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Citation for published version:

Masilkova, M, Weiss, ALEXANDER, Šlipogor, V & Konecná, M 2020, 'Comparative assessment of behaviorally derived personality structures in golden handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus oedipus*), and common marmosets (*Callithrix jacchus*)', *Journal of Comparative Psychology*. <https://doi.org/10.1037/com0000226>

Digital Object Identifier (DOI):

[10.1037/com0000226](https://doi.org/10.1037/com0000226)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Journal of Comparative Psychology

Publisher Rights Statement:

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Title: Comparative assessment of behaviorally-derived personality structures in golden-handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus oedipus*), and common marmosets (*Callithrix jacchus*)

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Abstract

One way to address questions about the origins and adaptive significance of personality dimensions is by comparing the personality structures of closely related species that differ in their socioecological circumstances. For the present study, we compared the personalities of captive golden-handed tamarins (*Saguinus midas*; N = 28), cotton-top tamarins (*Saguinus oedipus*; N = 20), and common marmosets (*Callithrix jacchus*; N = 17). All three species are New World monkeys of the family Callitrichidae. They thus share reproductive and behavioral characteristics but differ some in terms of their diet, habitat, and social organization. We expected that personality structures of closely related tamarin species would overlap more, both in terms of number of dimensions and their content, than either would overlap with the personality structure of common marmosets. We assessed personality using behavioral observations and compared the personality structures by means of cross-species correlations and fuzzy set analyses. Principal component analyses identified components that we labeled Agreeableness, Assertiveness, and Extraversion in golden-handed tamarins and common marmosets and components labeled Confidence and Extraversion in cotton-top tamarins. The greater personality similarities of the two phylogenetically more distant species suggest that differences in social organization, and in both habitat diversity and complexity, contributed to the evolution of personality. However, we also found that behaviors clustered in similar ways in the two tamarin species, suggesting that phylogenetic relatedness and genus-specific socioecological characteristics, such as the degree of reproductive competition, shaped personality structure in this primate family.

Keywords: marmoset, tamarin, primates, temperament, fuzzy set analysis

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Acknowledgements: We would like to thank the facilities involved in the project, namely Tierpark Berlin, Zoo Bojnice, Zoo Bratislava, Zoo Brno, Zoo Hodonín, Zoo Jihlava, Zoo Magdeburg, Zoo Ostrava, Zoo Plzeň, Zoo Praha, Zoo Ústí nad Labem, and Marmoset Lab at the Department of Behavioral and Cognitive Biology, University of Vienna. This study would not be possible without their collaboration. We are grateful to Mark James Adams for his support on “fuzzymonkey” package and Thomas Bugnyar for his valuable comments. This study was supported by grant 151/2016/P provided by Grant Agency of the University of South Bohemia.

Introduction

Personality traits in humans and animals are stable individual differences in behaviors, emotions, and thinking (Gosling, 2001; Pervin & John, 1997). Studies of human personality have found that personality traits (e.g., friendly, active) cluster into what have come to be known as personality facets (e.g., Gregariousness and Activity) that, in turn, cluster into broad personality dimensions or components (e.g., Extraversion) (Costa & McCrae, 1995). Although studies of nonhuman animals have yet to examine facets in detail, the evidence that personality traits cluster into higher-order dimensions is considerable (e.g., Fox & Millam, 2010; Selmann, Helle, Adams, Mar, & Lahdenperä, 2018; Gosling & John, 1999). Nonhuman personality research has also found that species differ with respect to how personality traits are organized into dimensions and that these differences appear to be attributable to phylogenetic relatedness and/or differences in species' behavior and socioecology (Adams et al., 2015; Morton et al., 2013; Uher, 2008; Weiss, 2018).

As is true for various physical or behavioral characteristics (Harvey & Pagel, 1991), by comparing personality structures of differently related species that share, to varying degrees, socioecological backgrounds, it is possible to address questions about the evolutionary bases of personality (Gosling, 2001; Gosling & Graybeal, 2007; Weiss, 2018). Specifically, if the personality dimensions of closely related species resemble one another, this would suggest that the way in which traits are organized into dimensions was inherited from a common ancestor. If, however, distantly related species with similar socioecologies have more similar personality dimensions than closely related species whose socioecologies differ, this would suggest that the organization of traits into dimensions is evolutionarily derived (Gosling, 2001; Gosling & Graybeal, 2007; Weiss, 2018). To take an example from the primate literature, studies using the

same or similar personality questionnaires have identified Openness dimensions in chimpanzees (Dutton, 2008; King & Figueredo, 1997) and rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011). Later, Openness was found in gorillas (Eckardt et al., 2015), bonobos (Weiss et al., 2015), and in four other macaque species (Adams et al., 2015). Further studies found Openness in two capuchin monkey genera (Manson & Perry, 2013; Morton et al., 2013; Robinson et al., 2016), in two squirrel monkey species (Wilson, Inoue-Murayama, & Weiss, 2018), and in common marmosets (Iwanicki & Lehmann, 2015; Koski, Buchanan-Smith, Burkart, Bugnyar, & Weiss, 2017; see however Inoue-Murayama, Yokoyama, Yamanashi, & Weiss, 2018). Thus, Openness, which is related to exploratory behavior, curiosity, and inventiveness, appears to be ancestral to anthropoid primates, perhaps because it aided survival in different and changing habitats and/or social environments. Species lacking Openness, such as orangutans (Weiss et al., 2011) and crested macaques (Adams et al., 2015), might have lost this dimension secondarily.

Differences in the organization of personality dimensions have also been linked to dominance hierarchies and social styles. For instance, a study of macaque monkeys found that the personality structures of despotic species with strict dominance hierarchies and strong nepotism, such as Japanese and rhesus macaques, resembled each other more than either resembled the personality structures of macaques with more relaxed and egalitarian social styles, such as Barbary macaques (Adams et al., 2015). Other differences in social organization have been associated with differences in personality structure. In cooperative breeders, such as common marmosets, a dimension related to social attentiveness and focus (Patience) has been identified. This dimension may be linked to the prosocial nature of marmoset social relationships, which are based on attentiveness to the needs of group members (Koski et al.,

2017). Apart from social organization, selective forces connected to cognitive abilities (Koski et al., 2017; Morton et al., 2013) and ecological variables, such as complexity of habitat or dietary spectrum (Mettke-Hofmann, Wink, Winkler, & Leisler, 2005; Mettke-Hofmann, Winkler, & Leisler, 2002), can also contribute to the shaping of personality structure.

Comparative studies of personality structures in primates require that a broad range of traits is measured in the same way in all species under study. The use of standardized questionnaires is one way to achieve this (e.g., Morton et al., 2013; Weiss et al., 2011). However, it is also possible to record a broad range of naturally occurring repeatable behaviors (common behaviors), which one would subject to data reduction analyses. Although there are studies on primates that report personality structures derived from the coding of common behaviors (Brent et al., 2014; Ebenau, von Borell, Penke, Ostner, & Schülke, 2020; Konečná et al., 2008; Martin & Suarez, 2017; Šlipogor, Burkart, Martin, Bugnyar, & Koski, 2020; Sussman, Ha, Bentson, & Crockett, 2013; Tkaczynski et al., 2018; Uher, Addessi, & Visalberghi, 2013), only Sussman and colleagues used this method to compare personality structures across species (Sussman et al., 2013).

The use of coding of common behaviors offers some advantages. For instance, it enables the direct comparison of the frequencies and durations of behaviors between individuals as well as species (Freeman, Gosling, & Schapiro, 2011). Using common behaviors in comparative personality research, however, requires detailed knowledge of the species' behavioral repertoires and the function of specific behaviors (Gosling, 2001; Uher, 2008), and this approach may not be feasible if the species that one wishes to compare have highly dissimilar repertoires.

For our study, we compared behaviorally-derived personality structures of three callitrichid species: golden-handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus*

oedipus), and common marmosets (*Callithrix jacchus*). The basal split between the *Saguinus* and the other Callitrichidae genera is dated ca. 14 million years ago and the *midas* and *oedipus* groups diverged ca. 5 million years ago (Buckner, Lynch Alfaro, Rylands, & Alfaro, 2015). Callitrichidae are a diverse family of small-bodied New World monkeys that share a unique set of reproductive and behavioral characteristics, including twinning, a large maternal to infant body-mass ratio, post-partum estrus, fast life history, reproductive suppression of subordinates, alloparental care of infants, and proactive prosociality (Burkart & Finkenwirth, 2015; Digby, Ferrari, & Saltzman, 2007).

There are also substantial differences between common marmosets and both tamarin species in their ecology. The main components of the callitrichid diet are fruits and animal prey. The specific diet composition, however, varies between genera (Digby et al., 2007). Marmosets are morphologically adapted to exploit plant gums and saps that make up the bulk of their diets (Rylands & de Faria, 1993). Common marmosets have also been documented to exploit alternative feeding resources, including leaves, prickly cladodes, fruits of cacti, and nectar of bromeliads (Abreu, De la Fuente, Schiel, & Souto, 2016; Amora, Beltrão-Mendes, & Ferrari, 2013). Their dietary flexibility, and the year-round availability of gums, enables common marmosets to inhabit a wide variety of seasonal habitats ranging from Atlantic rain forest to dry Caatinga thorn scrub forests (De la Fuente, Souto, Sampaio, & Schiel, 2014; Ferrari & Lopes Ferrari, 1989; Garber et al., 2019; Rylands & de Faria, 1993). Tamarins are dependent predominantly on highly seasonal fruits and animal matter and use plant gums and saps as fallback foods in seasons when fruit is scarce (Garber, 1993; García-Castillo & Defler, 2018). Both tamarin species, therefore, mostly inhabit primary and secondary forests, although golden-handed tamarins have also been reported to inhabit diverse forest types and habitats (Mittermeier

& van Roosmalen, 1981). The spatial distribution of the food resources exploited by these species influences the size of their home ranges, their daily group movements, and population densities. Specifically, compared to marmosets, tamarins have larger home ranges, longer daily paths, and lower population densities (reviewed in Digby et al., 2007; Ferrari & Lopes Ferrari, 1989).

In addition to these differences, although callitrichids live in small multimale-multifemale groups (Ferrari & Lopes Ferrari, 1989), there is a high degree of variability in the social organization of groups and populations. Marmosets form larger groups than tamarins (reviewed in Digby et al., 2007; Ferrari & Lopes Ferrari, 1989). Moreover, although the group sizes documented for cotton-top and golden-handed tamarins are comparable (Ferrari & Lopes Ferrari, 1989), researchers have observed two golden-handed tamarin groups merging temporarily to make up a single group (Thorington, 1968), suggesting that golden-handed tamarins may make up larger groups. Detailed knowledge of the social system of wild golden-handed tamarins, however, is not available. Differences in group dynamics between these species have been observed, too. In common marmosets, researchers have reported frequent changes in group membership due to high inter-group transfer (Scanlon, Chalmers, & Monteiro da Cruz, 1988). Moreover, in marmosets, females are more likely to leave the group (de Sousa, Albuquerque, Yamamoto, Araújo, & Arruda, 2009) whereas cotton-top tamarin groups are relatively stable with no sex differences in dispersion (Savage, Giraldo, Soto, & Snowdon, 1996).

Other differences between tamarins and marmosets concern reproduction. Callitrichids' reproductive systems are characterized by high reproductive skew. Within groups, there is one breeding female and the reproduction of other females in the group is suppressed (Digby et al.,

2007). Species differences in the degree of reproductive suppression are linked to ecological and physiological costs of infant rearing that are related to maternal to infant body-mass ratio and the size of home ranges (Díaz-Muñoz, 2016). Specifically, despite having twins twice a year, the infant care costs in marmosets are lower than those in tamarins, which give birth once per year (Díaz-Muñoz, 2016). As a result, reproductive suppression in marmosets is incomplete and stable groups with two parous females have been observed (reviewed in Yamamoto, Arruda, Alencar, de Sousa, & Araújo, 2009). The reproductive inhibition in tamarins, on the other hand, is strict with total suppression of ovulation of subordinate females (Ziegler, Savage, Scheffler, & Snowdon, 1987).

We used data from behavioral observations to compare the personality structures of captive common marmosets and golden-handed tamarins and also compared these to the personality structure found in a previous study of cotton-top tamarins (Masilkova, Weiss, & Konečná, 2018). To do so, we coded common behaviors defined in ethograms for these species. From observed behaviors, we created behavioral indices covering broad behavioral repertoires of species and representing general behavioral displays. We calculated the repeatabilities of these indices and then, to obtain personality dimensions, we subjected these indices to principal components analysis. To compare the personality dimensions and their overlap across species, we computed unit-weighted component scores and correlated these scores with one another (Morton et al., 2013; Weiss et al., 2011; Wilson et al., 2018). To identify personality facets, we performed fuzzy set analysis (Adams et al., 2015; Smithson & Verkuilen, 2006). We then compared how facets clustered into dimensions. Given their phylogenetic relatedness and socioecological similarities, we hypothesized that the personality structures of the tamarin species would overlap more, both in terms of the number of dimensions and in terms of their

facet content, than the structure of either tamarin species would overlap with that of common marmosets.

Methods

Subjects and Housing

The common marmosets ($N = 17$) included 12 males (age 1 to 16 years, $M = 7.5$, $SD = 4.9$) and five females (age 1 to 13 years, $M = 9.1$, $SD = 4.6$) from five groups housed at the Department of Behavioral and Cognitive Biology, University of Vienna (see Table S1 in the Supplementary materials). These subjects were housed in indoor-outdoor enclosures furnished with branches, wooden platforms, sleeping boxes and enrichment items, the latter being changed on a regular basis. Groups were fed once a day with a mixture of fresh fruits, vegetables, insects, milk products, and commercial food for callitrichids. Marmosets had *ad libitum* access to water. For more information on the marmosets' housing conditions see Šlipogor, Gunhold-de Oliveira, Tadić, Massen, and Bugnyar (2016).

The golden-handed tamarins ($N = 28$) included 15 males (age 1 to 11 years, $M = 4.7$, $SD = 3.3$) and 13 females (age 1 to 9 years, $M = 3.9$, $SD = 2.7$) from seven groups housed in Czech and German zoos (see Table S1). The cotton-top tamarins ($N = 20$) included 12 males (age 2 to 15 years, $M = 5.0$, $SD = 4.5$) and eight females (age 1 to 11 years, $M = 6.3$, $SD = 3.8$) from five groups housed in Czech and Slovak zoos (see Table S1). Tamarins were housed in spacious indoor enclosures equipped with branches, sleeping boxes, ropes, artificial or living plants, and enrichment objects. At the time of data collection, three groups of golden-handed tamarins (Brno, Hodonín, Magdeburg) and one cotton-top tamarin group (Ostrava) had access to an outdoor enclosure. Tamarins were provided a mixture of fresh and commercial food for callitrichids two to four times a day depending on the zoo. Water was available *ad libitum*.

Except for one female golden-handed tamarin whose origins and rearing background were unknown, the marmosets and tamarins were born in captivity and reared in family groups.

Personality Measures

Behavioral observations. For the behavioral observations, ethograms covering a broad behavioral spectrum of each species were compiled from the literature (common marmosets: Bezerra & Souto, 2008; Stevenson & Poole, 1976; Lipp, 1978; cotton-top and golden-handed tamarins: Masilkova et al., 2018). The ethograms included general behavioral categories common to all three species (e.g., locomotion and exploratory behavior) as well as species-specific behaviors (e.g., agonistic displays). The ethograms with definitions of behaviors selected for statistical analyses are provided in Supplementary materials (see Table S2). Behavioral observations were conducted between July 2011 and April 2016 by MM, who recognized the animals individually by their distinct body and facial features. Behaviors were recorded using a voice recorder (Olympus VN-8700PC Digital Voice Recorder). Observations of zoo-housed subjects were conducted in front of their enclosures from the visitor area. Observations of laboratory-housed subjects were made from an area in front of the enclosures.

The observer collected behavioral data using focal continuous recording with 30-minute sessions. In the case of social interactions, the directionality and identity of social partner were noted. Additionally, the observer carried out focal instantaneous sampling (Martin & Bateson, 2007) at 2-minute intervals within each session. During scans, the focal animal's behavioral states, the identity of its social partners, and the location (substrate) were recorded. As not all groups contained infants, social interactions with infants were recorded, but not included in our analyses. Only animals older than 12 months were observed as focal subjects ($N = 65$). Each focal animal was observed at least once a day and for a maximum of four times a day depending

on group size. If a focal animal was out of the observer's sight for more than 10 minutes, the focal session was discarded and replaced by a new one. The order of focal animals was randomized at the beginning of the observation period and counterbalanced so that every focal animal was observed evenly throughout the day. The focal sessions (12 per day) started between 07:15 and 09:30 and finished between 15:30 and 19:30 and so covered the daily activity of each group. Altogether, the total observation time was 170 hours for common marmosets ($M = 10$, $SD = 0$ h per subject), 399 hours for golden-handed tamarins ($M = 14.25$, $SD = 1.89$ h per subject), and 300 hours for cotton-top tamarins ($M = 15$, $SD = 0$ h per subject).

Behavioral indices. The observed behavioral data were analyzed in the form of behavioral indices. The selection of behavioral indices was driven by three criteria. First, we sought to cover as broad a repertoire across the species as possible so that we described the varying ways in which individuals could differ from one another. Second, where possible, we chose indices described in previous studies (Konečná et al., 2008; Masilkova et al., 2018). Third, we focused on general displays of behavior that facilitate comparison across species. This led us to omit one index (*Grimace^F*) from the list used by Masilkova et al. (2018) because this behavior was not present in common marmosets or golden-handed tamarins. This resulted in a list of 22 behavioral indices (see Table 1).

Behavioral indices were expressed as either i) frequencies of single behavior per hour (e.g., *Self-grooming^F*); ii) the proportion of scans reflecting duration of a single behavior (e.g., *Monitoring^P*); iii) as above but summarizing several behaviors (e.g., *Exploration^F*, *Affiliation^P*); iv) proportions of different types of behaviors (e.g., proportion of resting to active behaviors in *Resting^P*); or v) a variety of different behavior types (e.g., *Activity diversity^S*) computed as Shannon diversity indices (Shannon & Weaver, 1949). To capture the individual variation and

avoid zero-inflated data, behaviors were considered suitable for an index if they were observed in at least 75% individuals. In the case of rare but meaningful behaviors (as in iii), such as aggression and exploration (*Exploration^F*, *Contact aggression^F*, *Threats^F*), we grouped several behaviors from the same behavioral category that was defined in the ethogram to reach this limit (see Table 1 for details). Indices based on proportions of different types of behaviors or diversity measures (as in iv and v) provide more comprehensive information on individuals' behaviors by setting the behaviors in various relations to one another (Anestis, 2005; Konečná et al., 2008). Species differences in the raw behavioral values on each index are summarized in the Table S3. Because our measures were recorded in different units (i.e., frequencies, proportions, Shannon diversity indices), the behavioral indices were standardized before analyses so that they had a mean of zero and standard deviation of one.

“Insert [Table 1 here]”

Statistical Analyses

Unless stated otherwise, statistical analyses were performed in R version 3.5.0 (R Core Team, 2017). Analyses were performed separately for each species.

Repeatability. To test whether the behavioral indices were repeatable and thus represented personality traits, we first split the datasets into two (for marmosets) and three (for each tamarin species) subperiods of five hours of observation per individual. Next, we analyzed species-specific short-term repeatability using the package “rptR” (Stoffel, Nakagawa, & Schielzeth, 2017). The number of measurements for each individual (in this case subperiods) have been shown to have no effect on repeatability (Bell, Hankison, & Laskowski, 2009). The repeatability (Nakagawa & Schielzeth, 2010) was calculated using linear mixed-effects models with individual as a random factor. The *p*-values and 95% confidence intervals were obtained

from 1000 permutations and 1000 bootstrap runs. If a behavioral index had a statistically significant repeatability, but a confidence interval that included zero, we treated it with caution.

Identification of personality dimensions. We determined the number of dimensions to be extracted by inspecting scree plots and conducting Horn's parallel analysis (Horn, 1965) implemented in the package "paran" (Dinno, 2012). To identify the personality structure of each species, we conducted principal components analysis (PCA) using the "psych" package (Revelle, 2017). We subjected the resulting component matrices to orthogonal (varimax) and oblique (promax) rotations. We interpreted the oblique solution only if the correlations between components were non-negligible and the orthogonal and oblique solutions differed. The labels we chose for components were based on the component loadings. In addition, we used subscripts (*CM* for common marmosets, *GT* for golden-handed tamarins, and *CT* for cotton-top tamarins) to distinguish between components with the same name in different species.

Because our sample sizes were small, we also used MATLAB 9.5.0.944444 (R2018b) to extract dimensions for each species using regularized exploratory factor analysis (REFA), which is designed for small samples (Jung, 2013; Jung & Lee, 2011). We then compared the structures derived via REFA to those derived via PCA by means of targeted orthogonal Procrustes rotations (McCrae, Zonderman, Costa, Bond, & Paunonen, 1996).

Comparison of personality dimensions across species. To assess the overlap of dimensions between species, we computed unit-weighted component scores according to the species-specific personality structure. Unit-weighted scores are sums of scores on indices that loaded saliently (defined here as $\geq |0.4|$) on a component. Indices with negative salient loadings were weighted -1; indices with positive salient loadings were weighted 1; and all other indices were weighted 0 (Gorsuch, 1983). Next, we computed unit-weighted scores for each individual

according to the personality structure of the other species. For instance, unit-weighted scores for the common marmosets were calculated based on the components identified in golden-handed tamarins. We then compared each species' scores and the scores based on the other species' structure by means of Pearson correlations that were adjusted for the family-wise error rate using the Holm-Bonferroni adjustment for multiple comparisons (Holm, 1979).

Identification of personality facets. To obtain personality facets, we performed fuzzy set analysis using the R package “fuzzymonkey” (Adams, 2015). Following Adams et al. (2015), we defined fuzzy sets as facets of personality (clusters of indices) that combine to form higher-level personality units or dimensions. A fuzzy set is characterized as a list of objects (behavioral indices in our case) that belong to that list with a certain continuous degree of probability. This degree is measured as a membership value (m) ranging from 0 to 1, which represents a range rather than a binary yes/no classification (Smithson & Verkuilen, 2006; Zadeh, 1965). An index, thus, may belong to different fuzzy sets. To define which behavioral indices cluster into facets, we compared the overlap between semantically similar personality dimensions (X, Y, Z) of each species, based on the results of correlations of unit-weighted scores described above, using fuzzy intersections (\cap) between dimensions. We then computed the minimum loading, that is, the minimum degree of membership (\min), of each index on facet ($m_{X \cap Y \cap Z}$): $m_{X \cap Y \cap Z} = \min(m_X, m_Y, m_Z)$. The threshold for the salient inclusion of an index in a fuzzy set (facet) was computed by calculating the lower level of 95% confidence interval of a null distribution of index memberships of 100 randomly generated fuzzy intersects (Adams et al., 2015). Finally, we defined the facet more specifically by using the indices that had the greatest membership compared to other facets.

Comparison of personality facets across species. To test whether the dimensions across species are composed of similar clusters of behaviors, we compared the configuration of facets and behaviors in the personality structures of species.

Ethical Note

All zoos involved in this study are members of European Association of Zoos and Aquaria (EAZA). The husbandry conditions and animal welfare in all facilities were in accordance with the EAZA Best Practice Guidelines for Callitrichidae (Bairrão Ruivo & Stevenson, 2017) and in accordance with Austrian legislation in the case of common marmosets.

Results

Repeatability of Behavioral Indices

The repeatability estimates for the behavioral indices for each species are presented in Table S4. In each species, repeatabilities ranged from 0.00 to 0.96. The mean repeatability of behavioral indices was higher in golden-handed tamarins ($M = 0.72$, $SD = 0.15$) than in cotton-top tamarins ($M = 0.62$, $SD = 0.24$) and common marmosets ($M = 0.60$, $SD = 0.25$). Six indices (*Activity diversity*^S, *Carrying food away*^F, *Invite grooming(act)*^F, *Invite grooming(rec)*^F, *Substrate diversity*^S, and *Vigilance*^F) in common marmosets were not significantly repeatable. In golden-handed tamarins and cotton-top tamarins, all indices were significantly repeatable. Five indices (*Grooming(act)*^F, *Grooming(rec)*^F, *Invite grooming(rec)*^F, *Self-grooming*^F, and *Terminate grooming*^F) in cotton-top tamarins, although being significantly repeatable, contained 0 in the confidence interval (Masilkova et al., 2018). Given the purpose of the study, we retained all 22 indices in all three species for further analyses, but treated indices that were not significantly repeatable, and those which contained 0 in their confidence interval, with caution.

Personality Dimensions

Due to the lower number of subjects than indices, the correlation matrices of common marmosets and cotton-top tamarins were smoothed using the `cor.smooth` function to be positive definite (Revelle, 2017). The Keiser-Meyer-Olkin measure of sampling adequacy indicated that only around one-third to two-fifths of the variance in these behavioral indices might be caused by latent variables, that is, factors (common marmosets: KMO = 0.41; cotton-top tamarins: KMO = 0.31; golden-handed tamarins: KMO = 0.44). On the other hand, Bartlett's test of sphericity indicated that the correlations between indices were large enough to warrant the use of factor analysis (common marmosets: $\chi^2 = 1154.94$, $df = 231$, $p < 0.01$; cotton-top tamarins: $\chi^2 = 1012.12$, $df = 231$, $p < 0.01$; golden-handed tamarins: $\chi^2 = 570.84$, $df = 231$, $p < 0.01$).

The personality dimensions of common marmosets and golden-handed tamarins derived by REFA were identical (congruence coefficients close to 1.00 for all dimensions suggesting equality; Lorenzo-Seva & ten Berge, 2006) to those derived by PCA (see Tables S5 and S6, respectively), as was the case in cotton-top tamarins (see Masilkova et al., 2018). We therefore decided to interpret and further analyze the results from PCA as it is a more commonly used data reduction method (Konečná, Weiss, Lhota, & Wallner, 2012; Wilson et al., 2018).

Common marmosets. Parallel analysis and examination of the scree plot suggested retaining three components. The absolute intercorrelations of the components did not exceed 0.15 and the promax structure (see Table S7) did not differ from the varimax structure, so we interpreted the varimax solution. The components explained 57% of the variance.

The personality structure is presented in Table 2. The first component loaded predominantly on indices related to physical activity (positive loadings of *Activity diversity*^S and *Substrate diversity*^S) and social activity (positive loadings of *Approaches*^F and *Departures*^F, and negative loadings of *Passive affiliation*^P). High scorers also paid more attention to their

environment (positive loadings of *Exploration^F* and *Vigilance^F*). We therefore named this component “Extraversion_{CM}”. The second component was primarily characterized by positive loading on indices related to grooming interactions (e.g., *Grooming(act)^F*, *Terminate grooming^F*, and *Invite grooming(rec)^F*) and by a negative loading on *Contact aggression^F*. Therefore, we named this component “Agreeableness_{CM}”. The third component was characterized by positive loadings on indices including *Scent marking^F*, *Object sniffing^F*, and *Scratching^F*. Marmosets scoring high on this component also threatened others more often and solicited grooming from others more often. We thus labeled this component “Assertiveness_{CM}”.

Golden-handed tamarins. Parallel analysis and examination of the scree plot indicated that there were three components. The absolute intercorrelations of these components were less than 0.18 and the promax structure (see Table S8) did not differ from the varimax structure. We therefore interpreted the varimax solution. The three-component structure accounted for 60% of the variance.

The personality structure is displayed in Table 2. The first component had positive loadings on indices related to aggression (*Contact aggression^F*, *Threats^F*) and scent marking (*Scent marking^F*, *Object sniffing^F*). High scoring tamarins on this dimension also approached and left others more often. Therefore, we named this component “Assertiveness_{GT}”. The second component was characterized by loadings on affiliative behaviors, such as engaging in social play or being in contact or proximity with others (positive loadings of *Affiliation^P* and negative loadings of *Passive affiliation^P*), and on grooming interactions (e.g., positive loadings of *Grooming(act)^F* and *Terminate grooming^F*). We therefore labeled this component “Agreeableness_{GT}”. The third component had positive loadings on indices related to physical activity (*Activity diversity^S*) and behaviors directed to individuals’ environment (*Exploration^F*,

Monitoring^P, and *Vigilance*^F). High scoring tamarins were also active socially, that is, this component loaded positively on *Invite grooming(act)*^F. We thus named this component “Extraversion_{GT}”.

Cotton-top tamarins. The parallel analysis suggested extracting two components. Because the correlation between the promax-rotated components (see Table S9) was negligible (0.06), we interpreted the varimax solution. The two components accounted for 55% of the variance. The personality structure based on 22 indices (see Table 2) corresponded to the structure based on 23 indices published in Masilkova et al. (2018).

Cotton-top tamarin personality structure was characterized by a broad dimension, labeled Extraversion_{CT}, that loaded positively on activity (e.g., *Activity diversity*^S and *Exploration*^F) and most social behaviors (e.g., positive loadings of *Grooming(act)*^F, negative loadings of *Passive affiliation*^P) and a dimension, Confidence_{CT}, that reflected individuals’ confidence in social interactions (e.g., positive loadings of *Approaches*^F and *Contact aggression*^F) and interactions with environment (e.g., positive loadings of *Substrate diversity*^S).

“Insert [Table 2 here]”

Cross-Species Comparisons of Dimensions

The correlations of component scores of each species’ own structure and component scores based on other species’ structures are shown in Table 3. The significant correlations between the components are depicted in Figure 1. All significant correlations were positive. Agreeableness_{GT} was strongly correlated with Agreeableness_{CM} and to a lesser degree with Confidence_{CT} and Extraversion_{CT}. Similarly, slightly lower, but still strong correlations were found between Assertiveness_{GT} and Assertiveness_{CM}, and Assertiveness_{GT} and Confidence_{CT}. The correlation between Assertiveness_{CM} and Confidence_{CT} was not significant. Extraversion was

comparable across all three species with the strongest correlation between cotton-top tamarins and golden-handed tamarins (see Table 3). Furthermore, $Extraversion_{CT}$ was correlated with all the components of the other species except $Assertiveness_{GT}$. The correlations of $Extraversion_{CT}$ were, however, stronger with the components of golden-handed tamarins than of common marmosets.

“Insert [Table 3 here]”

Personality Facets

When creating fuzzy sets, the following abbreviations for dimensions were used: Ag = Agreeableness, As = Assertiveness, Co = Confidence, Ex = Extraversion. To indicate the species that sets refer to, we used the same subscripts that we used for components, and x to designate the fuzzy intersections of all three callitrichid species. The lower bound of the 95% confidence interval, generated by fuzzy intersections of randomly selected components, was $m(i) = |0.13|$. Thus, indices with membership $\geq |0.13|$ were considered to define a facet.

The memberships of indices in fuzzy sets are displayed in Table 4. Based on the significant correlations of component scores (see Table 3), we constructed a fuzzy intersection of the Extraversion components: $Ex_{CT} \cap Ex_{GT} \cap Ex_{CM}$ which was supported by the memberships of active and exploratory behavior ($Activity\ diversity^S$, $Exploration^F$), $Vigilance^F$, $Monitoring^P$ and negative values of $Invite\ grooming(rec)^F$ and $Departures^F$. We, thus, labeled this facet “activity/exploration $_x$ ”.

Because the component scores of Assertiveness of common marmosets and golden-handed tamarins were significantly correlated with $Extraversion_{CT}$ and $Confidence_{CT}$, we created and compared the fuzzy intersections for both options. Intersection $Co_{CT} \cap As_{GT} \cap As_{CM}$ was defined well by membership of indices related to contact aggression and physical proximity

(*Approaches^F*, *Contact aggression^F*). Therefore, we named this facet “aggression_X”. Intersection $Ex_{CT} \cap As_{GT} \cap As_{CM}$, on the other hand, was separable from aggression_X by the highest membership of behaviors related to visual or scent communication (*Threats^F*, *Object sniffing^F*, *Scent marking^F*). Thus, we labeled this facet “signals_X”. Both facets (aggression_X, signals_X) thus capture different aspects of dominance interactions. *Scratching^F* was present in both aggression_X and signals_X; however, the higher loading was on aggression_X (0.33 vs. -0.13).

Similarly, component scores of Agreeableness of common marmosets and golden-handed tamarins were correlated with Extraversion_{CT} and Confidence_{CT}. Therefore, two intersects were constructed. Intersection $Ex_{CT} \cap Ag_{GT} \cap Ag_{CM}$ described a facet labeled “grooming_X” clustering the initiation and termination of active social grooming behaviors (*Grooming(act)^F*, *Terminate grooming^F*). Intersect $Co_{CT} \cap Ag_{GT} \cap Ag_{CM}$ was characterized by membership of indices related to other socio-positive behaviors (*Affiliation^P*), demanding and receiving grooming (*Invite grooming(act)^F*, *Grooming(rec)^F*), and *Substrate diversity^S*. Due to capturing a more general sociable aspect of personality, we named this facet “sociability_X”. *Grooming(act)^F* and *Terminate grooming^F* loaded on both intersects, but grooming_X had higher membership (0.72 vs. 0.33 and 0.65 vs. 0.40, respectively). *Resting^P* had the same membership in both facets (-0.19).

Three indices (*Carrying food away^F*, *Passive affiliation^P*, *Self-grooming^F*) did not have a salient membership in any fuzzy intersects. In contrast, *Activity diversity^S*, *Affiliation^P*, *Substrate diversity^S*, and *Vigilance^P* had salient membership in several facets (see Table 4).

“Insert [Table 4 here]”

Cross-Species Comparisons of Facets

On the level of personality facets, there were similarities between tamarin species in how facets clustered into dimensions (for configuration of facets in dimensions, see Figure 1).

Specifically, all indices of the activity/exploration_X facet but one (*Departures*^F) were subsumed under the Extraversion dimension in golden-handed and cotton-top tamarins. In marmosets, on the other hand, *Departures*^F and other indices of the activity/exploration_X facet organized into Extraversion_{CM}, and two indices (*Monitoring*^P, *Invite grooming(rec)*^F) organized into Agreeableness_{CM}. Moreover, aggression_X was subsumed under Assertiveness_{GT} or Confidence_{CT} in tamarins. In marmosets, however, aggression_X was dispersed across all three dimensions. There were also similarities between golden-handed tamarins and common marmosets, namely signals_X and grooming_X were part of the Assertiveness and Agreeableness dimensions, respectively. In cotton-top tamarins, these facets clustered together with activity/exploration_X in Extraversion_{CT}. Indices of sociability_X blended into all personality dimensions in golden-handed tamarins and common marmosets. This differed from the pattern seen in cotton-top tamarins where this facet was classified under Confidence_{CT}.

“Insert [Figure 1 here]”

Discussion

We compared the personality structures of golden-handed tamarins, cotton-top tamarins, and common marmosets. At the level of personality dimensions, we found the greatest resemblance between golden-handed tamarins and common marmosets. Personality structures in these species comprised three dimensions, which we labeled Extraversion, Assertiveness, and Agreeableness. Personality structure in cotton-top tamarins, on the other hand, comprised two dimensions, which we labeled Extraversion and Confidence. Analyzing the personality structures at the level of facets revealed further similarities between golden-handed tamarins and common marmosets, but also between cotton-top and golden-handed tamarins. Specifically, signals_X was subsumed under Assertiveness and grooming_X under Agreeableness in common marmosets and

golden-handed tamarins. In both tamarin species, activity/exploration_X was included in Extraversion and aggression_X was included in Confidence_{CT} and Assertiveness_{GT}.

Either an Assertiveness or Confidence dimension was detected in all three species. Previous studies found similar dimensions in New World monkeys (e.g., Wilson et al., 2018), Old World monkeys (e.g., Adams et al., 2015), and great apes (e.g., Weiss et al., 2015). Thus, dimensions such as Assertiveness appear to be important for socially living primates. A similar dimension was probably present in the common ancestor of Old World and New World monkeys. Despite the high level of social cooperation, food sharing, rare intra-group aggressive events, and the rather egalitarian social relationships in callitrichids, the social systems of tamarins and marmosets are characterized by intense permanent reproductive competition where reproductive success depends on social dominance (Garber, 1997). Variation along Assertiveness might have evolved in response to these high levels of competition and cooperation.

The present findings indicate that the organization of personality facets into dimensions like Assertiveness or Confidence might have been affected by the different dominance hierarchies and social styles of these species. At the facet level, we found similarities between Assertiveness_{GT} and Confidence_{CT}; both dimensions consisted of a facet related to contact aggression and initiating social contact (aggression_X). However, this was not the case in common marmosets where indices of aggression_X were found in all the dimensions. This could be explained by tamarins' closer phylogenetic relatedness or by the greater degree of reproductive suppression of subordinates in tamarins compared to marmosets (Díaz-Muñoz, 2016). Specifically, the inhibition of reproduction might have led to aggression in tamarins being more related to other confidence-like traits. We also noted that tamarins, on average, displayed higher rates of contact aggression compared to marmosets (see Table S3). Assertiveness_{GT} and

Confidence_{CT} resembled the Assertiveness dimension described in squirrel monkeys (Wilson et al., 2018) and brown capuchin monkeys (Morton et al., 2013). As such, these dimensions may more closely resemble the ancestral forms of the dimension. In common marmosets, indices of contact aggression and initiating social contact loaded on Agreeableness_{CM} and Extraversion_{CM}, respectively; Assertiveness_{CM} was made up mostly of behaviors related to signals_X. Similar dimensions emerged in recent studies of common marmoset personality (as Assertiveness in Koski et al., 2017, Dominance in Inoue-Murayama et al., 2018, and behaviorally-derived Neuroticism in Iwanicki & Lehmann, 2015). The signals_X facet was, interestingly, also part of Assertiveness_{GT}. Compared to tamarins, marmosets live in larger groups (Digby et al., 2007; Ferrari & Lopes Ferrari, 1989) and thus may express Assertiveness more efficiently by olfactory communication (e.g., by scent marking). Tamarins, on the other hand, maintain close interactions with group members. The lack of detailed knowledge of wild golden-handed tamarin behavior and group composition prevents us from drawing strong conclusions.

Extraversion was also present and defined by activity/exploration_X in all three species. This facet captured behaviors related to activity, exploration, and interest in the surrounding environment. Across primates, activity and curiosity either load together on one dimension, such as Openness in squirrel monkeys (Wilson et al., 2018) and capuchin monkeys (Manson & Perry, 2013; Morton et al., 2013), on separate dimensions, such as Activity and Openness in macaques (Adams et al., 2015; Weiss et al., 2011), or Extraversion and Openness in chimpanzees and humans (Costa & McCrae, 1995; King & Figueredo, 1997), or together with other facets on Extraversion, such as in orangutans (Weiss, King, & Perkins, 2006). Why activity facets load on Extraversion in some species and on Openness in others, however, is unclear (Eckardt et al., 2015). Finally, the cluster of exploratory and active behaviors seems to be unique to New World

primates (with some exceptions, e.g., orangutans, Weiss et al., 2006), and might have been present in their common ancestor.

Because grooming_X and sociability_X were also included in Extraversion, we considered this dimension to be Extraversion rather than Openness as it resembled the broad Extraversion dimension of humans, chimpanzees, and orangutans (Costa & McCrae, 1995; King & Figueredo, 1997; Weiss et al., 2006). There were species differences, however, in the degree to which social behavior was included in this dimension. In cotton-top tamarins, Extraversion_{CT} was defined by grooming_X and signals_X. However, in common marmosets and golden-handed tamarins, social behavior accounted only for a small part of Extraversion, and in common marmosets, social behavior (*Affiliation^P*) even had negative loadings on the dimension. This narrowly defined variant of Extraversion resembled dimensions labeled Inquisitiveness (Koski et al., 2017) and Openness (Iwanicki & Lehmann, 2015) that were found in trait ratings of common marmosets.

Common marmosets and golden-handed tamarins are ecologically successful species (Pack, Henry, & Sabatier, 1999; Rylands, Coimbra-Filho, & Mittermeier, 1993). In fact, common marmosets are an invasive species and are a threat to native primate populations (Silva, Verona, Conde, & Pires, 2017). This narrowly defined variant of Extraversion, then, might have enabled common marmosets and golden-handed tamarins to cope with a wide range of environmental challenges, and so made it possible for them to occupy a variety of ecological niches (Abreu et al., 2016; Amora et al., 2013; De la Fuente et al., 2014). On the other hand, cotton-top tamarins, which lack this narrowly-defined variant of Extraversion, face extinction because they cannot deal with habitat loss and change by exploiting other niches (Savage et al., 2016). The inability of cotton-top tamarins to adapt to environmental changes might be because traits related to exploratory behavior are tied to traits related to grooming, and thus the cluster of

affiliative and exploratory behaviors may be more resistant to natural selection. In cotton-top tamarins, individuals with high scores on Extraversion_{CT} explore their environment more often, display a wider range of activities, and, at the same time, tend to engage more often in active affiliative behaviors. Alternatively, the greater frequency with which this species engages in social behaviors might reflect their higher activity levels.

Golden-handed tamarins and common marmosets, each, had a distinct Agreeableness dimension, which was associated with socio-positive behaviors. Dimensions related to Agreeableness or Sociability have been identified in other nonhuman primates (reviewed in Freeman & Gosling, 2010). Therefore, it seems probable that a dimension associated with sociable and friendly behavior was present in the common ancestor of primates. Agreeableness in our sample was characterized by grooming_x and had loadings of indices related to sociability_x. Behavioral indices based on grooming interactions were positively correlated with Agreeableness or Sociability dimensions in other primates, for example, mountain gorillas (Eckardt et al., 2015), Hanuman langurs (Konečná et al., 2008), and common marmosets (Šlipogor et al., 2020). Consistent with its function (Dunbar, 1991), the frequent grooming of others might be interpreted as one of the main behavioral expressions of Agreeableness in nonhuman primates.

It has been hypothesized that independent Agreeableness and Extraversion dimensions evolved in species with varying social environments or complex social systems (Eckardt et al., 2015). Although common marmosets and golden-handed tamarins do not have complex social systems, these species were observed to form dynamic groups that varied in size (Digby et al., 2007; Ferrari & Lopes Ferrari, 1989; Thorington, 1968) and in which group membership changed frequently (Pontes & Monteiro da Cruz, 1995; Scanlon et al., 1988). Moreover, captive

golden-handed tamarins in large groups show higher interindividual tolerance than other tamarin species. In cotton-top tamarins, however, indices related to social behaviors were either part of $Extraversion_{CT}$ or part of $Confidence_{CT}$. Studies on wild groups of cotton-top tamarins report that this species lives in small, stable and cohesive groups where unfamiliar conspecifics that attempt to join established groups might be chased away (Ferrari & Lopes Ferrari, 1989; French & Snowdon, 1981; Neyman, 1977; Savage et al., 2016). It is therefore possible that not only the complexity of the ecological niche, but also the complexity of the social niche might be reflected in personality structure and, in particular, the number of dimensions that are present (Koski, 2014; Lukaszewski, Gurven, von Rueden, & Schmitt, 2017). In solitary living primates or primates living in small cohesive groups, facets of Agreeableness might be subsumed under other dimensions.

At the content level, there were modest differences between species in what traits loaded on Agreeableness. In golden-handed tamarins, Agreeableness contained mostly socio-positive behaviors as was the case in squirrel monkeys (Wilson et al., 2018). On the other hand, common marmoset Agreeableness had negative loadings on monitoring and contact aggression, traits that were part of Extraversion in both tamarin species. Thus, monitoring in tamarins may be related to exploring the environment whereas monitoring in marmosets may reflect hostile staring (de Boer, Overduin-de Vries, Louwerse, & Sterck, 2013; Sutcliffe & Poole, 1984). The negative association between aggressive behavior and dimensions like Agreeableness was described in Barbary macaques (Konečná et al., 2012) and Hanuman langurs (Konečná et al., 2008). It also emerged in a study of trait ratings in common marmosets (Iwanicki & Lehmann, 2015).

Our study is not without limitations. The sample sizes were small and less variance in the indices was likely caused by personality dimensions than might be desirable. The present results

should therefore be interpreted with a degree of caution until studies on larger samples of callitrichids, including wild populations, are conducted. Furthermore, despite the relatively high repeatability estimates, there was also variation across species resulting in inclusion of indices that were not repeatable or contained zero in the confidence interval. Low repeatability estimate suggests that there was either no variability in the behavior among the individuals, that the individuals did not behave consistently, or that there was a large amount of error variance. Further studies should assess the repeatability of these indices over longer periods of time and over different contexts to further test whether they are measures of personality. Moreover, labels assigned to personality dimensions are hypotheses about the constructs that the dimensions represent and so should be considered tentative and subjected to further tests (Bell, 2007; Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Gosling, 2001; Koski, 2014). For instance, we labeled dimensions based on activity and exploration as Extraversion. In other marmoset studies using questionnaires, components composed of similar behaviors were labeled Inquisitiveness (Koski et al., 2017) and Openness (Iwanicki & Lehmann, 2015). Similarly, in studies of humans and primates, dimensions labeled Agreeableness tend to be associated with helpfulness, sympathizing with others, and being sensitive to others' needs (Goldberg, 1990; Weiss et al., 2006, 2009, 2015; Wilson et al., 2018). Sociability, a dimension that split from the facet of Extraversion, is characterized by being friendly and sociable. Examination of correlations between the scores on Agreeableness and the results of cooperative tasks could further clarify whether this dimension in common marmosets and golden-handed tamarins reflects Agreeableness or Sociability.

Given the existence of group level-similarity in personality in callitrichids (Koski & Burkart, 2015; Šlipogor et al., 2016), future studies should compare the personality structures at

the level of groups. Moreover, studies of other species or genera of callitrichids, such as lion tamarins, pygmy marmosets, or Goeldi's monkeys, would help us to better understand the phylogenetic roots of personality. Specifically, these species vary in their ecological and social niches, and so studying them could clarify how these factors influence personality structure. Focusing on specific socioecological variables, such as group size and dynamics, degree of reproductive competition, types of habitats, predation pressure, and other relevant selective forces can clarify still further the organization of personality structure.

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Table 1
Definitions of 22 Behavioral Indices Used for Data Reduction Analyses

Index	Data	Calculated as
<i>Activity diversity</i> ^S	I	Shannon diversity index of activity types
<i>Affiliation</i> ^P	I	Proportion of time focal subject spent by affiliative behaviors (contact, proximity, social play, allogrooming)
<i>Approaches</i> ^F	C	Frequency of approaching others
<i>Carrying food away</i> ^F	C	Frequency of carrying food away from others
<i>Contact aggression</i> ^F	C	Frequency of contact aggressive behaviors (general aggression, bite, beating, grab, grasp, chase, fight, push, displacement + tamarin face press or marmoset cuff)
<i>Departures</i> ^F	C	Frequency of leaving from others
<i>Exploration</i> ^F	C	Frequency of explorative behaviors (exploration, object manipulation, substrate searching)
<i>Grooming(act)</i> ^F	C	Frequency of grooming initiation by focal subject
<i>Grooming(rec)</i> ^F	C	Frequency of being groomed by others
<i>Invite grooming(act)</i> ^F	C	Frequency of inviting to groom
<i>Invite grooming(rec)</i> ^F	C	Frequency of being invited to groom
<i>Monitoring</i> ^P	I	Proportion of time watching the environment or other individuals
<i>Object sniffing</i> ^F	C	Frequency of sniffing an object or substrate
<i>Passive affiliation</i> ^P	I	Proportion of initiated passive affiliative behaviors (contact, proximity) to all affiliative behaviors
<i>Resting</i> ^P	I	Proportion of resting behaviors (rest, look, watch, sit, lie) to active behaviors (move, jump, cling, hang)
<i>Scent marking</i> ^F	C	Frequency of scent marking
<i>Scratching</i> ^F	C	Frequency of scratching
<i>Self-grooming</i> ^F	C	Frequency of self-grooming
<i>Substrate diversity</i> ^S	I	Shannon diversity index of substrate types
<i>Terminate grooming</i> ^F	C	Frequency of terminating grooming by a focal individual
<i>Threats</i> ^F	C	Frequency of threatening others: arched bristle display, frowning, + tamarins: open mouth display, headshake, tongue flick or marmosets: tufts flick stare, tufts forward, genital display
<i>Vigilance</i> ^F	C	Frequency of being alert

Note. ^F = frequency of behavior per hour, ^P = proportion, ^S = Shannon diversity index (Shannon & Weaver, 1949), C = data from continuous focal recording, I = instantaneous focal sampling data, (*act*) = behavior initiated by the focal animal, (*rec*) = received behavior of focal animal. Indices composed of species typical behaviors are in boldface.

Table 2

Personality Structures Based on Varimax Rotated PCA Component Loadings of Common Marmosets, Golden-Handed Tamarins, and Cotton-Top Tamarins

Behavioural index	Components								Communalities		
	Ext _{CM}	Agr _{CM}	Ass _{CM}	Ass _{GT}	Agr _{GT}	Ext _{GT}	Ext _{CT}	Con _{CT}	h ² _{CM}	h ² _{GT}	h ² _{CT}
<i>Activity diversity</i> ^S	0.71	-0.44	-0.21	0.04	0.36	0.55	0.89	0.27	0.74	0.44	0.86
<i>Affiliation</i> ^P	-0.53	0.33	-0.50	0.31	0.82	-0.04	-0.25	0.81	0.64	0.76	0.71
<i>Approaches</i> ^F	0.63	-0.16	0.40	0.93	0.04	-0.15	-0.03	0.84	0.58	0.89	0.71
<i>Carrying food away</i> ^F	0.63	-0.04	0.12	0.35	0.23	0.03	-0.17	0.66	0.41	0.18	0.46
<i>Contact aggression</i> ^F	-0.14	-0.68	0.18	0.86	-0.07	-0.12	-0.02	0.76	0.52	0.76	0.57
<i>Departures</i> ^F	0.78	0.07	0.11	0.71	0.31	-0.29	-0.13	0.92	0.63	0.68	0.87
<i>Exploration</i> ^F	0.87	-0.26	-0.12	-0.04	-0.09	0.53	0.88	-0.02	0.83	0.29	0.77
<i>Grooming(act)</i> ^F	0.19	0.79	-0.05	0.03	0.89	0.00	0.72	0.33	0.66	0.80	0.62
<i>Grooming(rec)</i> ^F	-0.23	0.65	0.11	0.11	0.59	0.18	0.07	0.62	0.48	0.40	0.38
<i>Invite grooming(act)</i> ^F	-0.03	0.47	0.52	0.04	0.23	0.81	0.22	0.45	0.50	0.71	0.25
<i>Invite grooming(rec)</i> ^F	-0.42	0.76	0.00	0.05	0.39	0.73	0.69	0.02	0.75	0.69	0.48
<i>Monitoring</i> ^P	0.20	-0.61	-0.06	0.05	-0.19	0.79	0.43	-0.10	0.42	0.65	0.19
<i>Object sniffing</i> ^F	0.06	0.36	0.77	0.70	-0.09	0.49	0.48	-0.35	0.73	0.74	0.35
<i>Passive affiliation</i> ^P	-0.88	-0.09	-0.04	0.24	-0.86	-0.02	-0.88	0.11	0.79	0.79	0.78
<i>Resting</i> ^P	0.10	-0.19	-0.03	-0.54	-0.22	-0.20	-0.64	-0.42	0.05	0.38	0.59
<i>Scent marking</i> ^F	-0.13	-0.08	0.93	0.79	-0.19	0.26	0.33	0.09	0.89	0.73	0.12
<i>Scratching</i> ^F	0.36	-0.13	0.75	0.33	0.05	-0.06	-0.13	-0.84	0.72	0.11	0.72
<i>Self-grooming</i> ^F	0.21	0.00	0.25	-0.03	0.70	-0.10	0.43	-0.24	0.10	0.50	0.24
<i>Substrate diversity</i> ^S	0.53	0.34	-0.18	-0.59	-0.49	0.45	0.32	0.57	0.43	0.79	0.42
<i>Terminate grooming</i> ^F	0.19	0.81	-0.06	0.05	0.93	0.03	0.65	0.40	0.69	0.87	0.58
<i>Threats</i> ^F	-0.18	-0.51	0.57	0.77	-0.25	-0.03	0.88	-0.08	0.61	0.66	0.78
<i>Vigilance</i> ^F	0.67	-0.04	0.15	-0.20	-0.17	0.62	0.71	-0.43	0.47	0.45	0.68
Explained Variance	23%	19%	15%	22%	22%	16%	29%	26%			

Note. Salient loadings $\geq |0.40|$ highlighted in bold. ^F = frequency of behavior per hour, ^P = proportion, ^S = Shannon diversity index, Agr = Agreeableness, Ass = Assertiveness, Con = Confidence, Ext = Extraversion, _{CM} = common marmosets, _{CT} = cotton-top tamarins, _{GT} = golden-handed tamarins.

Table 3

Pearson Correlations of Component Scores as Defined by Common Marmoset, Golden-Handed and Cotton-Top Tamarins Structures

	Cotton-top tamarins			Golden-handed tamarins		
Common marmosets	Confidence _{CT}	Extraversion _{CT}	Agreeableness _{GT}	Assertiveness _{GT}	Extraversion _{GT}	
Agreeableness _{CM}	0.21 [-0.44, 0.72]	0.23 [-0.44, 0.74]	0.81 [0.34, 0.96]	-0.26 [-0.77, 0.46]	-0.14 [-0.69, 0.51]	
Assertiveness _{CM}	0.07 [-0.49, 0.58]	0.32 [-0.38, 0.79]	-0.03 [-0.55, 0.52]	0.74 [0.16, 0.94]	0.15 [-0.52, 0.71]	
Extraversion _{CM}	0.40 [-0.30, 0.82]	0.75 [0.23, 0.94]	0.10 [-0.53, 0.66]	0.26 [-0.46, 0.78]	0.73 [0.17, 0.94]	
	Cotton-top tamarins			Common marmosets		
Golden-handed tamarins	Confidence _{CT}	Extraversion _{CT}	Agreeableness _{CM}	Assertiveness _{CM}	Extraversion _{CM}	
Agreeableness _{GT}	0.50 [0.02, 0.79]	0.65 [0.22, 0.87]	0.88 [0.66, 0.96]	-0.01 [-0.38, 0.37]	0.05 [-0.42, 0.50]	
Assertiveness _{GT}	0.71 [0.32, 0.89]	0.36 [-0.14, 0.71]	-0.15 [-0.60, 0.38]	0.77 [0.41, 0.92]	0.24 [-0.30, 0.67]	
Extraversion _{GT}	0.30 [-0.18, 0.67]	0.74 [0.38, 0.91]	0.17 [-0.37, 0.62]	0.39 [-0.16, 0.75]	0.70 [0.29, 0.90]	
	Golden-handed tamarins			Common marmosets		
Cotton-top tamarins	Agreeableness _{GT}	Assertiveness _{GT}	Extraversion _{GT}	Agreeableness _{CM}	Assertiveness _{CM}	Extraversion _{CM}
Confidence _{CT}	0.54 [-0.01, 0.84]	0.59 [0.03, 0.87]	0.08 [-0.43, 0.55]	0.25 [-0.32, 0.68]	-0.16 [-0.61, 0.36]	0.41 [-0.20, 0.79]
Extraversion _{CT}	0.74 [0.28, 0.92]	0.55 [-0.02, 0.85]	0.96 [0.87, 0.99]	0.61 [0.03, 0.88]	0.61 [0.04, 0.88]	0.80 [0.39, 0.94]

Note. Correlations in boldface are significant at $p < 0.05$. 95% confidence intervals are presented in brackets.

Table 4

Membership of Indices in Fuzzy Intersects (Facets) of Semantically Similar Dimensions for 3 Callitrichid Species

activity/exploration_x	$Ex_{CT} \cap Ex_{GT} \cap Ex_{CM}$
Behavioural index	m(i)
Vigilance^F	0.62
Activity diversity^S	0.55
Exploration^F	0.53
Invite grooming(rec)^F	-0.42
Substrate diversity ^S	0.32
Monitoring^P	0.20
Departures^F	-0.13
Scent marking ^F	-0.13
aggression_x	$Co_{CT} \cap As_{GT} \cap As_{CM}$
Behavioural index	m(i)
Approaches^F	0.40
Object sniffing ^F	-0.35
Scratching^F	0.33
Affiliation ^P	0.31
Contact aggression^F	0.18
Substrate diversity ^S	-0.18
Vigilance ^F	0.15
signals_x	$Ex_{CT} \cap As_{GT} \cap As_{CM}$
Behavioural index	m(i)
Threats^F	0.57
Object sniffing^F	0.48
Scent marking^F	0.33
Affiliation ^P	-0.25
Substrate diversity ^S	-0.18
Vigilance ^F	0.15
Scratching ^F	-0.13
grooming_x	$Ex_{CT} \cap Ag_{GT} \cap Ag_{CM}$
Behavioural index	m(i)
Grooming(act)^F	0.72
Terminate grooming^F	0.65
Invite grooming(rec) ^F	0.39
Activity diversity ^S	0.36

<i>Substrate diversity</i> ^S	0.32
<i>Threats</i> ^F	-0.25
<i>Affiliation</i> ^P	-0.25
<i>Invite grooming(act)</i> ^F	0.22
<i>Resting</i>^P	-0.19
<i>Monitoring</i> ^P	-0.19

sociability _x	$Co_{CT} \cap Ag_{GT} \cap Ag_{CM}$
Behavioural index	m(i)
<i>Grooming(rec)</i>^F	0.59
<i>Terminate grooming</i> ^F	0.40
<i>Substrate diversity</i>^S	0.34
<i>Grooming(act)</i> ^F	0.33
<i>Affiliation</i>^P	0.33
<i>Activity diversity</i> ^S	0.27
<i>Invite grooming(act)</i>^F	0.23
<i>Resting</i>^P	-0.19

Note. Only indices with membership $\geq |0.13|$ are presented. Bolded indices have the greatest membership in the fuzzy intersections representing the lower facets of personality. The negative or positive sign indicate the direction of loading and interpretation of index. m(i) = membership of index, _x = common callitrichid facet, _{CT} = cotton-top tamarins, _{GT} = golden-handed tamarins, _{CM} = common marmosets, *Ag* = Agreeableness, *As* = Assertiveness, *Co* = Confidence, *Ex* = Extraversion.

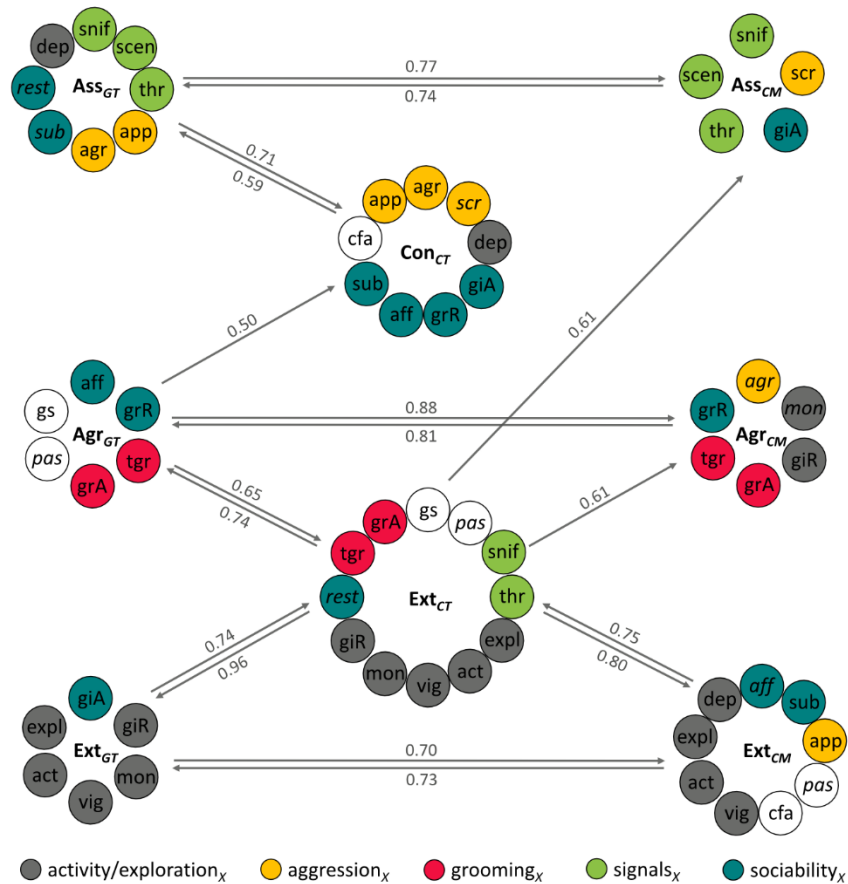


Figure 1. Personality structures of three callitrichid species ($_{CM}$ = common marmosets, $_{CT}$ = cotton-top tamarins, $_{GT}$ = golden-handed tamarins). Large circles represent the personality dimensions (Agr = Agreeableness, Ass = Assertiveness, Con = Confidence, Ext = Extraversion) that consist of small circles representing the indices loading (negative loadings in italics). Indices that did not load saliently on components are not depicted. The abbreviations of indices: act = *Activity diversity*^S, aff = *Affiliation*^P, agr = *Contact aggression*^F, app = *Approaches*^F, cfa = *Carrying food away*^F, dep = *Departures*^F, expl = *Exploration*^F, giA = *Invite grooming(act)*^F, giR = *Invite grooming(rec)*^F, grA = *Grooming(act)*^F, grR = *Grooming(rec)*^F, gs = *Self-grooming*^F, mon = *Monitoring*^P, pas = *Passive affiliation*^P, rest = *Resting*^P, scen = *Scent marking*^F, scr = *Scratching*^F, snif = *Object sniffing*^F, sub = *Substrate diversity*^S, tgr = *Terminate grooming*^F, thr = *Threats*^F, vig = *Vigilance*^F. Personality facets are depicted in different colors. Indices with white background did not have salient membership in any facet. The arrows and numbers represent significant cross-species correlations according to Table 3.

Supplementary material:

Comparative assessment of behaviorally-derived personality structures in golden-handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus oedipus*), and common marmosets (*Callithrix jacchus*).

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Journal of Comparative Psychology

Table S1. *Composition and Demography of Studied Groups*

Group	<i>n</i>	Adults	Subadults	Juveniles	Infants
Common marmosets	17				
Veli group ^a	2	1F, 1M	-	-	-
Ginevra group ^a	5	1F, 1M, 1M	1F, 1M	-	-
Pooh group ^a	4	1F, 1M, 2M	-	-	-
Sparrow group ^a	3	1F, 1M, 1M	-	-	-
Vento group ^a	3	3M	-	-	-
Golden-handed tamarins	28				
Brno	4	1F, 1F, 2M	-	-	-
Hodonín	4	1F, 1M, 1M	1M	1F	2M
Jihlava1	5	1F, 2F, 1M	1F	-	1F, 1M
Magdeburg	3	1F, 1M	1M	-	2M
Plzeň	2	1F, 1M	-	1F, 1M	-
Praha	7	1F, 1M, 3M	1F, 1M	1F, 1M	-
Tierpark Berlin	3	1F, 1M	1F	-	2M
Cotton-top tamarins	20				
Bojnice	4	1F, 1M	2M	2F	2F
Bratislava	3	1F, 1M, 1M	-	-	1F
Jihlava2	4	1F, 1M	1F, 1M	1M	1F, 1M
Ostrava	4	1F, 1F, 2M	-	-	-
Ústí nad Labem	5	1F, 1M, 2M	1F	-	1M

Note. Breeding individuals are indicated in bold. F = female, M = male, *n* = number of observed individuals, ^a housed at the University of Vienna. Age categories defined according to Cleveland & Snowdon (1984) in cotton-top tamarins, Moura (2003) in golden-handed tamarins, and Ingram (1977) in common marmosets.

Table S2. *Ethogram of Common Marmosets (Callithrix jacchus), Cotton-Top Tamarins (Saguinus oedipus), and Golden-Handed Tamarins (Saguinus midas) with Behaviors Used for Computing Behavioral Indices in Bold*

Behavior	Definition	Recording method	Species
<i>Locomotion/postures</i>			
Cling	individual hangs on tightly to vertical substrate using claws of both hands and feet (i.e., wire mesh, wall, tree trunks)	I	all
Hang	individual is suspended from wire mesh ceiling of enclosure or branch holding on using all limbs or legs	I	all
Jump	focal individual jumps to overcome gaps between substrates in the enclosure (i.e., branches, trunks, shelves, walls, ...); including change of substrate)	C, I	all
Lie	individual places its body in horizontal position with limbs hanging down or rested; on horizontal or slightly inclined substrate	I	all
Move	horizontal or vertical movement of more than 50 cm in a relaxed way; including walking, running and climbing; excluding chasing, playing and fleeing	C, I	all
Rest	sitting or lying in relaxed position with eyes open or closed; individual may be in proximity or contact with other individual	C, I	all
Sit	individual is in stationary position sitting on horizontal substrate	I	all
<i>Feeding/Food interactions</i>			
Approach - food	oriented approach towards individual possessing food item	C	all
Begging	scrounging the food from individual that is eating by fixing the food item with sight; may involve characteristic vocalization (moaning), touching or attempting to take the food item	C	all
Carry food away	calm leaving from proximity or contact and taking food away; e.g., from feeding bowl; excluding flee, play and startled locomotion	C	all
Co-feeding	joining other individual eating from the same feeding bowl	C, I	all
Contact - food	initiation of contact with individual possessing food item	C	all
Drinking	ingestion of liquids by drinking from water bowl/dispenser, licking wet surfaces or hands dipped in water	C, I	all
Eating	handling, chewing and active ingestion of food by swallowing it	C, I	all
Follow - food	individual follows the movement of another individual that possesses food to its proximity	C	all
Prey catching	catching invertebrates moving freely in the enclosure	C	all
Prey catching - attempt	unsuccessful attempt to catch invertebrates moving freely in the enclosure	C	all
Sharing food	voluntary sharing of food item with other individual resulting in eating together the same food item the possessor holds in hand or yielding the food item; often after begging	C	all
Stealing food	taking food from other individual's hand or mouth	C	all
Stealing food - attempt	unsuccessful attempt to steal food from hand or mouth of other individual	C	all
Substrate scanning	visual inspection of ground or wall in order to find food; individual might be on the ground or on substrate above the ground	C	all
Taking food from keeper	individual takes food from the zookeeper's hand	C	tamarins

Exploration/Object interactions

Approach - object	oriented approach towards individual possessing the object of interest	C	all
Attention	individual fixes its stare to the object of interest to examine it; usually followed by moving in direction of object	C	all
Contact - object	initiation of contact with individual possessing the object of interest	C	all
Follow - object	individual follows the movement of another individual that possesses the object to its proximity	C	all
General exploration	manipulative investigation of objects, enrichment or equipment of enclosure using hands or mouth	C, I	all
Object licking	individual licks surface, substrate or object	C	all
Object manipulation	manipulation of object (e.g., twigs, leaves, bark; excluding food) using hands or mouth; including looking at, sniffing and biting into the object	C, I	all
Stealing object	taking an object (e.g., twig, leaf, bark) from individual possessing it	C	all
Stealing object - attempt	unsuccessful attempt to possess an object that is held by other individual	C	all
Substrate searching	sitting on the ground and looking for the food in the substrate by using hands	C, I	all

Olfactory

Allomarking	scent marking over the body of another individual that might carry infants	C	all
Individual sniffing	smelling the body, face or anogenital region of other individual	C	all
Muzzle rubbing	pressing the oro-facial region onto the substrate and rubbing it with movements of head	C	all
Object sniffing	smelling the surface of substrate, objects, scent marks or food	C	all
Scent marking	rubbing the anogenital area against the substrate in a sitting position or by prolonged dragging the anogenital/suprapubic region along the substrate (may be accompanied by urine discharge) or rubbing the sternal area	C	all
Urine tasting	individual licks urine drops of another individual either left on substrate or while the individual is urinating or scent marking	C	all

Comfort

Face scratching	rubbing muzzle with hand	C	all
Head twist	individual stretches its head by tilting it back	C	all
Scratching	rapid rubbing of body using the claws of hand or foot; individual doesn't have to be visually focused on the scratched area	C	all
Self-grooming	using claws of hands or mouth to pick through its own skin or fur; including removing particles; individual is visually focused on the groomed area	C, I	all
Stretching	stretching the entire body or limbs; might be hanging from the branch or ceiling	C	all

Play

Joining in play	individual engages in ongoing social play of other individuals	C	all
Play with object	manipulation or biting into an object in the context of play	C, I	all
Social play	non-aggressive and active interaction of 2 or more individuals, including play chasing, play wrestling, displaying, biting, repeated jumping/falling from one branch to another together with others	C, I	all

Solicit play	attempt to attract the attention and involve other individual in playing; including staring, open mouth staring, tongue flicking, hide and seek, pushing the individual or jumping in front of the individual	C	all
Solitary play	repeated jumping and falling from one branch to another, swinging and bouncing on branches; excluding play with object	C, I	all
<i>Affiliative</i>			
Allogrooming	individual picks slowly through the fur or skin of other individual using the claws of 1 or both hands or mouth; including removing particles	C, I	all
Arm over	placing arm around other individual's upper body or shoulders	C	all
Contact	individual is in body contact or in comfortable reach of arm (<9 cm) with other individual	C, I	all
Huddling	animal lies across, sits or lies next to other individual in tight body contact; limbs can be intertwined	C	all
Invite grooming	individual lowers its body or stretches out on its back or side requesting grooming	C	all
Kiss	muzzle-muzzle contact of 2 animals; may involve tongue flicking	C	all
Licking individual	individual licks another individual's face, body or anogenital region; often an infant	C	all
Nuzzling	individual gently rubs its muzzle against other individual's face, body or anogenital region; may be accompanied by sniffing and licking	C	all
Proximity	individual is in the distance max. 30 cm from other individual	C, I	all
Waist clasping	placing both arms from behind around other individual's waist	C	all
<i>Sexual</i>			
Copulation	male mounts a female; including penile insertion and thrusting; sometimes accompanied by tongue flicking	C	all
Mounting	individual gets on back of other individual with arms around its waist; may include pelvic thrusts and tongue flicking	C	all
Lip smacking	individual is smacking its lips while fixing the gaze on another individual	C	marmosets
<i>Infant care</i>			
Climb off	infant climbs from the carrier to substrate or another carrier	C	all
Climb on	infant climbs on the back or side of potential carrier (from substrate or another carrier); limbs of infant are not in the contact with substrate; initiative of infant	C	all
Infant rejection	caretaker dislodges infant clinging to it or prevents infant to climb on by using scratching, biting, pushing, pulling infant's extremities or rolling the infant against substrate	C	all
Infant rejection - attempt	unsuccessful attempt to dislodge infant from back or prevent infant from climbing on	C	all
Invitation to carry	potential carrier attempts to entice the infant in order to carry it; including tongue flicking, lowering its body or piloerection	C	all
Nursing	infant is from the ventral side of the female suckling; infant's mouth is on the nipple of female	C	all
Solicit carrying	infant approaches potential carrier trying to climb on its back moaning; potential carrier is not interested	C	all
Taking infant on	potential carrier gathers infant from substrate or back of current carrier in order to carry it; initiative of potential carrier	C	all
Taking infant on - attempt	unsuccessful attempt of potential carrier to gather infant from substrate or back of the current carrier in order to carry it; infant refuses to climb on or the carrier refuses to transfer the infant; sometimes results in aggression	C	all

between caretakers

Dominance

Avoiding	individual while travelling changes the direction of its move in order to avoid another individual	C	all
Displacement	individual chases other individual away from potential source, e.g., food, water, sleeping box	C	all
Grasp	individual places its arm over the other individual's shoulder, head, upper body or touches other individual's face in dominant manner while slightly raising its body or head	C	all
Grimace	lip corners are pulled back, lower lip is retracted so the mouth is slightly open revealing dentition with pressed jaws; accompanied by vocalization	C	tamarins
Slit stare	individual stares at individual or object with eyelids half close; head is often slightly tilted backwards; mouth might be partially opened showing the teeth	C	marmosets
Tufts flatten	ear tufts remained flattened against the head	C	marmosets

Agonistic non-contact

Arched bristle display	individual stares at other individual, limbs flexed, vertebral column bent into high arch with fur piloerected; often accompanied by frowning; individual might be moving or vocalizing (in Masilkova et al., 2018 as "Body display")	C	all
Frown	individual stares at other individual and lowers its eyebrows; might be accompanied by tongue or ear flicking, vocalizations or in marmosets by erected tufts (in Masilkova et al., 2018 as "Facial threat")	C	all
Headshake	rapid turning the head from side to side on the horizontal plane; might be accompanied by teeth chattering	C	tamarins
Open mouth display	individual stares at another individual with mouth widely open exposing its teeth	C	tamarins
Tongue flick	protrusion and rapid rhythmical movements of the tongue tip up and down	C	tamarins
Genital display	individual turns, raises its tail and shows the genitals	C	marmosets
Tufts flick stare	movements of ear tufts forward and backward on the horizontal plane; individual fixes its stare at other individual	C	marmosets
Tufts forward	the ear tufts are held forward slightly erected; may precede the attack	C	marmosets

Agonistic contact

Beating	repeated pushing and hitting other individual using arms; other individual usually beats back	C	all
Bite	individual bites another individual with its teeth usually in limbs or head; teeth may or may not penetrate the skin	C	all
Chase	chasing other individual that is fleeing and trying to hide; rapid locomotion	C	all
Fight	aggressive physical confrontation of individuals; short fast struggle involving biting, wrestling, hitting, scratching, kicking; victim may scream	C	all
General aggression	any fast, aggressive act of behavior or unspecified physical assault of other individual that observer was not able to register in detail	C	all
Grab	individual grabs hair of other individual; may pull out strand of hair	C	all
Push	individual aggressively hits other individual using its hand; may push the other individual away	C	all
Face press	individual grabs the head of other individual and presses its open mouth to oponent's mouth	C	tamarins
Cuff	rapid and superficial scratching/hitting the other individual; usually to the	C	marmosets

neck region

Other social

Approach	individual comes in proximity to other individual	C	all
Attention - individual	fixed gaze on individual of interest; in context of hostility or curiosity	C	all
Departure	leaving from contact or proximity of other individual; excluding fleeing, displacement or carrying food or object away	C	all
Follow	individual follows the movement of other individual to its proximity	C	all
Teeth cleaning	individual uses its hands to open mouth of other individual and clean its teeth by using tongue; doesn't usually last long as groomee tries to recoil; often followed by aggression from groomee	C	all
Terminate grooming	individual ends the allogrooming	C	all

Other

Alert	vigilant observing of environment; individual is stationary and may turn its head from side to side	C, I	all
Leg stand	individual stands on hind legs staring in a fixed direction; might lean against an object with its hands	C	all
Looking	individual is stationary and calmly looks around	I	all
Out of sight	individual disappears from sight of observer to the box or separate part of enclosure	C, I	all
Vomiting	throwing up, usually after eating insect	C	all
Watching	individual observes particular object, place, animal or person	I	all
Gouging	individual grasps the substrate with its hand and gnaws into bark, branches or shelves with its teeth; often followed by scent marking	C	marmosets

Vocalizations

General alarm	individual vocalizes (Type E or H chirp) when startled or frightened	C	tamarins
Chirp	quiet call with series of high-pitched notes with each falling from high to low frequency and with variable time intervals between them; mouth is closed or slightly open	C	marmosets
Cough	low pitched non-tonal sound emitted with closed mouth	C	marmosets
Ek	very short call with few harmonics; uttered singly or in series	C	marmosets
Gecker	series of low pitched, harsh, staccato sounds; mouth closed or open with body vibrating noticeably	C	marmosets
Loud shrill	very loud whistle-like call of constant pitch with mouth widely open	C	marmosets
Moan	infant and juvenile insistent prolonged call; uttered singly or in series	C	marmosets
Phee	soft whistle with constant pitch emitted singly or in succession; mouth closed or partially open	C	marmosets
Scream	unevenly modulating call very unpleasant to human ear; uttered singly or in succession	C	marmosets
Tsik	brief sharp alarmed call; uttered singly or in series; rises slightly in pitch before dropping straight down; mouth half-open	C	marmosets
Tsik-Ek	very loud, sharp and rapid succession of tsik, ek and sometimes cough calls	C	marmosets
Twitter	rapid series of short notes uttered at intervals >0.1 s; loud sound emitted with open mouth	C	marmosets
Whirr	quiet call uttered with mouth almost closed and vibrating body; pleasant	C	marmosets

sound to human ear

Substrates

Branch	branch or stem of tree or bush; excluding vertical stems	I	all
Ceiling	roof or ceiling of enclosure enabling hanging or moving	I	all
Ground	floor of the enclosure		all
Other	other equipment of enclosure, e.g., ropes, pipes, toys, enrichment	I	all
Shelf	horizontal surfaces wider and longer than 10 cm, e.g., shelves, top of sleeping box	I	all
Trunk	vertical trunk or stem of any diameter	I	all
Wall	vertical wall (wire mesh, artificial rockwork) of enclosure enabling clinging and locomotion	I	all
Box	nesting box providing shelter	I	tamarins
Basket	nesting basket	I	marmosets

Note. C = continuous focal recording, I = instantaneous focal sampling.

Table S3. Descriptive Statistics of Behavioral Measures on 22 Behavioral Indices by Species

	Common marmoset				Golden-handed tamarin				Cotton-top tamarin			
	min	max	mean	SD	min	max	mean	SD	min	max	mean	SD
<i>Activity diversity</i> ^S	1.80	2.18	2.02	0.11	1.54	2.24	1.87	0.20	1.43	2.22	1.79	0.25
<i>Affiliation</i> ^P	0.14	0.68	0.31	0.13	0.07	0.49	0.28	0.10	0.06	0.49	0.22	0.15
<i>Approaches</i> ^F	0.80	11.00	5.46	3.27	2.73	48.75	13.10	9.84	2.00	30.20	9.86	7.66
<i>Carrying food away</i> ^F	0.10	1.10	0.38	0.26	0.00	1.59	0.71	0.46	0.00	2.40	0.77	0.71
<i>Contact aggression</i> ^F	0.00	3.80	1.10	1.04	0.07	14.00	2.35	2.78	0.07	12.87	3.04	3.19
<i>Departures</i> ^F	1.80	15.70	7.21	4.13	5.40	44.00	18.53	11.78	3.33	33.07	12.77	8.88
<i>Exploration</i> ^F	0.00	6.80	2.59	1.97	0.07	21.40	3.40	4.28	0.13	7.20	2.86	2.50
<i>Grooming(act)</i> ^F	0.30	7.20	2.63	2.09	0.53	18.00	4.73	4.51	0.00	2.93	1.02	0.80
<i>Grooming(rec)</i> ^F	0.20	6.20	2.09	1.56	0.20	12.38	4.28	2.77	0.00	4.60	1.58	1.22
<i>Invite grooming(act)</i> ^F	0.20	5.20	1.51	1.31	0.33	6.27	2.10	1.67	0.00	2.80	1.11	0.70
<i>Invite grooming(rec)</i> ^F	0.00	3.60	1.56	1.06	0.21	6.87	2.07	1.86	0.13	2.53	1.04	0.67
<i>Monitoring</i> ^P	0.06	0.29	0.13	0.06	0.01	0.21	0.06	0.05	0.02	0.17	0.10	0.04
<i>Object sniffing</i> ^F	3.90	19.10	8.06	4.04	0.67	14.63	5.70	4.07	1.13	8.00	2.93	1.78
<i>Passive affiliation</i> ^P	0.59	0.98	0.84	0.10	0.35	0.93	0.73	0.14	0.49	0.96	0.78	0.15
<i>Resting</i> ^P	1.45	6.78	3.76	1.31	1.19	12.15	3.76	2.10	1.49	10.30	4.61	2.41
<i>Scent marking</i> ^F	2.60	27.20	9.64	6.56	1.47	30.63	6.83	6.20	0.07	18.87	4.82	4.99
<i>Scratching</i> ^F	4.80	42.70	17.14	8.53	14.36	66.93	37.50	12.09	7.07	35.80	17.19	7.86
<i>Self-grooming</i> ^F	0.70	4.60	2.16	1.32	0.00	9.60	2.27	2.39	0.20	2.53	0.93	0.65
<i>Substrate diversity</i> ^S	1.37	1.81	1.61	0.13	0.14	1.43	0.85	0.36	0.14	1.27	0.88	0.27
<i>Terminate grooming</i> ^F	0.30	7.00	2.56	2.06	0.40	14.07	4.67	3.92	0.07	2.93	1.05	0.76
<i>Threats</i> ^F	0.00	20.90	3.20	4.91	0.20	17.13	1.73	3.21	0.07	4.47	1.40	1.16
<i>Vigilance</i> ^F	1.80	6.80	4.02	1.59	0.00	21.00	2.96	4.30	0.00	5.60	2.12	2.00

Table S4. Repeatability Estimates of 22 Behavioral Indices for Each Species

Behavioral index	Common marmoset			Golden-handed tamarin			Cotton-top tamarin		
	R ± SE	95% CI	<i>p</i>	R ± SE	95% CI	<i>p</i>	R ± SE	95% CI	<i>p</i>
<i>Activity diversity</i> ^S	0.21 ± 0.19	[0.00, 0.62]	0.20	0.60 ± 0.10	[0.36, 0.75]	0.001	0.69 ± 0.10	[0.44, 0.83]	0.001
<i>Affiliation</i> ^P	0.69 ± 0.14	[0.34, 0.88]	0.002	0.56 ± 0.11	[0.31, 0.73]	0.001	0.84 ± 0.06	[0.67, 0.92]	0.001
<i>Approaches</i> ^F	0.67 ± 0.15	[0.28, 0.86]	0.004	0.86 ± 0.05	[0.75, 0.93]	0.001	0.93 ± 0.04	[0.83, 0.96]	0.001
<i>Carrying food away</i> ^F	0.27 ± 0.20	[0.00, 0.64]	0.14	0.30 ± 0.12	[0.05, 0.51]	0.008	0.73 ± 0.10	[0.47, 0.86]	0.001
<i>Contact aggression</i> ^F	0.89 ± 0.07	[0.70, 0.96]	0.001	0.75 ± 0.08	[0.56, 0.85]	0.001	0.76 ± 0.09	[0.54, 0.88]	0.001
<i>Departures</i> ^F	0.78 ± 0.10	[0.53, 0.91]	0.002	0.85 ± 0.05	[0.72, 0.92]	0.001	0.93 ± 0.03	[0.85, 0.97]	0.001
<i>Exploration</i> ^F	0.77 ± 0.11	[0.49, 0.91]	0.002	0.84 ± 0.05	[0.70, 0.91]	0.001	0.77 ± 0.08	[0.57, 0.88]	0.001
<i>Grooming(act)</i> ^F	0.63 ± 0.15	[0.26, 0.84]	0.003	0.68 ± 0.09	[0.47, 0.80]	0.001	<i>0.29 ± 0.14</i>	<i>[0.00, 0.54]</i>	<i>0.02</i>
<i>Grooming(rec)</i> ^F	0.71 ± 0.13	[0.37, 0.88]	0.002	0.56 ± 0.11	[0.32, 0.74]	0.001	<i>0.26 ± 0.15</i>	<i>[0.00, 0.55]</i>	<i>0.03</i>
<i>Invite grooming(act)</i> ^F	0.40 ± 0.19	[0.00, 0.72]	0.06	0.68 ± 0.09	[0.47, 0.81]	0.001	0.37 ± 0.14	[0.07, 0.62]	0.004
<i>Invite grooming(rec)</i> ^F	0.26 ± 0.19	[0.00, 0.60]	0.13	0.70 ± 0.08	[0.50, 0.82]	0.001	<i>0.25 ± 0.14</i>	<i>[0.00, 0.52]</i>	<i>0.04</i>
<i>Monitoring</i> ^P	0.76 ± 0.11	[0.50, 0.90]	0.001	0.74 ± 0.08	[0.56, 0.85]	0.001	0.63 ± 0.12	[0.35, 0.79]	0.001
<i>Object sniffing</i> ^F	0.80 ± 0.10	[0.54, 0.92]	0.001	0.88 ± 0.04	[0.78, 0.93]	0.001	0.77 ± 0.08	[0.57, 0.88]	0.001
<i>Passive affiliation</i> ^P	0.53 ± 0.18	[0.06, 0.80]	0.01	0.62 ± 0.10	[0.39, 0.77]	0.001	0.45 ± 0.14	[0.15, 0.67]	0.002
<i>Resting</i> ^P	0.51 ± 0.18	[0.11, 0.79]	0.01	0.63 ± 0.10	[0.41, 0.78]	0.001	0.73 ± 0.09	[0.51, 0.85]	0.001
<i>Scent marking</i> ^F	0.89 ± 0.07	[0.71, 0.96]	0.001	0.82 ± 0.05	[0.68, 0.90]	0.001	0.79 ± 0.08	[0.60, 0.89]	0.001
<i>Scratching</i> ^F	0.81 ± 0.09	[0.56, 0.92]	0.001	0.76 ± 0.07	[0.58, 0.86]	0.001	0.82 ± 0.07	[0.64, 0.91]	0.001
<i>Self-grooming</i> ^F	0.67 ± 0.15	[0.30, 0.86]	0.003	0.61 ± 0.10	[0.39, 0.77]	0.001	<i>0.28 ± 0.14</i>	<i>[0.00, 0.55]</i>	<i>0.02</i>
<i>Substrate diversity</i> ^S	0.40 ± 0.20	[0.00, 0.75]	0.05	0.91 ± 0.03	[0.82, 0.95]	0.001	0.88 ± 0.05	[0.75, 0.94]	0.001
<i>Terminate grooming</i> ^F	0.61 ± 0.16	[0.19, 0.83]	0.01	0.68 ± 0.09	[0.47, 0.82]	0.001	<i>0.26 ± 0.14</i>	<i>[0.00, 0.53]</i>	<i>0.03</i>
<i>Threats</i> ^F	0.96 ± 0.03	[0.88, 0.98]	0.001	0.80 ± 0.06	[0.64, 0.89]	0.001	0.60 ± 0.12	[0.32, 0.77]	0.001
<i>Vigilance</i> ^F	0.00 ± 0.14	[0.00, 0.48]	0.50	0.94 ± 0.02	[0.89, 0.97]	0.001	0.51 ± 0.13	[0.19, 0.71]	0.001

Note. Significant results ($p < 0.05$) given in bold. Significant repeatability estimates with 0 in the confidence interval are in italics.

Table S5. Common Marmosets: Varimax-Rotated Solution of REFA and Congruence Between REFA and PCA Solutions

Behavioral index	Factor			h ²	Coefficient of congruence ^a
	Ext	Agr	Ass		
<i>Passive affiliation</i> ^P	-0.84	-0.09	-0.04	0.71	0.9999
<i>Exploration</i> ^F	0.82	-0.24	-0.11	0.75	0.9999
<i>Departures</i> ^F	0.74	0.07	0.10	0.57	1.0000
<i>Activity diversity</i> ^S	0.68	-0.41	-0.20	0.67	0.9999
<i>Vigilance</i> ^F	0.64	-0.04	0.14	0.43	0.9999
<i>Approaches</i> ^F	0.61	-0.16	0.37	0.53	0.9999
<i>Carrying food away</i> ^F	0.60	-0.04	0.11	0.37	0.9999
<i>Affiliation</i> ^P	-0.51	0.31	-0.46	0.57	1.0000
<i>Substrate diversity</i> ^S	0.49	0.32	-0.16	0.37	0.9998
<i>Terminate grooming</i> ^F	0.17	0.76	-0.05	0.60	1.0000
<i>Grooming(act)</i> ^F	0.17	0.74	-0.04	0.57	1.0000
<i>Invite grooming(rec)</i> ^F	-0.41	0.71	0.00	0.68	0.9999
<i>Contact aggression</i> ^F	-0.12	-0.64	0.17	0.45	1.0000
<i>Grooming(rec)</i> ^F	-0.22	0.61	0.10	0.43	0.9999
<i>Monitoring</i> ^P	0.20	-0.58	-0.06	0.38	1.0000
<i>Scent marking</i> ^F	-0.10	-0.08	0.86	0.75	0.9999
<i>Object sniffing</i> ^F	0.07	0.34	0.71	0.62	0.9998
<i>Scratching</i> ^F	0.36	-0.13	0.69	0.62	0.9997
<i>Threats</i> ^F	-0.15	-0.48	0.52	0.53	0.9999
<i>Invite grooming(act)</i> ^F	-0.03	0.44	0.48	0.43	0.9999
<i>Self-grooming</i> ^F	0.20	0.00	0.23	0.09	1.0000
<i>Resting</i> ^P	0.10	-0.17	-0.02	0.04	0.9982
Explained variance	20.77%	17.26%	12.68%		
Factor congruence	0.9999	0.9999	0.9999		

Note. Salient loadings $\geq |0.40|$ highlighted in bold. h^2 = communalities, ^a see Lorenzo-Seva & ten Berge (2006), Ext = Extraversion, Agr = Agreeableness, Ass = Assertiveness.

Table S6. *Golden-Handed Tamarins: Varimax-Rotated Solution of REFA and Congruence Between REFA and PCA Solutions*

Behavioral index	Factor			h ²	Coefficient of congruence ^a
	Ass	Agr ^b	Ext ^b		
<i>Approaches</i> ^F	0.88	0.05	-0.14	0.80	0.9999
<i>Contact aggression</i> ^F	0.82	-0.06	-0.12	0.69	1.0000
<i>Scent marking</i> ^F	0.75	-0.17	0.24	0.65	0.9999
<i>Threats</i> ^F	0.74	-0.23	-0.03	0.59	0.9999
<i>Departures</i> ^F	0.68	0.29	-0.27	0.62	0.9999
<i>Object sniffing</i> ^F	0.67	-0.08	0.46	0.66	1.0000
<i>Substrate diversity</i> ^S	-0.56	-0.47	0.42	0.71	0.9999
<i>Resting</i> ^P	-0.51	-0.21	-0.18	0.34	0.9999
<i>Terminate grooming</i> ^F	0.05	0.89	0.03	0.79	1.0000
<i>Grooming(act)</i> ^F	0.03	0.85	0.00	0.72	1.0000
<i>Passive affiliation</i> ^P	0.22	-0.81	-0.02	0.71	1.0000
<i>Affiliation</i> ^P	0.30	0.78	-0.04	0.69	1.0000
<i>Self-grooming</i> ^F	-0.02	0.67	-0.10	0.45	0.9999
<i>Grooming(rec)</i> ^F	0.10	0.56	0.17	0.36	1.0000
<i>Invite grooming(act)</i> ^F	0.04	0.22	0.75	0.62	1.0000
<i>Monitoring</i> ^P	0.04	-0.17	0.73	0.57	0.9999
<i>Invite grooming(rec)</i> ^F	0.05	0.37	0.68	0.60	1.0000
<i>Vigilance</i> ^F	-0.19	-0.16	0.57	0.39	0.9999
<i>Activity diversity</i> ^S	0.04	0.35	0.52	0.39	0.9999
<i>Exploration</i> ^F	-0.04	-0.08	0.49	0.25	1.0000
<i>Carrying food away</i> ^F	0.33	0.22	0.02	0.16	0.9998
<i>Scratching</i> ^F	0.31	0.05	-0.06	0.10	0.9999
Explained variance	20.19%	20.01%	13.78%		
Factor congruence	0.9999	0.9999	0.9999		

Note. Salient loadings $\geq |0.40|$ highlighted in bold. h² = communalities, ^a see Lorenzo-Seva & ten Berge (2006), ^b = loadings reflected, Ass = Assertiveness, Agr = Agreeableness, Ext = Extraversion.

Table S7. Common Marmosets: Promax-Rotated Solution of PCA and Correlations Between Components

Behavioral index	Component			h ²
	PC1	PC2	PC3	
<i>Passive affiliation</i> ^P	-0.90	-0.19	0.01	0.79
<i>Exploration</i> ^F	0.89	-0.16	-0.19	0.83
<i>Departures</i> ^F	0.79	0.16	0.06	0.63
<i>Activity diversity</i> ^S	0.73	-0.36	-0.27	0.74
<i>Vigilance</i> ^F	0.67	0.03	0.11	0.47
<i>Carrying food away</i> ^F	0.63	0.03	0.08	0.41
<i>Approaches</i> ^F	0.60	-0.10	0.36	0.58
<i>Substrate diversity</i> ^S	0.56	0.40	-0.20	0.43
<i>Affiliation</i> ^P	-0.49	0.27	-0.46	0.64
<i>Terminate grooming</i> ^F	0.21	0.83	-0.05	0.69
<i>Grooming(act)</i> ^F	0.21	0.81	-0.04	0.66
<i>Invite grooming(rec)</i> ^F	-0.41	0.71	0.04	0.75
<i>Contact aggression</i> ^F	-0.17	-0.70	0.17	0.52
<i>Grooming(rec)</i> ^F	-0.23	0.62	0.14	0.48
<i>Monitoring</i> ^P	0.20	-0.59	-0.09	0.42
<i>Resting</i> ^P	0.10	-0.17	-0.04	0.05
<i>Scent marking</i> ^F	-0.21	-0.10	0.94	0.89
<i>Object sniffing</i> ^F	0.00	0.36	0.78	0.73
<i>Scratching</i> ^F	0.30	-0.10	0.73	0.72
<i>Threats</i> ^F	-0.24	-0.54	0.57	0.61
<i>Invite grooming(act)</i> ^F	-0.07	0.46	0.54	0.50
<i>Self-grooming</i> ^F	0.19	0.02	0.24	0.10
Explained variance	23%	19%	15%	

Note. Salient loadings $\geq |0.40|$ highlighted in bold. h² = communalities. The correlations between promax-rotated components: PC1 vs PC2: -0.13, PC1 vs PC3: 0.15, PC2 vs PC3: -0.03.

Table S8. *Golden-Handed Tamarins: Promax-Rotated Solution of PCA and Correlations Between Components*

Behavioral index	Component			h ²
	PC1	PC2	PC3	
<i>Terminate grooming</i> ^F	0.94	-0.06	0.09	0.87
<i>Grooming(act)</i> ^F	0.90	-0.08	0.05	0.80
<i>Passive affiliation</i> ^P	-0.89	0.34	-0.06	0.79
<i>Affiliation</i> ^P	0.81	0.21	0.02	0.76
<i>Self-grooming</i> ^F	0.72	-0.11	-0.06	0.50
<i>Grooming(rec)</i> ^F	0.59	0.03	0.22	0.40
<i>Approaches</i> ^F	-0.01	0.94	-0.11	0.89
<i>Contact aggression</i> ^F	-0.12	0.88	-0.09	0.76
<i>Scent marking</i> ^F	-0.25	0.82	0.28	0.73
<i>Threats</i> ^F	-0.30	0.81	-0.01	0.66
<i>Object sniffing</i> ^F	-0.15	0.71	0.51	0.74
<i>Departures</i> ^F	0.27	0.68	-0.24	0.68
<i>Substrate diversity</i> ^S	-0.47	-0.54	0.40	0.79
<i>Resting</i> ^P	-0.18	-0.51	-0.23	0.38
<i>Carrying food away</i> ^F	0.21	0.33	0.05	0.18
<i>Scratching</i> ^F	0.03	0.32	-0.04	0.11
<i>Invite grooming(act)</i> ^F	0.22	0.00	0.82	0.71
<i>Monitoring</i> ^P	-0.20	0.05	0.78	0.65
<i>Invite grooming(rec)</i> ^F	0.38	-0.01	0.75	0.69
<i>Vigilance</i> ^F	-0.17	-0.19	0.60	0.45
<i>Activity diversity</i> ^S	0.36	-0.01	0.57	0.44
<i>Exploration</i> ^F	-0.09	-0.04	0.52	0.29
Explained variance	22%	22%	16%	

Note. Salient loadings $\geq |0.40|$ highlighted in bold. h² = communalities. The correlations between promax-rotated components: PC1 vs PC2: 0.18, PC1 vs PC3: -0.02, PC2 vs PC3: -0.04.

Table S9. Cotton-Top Tamarins: Promax-Rotated Solution of PCA and Correlation Between Components

Behavioral index	Component		h ²
	PC1	PC2	
<i>Activity diversity</i> ^S	0.90	0.20	0.86
<i>Exploration</i> ^F	0.88	-0.09	0.77
<i>Threats</i> ^F	0.88	-0.15	0.78
<i>Passive affiliation</i> ^P	-0.88	0.18	0.78
<i>Grooming(act)</i> ^F	0.72	0.28	0.62
<i>Vigilance</i> ^F	0.70	-0.48	0.68
<i>Invite grooming(rec)</i> ^F	0.70	-0.04	0.48
<i>Terminate grooming</i> ^F	0.66	0.35	0.58
<i>Resting</i> ^P	-0.65	-0.37	0.59
<i>Object sniffing</i> ^F	0.47	-0.38	0.35
<i>Self-grooming</i> ^F	0.43	-0.27	0.24
<i>Monitoring</i> ^P	0.43	-0.13	0.19
<i>Scent marking</i> ^F	0.33	0.07	0.12
<i>Departures</i> ^F	-0.12	0.93	0.87
<i>Approaches</i> ^F	-0.02	0.85	0.71
<i>Scratching</i> ^F	-0.14	-0.83	0.72
<i>Affiliation</i> ^P	-0.23	0.82	0.71
<i>Contact aggression</i> ^F	0.00	0.76	0.57
<i>Carrying food away</i> ^F	-0.15	0.67	0.46
<i>Grooming(rec)</i> ^F	0.08	0.61	0.38
<i>Substrate diversity</i> ^S	0.33	0.54	0.42
<i>Invite grooming(act)</i> ^F	0.23	0.43	0.25
Explained variance	29%	26%	

Note. Salient loadings $\geq |0.40|$ highlighted in bold. h² = communalities. The correlation between promax-rotated components: PC1 vs PC2: 0.06.

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