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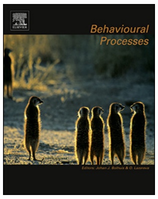

Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators?

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ABSTRACT

Measuring personality is being used to improved nonhuman primate welfare. To expand its use, it is important to identify traits that are shared between species and that measures are reliable, easy to use and less time consuming. Combining personality and other indicators strong validation of the results can be obtained. In the present study, we sought to determine if there is a link between physiological stress response (fecal cortisol metabolites), personality (ratings made by animal keepers and reaction to novel objects) and lateralization of the brain (hand preferences) on eight species of nonhuman primates: *Callithrix jacchus, Callithrix geoffroyi, Cebuella Pygmaea, Saguinus imperator, Saguinus oedipus, Leontopithecus rosalia, Pithecia pithecia* and *Nycticebus pygmaeus*. Personality assessments achieved good levels of interrater reliability and revealed three components of personality in our sample: fearfulness, activeness and aggressiveness. More exploratory individuals were more active, aggressive and showed higher cortisol metabolite levels. Right-handed subjects inspected novel objects sooner and the strength of the lateralization was linked with individual stress and the aggressiveness component. Our results highlight that there is a relation between personality, lateralization and physiological indicators in nonhuman primates, but although some aspects can be generalized across species and/or sexes others are species/sex dependent.

1. Introduction

It is generally recognized by the scientific community that animal welfare refers to the physical health, the behavior and the emotional state of animals (e.g., see Broom, 2014; Mendl, 2001). Because of that, measuring animal welfare is a complex task, it requires the combination of several indicators to provide enough information. From this perspective, many publications in recent years use a multimethod approach to address the welfare of several vertebrate species (Baird et al., 2016; Brando et al., 2018; Grand et al., 2012). In particular, for nonhuman primates, physiological measures of stress as the hypothalamic-pituitary-adrenal (HPA) axis activity (Behringer and Deschner, 2017; Novak et al., 2013), behavioral measures (Bloomsmith et al., 2018; Lutz, 2018) or a combination of behavioral and physical health (Cannon et al., 2016; Clay et al., 2018; Kummrow and Brüne, 2018; Robinson et al., 2018) are being used.

One of the behavioral indicators which have been suggested as a highly valuable tool to deepen our knowledge and to improve the assessment of animal welfare is personality (see Richter and Hintze, 2019 for a review). Defined as individual differences in behavior that are consistent over time and situations (Freeman and Gosling, 2010), personality has been widely studied in nonhuman primates (Blaszczyk, 2017 with *Chlorocebus pygerythrus*; Iwanicki and Lehmann, 2015 with *Callithrix jacchus*; Robinson et al., 2016 with *Sapajus apella* and *Cebus capucinus*; or Weiss et al., 2011b for a review on different species). The knowledge obtained in these studies is being used to improve nonhuman primate welfare (Coleman, 2012; Herrelko et al., 2012; Polgár et al., 2017; Tetley and O'Hara, 2012). However, despite the method used to evaluate personality (behavioral coding or trait rating), to expand their use as a tool in the animal welfare assessment, it is necessary that measures are reliable, easy to use and less time consuming (Freeman and Gosling, 2010; Watters and Powell, 2012).

Brain lateralization (i.e., hemispheric asymmetries in structure and/or function) has been suggested also to have practical implications to improve animal welfare (Rogers, 2010, 2011) with the left and right sides of the brain specialized to process information in different ways

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Table 1
Individual profiles.

Subject	Species	Sex [a]	Date of birth	HI	Z-score [b]	Hand [c]	FCM (ng/g) [d]
Subject 1	*Pithecia pithecia*	M	13-02-2000	−0.48	−2.69	L	654.9
Subject 2	*Pithecia pithecia*	F	29-11-2000	−0.44	−2.20	L	560.0
Subject 3	*Pithecia pithecia*	M	28-09-2014	−0.14	−0.84	N	716.4
Subject 4	*Nycticebus pygmaeus*	M	18-02-2012	0.18	0.96	N	395.2
Subject 5	*Nycticebus pygmaeus*	F	10-01-2012	0.56	3.18	R	373.7
Subject 6	*Leontopithecus rosalia*	M	11-08-2001	−0.79	−4.87	L	2624.8
Subject 7	*Leontopithecus rosalia*	M	08-02-2002	1.00	5.65	R	880.8
Subject 8	*Callithrix jacchus*	M	04-08-2015	0.94	5.30	R	1642.4
Subject 9	*Callithrix jacchus*	M	01-03-2015	−0.73	−4.01	L	2917.5
Subject 10	*Callithrix jacchus*	M	2012	−1.00	−5.39	L	1317.5
Subject 11	*Saguinus oedipus*	M	23-05-2004	−0.44	−2.47	L	1500.3
Subject 12	*Saguinus oedipus*	F	17-02-2005	0.60	3.28	R	1768.3
Subject 13	*Saguinus imperator*	M	18-05-2015	0.76	4.47	R	5067.5
Subject 14	*Saguinus imperator*	M	18-05-2015	0.60	3.55	R	2772.7
Subject 15	*Callithrix geoffroyi*	M	01-09-2010	0.76	4.35	R	517.0
Subject 16	*Callithrix geoffroyi*	M	01-09-2010	0.63	3.53	R	690.9
Subject 17	*Cebuella pygmaea*	M	18-02-2003	−0.08	−0.49	N	700.0
Subject 18	*Cebuella pygmaea*	F	07-02-2009	−0.64	−3.41	L	538.5

[a] M = Male, F = Female.

[b] Z-score ≥1.96 or ≤ −1.96 indicates significant hand preference ($p < 0.05$). Positive scores means right hand preferences and negative scores means left hand preferences.

[c] L = left hand preference, R = Right hand preference, N = No hand preference (ambi-preferent).

[d] Mean values for all the feces collected per individual.

and to control different categories of behavior and emotions (Leliveld et al., 2013). The right hemisphere is highlighted as being important in welfare since its activity involves physiological stress responses and the processing of negative emotions such as fear or aggressive behavior (Rogers, 2010). For nonhuman primates, several authors have found evidences of this relation between lateralization and stress (see Ocklenburg et al., 2016 for a review). There is also evidence of a connection between certain behaviors and the right and left hemispheres of the brain. For example, left-handed marmosets (*Callithrix jacchus, Callithrix geoffroyi*) have been shown to have negative cognitive bias (Gordon and Rogers, 2015), heightened fear (Braccini and Caine, 2009; Cameron and Rogers, 1999), reduced social responsiveness (Gordon and Rogers, 2010) and potential vulnerability to stress (Rogers, 2009) as compared to right-handed marmosets. Left-handed male rhesus macaques (*Macaca mulatta*) received more aggressive interactions, lower levels of grooming and were more likely to be submissive than right-handed males (Westergaard et al., 2003), although the opposite was the case for females (Westergaard et al., 2004). Similarly, right-hand preference in rhesus macaques was negatively correlated with stress reactivity (Westergaard et al., 2001). In chimpanzees (*Pan troglodytes*), right-handed individuals approached and touched novel objects faster than non-right-handed did (Hopkins and Bennett, 1994). For the perception of fear, *Callithrix jacchus* showed a right-hemisphere dominance displaying a larger left hemimouth, with or without vocalization, and a larger right hemimouth when producing a social contact call (Hook-Costigan and Rogers, 1998). On the contrary, in strepsirrhine species Scheumann and Zimmermann (2008) found that male but not female, mouse lemurs (*Microcebus murinus*) exhibited a significant right ear-left hemisphere bias when exposed to conspecific communication sounds of negative emotional valence. For *Otolemur garnetti*, Rogers et al. (1994) showed that individuals had left-eye dominance for viewing the tester or food through a grid, but eye preference did not correlate with handedness for food reaching in the same individuals; something also reported in common marmosets (Hook-Costigan and Rogers, 1995, 1998).

All these evidences suggest that measures of lateralization could be informative indicators in the welfare assessment of nonhuman primates. However, to define a reliable methodological framework, it is required the identification of lateralization measures capable of successfully reflect which hemisphere an individual has a propensity to use in different species. In this regard, hand preference for simple reaching has been proven to reflect it in nonhuman primates (for a detailed review see Rogers, 2018) and linked to different aspects of behavior and cognitive processes at individual level.

So, in this investigation we used a multimethod approach combining different indicators in the welfare assessment of eight species of nonhuman primates measuring: fecal cortisol metabolites (FCM) as a physiological indicator of stress (a powerful and noninvasive method used in many mammals, e.g., Barja et al., 2008, 2012; Casas et al., 2016; Sánchez-González et al., 2018a), individual personality (ratings made by animal keepers and reaction to novel objects) and lateralization of the brain (hand preferences).

To be able to standardize testing, it is important to identify traits shared between species in order to expand the animal welfare assessment (Hall et al., 2018). Therefore, the aim of this study was twofold. The first objective was to determine if there is a link between personality, stress response and lateralization treating data of all the subjects together, while our second goal was to identify tendencies between the variables that are sex, age or species dependent. We hypothesized that some aspects of personality would be present in all individuals and could be related to cortisol metabolite levels and laterality in the sample. We expected cortisol metabolite levels to be sex and/or species dependent (Barja et al., 2012; Novak et al., 2013) and therefore not related with laterality across sexes or species. However, we predicted that some general tendencies would be observed at the species level, expecting individuals with the higher cortisol metabolite levels, which approach later novel objects or with the greater scores in the fearful or neurotic dimension of personality to be left-handed.

2. Materials and methods

2.1. Subjects and housing

This study involved 18 individuals from eight different species of primates (Table 1): three species of marmosets: *Callithrix jacchus* (n = 3), *Callithrix geoffroyi* (n = 2), *Cebuella Pygmaea* (n = 2), three species of tamarins: *Saguinus imperator* (n = 2), *Saguinus oedipus* (n = 2), *Leontopithecus rosalia* (n = 2), one species of saki: *Pithecia pithecia* (n = 3) and one species of loris: *Nycticebus pygmaeus (n = 2).* Subjects were housed in pairs, with the exception of the three *Callithrix* *jacchus* and the family of sakis, at Faunia zoo (Madrid, Spain) in indoor enclosures. At the time of the study, the sakis had access to a naturalistic open enclosure inside the Tropical rainforest facility, which shared with macaws, toucans and scarlet ibis (*Eudocimus ruber*). *Saguinus oedipus* and *Callithrix geoffroyi* shared the enclosure with a pair of armadillos (*Euphractus sexcinctus* and *Chaetophractus villosus*), *Saguinus imperator* with a red-rumped agouti (*Dasyprocta leporina*) and *Callitrhix jacchus* with a hutia (*Capromys pilorides*). Loris lived on a reversed night cycle with red lights providing artificial night conditions for 12 h during daylight. During the remaining period, artificial day was created with white illumination. Feeding occurred during red light conditions. In all cases, animals were fed twice a day. Diet mainly consisted on fruit and vegetables like lettuce, chard, corn, pea, cauliflower, etc. Monkey chow, vitamin supplements (Protovit, Kabi complet, calcium or beta carotene for lion tamarins) and other complements as agar-agar, resins, gum arabic, gelatin or honey were also present. Eggs or cheese and live insects (crickets or mealworms) were provided on alternate days except for the loris where live insects were provided daily. In the afternoon, yogurt or multifruit baby food was offered. Water was available *ad libitum*.

2.2. Personality assessment

2.2.1. Questionnaires

In June 2017, each subject was rated on 27 personality adjectives (see Table 2) by 4 zoo keepers (two males and two females). Constraints we imposed to raters were to be long-term staff at the zoo and have more than one year of experience with the animals included in the study. Raters were asked to independently make their selections based on their overall impression of each individual's behavior patterns over time. They were sent a paper copy of the survey to fill out and return and asked to complete the survey separately and to not consult others when completing it. Personality adjectives were rated for each nonhuman primate on a 7-point Likert-type scale from 1 (the trait is not represented in the animal at all) to 7 (the trait is very strongly represented in the animal). We included traits based on previous studies on nonhuman primate personality (Byrne and Suomi, 2002; Iwanicki and Lehmann, 2015; Manson and Perry, 2013; Sussman et al., 2013; Weiss et al., 2011b) incorporating the ones mostly shared between articles on monkeys and marmosets. We also added 4 traits that focused on human–animal interactions, as humans can be an important element of a captive animal's environment (Baker et al., 2015). To be efficient we accommodated the questionnaire to the time dedicated for answering it.

Table 2
Definitions of the 27 adjectives rated in the personality questionnaires. Significant values were highlighted in bold face.

Trait	Definition	ICC[a] (3,k)
Active	**Moves around or explore a lot**	**0.59**
Aggressive	**Cause harm or threat, chases, bites, etc. other individuals**	**0.85**
Cautious	Interested in new situations, enrichment, etc. but it does not interact too much	0.42
Curious	**Quickly explores new things and situations**	**0.60**
Dominant	**Priority access to food or resources and control other individuals**	**0.72**
Effective	**Get what it wants**	**0.67**
Eccentric	Shows stereotypes or unusual mannerisms	0.20
Excitable	Overreacts to change	0.26
Fearful	**Retreats readily from others or from outside disturbances**	**0.59**
Flexible	Adapts well to changes, new situations.	−0.42
Insecure	Hhesitates to act alone; seeks reassurance from others	−0.16
Sociable	Seeks companionship of others	0.39
Irritable	**Reacts negatively with little provocation**	**0.60**
Inteligent	Acts with astuteness before situations	0.41
Jealous	**Seeks or tries to obtain what others possess, not paying attention at first until the partner gets it**	**0.57**
Lazy	**Takes time to move, strive to obtain food etc.**	**0.61**
Opportunistic	**Seizes a chance as soon as it arises**	**0.54**
Playful	**Initiates play and joins in when play is solicited or alone**	**0.87**
Persistent	**Continues in its efforts to carry out an action or prolongs it over time**	**0.51**
Solitary	Spends time alone	0.38
Subordinate	**Gives in readily to others**	**0.61**
Tense	Shows restraint in posture and movements	0.21
Relax	Shows calm in both posture and movements	−0.13
HA-Sociable	**Confident and willing to interact with humans, even getting on top**	**0.62**
HA-Cautious	Curious but keeps the distance with humans	0.19
HA-Nervous	**Uneasy with humans and keep the distances or try to hide**	**0.71**
HA-Aggressive	**Cause damage or attempt to assault humans**	**0.91**

[a] ICC designates intrA–Class correlation, a measure of reliability between raters.

2.2.2. Novel objects test

We tested individuals in their own permanent or family groups in their home cages. Following previous articles on nonhuman primates (Šlipogor et al., 2016; Hall et al., 2018), the experiment lasted for 7 min, after which the experimental stimulus was removed. We chose a multicolor dragon toy (14 cm long, 11 cm wide) as novel object 1, a black plastic spider (8 cm long, 8 cm wide) as novel object 2, and a red dragon-fly (7 cm long, 8 cm wings wide) with a black and yellow butterfly (6 cm long, 5 cm wide) as novel object 3. Each novel object was hung from a branch inside the enclosure with a straw rope during the test. After the zoo keeper hung the unfamiliar object, the observer recorded how long it took the animal to inspect the object. We defined inspection as a visual, olfactory, or tactile examination of the object within a minimum distance of 5 cm. The observer stood to one side of the enclosure during the test and timed with a stopwatch. Species were tested one at a time in a random order after having been fed to ensure that hunger was not a factor in the personality test outcome.

2.3. Hand preference

Hand preference was determined during normal feeding times by scoring the hand used to pick up pieces of food and take them to the mouth. Following the method used by Hook and Rogers (2000) and Gordon and Rogers (2015), a left or right score was recorded whether one hand held the food but repeated taking of the same item to the mouth using the same hand was recorded as only one score. If the animal took the item to the mouth using one hand and then changed it to the other hand, one right and one left score was recorded. If both hands were used simultaneously, we did not include these data in the calculation of hand preference. Each individual obtained a maximum of 13 scores per day having a range between 25 and 38 scores in total.

Left and right scores were used to quantify individual-level hand preference by the handedness index score (HI) and the binomial Z-score, computed for each subject as follows:

$$HI = {R - L}\Big/{N}\,;\ Z = {R - M}\Big/{\sqrt{N\cdot p\cdot q}}$$

being R and L the corresponding right and left scores, respectively; N the total number of responses registered for the subject ($R + L$); M was equal to $N/2$; and the value of p and q was 0.5.

HI varies between -1 (100% left hand use) and +1 (100% right hand use) and its absolute value (ABS-HI) was used to assess the strength of the hand preference (Hopkins, 2013; Llorente et al., 2009). Through the binomial Z-score, an individual was considered to have a significant hand preference if the Z-score was ≥ 1.96 or ≤ -1.96 ($p < 0.05$). Although there is some controversy regarding the threshold values that clearly separate right-handers, left-handers and ambi-preferents (Hopkins, 2013), we used the above criteria based on previous articles (Gordon and Rogers, 2015; Regaiolli et al., 2016) and corroborated that our results were equivalent using other thresholds reported in literature.

2.4. Cortisol metabolite levels

Fecal samples were collected during June and July 2017. Samples were collected during zoo operating hours (from 8:30 - 18:00 h) in the indoor enclosures and for the sakis also in the naturalistic open enclosure. Only fresh fecal samples were collected to prevent the action of environmental conditions and degradation by microorganisms (Washburn and Millspaugh, 2002; Barja et al., 2012). To identify individual feces, food coloring paste (Manuel Riesgo, S.A., Madrid, Spain) of two different colors (green and blue) were used. Fecal markers were hand-fed inside the mealworms always by the same person who also collected the fecal samples. The same color was fed to the same animal throughout the study from Monday to Thursday mornings (9:30–14:00) and fecal samples collected from Tuesday to Friday. Individual fecal samples were placed in Ziploc bags and stored in a freezer at −20 °C prior to analysis. Each animal had a total of 5 to 20 feces.

For the FCM extraction, fecal samples were unfrozen and dried until constant weight (60 °C, 21 h). We placed 0.5 *g* of dry feces in assay tubes with 1 ml of phosphate buffer and 1 ml of 80% methanol, then, they were shaken for 16 h and supernatants were centrifuged at 4000 r.p.m for 15 min. Pellets were discarded and the fecal extracts were stored at –20 °C until analyzed. We used a commercial cortisol enzyme immunoassay (DEMEDITEC Diagnostics GmbH, D-24145 Kiel, Germany) for the quantification. Parallelism, accuracy and precision tests have to be done to validate any enzyme immunoassay (Barja et al., 2012; Casas et al., 2016; Sánchez-González et al., 2018b). Parallelism was performed with serial dilutions of fecal extracts (1:32, 1:16, 1:8, 1:4, 1:2, 1:1) resulting in a curve parallel to the standard. Accuracy (recovery) was 97.1 ± 6.4%. Precision was tested through intra- and inter-assay coefficients of variation for fecal samples, being 11.9% and 13.6%, respectively. In each assay, we used a standard, whose cortisol metabolite concentration was known, included in the kit. FCM levels were expressed as ng/g dry feces.

2.5. Data analysis

Intr A–C lass correlation coefficients (ICC (3, k)) were calculated for each of the 27 adjective rated in the personality questionnaire to determine reliability between raters (Shrout and Fleiss, 1979). Adjective with an ICC (3, k) below 0.50 were considered as non-reliable and, therefore, the corresponding trait was not included in further analyses. A single score for the remaining personality adjectives was then calculated for each subject by averaging scores across raters.

To find relationships among the selected personality adjectives, we used the *k-Means* clustering algorithm (MacQueen, 1967; Xu and Wunsch, 2005). This unsupervised learning algorithm discovers underlying patterns in a dataset grouping similar data points together. The idea behind using this kind of analysis was grouping similar traits in a single personality component. To test internal consistency within the personality components identified by *k-Means*, we verified that the corresponding Cronbach's alpha was greater than 0.90. Finally, we computed the mean value of the scores obtained by the subject in all the traits included in the corresponding personality component. Hereafter, we call "coefficients" these mean values characterizing the components identified by the *k-Means* algorithm.

Once determined the hand preference, the characterizing FCM level in feces (estimated as the mean value for all the feces collected for a given subject) and the corresponding personality coefficients for all the subjects, we analyzed possible linear correlations among individual data by means of the Spearman's rank correlation (ρ). For that, we built a data matrix containing the following data for each subject: subject id; sex; age; HI; ABS-HI; Z-score; coefficients for the personality components; median latency to inspect novel objects (note that our tests consisted of presenting three different unfamiliar objects to each individual); and characterizing FCM level. In relevant cases with enough significant statistic, paired comparisons across attributes were assessed by Wilcoxon–Mann–Whitney (WMW) test. Additionally, Kruskal-Wallis test was used to analyze global relationships among species and individuals with different hand preference.

Finally, to determine the relative contribution of each individual factor to the variation in the two independent variables considered in our study, i.e., latency to approach novel objects and level of physiological stress, we performed bidirectional (forward/backward) stepwise logistic regressions to fit a General Linear Model (GLM) to the corresponding response variable considering as potential indicators different independent variables and their 2-way interactions. The algorithm started out with a GLM containing only a constant term and potential predictors were added or removed based on deviance as improvement criterion ($p < 0.01$). A comparison of the R-squared value between the final model and the final model minus a given predictor was used to determine the amount of variance in the response variable explained by the addition of that predictor to the model. Statistical data are reported as mean ± SE. The level of significance defined for all statistical tests was $p < 0.05$. All statistical analyses were performed in MATLAB R2018a for Linux.

3. Results

3.1. Hand preference and personality components

Z-score analysis revealed that 15 of our subjects presented a strong hand preference for picking up food (eight subjects were right-handed and seven left-handed), while three individuals were identified as ambipreferent because they did not present a preferred hand for picking up food (Table 1).

Regarding personality ratings, ICC (3, k) was greater than 0.5 for 16 out of 27 traits included in our personality questionnaire (see Table 2). Applying the *k-Means* algorithm to a dataset with the score obtained by every subject in these 16 personality traits, we obtained that the optimal number of clusters grouping similar traits was six (Table 3). Three of the suggested clusters only contained one trait (lazy, playful and subordinate), while the other three clusters contained two or more traits. The computation of the Cronbach's alpha for these latter corroborated internal consistency of the categorization suggested by *k-Means*. Then, in subsequent analyses, we considered lazy, playful and subordinate as individual personality adjectives; while, taking into account the traits they included, we correlated the other three suggested cluster with a personality component (fearfulness, activeness and aggressiveness, see Table 3) and computed the corresponding personality coefficient as described in Materials and Methods.

3.2. Relationships among independent variables

Correlation analysis among independent variables revealed some

Table 3
Groups of personality traits identified by the k-Means clustering algorithm maximizing the correlation among traits. Column α shows the corresponding Cronbach's alpha.

Personality Component	Personality traits	α
Fearfulness	Fearful, HA-nervous	0.916
Activeness	Active, curious, dominant, effective, opportunistic, persistent and HA-sociable	0.914
Aggressiveness	Aggressive, irritable, jealous and HA-aggressive	0.927
Lazy	Lazy	
Playful	Playful	
Subordinate	Subordinate	

Table 4
Spearman correlation coefficient between the individual's variables and the personality components/adjectives. Coefficients with a confidence level above 95% are highlighted in bold face.

Personality Component	Sex	Age	HI	ABS-HI	Z-score
Activeness	0.41 (p = 0.088)	−0.25 (p = 0.321)	−0.19 (p = 0.453)	0.19 (p = 0.442)	−0.18 (p = 0.461)
Aggressiveness	**0.44 (p = 0.049)**	−0.44 (p = 0.071)	−0.13 (p = 0.621)	**0.56 (p = 0.016)**	−0.10 (p = 0.691)
Fearfulness	0.065 (p = 0.801)	−0.31 (p = 0.212)	**0.42 (p = 0.048)**	0.21 (p = 0.412)	**0.45 (p = 0.046)**
Lazy	0.093 (p = 0.724)	−0.21 (p = 0.392)	**0.45 (p = 0.046)**	−0.01 (p = 0.971)	**0.44 (p = 0.046)**
Playful	0.37 (p = 0.133)	**−0.60 (p = 0.009)**	0.14 (p = 0.593)	0.06 (p = 0.821)	0.17 (p = 0.513)
Subordinate	0.00 (p = 1.000)	−0.20 (p = 0.421)	0.31 (p = 0.212)	−0.05 (p = 0.843)	0.32 (p = 0.194)

significant linear correlations between pairs of personality components. In particular, there was a moderate negative correlation between fearfulness and activeness ($\rho = -0.47$, $p = 0.049$); and positive correlations were found between fearfulness and lazy ($\rho = 0.49$, $p = 0.040$); activeness and playful ($\rho = 0.72$, $p < 0.001$); activeness and aggressiveness ($\rho = 0.71$, $p < 0.001$); and aggressiveness and playful ($\rho = 0.66$, $p = 0.003$). These correlations allowed us to identify and discuss some interesting general tendencies in our samples. For instance, the most active individuals tended also to be the most aggressive and playful, while subjects not very active tended to be fearful. Note that we did not find any significant linear correlation between the trait subordinate and any other personality component.

Analyzing relationships across individuals' features and personality components, we identified significant linear correlations (highlighted in bold face in Table 4) between sex and aggressiveness; age and playful; hand preference (i.e., both HI and Z-score) and fearfulness; hand preference and lazy; and ABS-HI and aggressiveness. A more detailed analysis of these relationships showed that our average male was more aggressive than our average female (aggressiveness coefficient = 2.64 ± 0.31 vs. 1.71 ± 0.09, WMW test $p_{aggressiveness} = 0.046$. Fig. 1A). It is important to also note the greater variability among males than among females. Similarly, right-handed individuals were in general more fearful and lazier than left-handers (fearfulness coefficient = 4.97 ± 0.21 vs. 3.89 ± 0.37, WMW test $p_{fearfulness} = 0.041$; lazy coefficient = 3.44 ± 0.21 vs. 2.50 ± 0.19, WMW test $p_{lazy} = 0.019$. Fig. 1B). Our results also pointed out that these correlations were highly modulated by the individual's species, being *S. imperator* (fearfulness coefficient = 5.81 ± 0.19; lazy coefficient = 3.75 ± 0.00), *N. pygmaeus* (fearfulness coefficient = 5.50 ± 0.50; lazy coefficient = 3.75 ± 0.25), and *C. geoffroyi* (fearfulness coefficient = 4.75 ± 0.38; lazy coefficient = 3.87 ± 0.13) the species more fearful and lazier with all the individuals right-handed or with no hand preference (Table 1). A moderate positive correlation between ABS-HI and aggressiveness was also observed suggesting that the higher the strength of the lateralization, the more aggressive an individual was (Fig. 1C). Finally, we found a highly significant negative correlation between age and the playful coefficient (cf. Table 4). No additional significant correlations were detected.

3.3. *Latency to inspect novel objects and cortisol metabolite levels*

Morning and afternoon cortisol metabolite levels showed no significant differences (WMW test $p = 0.075$). Similarly, no significant linear correlations were found between the minimum ($\rho = -0.18$, $p = 0.493$), maximum ($\rho = -0.20$, $p = 0.432$) and median ($\rho = -0.38$, $p = 0.121$) response time to novel objects and the characteristic FCM level. However, our analysis revealed other relevant trends regarding the inspection of novel objects. First, right-handed individuals approached novel objects significantly sooner than left-handers (27.4 ± 6.0 s vs. 187.9 ± 58.3 s, WMW test *p-value* = 0.040. Fig. 2A, blue traces), while males did it sooner than females (71.9 ± 25.0 s vs. 217.0 ± 98.9 s, WMW test *p-value* = 0.004. Fig. 2B, blue traces**)**. Note also the greater variability in the range of response times of left-handed individuals as compared to individuals with a right preference. Second, regarding the personality components, we found moderate negative correlations between the response to novel objects and how aggressive ($\rho = -0.43$, $p = 0.044$), active ($\rho = -0.50$, $p = 0.037$) and/or playful ($\rho = -0.41$, $p = 0.044$) the individual was. These were component of personality related to sex, which emphasized dependence of the response to new objects on the individual's sex.

Regarding the level of physiological stress, we found certain dependence on the species (Fig. 2C). Although in some species FCM levels showed a significant variability among individuals, we might consider that each species had a different basal FCM level. This could be the main factor influencing the cortisol metabolite levels in our primates, but the analyses also suggested that additional stressors could influence the stress response. For instance, we found a moderate linear correlation between the FCM levels and the aggressiveness component of personality ($\rho = 0.50$, $p = 0.035$). Note that, unlike response to new objects, this correlation was positive. Thus, in general, the more aggressive an individual was, the greater the cortisol metabolite level in its feces. Regarding the sex, although males in general had a greater

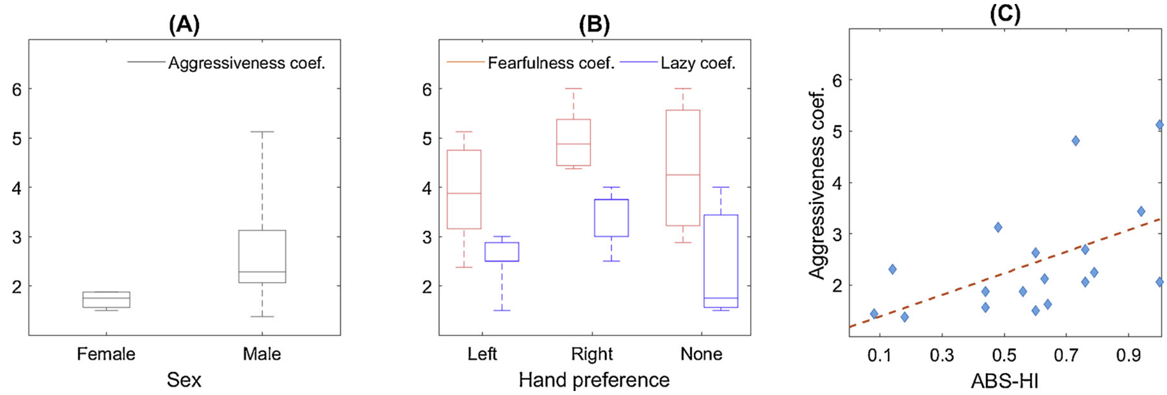

Fig. 1. (A) Boxplot comparing the aggressiveness coefficient for females and males. (B) Boxplot comparing the fearfulness and lazy coefficients in relation to the individuals' hand preference. (C) Positive linear correlation between ABS-HI and the aggressiveness coefficient.

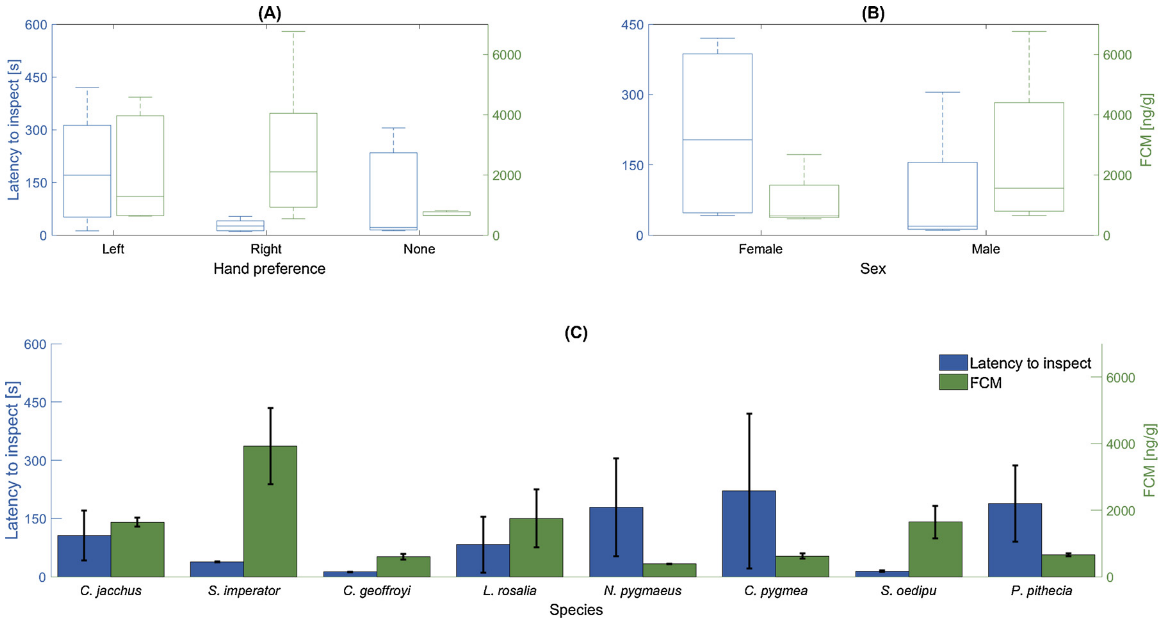

Fig. 2. Boxplot comparing the latency to inspect a new object and the FCM level as a function of hand preference (A) and sex (B). (C) Comparison of the same variables, but now in terms of median values (± SE), in the case of the different species considered in the study.

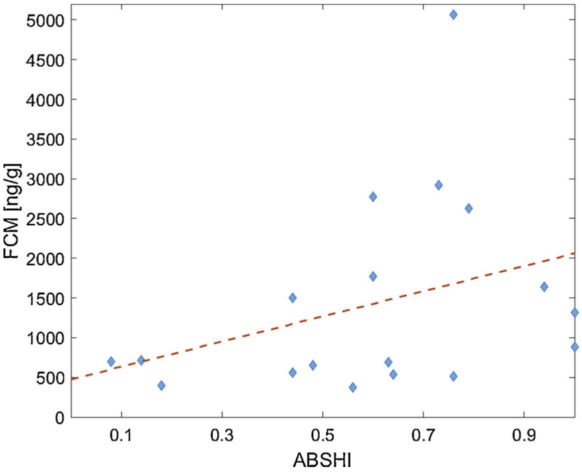

Fig. 3. Positive linear correlation between ABS-HI and the FCM level.

level of cortisol metabolites in feces than females (2421 ± 537 *ng/g* vs. 1121 ± 518. Fig. 2B), WMW test indicated that the difference was not statistically significant (*p-value* $= 0.061$). For lateralization, no dependence on hand preference was detected in the case of the FCM level (cf. Fig. 2A), but ABS-HI showed a moderate positive correlation with the physiological stress ($\rho = 0.48$ with $p = 0.042$. Fig. 3).

Finally, although the correlation coefficients indicated that there was not a linear correlation between latency to inspect novel objects and physiological stress level, an intriguing result pointing to some kind of relationship between them can be observed in panels A–C of Fig. 2. The greater FCM levels in a group usually corresponded to the lower response times to novel objects (cf. right-handed individuals, males or *S. imperator*). The computation of GLMs corroborated the existence of this relationship. On one hand, a GLM including the FCM levels ($p = 0.022$), the coefficients for the activeness ($p = 0.001$), the aggressiveness ($p = 0.003$) and the playful ($p < 0.001$) component of personality and the interaction aggressiveness*playful ($p = 0.003$) as predictors explained approximately 99% ($R^2 = 0.987$) of the variability in latency to approach and inspect novel objects with significant $p < 0.001$. On the other hand, significant factors explaining the variation found in the physiological stress level were latency to inspect novel object ($p = 0.034$) and, again the coefficients for the activeness ($p = 0.006$), aggressiveness ($p = 0.023$) and playful ($p = 0.011$) components of personality. In this case, the model was significant with a *p-value* of 0.003 and explained around 78% ($R^2 = 0.782$) of the variability in the FCM levels. It is important to note that GLMs did not find sex, species or hand preference as significant predictors. A possible explanation is that, as we indicate above, some personality components were highly correlated with these variables and, therefore, they were redundant in the model. This could be corroborated by creating GLMs that did not include personality components. Sex, hand preference and species became significant predictors for GLMs created in this way, although these GLMs explained less variability in the corresponding response variable than those including the personality components (77% of the variability with a *p-value* $= 0.008$ in the case of latency to inspect novel object; and 63% being *p-value* $= 0.036$ for the FCM level).

4. Discussion

To our knowledge, this is the first study to measure lateralization, personality and physiological stress with all of the species of nonhuman primates that we investigated trying to find a common pattern in the welfare assessment. This multimethod approach also allowed us to validate results especially when comparing different species suggesting that the interpretation of some personality aspects must be analyzed cautiously.

4.1. *Personality assessment*

Personality rating system and novel object test were shown a reliable way to characterize individual personality differences in our nonhuman primates. This result is in line with previous investigations providing successful outcomes with species of marmosets and tamarins – such as *Callithrix jacchus* (Iwanicki and Lehmann, 2015; Šlipogor et al., 2016; Koski and Burkart, 2015; Koski et al., 2017) or *Saguinus oedipus* (Franks et al., 2013) – and with other species of strepsirrhine primates – such as *Microcebus murinus* (Dammhahn, 2012). In addition, in our particular case, relationships among personality traits with good reliability between raters revealed three components, which reflected fearful, active and aggressive characteristics in our sample. These personality components could be translated into some of the Five Factor Model dimensions (Costa and McCrae, 1992) that many investigators use to asses personality in nonhuman animals (Gosling and John, 1999). According to this, our selected adjectives for the fearfulness component (see Table 3) would correspond to the neuroticism dimension. Given the high positive correlation observed in subsequent analyses with the lazy adjective, with a larger sample, we would expect it to be included in the fearfulness component and therefore in the neuroticism dimension too. Similarly, the activeness component, which would likely also contain the playful adjective with a larger sample, would correspond to the openness to experience dimension; while the aggressiveness component would correspond to the antagonism dimension (i.e., the opposite of the agreeableness dimension). These findings agree with results of studies with common marmosets (Inoue-Murayama et al., 2018) and other nonhuman primate species – such as capuchins or bonobos (Robinson et al., 2016; Weiss et al., 2015) – which suggests certain degree of consistency in the major dimensions of personality across many primate species (Capitanio, 2004; Gosling, 2001; Freeman and Gosling, 2010).

The neuroticism dimension, however, is usually related not only to fearfulness and nervousness, but also to vulnerability to stress (Gosling and John, 1999). Therefore, we would expect to correlate this component of personality with the FCM level in our samples. In contrast, in our case higher cortisol metabolite levels were mainly associated with the aggressiveness and activeness components of personality: more aggressive and anxious temperaments tend to be associated with higher cortisol levels (Capitanio et al., 2004; Erickson et al., 2005). This connection is consistent with studies on common marmosets where the sociability dimension of personality, equivalent to our activeness component, was associated with higher hair cortisol levels (Inoue-Murayama et al., 2018). In fact, in our primates, these components of personality were related to the latency to inspect novel objects being in general the subjects more aggressive, more active and more playful the ones which inspected sooner the novel objects. In this line, Šlipogor et al. (2016) identified not only bolder marmosets to spend more time close to the stimuli and showed more stress behaviors, but also obtained variables related to subjects' activity and to their stress responses load on the same component. For cotton-top tamarins also promoted-individuals (tendency to be motivated by gains over safety) approached the novel enrichment objects faster than other monkeys (Franks et al., 2013), and for macaques lower confidence was associated to lower cortisol in the morning (Capitanio et al., 2004). Therefore, it seems that more exploratory nonhuman primates tend to be bolder, more confident, active and aggressive, which, consequently, exposes them to more stressful situations, showing higher cortisol metabolite levels. In contrast, Byrne and Suomi (2002) found aggressive, confident, curious, effective and opportunistic personality traits, all negatively correlated with cortisol reactivity levels in juvenile capuchin monkeys; while the correlation with apprehensive, fearful, insecure, submissive and tense was positive. These contradictory results could be due to how we interpret fear, which has been usually linked to anxiety in nonhuman primates (see Barros and Tomaz, 2002 for a review) and separated totally from confidence or boldness (Carter et al., 2012; Weiss et al., 2011a). From this perspective, more fearful/anxious animals would show higher physiological stress levels than more confident or bolder subjects. However, in our sample, we observed the opposite because our fearfulness component could be representing the shyness individuals, which would not necessarily have to be the anxious ones. In fact, individual data in our sample support this hypothesis with the loris, geoffroy and pygmy marmosets rated within the highest in fear or lazy traits, also the ones with lower cortisol levels and for pygmy marmosets, and loris also the ones with longer latencies to approach novel objects. It is true that emperor and lion tamarins were rated one of the highest in fear and presented the higher cortisol levels too. This result supports our hypothesis that the fearfulness component must be analyzed cautiously because confounding factors in terminology or in the interpretation of the fear trait (especially when comparing different species as it is our case) could apply, and using a physiological measure or multiple assays can validate the results in the assessment of animal personality (Carter et al., 2012; Gosling, 2001; Uher, 2008; Uher and Asendorpf, 2008).

It would be interesting in future research to test personality differences between species (e.g., Baker et al., 2015; Manson and Perry, 2013; Morton et al., 2013; Robinson et al., 2016), something not possible for us due to our small sample size. Nonetheless, even in our data, it appears that although some aspects of personality could be generalized across species, others as fearfulness could be modulated by the species. Likewise, sex was detected to affect temperament in nonhuman primates, being for example female macaques more cautious and more novelty averse than males (Montgomery et al., 2005; Sussman et al., 2013), male marmosets lower than females in patience (Koski et al., 2017) and, in general, males in many species more aggressive than females (Schuett et al., 2010). These articles agree with what we detected in our sample with males being more aggressive, approaching sooner novel objects and with higher cortisol metabolite levels in general than females. Otherwise, studies with marmosets found that females were faster in exploratory behavior (Yamamoto et al., 2004) and Koski and Burkart (2015) reported no differences in exploration tendency between sexes. All these evidences suggest that not only the species, but also sexual selection or even the species-by-sex interaction could play a role in personality (Schuett et al., 2010; Sussman et al., 2013) and therefore it would be interesting to address these differences in future research with larger samples.

The age was only related with the playful trait and seems very logical that although all the subjects were adults, the youngest individuals were the most playful. The only personality trait which was not related with anything was subordinate. This could be explained because we were not able to analyze social status or dominance due to the small sample size within a species and because all the subjects were grouped in pairs or trios. Nevertheless, influence of social environment in nonhuman primates is a relevant aspect to investigate in future research as previously reported in common marmoset (Koski and Burkart, 2015; Šlipogor et al., 2016) and even affect the HPA axis function as it has been shown in macaques (Kohn et al., 2016).

What it seems clear is that personality is an important element in the welfare assessment. Results of this work support that there is a relation between personality and physiological indicators or health in nonhuman primates (e.g., Capitanio, 2011; Robinson et al., 2017, 2018), something that has been also proved in humans (see Mehta and Gosling, 2008 for a review).

4.2. *Lateralization*

Our finding that individual strength lateralization was linked with individual stress was a surprising result that agree with previous studies on sharks (Byrnes et al., 2016), sheeps (Morgante et al., 2007) or even in humans, where an increase of lateralization was showed after acute stress (Brüne et al., 2013). In contrast, rhesus monkeys (*Macaca mulatta*) with higher cortisol reactivity evinced less hemispheric brain asymmetry (Short et al., 2014) and Westergaard et al. (2003) showed for these nonhuman primates a negative correlation between ABS-HI scores and plasma ACTH concentrations, although positive correlations were detected with the aggressive behavior as we did. One possible explanation for these differences has been related to the corpus callosum function on the contralateral hemisphere in the brain because depending on callosal subregions and fiber type, either an inhibitory influence (enhancing lateralization) or an excitatory influence (diminishing lateralization) could be executed (Van der Knaap and Van der Ham, 2011). Nevertheless, as Ocklenburg et al. (2016) pointed out, there are evidences of a relation between stress and lateralization for humans and nonhuman animals but more empirical research is needed to explain it.

Unlike the strength of hand preference, its direction, as expected in all the species analyzed, was not directly related with FCM levels. However, it was linked to other of the welfare indicators analyzed. In general, right-handed subjects inspected novel objects sooner than left-handed or individuals with no hand preferences. These results agree with previous studies on chimpanzees (Hopkins and Bennett, 1994), common marmosets (Cameron and Rogers, 1999) or Geoffroy´s marmosets (Braccini and Caine, 2009). Moreover, right-handers have been described in literature as proactive, while left-handers as reactive personality types (Rogers, 2009; 2010). On the contrary, right-handed subjects in our sample were also more fearful and lazier, attributes that clearly correspond to reactive personality types. This could again be result of the species differences above explained, which highlights the importance of the species in explaining laterality differences. Consequently, in our sample we only could see some tendencies. For example, the species with the highest FCM levels were *S. imperator*, *S. oedipus* and L. *rosalia*; and the ones with the lowest *N. pygmaeus* and *C. geoffroyi.* For L. *rosalia,* the righ-handed individual showed lower FCM levels than the left-handed individual as other studies reported with common marmosets (Rogers, 2009). Additionally, our right-handed lion tamarin exhibited an abnormal repetitive behavior of head rolling and this could explain why in the same environment this individual had lower FCM levels: perform the abnormal repetitive behavior has been shown as a way to liberate stress (e.g., Kelly et al., 2009; Mason and Latham, 2004; Tiefenbacher et al., 2000). Nevertheless, we do not know if there is a connection between lateralization and how to cope with stress and with the frequency to express abnormal repetitive behaviors. Tomaz et al. (2003) suggested that marmosets show a stronger activation of the right hemisphere under acute stress. If these differences result in different strategies to manage stress remains unknown and it would be interesting to address these issues in future studies. For *S.oedipus* and *C. jacchus*, although we had right- and left-handed individuals, no clear tendencies could be commented due to differences in sex (our female cotton top tamarin was right-handed and the male left-handed) and to the non homogeneous distribution of FCM values as a function of lateralization (the right-handed common marmoset presented higher FCM levels than one of the left-handed but also lower levels than the other left-handed).

Three subjects in our colony did not present a preferred hand for picking up food: one member of *N. pygmaeus*, of *C. pygmaea* and of *P. pithecia.* Interestingly, these are species for which previous authors had also noted weak or no significant hand preferences. Smith and Thompson (2011) found for a population of wild sakis more ambidextrous individuals than expected and other authors suggested that prosimians, small-bodied, quadrupedal primates or gum feeding species could prefer mouth retrieval of food and be less manually lateralized (Papademetriou et al., 2005; Scheumann et al., 2011; Singer and Schwibbe, 1999). In contrast, recent studies on strepsirrhine species found manual lateralization on several species as red fronted lemurs (Schnoell et al., 2014), ring tailed lemurs (Regaiolli et al., 2016) and slow lorises (Poindexter et al., 2018). In addition to this controversy, some authors claim that complex bimanual tasks are better than unimanual tasks for investigating manual asymmetries (Canteloup et al., 2013; Hopkins et al., 2011; Llorente et al., 2009, 2011), while other works in literature point out that hand preference for simple reaching reflects more frequent use of the opposite hemisphere of the preferred hand (Gordon and Rogers, 2010, 2015; Rogers, 2018) being very consistent with a mean strength of 80–90% (Rogers, 2009). To solve these discrepancies, more studies are needed considering the effects of sex, rearing history, age and/or feeding ecology in explaining differences between unimanual versus bimanual coordinated behaviors and in the direction of handedness not only at individual and population levels, but also at a species or cross-species level among primates (Meguerditchian et al., 2012). Consequently, we propose for future studies with large samples the combination of unimanual and bimanual tasks as measures of lateralization, which could not only help to explain the divergent patterns of handedness reported in the nonhuman primate literature, but also serve better as indicator in the welfare assessment.

5. Conclusions

This study demonstrates that personality is an important element in the welfare assessment and that there is a relation between personality, lateralization and physiological indicators in nonhuman primates. In our sample, more exploratory individuals were more active, aggressive, playful and showed higher cortisol metabolite levels in feces. Even the strength of lateralization, independently of the direction, was associated with stress and the aggressiveness component. However, although some aspects can be generalized across species and/or sexes, others seem to be species/sex dependent. More studies are needed specially to elucidate the connection with lateralization, which could explain differences in how individuals react and manage physiological stress.

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