Personality traits modulate stress responses after enclosure change of captive capuchin monkeys (Sapajus libidinosus)

Vitor Hugo Bessa Ferreira, Elanne de Paiva Fonseca, Ana Cecilia Correia Santos das Chagas, Luiz Guilherme Mesquita Pinheiro, Maria Bernardete Cordeiro de Sousa, Hélderes Peregrino Alves da Silva, Nicole Leite Galvão-Coelho, Renata Gonçalves Ferreira

Personality traits modulate stress responses after enclosure change of captive capuchin monkeys (*Sapajus libidinosus*)

Vitor Hugo Bessa Ferreira[1,2,3*], Elanne De Paiva Fonseca[1], Ana Cecilia Correia Santos Das Chagas[1], Luiz Guilherme Mesquita Pinheiro[1], Maria Bernardete Cordeiro de Sousa[1,4], Hélderes Peregrino Alves Da Silva[1], Nicole Leite Galvão-Coelho [1], Renata Gonçalves Ferreira[1*].

1. Department of Physiology and Behavior, Psychobiology Graduation Program, Federal University of Rio Grande do Norte, Caixa Postal, 1511, Natal, RN 59078-970, Brazil
2. Yncréa Hauts-de-France, ISA Lille, 48 bd Vauban 59046 Lille Cedex, France
3. INRAE, CNRS, IFCE, Université de Tours, Centre Val de Loire UMR Physiologie de la Reproduction et des Comportements, 37380 Nouzilly, France
4. Brain Institute, Federal University of Rio Grande do Norte, Central Campus, 3000 -Natal, RN 59078-970, Brazil

Corresponding Authors:

Renata G Ferreira and Vitor H B Ferreira

Email: renata.ferreira@pq.cnpq.br; vitor@zootecnista.com.br

Depto. de Fisiologia & Comportamento – PPg em Psicobiologia

Centro de Biociências – Universidade Federal do Rio Grande do Norte

Av. Senador Salgado Filho, 3000 Campus Universitário

Natal, Rio Grande do Norte, Brasil

ZIP code: 59. 078-970

PO Box: 1511

Phone: + 55 84 3215-3409

Fax: + 55 84 3211-9206

ABSTRACT

Husbandry procedures may cause behavioral and physiological changes to animals living in captivity. However, an individual´s reaction is not uniform and may be related to different coping strategies. In this study, we analyzed whether and how 12 adult captive capuchin monkeys (*Sapajus libidinosus*) varying in four personality axes ('Feeding', 'Sociability', 'Exploration', and 'Activity') differed in their stress responses to an enclosure change. Behavioral data and fecal samples of the individuals were collected for two months before (97 h and 246 fecal samples) and 14 days after the enclosure change (52 h and 666 fecal samples). We used Akaike Information Criteria to select the best linear regression models having personality axes and the period after enclosure change as predictive factors and behaviors potentially indicative of stress (BPIS) and levels of fecal glucocorticoid metabolites (FGM) as the response variables. Best models indicate that specific personality axes acted as a buffer and improved individual stress coping, mainly at the physiological level. More sociable and more active individuals did not show the peak of FGM levels as that exhibited by their less sociable and less active counterparts on the first day of the enclosure change. The link between exploration and resilience to acute stress was less clear: more exploratory individuals showed an increase in FGM levels during the first week of enclosure change, while the less exploratory ones showed a later increase, during the second-week post-enclosure change, suggesting a lesser capacity to recover from stressful stimuli in these individuals. The results presented in this study build on growing literature showing that animals differ in their behavioral profiles and that these differences relate to resilience to environmental disturbances, which may impact individual survival and reproduction, resulting in less genetic diversity of captive colonies and increased issues related to research replicability. We argue that these interindividual differences must be considered in husbandry decisions and during research data collection for the sake of animal welfare and reliable science.

Keywords: Animal personality; Animal welfare; Captivity; Enclosure change; Individual differences; Primates.

1. INTRODUCTION

Captive animals are usually subjected to several husbandry procedures that have been demonstrated to result in both behavioral and physiological changes, indicative of distress (Morgan and Tromborg, 2007). One common procedure is the enclosure change of individuals or whole groups for practical or experimental purposes, which forces animals to cope and adapt to new environments (Kuehnel et al., 2012; Matheson et al., 2005). Enclosure change of rhesus monkeys (*Macaca mulatta*) may, for example, increase heart rate, growth hormone levels and leukocyte responses (Balcombe et al., 2004). Leopard cats (*Felis bengalensis*) moved to new cages also showed marked changes in cortisol levels and signs of behavioral arousal, such as increased stereotypic pacing and higher frequencies of hiding (Carlstead et al., 1993). These impacts on animal behavioral and physiological functioning may, in turn, influence research outcomes, as the time for each species to come back to baseline values may vary greatly: for Tonkean macaques (*Macaca tonkeana*), enclosure change stress induced faecal cortisol increase, but hormone levels were back to baseline only a few days after enclosure change (Cinque et al., 2017). On the other hand, for common marmosets (*Callithrix jacchus*), the impacts can be long-lasting: Kuehnel et al. (2012) detected elevated faecal cortisol, decreased lymphocyte count, and 3% weight loss, up to four weeks after enclosure change, suggesting that this time was not enough for animals to recover.

Besides between-species differences, individual characteristics also interfere with how an animal copes with stress. In their classical studies, Koolhaas et al. (1999) showed that when individual laboratory mice and rats react to stress, they may exhibit two stress-coping strategies. One, labeled "proactive," refers to a more aggressive and active reaction. These individuals are prone to the development of behavioral routines, thriving in more stable environments. On the other hand, individuals displaying the "reactive" strategy display more avoidance behaviors, are more inactive, and more prone to act flexibly due to its high attentional state to environmental changes. At the physiological level, proactive individuals, unlike reactive ones, exhibit a weak activity and reactivity of the hypothalamic-pituitary-adrenal axis (HPA) showing low corticosterone levels, but a strong reactivity of the sympathetic nervous system, associated to a higher release of catecholamines

(norepinephrine and adrenaline). Although these two strategies are different at multiple levels, they have both the same aim: allow the animal regain control over the stressful situation (Koolhaas et al., 1999). Subsequently, Koolhaas et al. (2007) considered the covariation between the behavioral and physiological axes that make up the stress response, designing a two tier model with coping style and emotionality as two independent dimensions, drawing four response profiles : docile, shy, bold and panicky.

Beyond the proactive-reactive axis, other dimensions of individual differences (or personality traits) may influence the individual reaction to stress. African elephants (*Loxodonta africana*) scoring high on the 'fearful' component exhibited higher morning salivary cortisol than those scoring high for the 'sociable', 'effective' and ‘aggressive’ components (Grand et al., 2012). More explorative and playful capuchin monkeys showed less cortisol reactivity in response to being separated from the group compared to their less explorative and playful counterparts (Byrne and Suomi, 2002). Individual differences were also found in captive Diana monkeys (*Cercopithecus diana*) when exposed to a high density of zoo visitors, with some individuals displaying more behaviors potentially indicative of stress (BPIS). Other individuals, in contrast, increased the display of positive behaviors, such as playing, evidencing different patterns of behaviors through which individuals cope with stress (Barlow et al., 2007).

Primates in zoos, aquariums, or wildlife rescue centers may be relocated several times during their lifetime, both within and between different establishments (Matheson et al., 2005). These relocations are not without consequences for the individuals and are known to increase the exhibition of BPIS, such as self-injurious and self-abuse behaviors, and the levels of stress hormones (Davenport et al., 2008; Gottlieb et al., 2013; Linden et al., 2018; Rommeck et al., 2009). In Europe, most of the captive capuchin monkeys (*Sapajus spp.*) in zoos were relocated to different places at least once in their lives, reaching up to five changes for a single individual (Dufour et al., 2011). According to Levacov et al. (2011), between 1996 and 2006, in Brazil alone, 4631 primates were sent to CETAS (Wild Animal Rescue Center), of which approximately 1301 (28.1%) of these were of the *Sapajus* genus. The frequent arrival of individuals in these centers, the formation of new groups, and the

112 relocation of groups or individuals is, therefore, a customary activity that may impact individual
113 welfare significantly.
114 The current literature on capuchin monkey enclosure change indicates significant changes
115 when individuals face a novel environment. These changes included mainly increased resting, social
116 proximity and social behaviors, compared to the period pre-enclosure change (Dufour et al., 2011;
117 Matheson et al., 2005). However, these studies did not consider physiological changes, nor possible
118 influences of between-individual differences in coping with stress. In an earlier experiment (Ferreira et
119 al., 2018), we showed that captive capuchin monkeys differed behaviorally along four axes of genus-
120 normative behavioral patterns (GNB). These GNB axes were labeled: 'Feeding', 'Sociability',
121 'Exploration', and 'Activity'. 'Sociability' and 'Exploration' were related to lower basal fecal
122 glucocorticoid metabolite (FGM) levels. 'Activity' correlated to higher basal FGM levels. 'Activity'
123 was also related to the type of BPIS exhibited with more active individuals performing more short-
124 duration BPIS, while less active individuals performed more long-duration BPIS. In the present study,
125 we took advantage of a planned within-facility enclosure change of animals studied in Ferreira et al.,
126 2018, and we analyzed whether and how individual captive capuchin monkeys (*Sapajus libidinosus*)
127 with different personalities react behaviorally and physiologically to being moved to a new enclosure.
128 Based on the coping styles literature and previous studies on capuchin monkeys (Byrne and Suomi,
129 2002; Ferreira et al., 2018; Koolhaas et al., 1999), we predicted that less active, less sociable and less
130 explorative individuals would be more impacted by the enclosure change, with an increase in both
131 BPIS exhibition and FGM levels, compared to their more active, more sociable and more explorative
132 conspecifics.
133
134 ## 2. METHODS
135
136 ### 2.1. SUBJECTS AND HOUSING
137
138 Our study comprised two groups of capuchin monkeys (*Sapajus libidinosus*) under the care of
139 the Wildlife Rescue Center (CETAS) of Cabedelo, in the state of Paraiba, Brazil. Group A contained

nine adult individuals (six males and three females), and Group B contained six individuals, four adults (two males and two females), and two juveniles (one male and one female). Only 12 adult individuals, out of the 15 animals initially available, were included in the analyses. Data from the two juveniles were not collected, and one adult female from Group B was housed individually after enclosure change and was therefore excluded from our analysis.

The environment provided to both groups was similar: barren, non-enriched enclosures of equal size (4.60 m x 3.15 m x 2.40 m), with concrete floor and barred walls allowing an outside view, and limited presence of humans (only caretakers and researchers had contact with these animals). Individuals were identified by their physical characteristics (color, size, and shape of the head and body). The exact age, the origin of the animals, and the amount of time each animal spent in these environments could not be determined; therefore, these parameters were not considered for analyses.

2.2. BASELINE DATA COLLECTION

Behavioral and physiological baseline data of adult individuals were collected three workdays per week, over two months before group enclosure change. The collection of data followed the same procedure as (Ferreira et al., 2018): 'focal animal' method (Altmann, 1974), with two 10-minute sessions, one in the morning and one in the afternoon, per individual and records at every 30-second intervals, totaling 40 daily behavioral records (states) per animal. In this study we focused only in BPIS. The BPIS were divided into two types: states (behavior lasting more than 5s: “Pacing”, “Self-grooming”, and “Crouching/self-clasp/huddle”) and events (behavior lasting less than 5s: “Head twirl”, “Pirouette”, and “Self-scratching”). Four BPIS could be described as either states or events, depending on their duration (“Boucing/rocking”, “Ingestion/Manipulation of urine, feces, and sperm”, “Masturbation/auto-erotic”, and “Sexual Display to humans”, see full BPIS ethogram in Tables 1). BPIS events were quantified in 'all occurrences', that is, every event of selected behaviors was recorded within the 10 min focal sampling.

(Table 1 about here)

All occurrences of agonistic behaviors between all individuals (focal and/or non-focal individuals), and the identity of participants, were recorded in order to calculate the dominance hierarchy for each group. The daily observation started 30 minutes after the meal to avoid biased data for food-related behavior, from 08:00 to 17:00, approximately. The total time of behavioral collection was of 78 hours in Group A and 19 hours in Group B (Mean Group A: 8.6 hours/individual; Mean Group B: 6.3 hours/individual).

In a previous experiment (Ferreira et al., 2018), to determine captive capuchin monkey personality axes, behavioral data on 12 genus normative behaviors (GNB, see the full GNB ethogram in Table S1 in the supplementary material) from 25 captive capuchin individuals (including the two groups that were submitted to enclosure change) were analyzed through a principal component analysis (PCA), generating four components labeled 'Feeding', 'Sociability', 'Exploration', and 'Activity' (see Table S2 in the supplementary material for the PCA structure matrix, its components and the explained variance). Each individual received a score within each component (regression method). The scores for our 12 relocated individuals were subsequently used for enclosure change analyses (see Data analysis section).

The fecal collection was conducted opportunistically (morning and afternoon) at least three times per week, during the behavioral observation. After seeing the defecation and identifying the individual, the researcher entered the enclosure and collected the fecal samples within two hours after defecation. The feces were packed in Eppendorf tubes and identified by the name of the animal, time of defecation, time of collection, and date. Samples were frozen at −5 °C within two hours after defecation until analyses (Ferreira et al., 2018). In total, 246 samples of feces from 12 adult monkeys were collected (average of 20.5 samples per individual). Data analysis on the large sample size (25 individuals) did not show circadian variation in FGM levels across the day (Ferreira et al., 2018).

2.3. ENCLOSURE CHANGE DATA COLLECTION

Due to enclosure renovation, the groups were relocated to new enclosures within the same

196 facility on January 16, 2016, between 6:30 and 7:30 am. Individuals were captured one by one by a
197 caretaker using a net and were immediately released into the new enclosures (less than 30 m apart).
198 These new enclosures were of the same size for both groups (4.65m x 2.30m x 2.63m) and, similar to
199 the previous enclosure, they were barren and non-enriched. The behavioral observation was performed
200 over the next 14 days (with the exception of the third day post-enclosure change, which was excluded
201 due to heavy rain) in the new enclosure, and similarly to the first period, the adult animals were
202 observed 10 minutes in the morning and 10 minutes in the afternoon. As the time to peak FGM
203 excretion after a stressful incident can vary 1.5–8.5 h among captive capuchin monkeys (Mendonça-
204 Furtado et al., 2017), fecal sample collection on the first and second days of the enclosure change
205 started from 7:30 am and ended by 6:00 pm. From the fourth day and until the end of the second week,
206 fecal sample collection occurred between 8:00 am and ended by 3:00 pm.
207 This phase comprised a total of 52 observation hours, with an average of 4.3 observation hours
208 per individual and a total of 666 fecal samples was collected, averaging 55.5 (±8.79) samples per
209 animal.
210
211 **2.4. GLUCOCORTICOID METABOLITES MEASUREMENT**
212
213 The protocol for glucocorticoid metabolite analyses followed the same procedures as
214 described in (Ferreira et al., 2018), following the methods of (Munro and Stabenfeldt, 1984) and
215 (Sousa and Ziegler, 2000) and previously validated for this species based in (Mendonça-Furtado et al.,
216 2017). Intra and inter-assays coefficient of variation (CV) for high and low concentration pools were
217 2.58% and 1.47%, and 19.09% and 16.76%, respectively (n= 19 plates). Intra and inter-assays CV for
218 high and low concentration pools were 1.7% and 1.8%, and 18.25% and 16.66%, respectively (n= 27
219 plates). Additional comparisons of pool values pre- and post-enclosure change showed that fecal
220 samples in both conditions were similarly measured, intra and inter-assays CV for high and low
221 concentration pools were 1.7% and 2%, and 18.92% and 19%, respectively (n= 46 plates).
222
223

2.5. DATA ANALYSIS

For statistical analyses, all BPIS events were summed together to form a single variable (Total Event BPIS henceforth). The same was done for all BPIS states (Total State BPIS henceforth). The 12 adult individuals were separated into two equal groups of six individuals based on the regression scores of each personality axis, above and below median values on each component (Table 2) having a high value meaning that the component fits the individual adequately. For example, 'Sociability' was positively composed of 'Grooming', 'Social play' and 'Sexual display', and negatively composed of 'Scan environment/Alert'. Thus, an individual scoring high for 'Sociability' exhibits a high frequency of social behaviors and are less alert towards its environment than individuals scoring low in this axis.

(Table 2 about here)

The dyadic events of agonism were used to calculate the dominance hierarchy using the SOCPROG 2.4 software (Whitehead, 2008), and the dominance index used was the MDS (Modified David's Score) (De Vries et al., 2006).

Individual FGM values were compiled into four indices to analyze the impact on stress physiology: median, mean, maximum, and minimum (Ferreira et al., 2018). All outliers (values more than three interquartile ranges) within each variable were excluded in order to obtain a more reliable database.

According to previous literature on animal enclosure change and capuchin monkeys FGM analyses (Cinque et al., 2017; Mendonça-Furtado et al., 2017; Watson et al., 2005), the FGM repeated measures were assessed in four different periods, named baseline (before enclosure change), day 1, week 1 (from day 2 to day 7) and week 2 (from day 8 to day 14) after the enclosure change. When necessary, variables were log-transformed, and normality of residuals was checked using the Shapiro-Wilk test.

In a first step, to verify for overall impacts of enclosure change, without taking into account individual differences, we ran linear mixed models (LMM, 'lmerTest' R package) for each of our

252 FGM and BPIS variables including, as fixed factors, only 'period' (baseline, day 1, week 1 and week
253 2), 'group' (A and B), 'sex' (male and female) and 'dominance', as well as all possible two-way
254 interactions with 'period'. For each variable studied (FGM and BPIS), we created eight different
255 models. The simplest model contained only period, and the most complex model all the fixed factors
256 and their interactions with the period. Final models were selected based on Akaike's Information
257 Criterion (AIC): when the difference between AIC models was equal or lower than 10, we choose the
258 model with fewer variables (Burnham et al., 2011). The second step was to verify enclosure change
259 impacts on different personalities: BPIS and FGM variables were then reanalyzed based on the model
260 chosen on the first step, and each of the GNB axes (Feeding, Sociability, Exploration, and Activity)
261 were then included, one-by-one, as well as two-way interactions between each GNB axis and Period.
262 As our main interest were these interactions, significant main effects of Period or GNB axis only,
263 within these models, were not considered. The subject ID was included as a random factor in all
264 models. When interactions or main effects were significant, *post hoc* ANOVA comparisons of
265 estimated marginal means ('emmeans' R package) were carried out with Tukey adjustment. All
266 analyses were conducted using R version 3.6.1. Statistical significance was accepted at $p \leq 0.05$ and
267 trends at $p < 0.09$. Results are presented as raw mean ± standard deviation.
268
269 ## 3. RESULTS
270
271 All models and their AIC can be found in the supplementary electronic material (Table S3).
272 The selected best models for both first and second step analyses can be found in Table 3.
273
274 (Table 3 about here)
275
276 ### 3.1. OVERALL IMPACTS OF ENCLOSURE CHANGE
277
278 Independent of individual sex, dominance rank, and group, the enclosure change period tended
279 to impact the exhibition of Total State BPIS, but not Total Event BPIS (Figure 1a, Table 3). Post-hoc

analysis showed a trend for an increase in the display of Total State BPIS on the first day of enclosure change compared to baseline ($F_{3,36} = 2.33$, $p = 0.08$, Figure 1b).

Enclosure change period affected significantly median ($F_{3,34.081} = 7.21$, $p < 0.001$), maximum ($F_{3,36} = 7.29$, $p < 0.001$), and minimum ($F_{3,32.403} = 10.85$, $p < 0.001$), but not mean FGM values ($F_{3,34.296} = 1.02$, $p = 0.39$, Figure 2a, Table 3). Post-hoc analysis on the median and minimum FGM revealed values increased significantly on the first day of enclosure change, returning to baseline since Week 1 (Figures 2b and 2c). Maximum values, on the other hand, increased significantly only from Week 1, compared to Baseline and Day 1, returning to baseline on Week 2 (Figure 2d).

(Figure 1 and 2 about here)

4.1. INDIVIDUAL DIFFERENCES IN REACTION TO ENCLOSURE CHANGE

Although we found a significant interaction between Period and Activity influencing Total Event BPIS ($F_{3,36} = 4.36$, $p = 0.01$), *post-hoc* analysis of these interactions did not reveal any differences between periods, nor between more and less active individuals. No significant interaction was found between the period and the other three GNB axes for BPIS events or Total State BPIS (Table 3).

The FGM mean levels were not affected by any of the interactions between the Period and the four GNB axes ($p > 0.05$). There was an influence of the interaction between Period and Sociability on FGM median values ($F_{3,33.967} = 4.26$, $p = 0.01$). *Post-hoc* analysis showed that less sociable individuals presented higher FGM median levels during the first day of enclosure change than more sociable ones, and then returned to baseline within Week 1. This peak and fluctuation were not observed in more sociable animals (Figure 3a). These results were similar for the influences of interaction between Period and Activity on FGM minimum values ($F_{3,32.056} = 5.71$, $p < 0.01$). On the first day of the enclosure change, more active animals showed lower FGM minimum levels compared to less active individuals. Less active animals showed an FGM peak on Day 1 but returned to baseline from Week 1 (Figure 3b). FGM maximum values were influenced by the interaction between Period and

Exploration ($F_{3,36} = 4.86$, $p < 0.01$). For more exploratory individuals, maximum FGM values peaked on Week 1 after the enclosure change, returning to baseline during Week 2, while for less exploratory individuals, FGM levels peaked only at Week 2 (Figure 3c).

(Figure 3 about here)

4. DISCUSSION

Our study shows the existence of marked behavioral and physiological changes resulting from enclosure change, which corroborates previous results found in the literature of capuchin monkeys (Byrne and Suomi, 2002; Dufour et al., 2011; Matheson et al., 2005). However, the acute stress of enclosure change seems to be perceived differently for different individuals, which supports findings on the relationship between animal personality and stress susceptibility (Cavigelli, 2005; Koolhaas et al., 1999).

Unlike Dufour et al. (2011), who did not found differences in the BPIS exhibition before and after relocating a group of captive capuchin monkeys, our animals tended to spend more time exhibiting BPIS on the first day of the enclosure change. This increase corroborates the idea that some unusual behaviors, mainly stereotypies, are signs of stress, with animals reverting to self-directed and/or repetitive behaviors in an attempt to cope with or divert focus from an unpleasant situation (mantra-like effect - Mason, 1991; Mason and Latham, 2004), in our study, the enclosure change. The decrease in BPIS to baseline in Weeks 1 and 2 after enclosure change, however, does not mean lack of stress, since increases in FMG levels were detected up to 2 weeks after enclosure change. It is possible that individuals have turned to other ways of coping with the enclosure change stress, such as increasing grooming or spending more time in proximity to other group members (Dufour et al., 2011; Matheson et al., 2005). Alternatively, as BPIS in captivity develop mainly in response to chronic physical and social stress (Mason, 1991), they may not be the best indicator of an acute stress response.

In our previous study (Ferreira et al. , 2018), which included these same two groups, we showed that more sociable individuals present lower basal FMG levels than less sociable groupmates. This personality trait seems also to confer greater resilience to the acute stress to face enclosure change. In the present study, more sociable individuals did not show the peak of FGM levels that was exhibited by their less sociable counterparts on the first day of the enclosure change. Affiliative behaviors in animals may act as a buffer against stress, by the action of oxytocin in reducing the activation of the HPA axis (DeVries et al., 2003; Quirin et al., 2011), which may explain the physiological stability presented by more sociable animals. The level of sociability is also related to the amount of aggression an individual receives: under stressful situations, less sociable monkeys may be specifically targeted for aggression, while under low stress, predictable situations, they receive the same or lower amounts of aggression compared to more sociable individuals (Boyce et al., 1998), which offers a further explanation of why our less sociable captive monkeys may be facing increased enclosure change stress.

Our previous study also showed that more active individuals have higher FGM maximum levels, and that activity was related to the exhibition of stress behaviors, with more active individuals being more stereotyped than less active ones (Ferreira et al., 2018). Here, more active individuals, similar to the more sociable ones, were less impacted by the enclosure change, showing less fluctuation of minimal FGM levels compared to less active individuals. These more active and stereotyped individuals fit well within the proactive coping style concept (Ijichi et al., 2013). Therefore, the proactive individuals from Koolhaas et al., (1999) and our active animals are expected to share common physiological traits, such as a low HPA reactivity when facing stress, expressed by low corticosterone release. The greater stability in minimum FGM levels of the most active individuals when compared to the least active ones, detected in the current study, was therefore expected and is in line with our initial prediction.

Studies suggest that exploratory behavior indicates an individual's higher adaptive capacity to its environment (Smith and Blumstein, 2008). Positive correlations between survival after reintroduction and exploration were described in voles (Banks et al., 2002) and Sprague-Dawley rats (Cavigelli, 2005). More innovative, active, and curious capuchin monkeys attain better performance in

363 positive reinforcement training (Morton et al., 2013). For juvenile capuchin monkeys, Byrne and
364 Suomi (2002) found a negative correlation between exploratory behavior and cortisol reactivity
365 between two months and four years of age. Our analyses suggest that the link between exploration and
366 resilience to acute stress is not clear. More exploratory individuals showed an increase in FGM levels
367 during the first week of enclosure change, while the less exploratory ones showed a later increase
368 occurring only during the second week post-enclosure change. One possibility is that less explorative
369 individuals employed a more delayed strategy ("shy" type), therefore managing the stress of a new
370 environment later than the more explorative individuals, which seemed to exhibit a "bold" strategy
371 (Ferrari et al., 2013). An acute stress response is essential for individual adaptation and beneficial for
372 healthy animals (McEwen, 2005). The delayed response of less exploratory could be the start of a
373 chronic stress response, suggesting that these individuals have an inefficient capacity to recover from
374 stress, which characterizes a susceptible profile. A longer observation is required to confirm this
375 hypothesis. Another possibility is that, since the pre- and post-enclosure environments were barren,
376 non-enriched, and did not offer anything new for individuals to explore and cope with the enclosure
377 change procedure, this component may not be adequate to describe and differentiate individuals in
378 these particular conditions.

379 It is important to state that, although individual differences are accentuated during periods of
380 environmental change (when individuals try regain control over the changing situation), highly
381 stressful situations may constraint behavioral and elicit similar responses from most individuals (Caspi
382 and Moffitt, 1993). Offering individuals ways to cope with stress within their enclosure through
383 environmental enrichment, for example, may reduce the enclosure change stress and allow more
384 different and nuanced responses between individuals (Benaroya-Milshtein et al., 2004; Carlstead and
385 Shepherdson, 2009).

386 To further understand the influences of personality in coping with stressful situations in
387 captivity, it is essential to consider that individuals vary along with multiple personality traits. As the
388 four components of personality here analyzed were independent and not significantly correlated
389 (Ferreira et al., 2018), we analyzed them separately. However, the same individual may score high in
390 sociability and activity, and low in feeding and exploration, for example. Future analyses with larger

samples may allow comparisons of multiple personality axes simultaneously and offer a complete picture of the phenomena.

Our results also show the importance of looking at physiological data from different perspectives, beyond the mean, since we would not have noticed any change in the animals' physiological reactions if we had considered only the FGM mean values. In contrast, by considering only FGM median and minimum values, we would be led to think that these stress responses were limited to the day of the enclosure change, as it was the case for some primates (Cinque et al., 2017; Watson et al., 2005). However, FGM maximum values showed that, for different personalities, stress might last to up to two weeks.

Reactivity to stress mainly involves the HPA axis and the sympathetic system, and these two systems can be activated differently depending on phenotypic characteristics, sex, age and nature, and context of the stressor. Therefore, during the stress response, both can be activated, or only one of the two, or both may not show significant activation (Godoy et al., 2018; Joëls and Baram, 2009). In this way, the investigation of the two systems simultaneously can bring better assessments of the response profiles in mammals in the face of the challenges to which they are submitted. Thus, as the consideration of only one physiological index may lead to misleading conclusions, we recommend researchers to use different indices as well as other variables when analyzing physiological data related to a stress response.

The results presented in this study build on growing literature showing that animals differ in their behavioral profile and that these differences relate to resilience to environmental disturbances (Smith and Blumstein, 2008; Wingfield, 2013). More sociable and more active individuals seem to cope better with this type of husbandry stress, while the enclosure change of less sociable and less active individuals should be avoided or differently managed since they are significantly impacted. These interindividual differences in personality and stress coping styles of captive animals affect survival and reproduction, which may impact the genetic diversity of captive colonies, particularly those of endangered species (Watters and Powell, 2012; Wielebnowski, 1999).

Finally, within the scientific scope, the loss of genetic variation and the disappearance of more vulnerable individuals due to stressful conditions can lead to an involuntary standardization of the

animals studied. A high standardization and low within-experiment variation are one of the factors pointed out as responsible for the low reproducibility and translational failures of animal experimentation, since it may result in findings that are statistically significant but not easily generalized to experiments in different conditions (Richter, 2017). Since individual differences may affect research validity, reliability, and replicability (Koolhaas et al., 1999), husbandry decisions and research data collection need to take them into serious consideration for the sake of animal welfare and reliable science.

ACKNOWLEDGEMENTS

We thank the CETAS Cabedelo for permission to work within their facilities and for all logistical support during data collection. VHBF was supported by a postgraduate scholarship from the Brazilian National Council for Scientific and Technological Development - CNPQ - during this research (133216/2015-2). This research was funded by CNPq Universal (4403041-2014-8) and Fundação Grupo Boticário (0973-2013.1) to RGF.

434 **BIBLIOGRAPHY**

435

436 Balcombe, J.P., Barnard, N.D., Sandusky, C., 2004. Laboratory Routines Cause Animal Stress. J. Am.
437 Assoc. Lab. Anim. Sci. 43, 42–51.
438 Banks, P.B., Norrdahl, K., Korpima, E., 2002. Mobility decisions and the predation risks of
439 reintroduction. Biol. Conserv. 103, 133–138.
440 Barlow, C.J., Caldwell, C.A., Lee, P.C., 2007. Individual differences and response to visitors in zoo-
441 housed Diana monkeys (Cercopithecus diana diana), in: Dow, S., Clarck, F. (Eds.), Proceedings
442 of the 8th Annual Symposium on Zoo Research (Pp. 131–142). British and Irish Association of
443 Zoos and Aquariums, London, UK.
444 Benaroya-Milshtein, N., Hollander, N., Apter, A., Kukulansky, T., Raz, N., Wilf, A., Yaniv, I., Pick,
445 C.G., 2004. Environmental enrichment in mice decreases anxiety, attenuates stress responses and
446 enhances natural killer cell activity. Eur. J. Neurosci. 20, 1341–1347.
447 https://doi.org/10.1111/j.1460-9568.2004.03587.x
448 Boyce, W.T., Neill-wagner, P.O., Price, C.S., Raines, M., Suomi, S.J., 1998. Crowding Stress and
449 Violent Injuries Among Behaviorally Inhibited Rhesus Macaques. Am. Phychological Assoc. 17,
450 285–289.
451 Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference
452 in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol.
453 Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6
454 Byrne, G., Suomi, S.J., 2002. Cortisol reactivity and its relation to homecage behavior and personality
455 ratings in tufted capuchin (Cebus apella) juveniles from birth to six years of age.
456 Psychoneuroendocrinology 27, 139–154. https://doi.org/10.1016/S0306-4530(01)00041-5
457 Carlstead, K., Brown, J.L., Seidensticker, J., 1993. Behavioral and Adrenocortical Responses to
458 Environmental-Changes in Leopard Cats (Felis-Bengalensis). Zoo Biol. 12, 321–331.
459 https://doi.org/10.1002/zoo.1430120403
460 Carlstead, K., Shepherdson, D., 2009. Alleviating stress in zoo animals with environmental
461 enrichment., in: Moberg, G.P., Mench, J.A. (Eds.), The Biology of Animal Stress: Basic

462 Principles and Implications for Animal Welfare. CABI, Wallingford, pp. 337–354.
463 https://doi.org/10.1079/9780851993591.0337
464 Caspi, A., Moffitt, T.E., 1993. When Do Individual Differences Matter? A Paradoxical Theory of
465 Personality Coherence. Psychol. Inq. 4, 247–271. https://doi.org/10.1207/s15327965pli0404_1
466 Cavigelli, S., 2005. Animal personality and health. Behaviour 142, 1223–1244.
467 https://doi.org/10.1163/156853905774539355
468 Cinque, C., De Marco, A., Mairesse, J., Giuli, C., Sanna, A., De Marco, L., Zuena, A.R., Casolini, P.,
469 Catalani, A., Thierry, B., Cozzolino, R., 2017. Relocation stress induces short-term fecal cortisol
470 increase in Tonkean macaques (Macaca tonkeana). Primates 58, 315–321.
471 https://doi.org/10.1007/s10329-016-0590-7
472 Davenport, M.D., Lutz, C.K., Tiefenbacher, S., Novak, M.A., Meyer, J.S., 2008. A Rhesus Monkey
473 Model of Self-Injury: Effects of Relocation Stress on Behavior and Neuroendocrine Function.
474 Biol. Psychiatry 63, 990–996. https://doi.org/10.1016/j.biopsych.2007.10.025
475 De Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of
476 dominance hierarchies. Anim. Behav. 71, 585–592.
477 https://doi.org/10.1016/j.anbehav.2005.05.015
478 DeVries, A.C., Glasper, E.R., Detillion, C.E., 2003. Social modulation of stress responses. Physiol.
479 Behav. 79, 399–407. https://doi.org/10.1016/S0031-9384(03)00152-5
480 Dufour, V., Sueur, C., Whiten, a., Buchanan-Smith, H.M., 2011. The impact of moving to a novel
481 environment on social networks, activity and wellbeing in two new world primates. Am. J.
482 Primatol. 73, 802–811. https://doi.org/10.1002/ajp.20943
483 Ferrari, C., Pasquaretta, C., Carere, C., Cavallone, E., von Hardenberg, A., Réale, D., 2013. Testing
484 for the presence of coping styles in a wild mammal. Anim. Behav. 85, 1385–1396.
485 https://doi.org/10.1016/j.anbehav.2013.03.030
486 Ferreira, V.H.B., Silva, C.P.C. Da, Fonseca, E.D.P., Chagas, A.C.C.S. Das, Pinheiro, L.G.M.,
487 Almeida, R.N. De, Sousa, M.B.C. de, Silva, H.P.A. Da, Galvão-Coelho, N.L., Ferreira, R.G.,
488 2018. Hormonal correlates of behavioural profiles and coping strategies in captive capuchin
489 monkeys (Sapajus libidinosus). Appl. Anim. Behav. Sci. 207, 108–115.

490 https://doi.org/10.1016/j.applanim.2018.07.002
491 Godoy, L.D., Rossignoli, M.T., Delfino-Pereira, P., Garcia-Cairasco, N., Umeoka, E.H. de L., 2018. A
492 comprehensive overview on stress neurobiology: Basic concepts and clinical implications. Front.
493 Behav. Neurosci. 12, 1–23. https://doi.org/10.3389/fnbeh.2018.00127
494 Gottlieb, D.H., Capitanio, J.P., Mccowan, B., 2013. Risk factors for stereotypic behavior and self-
495 biting in rhesus macaques (Macaca mulatta): Animal's history, current environment, and
496 personality. Am. J. Primatol. 75, 995–1008. https://doi.org/10.1002/ajp.22161
497 Grand, A.P., Kuhar, C.W., Leighty, K.A., Bettinger, T.L., Laudenslager, M.L., 2012. Using
498 personality ratings and cortisol to characterize individual differences in African Elephants
499 (Loxodonta africana). Appl. Anim. Behav. Sci. 142, 69–75.
500 https://doi.org/10.1016/j.applanim.2012.09.002
501 Ijichi, C.L., Collins, L.M., Elwood, R.W., 2013. Evidence for the role of personality in stereotypy
502 predisposition. Anim. Behav. 85, 1145–1151. https://doi.org/10.1016/j.anbehav.2013.03.033
503 Joëls, M., Baram, T.Z., 2009. The neuro-symphony of stress. Nat. Rev. Neurosci. 10, 459–466.
504 https://doi.org/10.1038/nrn2632
505 Koolhaas, J.M., De Boer, S.F., Buwalda, B., Van Reenen, K., 2007. Individual variation in coping
506 with stress: A multidimensional approach of ultimate and proximate mechanisms. Brain. Behav.
507 Evol. 70, 218–226. https://doi.org/10.1159/000105485
508 Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De
509 Jong, I.C., Ruis, M. a W., Blokhuis, H.J., 1999. Coping styles in animals: Current status in
510 behavior and stress- physiology. Neurosci. Biobehav. Rev. 23, 925–935.
511 https://doi.org/10.1016/S0149-7634(99)00026-3
512 Kuehnel, F., Grohmann, J., Buchwald, U., Koeller, G., Teupser, D., Einspanier, A., 2012. Parameters
513 of haematology, clinical chemistry and lipid metabolism in the common marmoset and
514 alterations under stress conditions. J. Med. Primatol. 41, 241–250. https://doi.org/10.1111/j.1600-
515 0684.2012.00550.x
516 Levacov, Diana, Jerusalinsky, L., Fialho, M. de S., 2011. Levantamento dos primatas recebidos em
517 Centros de Triagem e sua relação com o tráfico de animais silvestres no Brasil, Sociedade. ed, A

518 Primatologia No Brasil. Belo Horizonte, MG. https://doi.org/10.13140/2.1.3425.1200
519 Linden, J.B., Isbell, L.A., Capitanio, J.P., Mccowan, B., 2018. Coping style and cortisol levels in
520 infancy predict hair cortisol following new group formation in captive rhesus macaques (Macaca
521 mulatta) 1–13. https://doi.org/10.1002/ajp.22938
522 Mason, G.J., 1991. Stereotypies and suffering. Behav. Processes 25, 103–115.
523 https://doi.org/10.1016/0376-6357(91)90013-P
524 Mason, Georgia J., 1991. Stereotypies: a critical review. Anim. Behav. 41, 1015–1037.
525 https://doi.org/10.1016/S0003-3472(05)80640-2
526 Mason, G.J., Latham, N.R., 2004. Can't stop, won't stop: Is stereotypy a reliable animal welfare
527 indicator? Anim. Welf. 13, 57–69.
528 Matheson, M.D., Fragaszy, D.M., Johnson-Pynn, J.S., 2005. Response to novel housing in two groups
529 of captive tufted capuchin monkeys (Cebus apella). Primates. https://doi.org/10.1007/s10329-
530 005-0128-x
531 McEwen, B.S., 2005. Stressed or stressed out: What is the difference? J. Psychiatry Neurosci. 30,
532 315–318.
533 Mendonça-Furtado, O., Izar, P., Palme, R., 2017. Validation of an Enzyme Immunoassay for
534 Measuring Fecal Cortisol Metabolites of Bearded (Sapajus libidinosus) and Black (Sapajus
535 nigritus) Capuchins. Int. J. Primatol. https://doi.org/10.1007/s10764-017-9993-6
536 Morgan, K.N., Tromborg, C.T., 2007. Sources of stress in captivity. Appl. Anim. Behav. Sci. 102,
537 262–302. https://doi.org/10.1016/j.applanim.2006.05.032
538 Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., 2013. Taking personality selection bias seriously in
539 animal cognition research: a case study in capuchin monkeys (Sapajus apella). Anim. Cogn. 16,
540 677–684. https://doi.org/10.1007/s10071-013-0603-5
541 Munro, C., Stabenfeldt, G., 1984. Development of a microtitre plate enzyme immunoassay for the
542 determination of progesterone. J. Endocrinol. 101, 41–49. https://doi.org/10.1677/joe.0.1010041
543 Quirin, M., Kuhl, J., Düsing Rainer, R., 2011. Oxytocin buffers cortisol responses to stress in
544 individuals with impaired emotion regulation abilities. Psychoneuroendocrinology 36, 898–904.
545 https://doi.org/10.1016/j.psyneuen.2010.12.005

546 Richter, S.H., 2017. Systematic heterogenization for better reproducibility in animal experimentation.
547 Lab Anim. (NY). 46, 343–349. https://doi.org/10.1038/laban.1330
548 Rommeck, I., Anderson, K., Heagerty, A., Cameron, A., McCowan, B., 2009. Risk Factors and
549 Remediation of Self-Injurious and Self-Abuse Behavior in Rhesus Macaques. J. Appl. Anim.
550 Welf. Sci. 12, 61–72. https://doi.org/10.1080/10888700802536798
551 Smith, B.R., Blumstein, D.T., 2008. Fitness consequences of personality: A meta-analysis. Behav.
552 Ecol. 19, 448–455. https://doi.org/10.1093/beheco/arm144
553 Sousa, M.B.C., Ziegler, T.E., 2000. Influência da variação diurna no sangue e do estresse na excreção
554 fecal de esteróides em Callithrix jacchus. A Primatol. No Bras. 6, 319–331.
555 Watson, S.L., McCoy, J.G., Stavisky, R.C., Greer, T.F., Hanbury, D., 2005. Cortisol response to
556 relocation stress in Garnett's bushbaby (Otolemur garnettii). Contemp. Top. Lab. Anim. Sci. 44,
557 22–24.
558 Watters, J. V, Powell, D.M., 2012. Measuring animal personality for use in population management in
559 zoos: suggested methods and rationale. Zoo Biol. 31, 1–12. https://doi.org/10.1002/zoo.20379
560 Wielebnowski, N.C., 1999. Behavioral differences as predictors of breeding status in captive cheetahs.
561 Zoo Biol. 18, 335–349. https://doi.org/10.1002/(SICI)1098-2361(1999)18:4<335::AID-
562 ZOO8>3.0.CO;2-X
563 Wingfield, J.C., 2013. The comparative biology of environmental stress: Behavioural endocrinology
564 and variation in ability to cope with novel, changing environments. Anim. Behav. 85, 1127–
565 1133. https://doi.org/10.1016/j.anbehav.2013.02.018
566

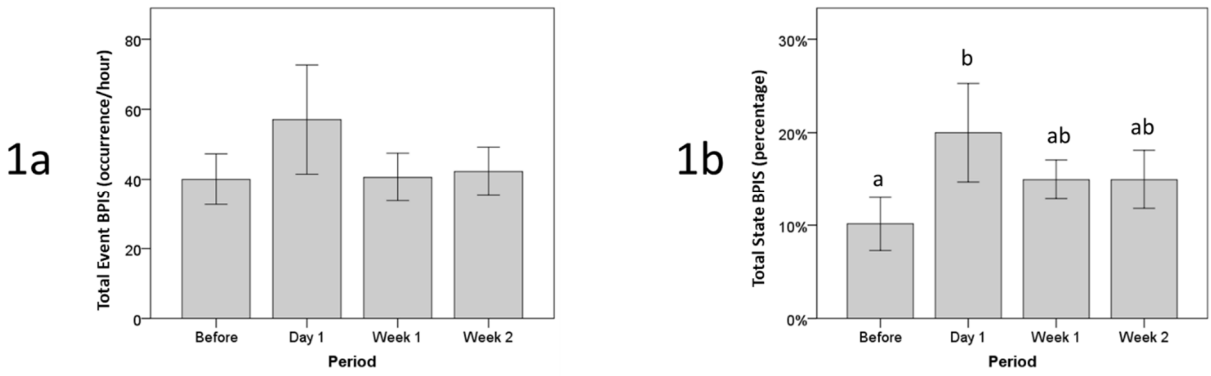

Figure 1: Behaviors potentially indicative of stress (BPIS) over four periods, before and after enclosure change (Day 1, Week 1, and Week 2) of 12 captive capuchin monkeys. 1a- Events (occurrences per hour), and 1b- States (percentage). Different letters indicate trend differences (*post-hoc* ANOVA) between periods. Data are presented as raw means ± SD.

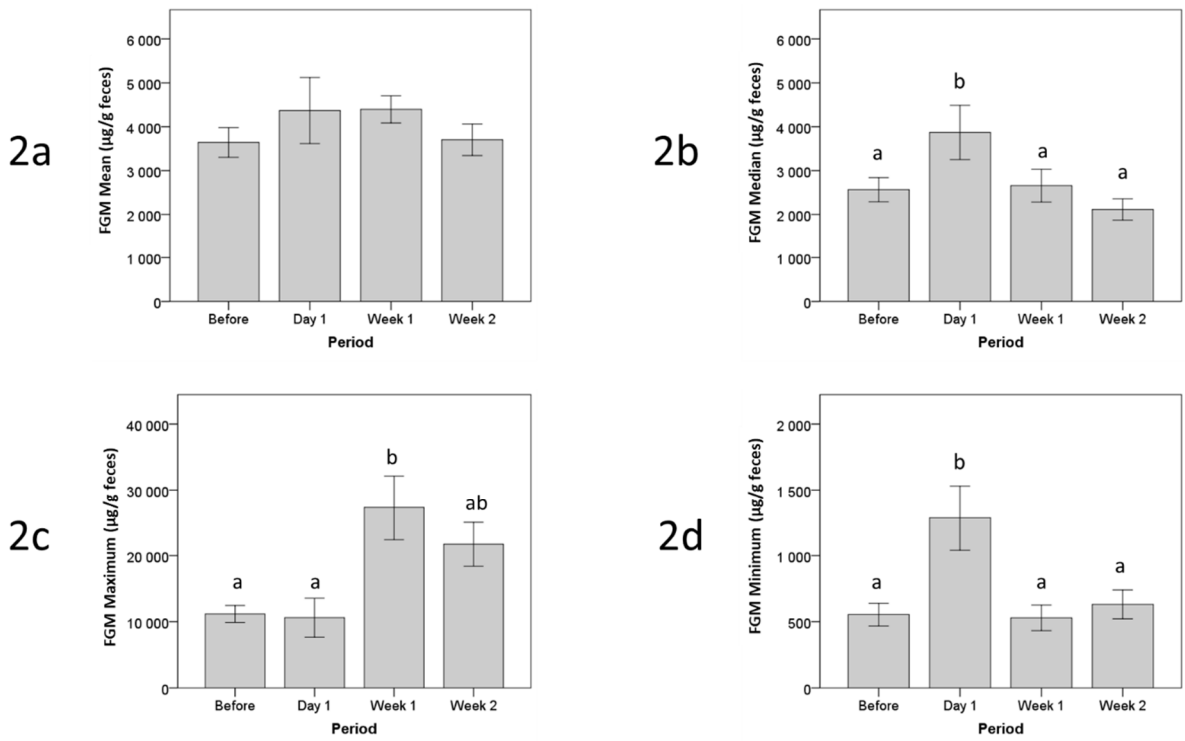

Figure 2: Fecal glucocorticoid metabolite (FGM) values over four periods, before and after enclosure change (Day 1, Week 1, and Week 2) of 12 captive capuchin monkeys. 2a- FGM Mean values, 2b- FGM Median values, 2c- FGM Maximum values, and 2d- FGM Minimum values. Different letters indicate significant (*post-hoc* ANOVA) differences between periods. Data are presented as raw means ± SD.

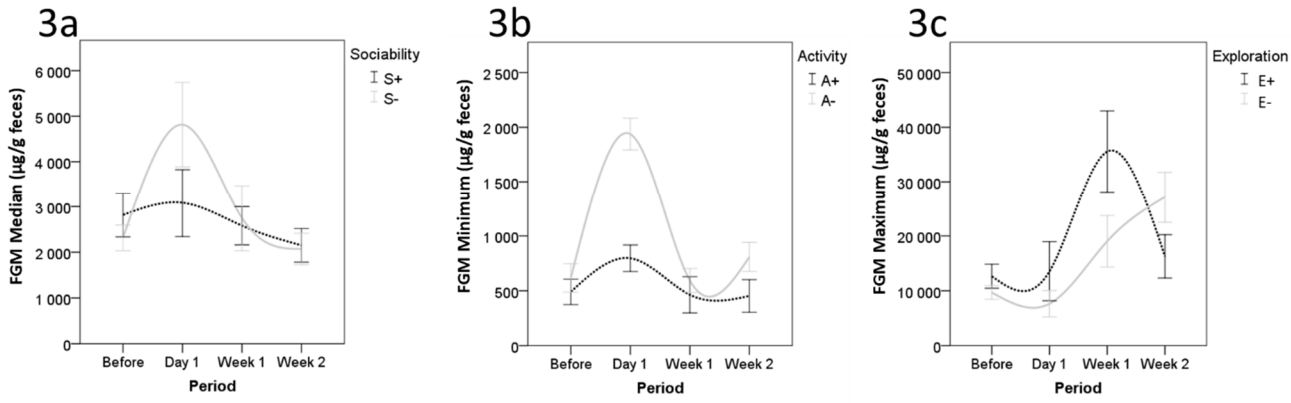

Figure 3: Fecal glucocorticoid metabolite (FGM) values over four periods, before and after enclosure change (Day 1, Week 1, and Week 2) of captive capuchin monkeys with different personality traits. 3a) FGM Median values for more and less sociable individuals (S+ and S-, respectively), 3b) FGM Minimum values for more and less active individuals (A+ and A-, respectively), 3c) FGM Maximum values for more and less explorative individuals (E+ and E-, respectively). Data are presented as raw means ± SD.

Table 1: Ethogram of Behaviors Potentially Indicative of Stress (BPIS)

Behavior	Description	Type*
Pacing	Walk or run repeatedly covering the same routine-like circuit inside the enclosure without an obvious goal. This behavior is commonly described for captive animals, especially carnivores and primates	State
Boucing/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 5s. In wild tend to occurs after an animal received intense aggression. In captivity, it may occur without prior aggression. Scream may occur.	Event/State
Head twirl	The subject turns his head sideways and upwards repeatedly (the animal may be stationary or locomotion).	Event
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.	Event
Self-grooming	Animal repetitively manipulates its own fur with the hand or mouth.	State
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 centimeters away.	State
Ingestion/Manipulation of urine, feces, and sperm	Manipulate, lick and eating/drinking of urine, feces and sperm.	Event/State
Masturbation/auto-erotic	The stimulation or manipulation of one's own genitals	Event/State
Self-scratching	Short bouts of manipulation of its own fur with the hand or mouth.	Event
Sexual Display to humans	Similar to sexual display (see above) but directed to humans	Event/State
Total State BPIS	Sum of all BPIS states	
Total Event BPIS	Sum of all BPIS events	

*State ≥ 5 seconds; Event < 5 seconds

Table 2: Group composition and individual characteristics, scores, and classification on each of the studied behavioral components.

Subject	Group	Sex	MDS	Feeding	Sociability	Exploration	Activity
Gal	A	Female	-12.95	F+ (1.35)	S+ (0.18)	E+ (-0.14)	A+ (0.29)
Sandy	A	Female	4.26	F+ (1.83)	S+ (-0.18)	E- (-0.31)	A- (-0.6)
Ines	A	Female	-11.53	F- (-0.17)	S+ (-0.05)	E+ (-0.08)	A- (-0.04)
Buraco	A	Male	18.14	F- (-0.09)	S+ (0.13)	E- (-0.68)	A- (-1.06)
Maguila	A	Male	13.77	F- (0.44)	S- (-0.89)	E- (-0.58)	A- (-0.82)
Sanfona	A	Male	-1.57	F+ (0.69)	S- (-0.52)	E+ (0.37)	A+ (0.06)
Libi	A	Male	-8.25	F- (-0.13)	S- (-0.39)	E+ (-0.3)	A+ (0.74)
Junior	A	Male	4.81	F- (-0.87)	S+ (-0.14)	E+ (-0.26)	A+ (0.24)
Claudio	A	Male	-6.69	F+ (1.85)	S- (-0.32)	E+ (-0.18)	A- (-0.41)
Jony	B	Female	2.46	F+ (1.74)	S+ (1.35)	E- (-0.51)	A+ (0.04)
Catra	B	Male	4.31	F- (-0.53)	S- (-0.2)	E- (-0.51)	A- (-0.1)
Ramos	B	Male	-0.68	F+ (1.03)	S- (-0.22)	E- (-0.46)	A+ (1.71)

MDS: Modified David's Score. F+, S+, E+, A+ represent individuals scoring above the median in the component. Score high means that the component fits the individual adequately (the individual exhibits the component behaviors frequently). F-, S-, E-, A- represent individuals scoring below the median for this component, that is, the individual is less likely to exhibit the behaviors of the component frequently.

Table 3: Selected models tested during first and second steps of data analysis.

BPIS	First step (Overall analysis)	Second step (Individual analysis)
Total Event BPIS	Period, AIC = 12.4496, $F_{3,36}$ = 0.048, p = 0.98	Period*Feeding, AIC = 18.2123, $F_{3,36}$ = 0.74, p = 0.53 Period*Sociability, AIC = 19.8440, $F_{3,36}$ = 0.18, p = 0.90 Period*Exploration, AIC = 15.1247, $F_{3,36}$ = 1.73, p = 0.17 **Period*Activity, AIC = 9.1406, $F_{3,36}$ = 4.36, p = 0.01**
Total State BPIS	Period, AIC = -166.0203, $F_{3,36}$ = 2.33, p = 0.08	Period*Feeding, AIC = -161.0952, $F_{3,36}$ = 0.58, p = 0.62 Period*Sociability, AIC =-161.8954, $F_{3,36}$ = 0.84, p = 0.47 Period*Exploration, AIC = -159.3328, $F_{3,36}$ = 0.43, p = 0.72 Period*Activity, AIC = -165.2017, $F_{3,36}$ = 1.31, p = 0.28
FGM	First step (Overall analysis)	Second step (Individual analysis)
Mean	Period, AIC = 796.4230, $F_{3,34.296}$ = 1.02, p = 0.39	Period*Feeding, AIC = 799.3571, $F_{3,34.193}$ = 0.35, p = 0.78 Period*Sociability, AIC = 800.6390, $F_{3,34.214}$ = 1.20, p = 0.32 Period*Exploration, AIC = 801.9305, $F_{3,34.308}$ = 0.85, p = 0.47 Period*Activity, AIC = 799.4531, $F_{3,34.342}$ = 0.49, p = 0.68
Median	**Period, AIC = 771.9406, $F_{3,34.081}$= 7.21, p < 0.001**	Period*Feeding, AIC = 772.4476, $F_{3,34.077}$ = 0.90, p = 0.44 **Period*Sociability, AIC = 768.8430, $F_{3,33.967}$ = 4.26, p = 0.01** Period*Exploration, AIC = 776.3155, $F_{3,34.080}$ =1.14, p = 0.34 Period*Activity, AIC = 773.9522, $F_{3,34.164}$ = 0.31, p = 0.81
Maximum	**Period, AIC = 1042.006, $F_{3,36}$ = 7.29, p < 0.001**	Period*Feeding, AIC = 1046.393, $F_{3,36}$ = 0.82, p = 0.49 Period*Sociability, AIC = 1047.242, $F_{3,36}$ = 0.95, p = 0.42 **Period*Exploration, AIC = 1036.763, $F_{3,36}$ = 4.86, p < 0.01** Period*Activity, AIC = 1046.378, $F_{3,36}$ = 1.06, p = 0.37
Minimum	**Period, AIC = 639.9824, $F_{3,32.403}$ = 10.85, p < 0.001**	Period*Feeding, AIC = 640.9610, $F_{3,32.611}$ = 1.66, p = 0.19 Period*Sociability, AIC = 646.6376, $F_{3,32.612}$ = 0.45, p = 0.45 Period*Exploration, AIC = 644.0195, $F_{3,32.308}$ = 1.39, p = 0.26 **Period*Activity, AIC = 627.7545, $F_{3,32.056}$ = 5.71, p < 0.01**

First step consisted of verifying for overall impacts of enclosure change, without taking into account individual differences. Models included as fixed factors ‘Period’ (baseline, day 1, week 1 and week 2), ‘Group’ (A and B), ‘Sex’ (male and female) and ‘Dominance’, as well as all two-way interactions with ‘Period’. Final models were selected based on Akaike’s Information Criterion (AIC): when the difference between AIC models was equal or lower than 10, we choose the model with fewer variables. Second step consisted of verifying impacts of enclosure change on individual differences, BPIS and FGM variables were reanalyzed based on the model chosen on the first step, and each of the GNB axes (Feeding, Sociability, Exploration, and Activity) were then included, one-by-one, as well as two-way interactions between each GNB axis and Period. Significant models are in bold.