females.

3.2. PCA analysis of BPIS and correlation with GNB

After removal of outliers (i.e., those individuals whose standardized factor regression values were greater than 3), Kaiser-Meyer-Olkin measures (KMO = 0.623) and Bartlett's test of sphericity ($X^2 = 84.280$, $p < 0.001$) indicate adequacy of sampling ($n = 109$). Data reduction analyses using PCA with direct oblimin rotation yielded five factors (Table 4). The mean absolute value of correlation coefficients between components was 0.051 which is lower than the mean component intercorrelations described for personality dimensions in capuchins.

The first factor reflected a high occurrence of pacing and a low occurrence of self-grooming. We labelled this factor Restless. This factor significantly positively correlated to GNB locomotion and agonism given, but negatively to feeding and vigilance (see Tables 4 and 5). A second factor, labelled Self-narcotizing/fear was loaded positively on masturbate and scream. This factor correlated

Table 4
Loading Items on Direct Oblimin rotated components, and variance explained.

	Component				
	Restless	Self-narcotizing/fear	Self-protection	Stereotyped	Help-seek
Pacing	**.839**	–.043	–.275	–.067	–.109
Selfgrooming	**–.813**	–.172	–.319	.099	–.021
Masturbation	–.070	**.754**	–.082	–.237	–.046
Scream	.174	**.740**	.024	.065	.067
Crouching	.005	–.081	**.960**	.024	–.036
Ingestion UFE	–.003	–.065	–.197	**–.696**	–.330
Head-shaking	–.065	–.102	–.097	**.645**	–.203
Pirouette	–.048	–.091	.000	**.439**	–.132
Bouncing	.017	–.161	–.007	–.094	**.787**
Sexual display to humans	–.198	.357	–.006	–.143	**.559**
% Variance explained	15.54	13.35	11.60	10.91	10.52

Table 5
Correlation analyses between BPIS Factors and activity budget states.

	Restless	Self-narcotizing/fear	Self-protection	Sterotyped	Help-seek
	r	*r*	*r*	*r*	*r*
Feeding	**−0.196***	0.06	0.152	0.184	0.066
Vigilance	**−0.194***	0.069	**−0.201***	**−0.318*****	0.17
Locomotion	**0.205***	0.039	0.031	0.031	−0.095
Social positive	−0.147	−0.023	0.099	0.019	−0.109
Inactivity	0.077	−0.037	**0.244***	**−0.244****	0.106
Manipulate environment	−0.082	0.056	−0.055	**0.219***	−0.126
Solitary play	−0.094	−0.04	0.079	0.115	−0.101
Agonism received	0.011	0.012	−0.094	**−0.252****	0.021
Agonism given	**0.213***	**0.262*****	−0.101	**−0.339*****	−0.146

Values in bold indicate significant results.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table 6
Comparison of BPIS factors by sex.

	$F_{1,108}$	P	R^2
Restless	2.437	0.121	0.045
Self-narcotise/fear	0.002	0.966	0.066
Self-protection	0.246	0.611	0.071
Stereotyped	0.688	0.409	0.052
Help-seek	1.531	0.219	0.096

significantly and positively to agonism given. A third factor loaded strongly on crouch and was labelled Self-protection. This factor significantly positively correlated with inactivity and negatively with vigilance. The fourth factor, labelled Stereotyped, was characterised by high loading on head-shaking and pirouette, low-loading on ingest UFE, and correlated positively to manipulate environment, and negatively to vigilance, inactivity, agonism received and agonism given. A final fifth factor was labelled Help-seek and loaded strongly on bounce and sexual display to humans. No sex effect was found on the components of BPIS (Table 6)

4. Discussion

In this work we recorded 10 behaviours that are potentially indicative of stress (BPIS) in a sample of 123 captive capuchin monkeys. We found them to comprise one fifth (mean of 17%) of an individual's activity budget. Individuals exhibited a mean of three different types of BPIS at a rate of one BPIS at every two minutes. The proportion of BPIS is similar to that described for captive groups occupying similar sized areas (BPIS occupied 10% of scans in a captive *S. apella* group of 12 animals studied by Uylan et al., 2006); lower than that described for single housed capuchins (Boinksy et al., 1999 describes 54% of instantaneous scans with BPIS taken in eight single housed capuchins—*S. apella*), and much higher than that observed in wild or reintroduced capuchins, in which stress related behaviour such as scream and bouncing compose less than 1% of the activity budget (Ferreira et al., 2008; Verderane, 2010).

The existence of sex differences in presentation of BPIS is equivocal. For example, Nash et al. (1999) reported sex differences in a large sample ($N = 268$) of captive chimpanzees, whereas Birkett and Newton-Fischer (2011) report a lack of sex differences in 40 zoo kept chimpanzees. Bowers et al. (1998) identified five reactive and 10 proactive animals in a sample of 16 longtailed monkeys (*Macaca fascicularis*), but no sex differences were detected. We found no sex difference in the proportion and frequency of BPIS in our sample of over 100 animals, but females housed in male biased groups exhibited a more rich BPIS repertoire than males or females in female biased or sex-balanced groups. If BPIS are related to behavioural styles, this general lack of sex difference was expected given the absence of major sex differences in personality dimensions described in captive *S. apella* (Uher et al., 2013).

Identifying differences in reaction to stressful circumstances is a necessary first step for further research on the cumulative stress supported by individuals when they face environmental changes or relocation attempts (Mcdougal et al., 2005; Teixeira et al., 2007; Winfield, 2013). Notwithstanding their adaptive relevance, behaviours that indicate attempts to cope with stress (ideally) occupy a minor part of an individual's time and are not the predominant categories in animals activity budget, hence, they are difficult to study in the wild. Besides, greater plasticity at species and individual level in behavioural profiles is expected in long-lived, highly cognitive species that occupy diverse biomes and that exhibit high social behaviour learning, such as capuchin monkeys (Dukas, 2013).

Our PCA analyses detected five components summarising variation in BPIS between individuals, two of which may be related to the two basic coping strategies described in several other species (Koolhaas et al., 1999, 2010): Restless, characterised by high pacing (a routine like movement), low self-grooming, and a positive correlation with locomotion and aggression given, may reflect the Proactive coping strategy; Self-protection, characterised by high proportion of crouching behaviour, correlated to high inactivity and low vigilance, may reflect the Reactive coping strategy.

However, in addition to these potential proactive/reactive coping styles, our PCA analysis indicated the existence of three other components that could represent other types of coping response in these captive capuchins: Stereotyped, Self-narcotizing/fear, and Help-seek.

Ijichi et al. (2013) propose that stereotypic behaviour is a second step in a proactive coping response to chronic suboptimal environment. In their attempt to avoid an uncontrollable stressor, proactive individuals may become stuck in a fixed sequence of behaviour that is self-rewarding. Reactive individuals are less likely to exhibit the active responses that may develop into stereotyped behaviour and may instead try to cope with chronic stress by decreasing their perception of and vigilance for triggering stimuli and, when failing to cope, might develop a "learned helplessness" depression-like state. Our analysis did not group stereotypic head-twirls and pirouette with pacing which is more characteristic of a proactive coping strategy. Pomerantz et al. (2012) found that head-twirls, but not pacing, predicted pessimistic judging bias in ambiguous test, which is a cognitive index for poor-welfare. Whether stereotypy is a second step in the coping strategy of proactive animals or a different form of reaction requires further analyses.

With respect to Self-narcotizing/fear and Help-seek, Fragaszy et al. (2004) describe that masturbation is a rare behaviour both in captivity and in wild (although they did not offer rates). In our sample we detected a mean frequency of one masturbation record at every 2 h. These authors also report that sexual displays can occur outside sexual context, with capuchins presenting eye brow raising, head tilt and chest rubbing after a fight and during reconciliation. It is possible that the sexual behaviour directed at humans (a component of the help-seek factor) may indicate an affiliative display with calming effects similar to the observed between capuchins themselves.

Although we found five dimensions that could be labelled as coping responses, it is not possible to map them simply onto the five personality dimensions previously identified in capuchins (Manson and Perry, 2013; Morton et al., 2013a,b). For example, high aggression is characteristic of the Extroversion/Assertive personality dimension, however, both Restless and Self-narcotizing/Fear were positively correlated to high agonism given. Self-protecting animals presented low vigilance which is typical of both Openness and Sociable personality dimensions. Manipulate the environment was positively correlated with the Sterotyped component, a trait found in Assertive dimension, but close to innovative and persistence items of the Openness dimension. Increased vigilance, found in Neurotic dimension, marginally correlated to Help-seek BPIS, but increased vigilance is also found in the Creative and Curious items on Openess and Sociable personality dimensions. While it is suggested that personality dimensions correlate to predisposition to certain types of psychopathology (Cavigelli, 2005; Capitanio, 2010) further investigation is needed to evaluate whether individual differences identified here do or do not map on to stress-induced coping strategies in animals.

Nonhuman primates have been used as models for psychiatric disorders for many decades (Nelson and Winslow, 2009). In a study of captive chimpanzees Brune et al. (2006) compared nonverbal cues, such as expressions, body postures and behaviors, with descriptions of the catalogue of human diseases, and found similarities with depression, anxiety, eating and post-traumatic disorders. They argue that studies of these abnormal behaviors in primates and other species will substantially promote understanding of mental well-being, therapy, and prevention of psychopathology in humans. However, Boyle et al. (2008) argue that behaviour is a surface trait, and that there is a need to find the source trait (eg. physiology) of the different coping strategies. The matching of BPIS and other physiological indices of stress (e.g. cortisol) has long been a problematic issue (Broom, 1991; Mason and Rushen, 2006). Part of this mismatch can be attributed to between-individuals differences in stress coping strategies. The possibility that there are a number of different ways of responding to challenging situations should be taken into account when searching for behavioural, physiological or cognitive stress related indices, and their consequences for successful coping with challenges.

5. Conclusion

We identified five components of stress related behaviors in a large sample of capuchin monkeys housed in captive conditions. Two of the patterns resemble the two coping strategies described in several other species (Restless/Proactive and Self-protection/Reactive), and could reflect a basic dichotomy in stress-reactivity that is conserved across species. We also detected three other components: Self-narcotize/fear, Sterotyped and Help-seek. No sex differences in these components was found. Although we tried to spread our observations over a 4 week period, further work is required to establish the cross-time, cross-context stability of the BPIS observed in this study. Whether these five strategies vary in robustness, responsiveness and resilience in coping with stress in the wild, whether other species also show a varied set of strategies that goes beyond the Proactive/Reactive axis, whether this relates to plasticity in behaviour and cortical development, and what the physiological and cognitive correlates of these coping strategies are remain questions for further research.

Conflict of interest

The author declare there is no conflict of interest.

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