Personality, Subjective Well-Being, and the Serotonin 1a Receptor Gene in Common Marmosets (*Callithrix jacchus*)

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Abstract

In a previous study of laboratory housed common marmosets (*Callithrix jacchus*), we found that correlations among personality traits indicated the presence of factors that we labeled Dominance, Sociability, and a Neuroticism. Unlike two other studies of this species, we did not find a Conscientiousness, Openness, or Patience factor. Because this discrepancy may have been attributable to the fact that many purported markers of Conscientiousness were excluded because of concerns about reliability, we followed up this study by increasing the sample size from 77 to 128. In addition to this, as we did in our previous study, we gathered data on subjective well-being in these subjects. We also investigated polymorphisms related to the serotonin 1a receptor. We found three personality factors—Sociability, Dominance, and Negative Affect—like those found in our previous study and in other studies of this species. We also found an Openness factor and a factor that we labeled "Impulsiveness", which resembled, but was not identical to, Conscientiousness. In addition, there was evidence for two higher-order factors: Pro-sociality and Boldness. Further analyses could not rule out the possibility that the higher-order factors represented a higher-level of personality organization. Correlations between the first- and higher-order factors and the subjective well-being measures were consistent with the definitions of the factors. There were no significant associations between personality and genotype. These results are consistent with the possibility that, perhaps because common marmosets are cooperative breeders, personality structure in this species is more labile than in other nonhuman primates and in humans.

Keywords: behavioral characters, behavioral syndrome, callitrichid, rating, temperament

Introduction

Common marmosets (*Callithrix jacchus*) are small New-World monkeys found in South America where they inhabit a wide range of habitats [1, 2]. Because of their small size, fast life history, and other physical and physiological characteristics, common marmosets are becoming an increasingly popular animal model in biomedical research [3], although some [e.g., 4] have highlighted the shortcomings of marmoset models.

Common marmosets are also becoming popular subjects for research on cognition and personality. This trend has been driven partly by findings that common marmosets display behaviors and capabilities once believed to be exclusive to humans and great apes. Common marmosets, for example, exhibit high levels of spontaneous cooperative behavior [5, 6] and can discriminate between third parties that do and do not reciprocate [7]. These capabilities, and others, are believed to have evolved in common marmosets because they, like other callitrichids, but unlike other nonhuman primates, are cooperative breeders [see 8 for a review]. In species that are cooperative breeders, rather than disperse and mate, the adult siblings and offspring of mating pairs often stay within the family unit to help raise offspring, and so delay or forego reproduction [9].

Studies of common marmosets have revealed the presence of stable personality traits [10, 11], although one study found that these traits can be modified via social facilitation or social group effects [12]. Studies have also found that personality traits in common marmosets are heritable and related to well-being [13], associated with the strength of laterality [14], and the binding potential of serotonin transporters in the brain [15]. Moreover, different methods, namely those based on behavioral observations and ratings, show evidence of convergent and discriminant validity in that they are correlated when both assess the same psychology construct, and uncorrelated when they do not, respectively [16, 17]. However, at

least one study has found that evidence for convergent and discriminant validity is not consistent across different samples [16].

One area of personality research to which studies of common marmosets have contributed is the attempt to reconstruct the evolutionary history of personality structure using the comparative method [18, 19]. Personality structure refers to the fact that statistical methods, including factor analysis and principal components analysis [20], but also others [e.g., 21], reveal that individual traits group into higher-order factors, which represent personality *domains*. For example, in humans, factor analysis has shown that traits such as 'fearful', 'vulnerable' and 'anxious' describe the Neuroticism domain while traits such as 'active', 'social', and 'assertive' describe the Extraversion domain [22, 23].

Like findings in other nonhuman primate taxa, including *Macaca* [24], *Pan* [25], *Saimiri* [26], *Sapajus* and *Cebus* [27-29], and other Callitrichids [30], four studies of common marmosets [13, 17, 31, 32] have yielded findings consistent with the notion that that the socioecology of a species influences that species' personality structure [see 33 for a discussion]. Despite differences in the origins and housing of subjects, and in how personality was measured, the five sets of data from these four studies revealed overlapping personality domains (see Figure 1): all five revealed domains related to sociability [13, 17, 31, 32]; four revealed domains related to aggressiveness and competitive prowess [13, 17, 31, 32]; three revealed domains related to anxiety and vigilance [13, 17, 32]; two revealed domains related to exploratory tendencies [17, 31]; and two revealed domains related to self-control [17, 31]. In addition, two of these studies found a domain—Perceptual Sensitivity [17] and Patience [31]—that had not been found in other species.

The most striking finding from these studies common marmoset personality is that, although many primate and non-primate species exhibit individual differences in traits related to self-control [34, 35], these traits formed one or two broad domains. Similar domains had

only been found previously in humans *Homo sapiens* [e.g., 36], chimpanzees *Pan troglodytes* [37-42], bonobos *Pan paniscus* [25], and brown capuchin monkeys *Sapajus apella* [28], all of which are known for having larger brains. Consequently, the findings in common marmosets led the researchers to conclude that the cognitive and behavioral demands associated with cooperative breeding may have led to the evolution of these domains in a small-brained primate [31].

The results from the four studies of common marmosets, however, were not entirely consistent. Specifically, although they found evidence that marmosets possess up to seven domains, they varied with respect to which subset of these domains they found. This variation may be attributable to the fact that, asides perhaps from one study [31], these studies did not sample enough traits or individuals to capture all the ways in which individuals may differ in their personality.

To address whether this was the case, we followed up our earlier study of personality in 77 (68 male and 9 female) common marmosets housed at the Kobe, Japan campus of the Institute of Physical and Chemical Research (RIKEN) [13]. In that study, we did not find a Conscientiousness, Patience, or, for that matter, an Openness domain. One reason why we may not have found those domains is that several items related to these domains were removed because they had interrater reliability estimates that were less than zero [13]. This can happen if there is not enough between-subjects variance in traits or a large amount of error variance [43].

A low level of between-subjects variance may come about when unmeasured influences, for example in how animals are housed or bred, overwhelm or make it difficult to observe or perceive individual differences in one or more traits. However, a study that compared common marmosets that lived in a laboratory to those that lived in the wild [44]

suggests that this does not happen. A low level of between-subjects variance may also come about because the personalities of individuals conform to that of their group [12].

In the present study, we attempted to rule out the possibility that low between-subjects variance was responsible for the inconsistency between our previous study that only found evidence for three domains—Dominance, Sociability, and Neuroticism—and the studies that found additional domains, including Conscientiousness. We therefore increased the between-subjects variance in the RIKEN sample by increasing the sample size by approximately two-thirds, which also led to our nearly doubling the ratio of females to males.

In addition to trying to find these additional domains in the common marmosets housed at RIKEN, we examined associations between any personality domains that we identified and a measure of subjective well-being. Previous studies in humans [45, 46] and in nonhuman primate species, including chimpanzees [40, 47, 48], orangutans *Pongo* spp. [49], rhesus macaques *Macaca mulatta* [50], brown capuchin monkeys [51], and common marmosets [13], have shown a consistent pattern of relationships between personality and measures of well-being or welfare. Specifically, personality domains associated with gregariousness, assertiveness, activity, and other traits associated with Extraversion [52] were related to higher subjective well-being and personality domains made up of traits associated with vigilance, fearfulness, anxiety, and other traits associated with Neuroticism [53] were associated with lower subjective well-being. By testing for associations between the personality domains and subjective well-being in this study, then, we could assess the degree to which the personality domains we find are measures of distinct psychological constructs.

Finally, we tested whether a set of genetic polymorphisms were associated with personality. A previous study found that lower Dominance and lower Neuroticism in common marmosets were both associated with the AA genotype of the μ-opioid receptor gene; lower Neuroticism was additionally associated with the short form of the arginine

vasopressin receptor 1A gene [13]. For the present study we focused on single nucleotide polymorphisms (SNPs) of the serotonin receptor 1a gene. A study of chimpanzees identified a SNP (rs25209664: C743A) that caused a proline to glutamine substitution at the 248th amino acid of the serotonin receptor 1a gene. This polymorphism was associated with aggression and sociability: chimpanzees who possessed two C alleles engaged in less social grooming and were rated as more anxious [54]. This study also found evidence for some interactions: males with the CC genotype displayed more often and, of chimpanzees with the AC genotype, mid-ranking individuals had lower proximity scores [54].

Method

Subjects

Subjects were 128 common marmosets (99 males, 29 females) that ranged in age from 1.6 to 15.1 (mean = 4.8, SD = 2.7). Subjects were recruited in three waves. The 77 subjects from the first wave had taken part in a similar previous study [13] and included 68 males and 9 females ranging in age from 1.5 to 15.1 years (mean=6.0, SD=2.6). Subjects from the second and third waves were born at RIKEN. The 24 subjects from the second wave included 17 males and 7 females ranging in age from 1.7 to 4.5 years (mean = 2.6, SD = 0.7) and the 27 subjects from the third wave included 14 males and 13 females ranging in age from 2.0 to 4.9 years (mean = 3.0, SD = 0.8).

Animal Housing and Husbandry

Subjects were housed in the RIKEN Center for Biosystems Dynamics Research in Kobe, Japan. One hundred and twelve subjects were born at the center, six were supplied by CLEA Japan Inc. (Tokyo, Japan), and 10 were supplied by Japan Wild Animal Laboratory Limited (Amami, Japan). Subjects sourced from other facilities had lived in the center for at least three years prior to this study.

At RIKEN, subjects were housed in breeding rooms that had a 12 h light-dark cycle (light: 08:00–20:00). Enclosures (1630 × 760 × 831 mm for families, 660 × 650 × 600 or 660 × 450 × 600 mm for pairs or individuals) had wooden perches, a plastic cube-shaped shelter, a food tray, and a water dispenser. There were around twenty cages in each breeding room and so even if animals were individually housed, they were exposed to visual, auditory, and olfactory stimulation from conspecifics. The temperature and humidity in the breeding room were maintained at approximately 28°C and 50%, respectively. In the morning and afternoon, subjects received solid food (CMS-1, CLEA Japan, Inc., Tokyo, Japan) mixed with an appropriate amount of water to soften it, powdered milk formula, honey, gluconic acid, calcium, vitamin C, and lactobacillus probiotic. Food in the afternoon was softened into a paste by soaking it in water and then stirring it. Once a week subjects' diets were supplemented with chopped and boiled eggs or bananas.

Animal Rearing

Animals reared by their parents and/or their family members, including one to five older brothers or sisters, were reared in family cages. At around 14 days after birth, when they were still infants, these subjects were fed a food paste in the afternoon. When these individuals were between 6 and 15 months old, to ensure that they were provided with the required amount of space, they were transferred from their family cage to a home cage (0.21 to 0.43m^2 floor space per animal). Animals living in these home cages were same-sex, mixed-age peers. Individuals that were to be used in brain imaging [55] or in behavioral studies, and individuals that did not get along with their partners, were single housed.

Animals that were not reared by their parents, for example, in the event of a triplet birth or parental neglect, were hand-reared in climate-controlled rearing cages by human caregivers. This procedure has been described elsewhere [13]. In short, these animals were housed in a thermal insulation box and a towel roll from one day to 21 days after birth. Then,

from 21 days after birth to weaning, these animals were housed in a wire-mesh box sized 390 × 230 × 300 mm furnished with a hammock, perches, a towel roll, a feeding dish, and a water bottle. These animals were breastfed on the day of their birth and then bottle-fed until weaning. A food paste was introduced at around 28 days and then animals were weaned fully 50 to 70 days after birth. After weaning, these animals were housed in a home cage with peers or individually in the breeding room.

Of the 77 subjects from the first wave, 30, including 23 parent-reared and seven hand-reared subjects, were housed in a family group (n = 13) or with same-sex peers (n = 17). The remaining 47 subjects, including 33 that were parent-reared, 13 that were hand-reared, and one with an unknown rearing history, were single-housed. Of the 24 subjects from the second wave, 22, including 18 that were parent-reared, 3 that were hand-reared, and one with an unknown rearing history, were housed in a family group (n = 7), with an opposite sex marmoset for breeding (n = 2), or with same-sex peers (n = 13). The remaining two subjects from the second wave were parent-reared and single-housed. Of the 27 subjects from the third wave, 25 parent-reared subjects and one hand-reared subject were housed in a family group (n = 1), with an opposite-sex marmoset for breeding (n = 4), with same-sex peers (n = 19), or single-housed (n = 2). The remaining subject was parent-reared and single-housed.

Ratings

Questionnaires

Personality. To assess personality, we used the Hominoid Personality Questionnaire (HPQ).[1] Each of the HPQ's 54 items consists of a trait adjective paired with one to three sentences that set the adjective in the context of primate behavior. For example, "**FEARFUL**" (boldface and capitals in the original) is paired with the descriptor sentence "Subject reacts excessively to real or imagined threats by displaying behaviors such as

[1] The HPQ can be obtained at https://extras.springer.com/2011/978-1-4614-0176-6.zip

screaming, grimacing, running away or other signs of anxiety or distress." The HPQ's instructions ask raters to **a)** judge the standing of each animal on each trait based on the animal's behavior and interactions with others, and the rater's own judgement of what constitutes average behavior for this species, **b)** assign a rating of 1 ("Displays either total absence or negligible amounts of the trait.") to 7 ("Displays extremely large amounts of the trait.") to each item, and **c)** not discuss their ratings with their fellow raters.

A description of the HPQ's development can be found elsewhere [56]. Briefly, the HPQ grew out the 48-item Orangutan Personality Questionnaire [49], which grew out of the 43-item Chimpanzee Personality Questionnaire [39]. Forty-one of the HPQ's 54 items were sampled from Goldberg's [57] trait terms of the five major domains of human personality [39]. The remaining 13 items were adapted from items [58] or facets [59] from other human personality inventories, or were created for by the authors of these instruments [39, 40, 49].

For this study, we used a version of the HPQ that had been translated into Japanese using a back-translation procedure. A study of chimpanzees revealed that the translation did not affect the HPQ's psychometric properties [40].

Subjective Well-Being. Ratings were made on a four-item scale that was based on a questionnaire used to measure subjective well-being in captive chimpanzees [47]. Each item was devised to assess a different concept of subjective well-being that had been described in the human literature [47, 60-64]. The first item (moods) concerned the extent to which an individual experienced positive versus negative affect. The second item (social) concerned whether the individual experienced pleasure from social interactions. The third item (goals) concerned whether the individual was able to achieve its goals, bearing in mind that different individuals may have different, personal goals. The fourth item (be marmoset) asked raters how "happy" they would be if they were that marmoset for a week and was thus meant to measure global satisfaction. The subjective well-being scale's instructions asked raters to

assign a rating of 1 ("Displays either total absence or negligible amounts of the trait or state.") to 7 ("Displays extremely large amounts of the trait.") to each item. The instructions also request that raters do not discuss their ratings.

For this study, we used a version of the subjective well-being questionnaire that had been translated into Japanese using a back-translation procedure. A study of chimpanzees revealed that the translation did not affect this questionnaire's psychometric properties [40].

Raters and Ratings

We asked three keepers (two men and one woman) who had completed the questionnaires in the first wave of data collection [see 13 for details] completed the questionnaires for the second and third wave of data collection. The keepers did not know the results of the previous study or the purpose of collecting the data. The keepers had known the subjects they rated for 1.1 to 9.8 years (mean = 3.7 years, SD = 2.2). Two keepers (one man and one woman) rated all 128 subjects and the third rated 81 subjects. This resulted in a total of 337 ratings or an average of 2.63 ratings per subject. There were no missing ratings data.

Genotyping

A buccal swab was taken from each subject and kept in a 90% ethanol solution until DNA extraction. DNA was extracted by DNeasy Blood and Tissue kit (Qiagen, CA, USA). PCR amplification was conducted in a 10 µl (the total volume) reaction mixture containing 10ng of DNA template, 0.4 µM of each primer (forward: 5'-tggattcccttcctccgaaa-3', reverse: 5'-aggtgttgattccctagggt-3'), 0.5U of LA Taq DNA polymerase, 400 µM of dNTPs, and GC buffer I (TaKaRa, Shiga, Japan). After denaturing DNA samples at 95°C for 1 min, we set up 40 cycles of 95°C for 30 seconds, 60°C for 30 seconds, 74°C for 1 minute, and a final extension at 74°C for 10 minutes. A total of 1,473 base pair fragments including whole single exon region were amplified. We then sequenced the polymerase chain reaction products, both forwards and backwards, using 3130xl Genetic Analyzer (Applied Biosystems, CA, USA).

The internal primer 5'-tcatgctggttctctatggg-3' was also used for sequencing. Primers were designed based on the NCBI Reference Sequence NC_013897. In the end, we identified three novel SNPs (G840C, G841A, and T901A) in the third intracellular region of the receptor (see Figures 2 and 3). G840C was a synonymous SNP coding alanine at the 280th amino acid sequence, G841A was a nonsynonymous SNP that caused a methionine substitution at the 281st amino acid sequence, and T901A was a nonsynonymous SNP that caused a serine to threonine substitution at the 301st amino acid sequence.

Analyses

We conducted the analyses using version 3.6.3 of R [65]. We used functions from version 1.9.12 of the psych package [66], version 1.0.7 of the EFA.MRFA package [67], and some custom functions.

Item Interrater Reliabilities

We used a custom function in R to compute the interrater reliabilities of the HPQ and subjective well-being questionnaire items. This function computed two intraclass correlations (*ICC*s) described by Shrout and Fleiss (43). The first, *ICC*(3,1), indicates the reliability of individual ratings, that is, it is an estimate of the reliability of the rating from a single rater. The second, *ICC*(3,*k*), indicates the reliability of the mean rating coming from *k* raters, which was equal to 2.63 in the present study. We excluded items that had reliabilities that were not greater than zero [see 56 for a discussion].

Exploratory Factor Analyses

Personality. We conducted these analyses on the aggregate (mean) of personality ratings for the 128 subjects. Simulation studies [68-70] have shown that the number of subjects required for satisfactory recovery of factors is a function of item communalities, item loadings, and the item:factor ratio, and that the subject:item ratio is irrelevant. Previous rating-based studies of common marmoset personality [13, 17, 31] have found that between

72% and 97% of questionnaire items were reliable, a total of three to five factors, median salient loadings of around .6 or .7, and communalities that were between wide and high [see ref 69 for definitions of these types of communalities]. As such, we have a large enough sample size to conduct factor analyses on these data.

Before extracting factors using the maximum likelihood procedure, we determined how many factors to extract. To do so, we used the fa.parallel function from the psych package to generate a scree plot, which we inspected, and to conduct a parallel analysis [71] in which we compared eigenvalues from a principal components analysis of our data to the distribution of 1000 eigenvalues generated from principal components analysis of resampled and randomly generated data. We used principal components analysis for our parallel analysis because a recent study showed that the number of dimensions identified in this manner is more accurate [72]. In addition, we used the VSS function from the psych package to determine, for one to eight factor solutions, which had the lowest Bayesian Information Criterion [BIC; 73], and the hullEFA function from the EFA.MRFA package to determine the number of factors via the Hull method [74], which is known to perform well with personality data [75]. Finally, we inspected the factors obtained to ensure that they were interpretable.

After we extracted factors using the fa function from the psych package, we applied an oblique (promax) and an orthogonal (varimax) rotation. If the promax rotation yielded factors that were strongly correlated and/or a different structure, we retained and interpreted those factors. Otherwise, we retained and interpreted the varimax-rotated factors.

In interpreting the factors, we specified that salient loadings were those equal to or greater than |0.4|. We labeled factors based on our interpretations of them and attempted to find suitable labels from previous findings in common marmosets, and, if none were available, from studies of nonhuman primates and humans. If we could not find a label from these sources, we devised our own.

In addition to conducting this first-order factor analysis, we found evidence (results to be discussed) suggesting that there may be second-order personality factors underlying these data. We thus conducted an exploratory factor analyses of the inerfactor correlation (Phi) matrix obtained from the promax-rotated factors. For the same reason, we conducted an additional item-level factor analysis as a robustness check.

Subjective Well-Being. We conducted a maximum likelihood factor analysis using the fa function on aggregated (mean) ratings for all 128 subjects. Previous work in 77 of these subjects revealed a single factor [13].

Unit-Weighted Factor Scores

For the remaining analyses, we used a custom R function to compute unit-weighted factor scores [20, 76] for the personality and subjective well-being data. This involved, for each item, finding the largest salient factor loading. If that loading was positive, we assigned it a weight of +1. If that loading was negative, we assigned it a weight of -1. In all other cases, we assigned a weight of zero. After We then summed the weighted item ratings.

Factor Reliabilities

For the first- and second-order personality factors, and for subjective well-being, we used the same custom function to compute Shrout and Fleiss's *ICC*(3,1) and *ICC*(3,*k*) for the items to compute these *ICC*s. As with the item-level analyses, *k* was equal to 2.63. In addition, we used the alpha function from the psych package to compute Cronbach's alpha (α), a measure of the internal consistency reliability of a scale, and the omega function to compute McDonald's omega hierarchical (ω_h), a measure of the degree to which a general factor saturates a scale's items.

Personality Factor Comparisons

To compare the first- and second-order factors to factors found in previous studies of common marmoset personality [13, 17, 31], we first generated unit-weighted factor scores

based on the personality structures described in these other studies. Because there was not a total overlap of questionnaire items across these studies, we sometimes had to substitute items that were similar in meaning or in the constructs that they purportedly assessed. Details about how these scores were created can be found in Table S1. After computing these unit-weighted factor scores, we obtained correlations between the scores based on the factor loadings from the present study and the scores based on component and factor loadings from previous studies. We compared the absolute magnitudes of these correlations and highlighted the highest correlation or, in the case where the confidence intervals of two or more correlations overlapped, highest correlations.

Personality-Subjective Well-Being Associations

We used Pearson correlation coefficients to examine associations between the first- and second-order personality factors and, both, the subjective well-being items and the total of these items. We used Holm's method [77] to adjust for familywise error rates.

Genetic Associations

To examine the genotype-personality associations, for the first- and second-order personality factors, we fit linear models using the lm function. For these analyses, we standardized the personality factor scores (mean = 0, SD = 1). The variables in the models included sex (male = 1, female = 0), age in years, and a categorical variable that indicated genotype. Because there were problems with genotyping four subjects, these individuals were excluded from the analyses. In addition, the G840C genotypes for two subjects and T901A genotype for one subject were unclear, and so these individuals were not included in tests of associations between personality and the G840C and T901A genotype, respectively. Finally, only one subject had the AA version of G841A and only nine subjects had the GA version of this genotype. We therefore did not examine associations between these genotypes and personality.

Although subjects were related, we did not test for the effect of genotypes within the context of an animal model [cf. 13]. Moreover, because we conducted multiple, sometimes non-independent, tests, we used the Bonferroni correction to adjust for familywise error rates.

Ethics

This study complied with the current laws of Japan, including the Act on Welfare and Management of Animals. All experimental and husbandry procedures were performed in accordance with RIKEN's Guidelines for Conducting Animal Experiments, and in accordance with the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines. All procedures were approved by the Animal Care and Use Committee of the Kobe Institute of RIKEN (MA2009-10-16).

Results

Interrater Reliabilities of Items

Personality

The interrater reliabilities of the 54 HPQ items are presented in Table 1. The reliabilities of individual ratings and of mean ratings for the items 'anxious', 'persistent', 'quitting', and 'unperceptive' were negative, and so we excluded these items from further analyses. Although the reliability of mean ratings for the items 'innovative' and 'decisive' were equal to 0.01, the reliabilities of individual ratings for these items were less than 0.01, and so we decided to exclude those items from further analyses.

Of the remaining 48 items, the interrater reliabilities of individual ratings ranged from 0.02 ('inventive') to 0.45 ('sociable'). The mean and standard deviation for these estimates were 0.21 and 0.11, respectively. The interrater reliabilities of mean ratings for the remaining items ranged from 0.06 ('inventive') to 0.68 ('sociable'). The mean and standard deviation for these estimates were 0.40 and 0.16, respectively.

Subjective Well-Being

The interrater reliabilities of individual ratings were 0.16, 0.10, 0.15, and 0.14 for the moods, social, goals, and global well-being items, respectively. The corresponding reliabilities of mean ratings were 0.33, 0.23, 0.32, and 0.30.

Maximum Likelihood Exploratory Factor Analyses

Personality

First-Order Analysis. The scree plot (see Figure S1) and parallel analysis indicated that there were five factors. The Hull method (see Figure S2) also indicated that there were five factors, and BIC achieved a minimum with five factors. We therefore extracted five factors.

A promax rotation of the five-factor solution yielded two interfactor correlations that were large (rs $\geq$ |0.5|) and two that were medium-sized (rs $\geq$ |0.3|). The mean and standard deviation of the absolute interfactor correlations were 0.26 and 0.20, respectively. Comparison of the varimax- and promax-rotated factors revealed that the congruence coefficients for two factors fell below 0.95 (see Table S2) and an inspection of the loadings indicated that the promax-rotated factors differed some from their varimax-rotated counterparts. Given these results, we interpreted the promax-rotated factors (see Table 2), which explained 63% of the variance (the varimax-rotated factors are presented in Table S3).

The first factor loaded on items related to high Extraversion and high Agreeableness in humans [e.g., 57]. This factor resembled the Sociability factor in one study [13] and the Agreeableness factor from two other studies [17, 31] of common marmosets.

The second factor loaded on items related to high Extraversion and low Agreeableness in humans [e.g., 57]. Compared to other studies of common marmosets, it is best described as a narrow version of factors labeled Dominance [13], Extraversion [17], and Assertiveness [31]. To be consistent with a prior study of a subset of these subjects [13], we labeled this factor Dominance.

The third factor had positive loadings on items related to high Neuroticism and low Conscientiousness in humans, and also negative loadings on items related to low Neuroticism and high Conscientiousness [e.g., 57]. In a previous study of a subsample of these animals [13], the Dominance and Neuroticism factor loaded on some of these items. Compared to other studies of common marmosets, it resembled most closely the factors labeled Conscientiousness and Patience in one study [31] and the Conscientiousness factor in another [17]. Humans that are high in Neuroticism and low in Conscientiousness are described as exhibiting an undercontrolled style of impulse control [78]. We thus labeled this factor Impulsiveness.

With the exception of a negative loading on the item cautious, the fourth factor loaded primarily on items related to high Openness in humans [e.g., 57]. Previous studies of common marmosets have labeled factor such as these Openness [17] and Inquisitiveness [31]. We therefore labeled this factor Openness.

The fifth factor loaded on items related to low Extraversion and high Neuroticism in humans [e.g., 57]. In the previous study of a subset of these animals [13], Neuroticism had a positive loading on many of these items. In all three previous studies of this species, factors such as Dominance, Assertiveness, and Conscientiousness had negative loadings on these items [13, 17, 31]. Given that this factor combined aspects of high Neuroticism and low degrees of Assertiveness or social prowess, we labeled it Negative Affect.

Second-Order Analysis. Because there were several non-negligible correlations between the just-described factors, we factor analyzed the factor intercorrelation (Phi) matrix. This enabled us to test whether there were any second-order factors.

Inspection of the scree plot (see Figure S3) and parallel analysis indicated that there were two factors; BIC was lowest for the two-factor solution.[2] We also tried to extract a single 'general' factor, but this solution exhibited poor fit (root mean square of the residuals = 0.14), and the factor did not have a salient loading on Openness or on Negative Affect. A promax rotation of the two-factor solution indicated that they were close to being orthogonal, and the loadings of the varimax-rotated factors were nearly identical to those of the promax-rotated factors (see Table 3). We therefore interpreted the varimax-rotated factors, which accounted for 49% of the variance. After reflecting (multiplying loadings by -1) the first factor, it had a positive loading on Sociability and a negative loading on both Dominance and Impulsiveness. We thus labeled this factor Pro-sociality. The second factor had a positive loading on Openness and a negative loading on Negative Affect. We thus labeled this factor Boldness.

Robustness Checks. Previous studies of common marmosets did not find evidence higher-order factors, that is, interfactor correlations tended to be modest [13, 17, 31]. Therefore, to investigate these findings further, we conducted two robustness checks.

The first check was to test whether the higher-order factors reflected the structuring of data collection. Specifically, because different subjects were rated in each wave, this may have led raters to rate the subjects belonging to each wave as resembling one another more than they did subjects in other waves. To test this, we residualized the 48 reliable items on a categorical variable that represented whether the subject was rated in the first, second, or third wave. We then factor analyzed the residualized item scores.

Inspection of the scree plot (see Figure S4) suggested that there were four or five factors and parallel analysis indicated that there were four factors. The Hull test indicated that

[2] We did not conduct a Hull test because the hullEFA function cannot be used to examine correlation matrices.

there were two factors (see Figure S5). The BIC was lowest for a five-factor solution. We therefore examined promax-rotations after extracting two, four, and then five factors.

For the two-factor solution (see Table S4), the first factor loaded predominantly on items onto which the factors Sociability, Dominance, and Impulsiveness had loaded. It therefore resembled the higher-order factor Pro-sociality. The second factor loaded predominantly on items onto which the factors Openness and Negative Affect had loaded. It therefore resembled the higher-order factor Boldness. For the four-factor solution (see Table S5), the first, third, and fourth factors resembled Sociability, Negative Affect, and Openness. The second factor loaded predominantly on items related to high Dominance and high Impulsiveness. The five-factor solution yielded five factors that resembled the five factors that has been found earlier (see Table S6).

The similarity, as indicated by Tucker's congruence coefficients, between the five factors obtained before and after item scores were residualized were equal to or greater than 0.98, suggesting that these were the same factors (see Table S7). Factor analysis of the residualized item scores, then, revealed either the same structure (the five-factor solution) or structures in which there were stronger associations between factors (the two- and four-factor solutions). These results are not consistent with the possibility that the higher-order factors reflect the fact that we collected these data in three stages.

The second check was to test whether the second-order factors are general evaluative factors used by raters [cf. 79]. To do so, we factor analyzed ratings from each of the three raters separately. We also factor analyzed a weighted correlation matrix from which removed possible effects of raters:

$$\mathbf{R}_w = \frac{1}{N}\sum_{i=1}^{k}\mathbf{R}_i n_i$$

where $\mathbf{R}_w$, the weighted correlation matrix, is the sum of the products of the correlation matrices of each of $k = 3$ raters, $\mathbf{R}_i$, and the subjects, n_i rated by that individual rater, divided by the total number of subjects, N.

For ratings from one keeper who rated all the subjects, the scree plot (see Figure S6), parallel analysis, BIC, and Hull method (see Figure S7) indicated that there were five factors. We thus extracted five factors and subjected them to a promax rotation (see Table S8). The factors resembled those obtained in the initial factor analysis and the interfactor correlations were similar in magnitude. We then conducted a second-order factor analysis in which we forced a two-factor solution. Although one second-order factor just missed our criterion for a salient loading on a first-order factor, these factors resembled Pro-sociality (reversed) and Boldness (see Table S9).

For ratings from the second keeper who rated all the subjects, the scree plot (see Figure S8) indicated that there were five factors and parallel analysis, the BIC, and the Hull method (see Figure S9) indicated that there were four factors. We thus extracted four factors and subjected them to a promax rotation (see Table S10). The first factor appeared to be a Dominance versus Agreeableness, the third factor was Gregariousness (a narrow facet of Extraversion), and the last two factors were difficult to interpret. The interfactor correlations were not consistent with there being a second-order factor.

For ratings from the keeper who rated 81 subjects, the scree plot (see Figure S10) and parallel analysis, the BIC, and Hull method (see Figure S11) indicated that there were three factors. We thus extracted three factors and subjected them to a promax rotation (see Table S11). These factors included Agreeableness versus Dominance, Extraversion, and Negative Affect/Impulsiveness, respectively.

For the weighted correlation matrix, the scree plot indicated that there were five factors (see Figure S12) and both the parallel analysis, and the BIC indicated that there were

three factors. We thus extracted three factors and subjected them to a promax rotation (see Table S12). The first and third factors loaded on many of the traits that belonged to the factors that made up the second-order Pro-sociality and Boldness domains, respectively. The second factor was an Impulsiveness factor. The correlation between the first and third factors was low, but the correlation between Impulsiveness and Pro-sociality was between medium and large, and therefore was consistent with the definitions of these factors.

We then extracted five factors and subjected them to a promax-rotation (see Table S13). The five factors resembled those from our initial factor analyses as did the interfactor correlations. The scree plot indicated that there were two factors (see Figure S13) as did both the parallel analysis and the BIC. The first higher-order factor was, when reflected, a Pro-sociality factor. The second higher-order factor was a Boldness factor (see Table S14).

Subjective Well-Being

Inspection of the scree plot (see Figure S14), parallel analysis, and the BIC all indicated that there was a single factor.[3] This factor explained 67% of the variance and had salient loadings on all four items (see Table 4).

Reliabilities of Factors

Personality

The interrater reliabilities of the individual ratings for Sociability, Dominance, Impulsiveness, Openness, and Negative Affect were 0.52, 0.39, 0.28, 0.26, and 0.25, respectively. The interrater reliabilities of mean ratings for these factors were 0.74, 0.63, 0.50, 0.48, and 0.46, respectively. For Pro-sociality and Boldness, respectively, the interrater reliabilities of individual ratings were 0.45 and 0.30, and the interrater reliabilities of mean ratings for these second-order factors were 0.69 and 0.53.

[3] We conducted a Hull test for this analysis, too, but doing so produced a warning, which we suspect was attributable to there only being four items. The Hull test nevertheless indicated that there was one factor.

The internal consistency reliability (Cronbach's α) for Sociability, Dominance, Impulsiveness, Openness, and Negative Affect were 0.95, 0.95, 0.88, 0.85, and 0.81, respectively. The degree to which a general factor saturated these factors (McDonald's ω_h) was 0.81, 0.85, 0.75, 0.80, and 0.68, respectively.

Subjective Well-Being

For the total subjective well-being score, the interrater reliability of individual ratings was 0.21 and the interrater reliability of the mean of ratings 0.41. Cronbach's α for this scale was 0.87 and McDonald's ω_h was 0.13.

Personality Factor Comparisons

Iwanicki and Lehmann (17) found four factors. Compared to our first-order factors, their Extraversion factor overlapped with Dominance and Negative Affect, their Agreeableness factor overlapped with Sociability and (low) Dominance, their Conscientiousness factor overlapped with Sociability, and their Openness factor overlapped with the same-named factor that we found (see Table 5). Compared to our second-order factors, Iwanicki and Lehman's Extraversion overlapped with (low) Pro-sociality and high Boldness; their Agreeableness and Conscientiousness factors overlapped with Pro-sociality; and their Openness factor overlapped with Boldness (see Table 6).

Koski, Buchanan-Smith (31) found five factors. Compared to our first-order factors, their Conscientiousness factor overlapped with (low) Dominance and (low) Impulsiveness; their Agreeableness factor overlapped with Sociability; their Assertiveness factor overlapped with (low) Sociability, Dominance, and (low) Negative Affect; their Patience factor overlapped with Sociability; and their Inquisitiveness factor overlapped with Openness (see Table 5). Compared to our second-order factors, their Conscientiousness, Agreeableness, and Patience factors all overlapped with Pro-sociality; their Assertiveness factor overlapped with

Boldness and (low) Pro-sociality; and their Inquisitiveness factor overlapped with Boldness (see Table 6).

Inoue-Murayama, Yokoyama (13) found three factors. Compared to our first-order factors, their Dominance factor overlapped with Dominance; their Sociability factor overlapped with Sociability; and their Neuroticism factor overlapped with Negative Affect (see Table 5). Compared to our second-order factors, their Dominance and Sociability factors overlapped with low and high Pro-sociality, respectively; their Neuroticism factor overlapped with (low) Boldness (see Table 6).

Personality and Subjective Well-Being Associations@@@

The correlations between the subjective well-being items and the personality factors are presented in Table 7. Sociability was significantly associated with higher scores on all four items and the total subjective well-being score. Dominance was not significantly related to any of the scale's items or the factor. Impulsiveness was significantly related to lower, and Openness was significantly related to higher, balance of positive versus negative moods, how happy raters thought they would be if they were the marmoset, and the total subjective well-being score. Negative Affect was negatively related to how happy raters would be how happy raters thought they would be if they were the marmoset. Of the second-order factors, Pro-sociality was significantly associated with being rated as higher on all items save for the ability to achieve goals, and the total subjective well-being score. Boldness was not significantly associated with the pleasure subjects derived from social interactions, but it was significantly related to being higher in the other three items and in the total subjective well-being score.

Personality-Genotype Associations

G840C Genotypes

Twenty-seven subjects had the GG genotype, 23 had the CC genotype, and 72 were heterozygous. In the first set of analyses, we compared subjects with the GC genotype and subjects with the GG genotype to those with the CC genotype. Compared to subjects with the CC genotype, subjects with the GC or GG genotypes were significantly higher in Dominance; these associations, however, did not prevail correction for multiple tests (see Table S15). In a second set of analyses, we compared the 95 subjects who were carriers of the C allele (CC or GC genotype) to the 27 subjects with the GG genotype. None of the comparisons were statistically significant (see Table S16). In a third set of analyses, we compared the 99 subjects who were carriers of the G allele (GG or GC genotype) to the 23 subjects with the CC genotype. Carriers were significantly higher in Dominance, but this effect did not prevail correction for multiple tests (see Table S16).

T901A genotypes

Twelve subjects had the TT genotype, 35 had the AA genotype, and 76 were heterozygous. Because of this imbalance in the number of subjects, we only compared the 88 subjects who carried the T allele to the 35 subjects with the AA genotype. None of the comparisons were statistically significant (see Table S17).

Discussion

We found five personality domains—Sociability, Dominance, Impulsiveness, Openness, and Negative Affect—in common marmosets and higher-order domains that we labeled Pro-sociality, which had a positive loading on Sociability and negative loadings on Dominance and Impulsiveness, and Boldness, which had a positive loading on Openness and a negative loading on Negative Affect. The interrater reliabilities of these domains were comparable to what has been found in studies of other primate species [80], including humans [e.g., 81] and they were related to subjective well-being and its constituent items in

ways consistent with their meaning. We found no strong evidence that either personality or subjective well-being was associated with polymorphisms of the serotonin 1a receptor gene.

The personality domains that we found in the present study overlapped, although not completely, with those found in prior studies of common marmosets. Openness resembled eponymous domains, or a domain labeled Inquisitiveness, identified in previous studies [13, 17, 31, 32]. Moreover, although we did not find a clear Conscientiousness factor, as did two previous studies [17, 31], Impulsiveness and Pro-sociality overlapped with Conscientiousness in that all three were related to behavioral consistency and reliability, prosociality, tolerance, and low levels of aggression [17, 31]. Impulsiveness, however, was also related to emotionality and reactivity whereas Conscientiousness was not. Finally, Dominance, Sociability, and Negative Affect resembled domains found in earlier studies [13, 17, 31, 32]. On the other hand, although they may have been represented by Pro-sociality, we did not find strong evidence for a Patience [31] or a Perceptual Sensitivity [17] (which may be the same construct [31]) domain.

Unlike past rating-based studies that did not find higher-order factors in common marmosets [13, 17, 31], we found two second-order factors. In follow-on analyses, we found that these higher-order domains partly reflect a tendency for raters to see some traits as more correlated than others. However, these analyses could not exclude the possibility that these domains represent a higher-level of personality organization, perhaps reflecting group personalities [cf. 12]. Although there have been reports of higher-order factors of human personality [e.g., 82], including the so-called “general factor of personality” [e.g., 83], these reports have been criticized [e.g., 84, 85, 86]. The problems that affect human studies that purportedly find higher-order personality factors were absent in the present study: each animal was rated by two or three keepers, the correlations among the latent variables were considerable, and adjusting for rater effects increased rather than decreased some correlations

among factors. Nevertheless, because second-order factors were not identified in other studies of common marmosets [13, 17, 31, 44], including one that included 77 of the same animals, prior to interpreting the meaning of this phenomenon, we urge an attempt to replicate these findings and an analysis of similar data using more flexible modeling techniques [e.g., 11].

The findings from the present study are consistent with the possibility that common marmosets evolved a personality structure that includes a domain or domains associated with self-control that are found in larger-brained primate species, such as brown capuchin monkeys [28], chimpanzees [39], and humans [59]. As these species share only a very distant common ancestors with Callitrichids, and have very different socioecologies, these traits are not likely to be homologous. Instead, the presence of traits related to self-control in common marmosets likely reflects convergent evolution that was driven by the need for individuals to meet the demands associated with cooperative breeding. Although, it is worth noting that there is still variability between studies in how these traits group together, studies that examine the role that factors such as Conscientiousness, Patience, or Impulsivity play in infant rearing, especially by helpers, among common marmosets are needed to test this hypothesis.

As in our study of a subsample of these subjects [13], we found personality-subjective well-being correlations that were consistent with those found in studies of humans [45, 46] and nonhuman primates [40, 47-51]. These findings, and those in humans and great apes that indicate that a common genetic background underlies these traits [87-92], are consistent with the possibility that these relationships are ancestral.

Our failure to find association between SNPs related to the serotonin 1a receptor gene and either personality domains is not consistent with previous findings of an association between this genotype and personality in chimpanzees [54]. It is possible that our failure to

find such associations resulted from the personality measure that we used. However, as the associations between personality and serotonin-related genes in humans are likely false positives [93], we suspect that we did not find significant associations because there were none.

This study had shortcomings. First, nearly 40% of the subjects were single housed. Behaviors related to some of the traits might therefore have been rare or absent, and so we still may not have been capturing enough between subject variation. Second, the factor structure was compared to studies that used different, although partly overlapping, instruments. It is unclear to what degree the use of different measures may have obscured similarities or blurred differences between the structures in these studies. This limitation also prevented us from using other statistical methods to directly compare these structures. Third, we judged that it was worth reporting the genetic associations so that they may contribute to future meta-analyses, as we alluded to previously, to identify genetic effects considerably larger sample sizes are needed. Fourth, the interrater reliabilities of the subjective well-being variables were lower than those reported in other nonhuman primate species, for example, chimpanzees [40, 47].

The cliché that a study's findings can yield more questions than answers is well-suited for the present case. Nevertheless, these findings highlight the need for (and promise of) large collaborative studies if we are to understand the proximate and ultimate origins of personality structure in common marmosets, and other species, including ours.

Data Availability

Data needed to reproduce the analyses are available via the Open Science Foundation website: https://osf.io/ysrja/.

Table 1
Interrater Reliabilities of Items from the Hominoid Personality Questionnaire

Item	*ICC*(3,1)	*ICC*(3,*k*)
Sociable	0.45	0.68
Sympathetic	0.43	0.66
Solitary	0.43	0.67
Protective	0.42	0.66
Helpful	0.38	0.62
Friendly	0.36	0.60
Aggressive	0.34	0.57
Gentle	0.34	0.58
Irritable	0.33	0.57
Affectionate	0.32	0.55
Stingy/greedy	0.29	0.51
Dominant	0.28	0.50
Individualistic	0.28	0.51
Submissive	0.28	0.51
Imitative	0.28	0.51
Independent	0.27	0.50
Excitable	0.26	0.48
Conventional	0.26	0.48
Bullying	0.23	0.44
Impulsive	0.23	0.44
Dependent/follower	0.23	0.44
Defiant	0.23	0.45
Stable	0.21	0.41
Jealous	0.21	0.41
Cautious	0.19	0.39
Active	0.19	0.38
Fearful	0.18	0.37
Autistic	0.18	0.36
Thoughtless	0.17	0.36
Erratic	0.17	0.35
Playful	0.16	0.33
Intelligent	0.16	0.33
Reckless	0.15	0.32
Curious	0.14	0.30
Sensitive	0.14	0.30
Inquisitive	0.13	0.28
Cool	0.13	0.29
Predictable	0.13	0.28
Lazy	0.11	0.25
Timid	0.10	0.22
Clumsy	0.09	0.21
Disorganized	0.09	0.20
Vulnerable	0.07	0.16

Unemotional	0.06	0.15
Distractible	0.05	0.13
Manipulative	0.05	0.12
Depressed	0.04	0.09
Inventive	0.02	0.06
Innovative	0.00	0.01
Decisive	0.00	0.01
Anxious	-0.03	-0.08
Persistent	-0.06	-0.19
Quitting	-0.08	-0.24
Unperceptive	-0.12	-0.39

Table 2

Pattern Matrix from the First-Order Factor Analysis of the Hominoid Personality Questionnaire

	Factor Loadings					
Item	Soc	Dom	Imp	Opn	Neg	h^2
Helpful	**0.89**	0.10	-0.05	0.09	-0.08	0.79
Sympathetic	**0.83**	-0.01	-0.07	0.07	0.08	0.76
Protective	**0.80**	0.01	0.02	0.02	-0.15	0.66
Individualistic	**-0.78**	0.09	-0.05	0.13	0.25	0.71
Dependent/follower	**0.77**	0.06	-0.05	0.23	0.39	0.69
Independent	**-0.73**	0.27	-0.31	0.10	0.08	0.62
Imitative	**0.72**	0.04	0.07	0.20	0.18	0.49
Solitary	**-0.71**	0.05	-0.04	-0.17	0.34	0.74
Affectionate	**0.64**	-0.09	-0.16	0.21	0.12	0.65
Sensitive	**0.64**	-0.08	-0.17	-0.02	0.04	0.61
Sociable	**0.62**	-0.27	-0.16	0.16	-0.15	0.85
Conventional	**0.60**	0.11	-0.33	-0.13	0.19	0.62
Intelligent	**0.59**	0.26	-0.18	0.00	-0.19	0.39
Gentle	**0.50**	-0.35	-0.24	0.15	0.09	0.83
Reckless	**-0.50**	-0.16	0.39	0.38	-0.03	0.62
Friendly	**0.49**	**-0.46**	-0.15	0.13	0.02	0.86
Jealous	0.02	**0.92**	-0.04	0.21	0.15	0.83
Stingy/greedy	-0.08	**0.87**	-0.06	0.28	0.15	0.86
Bullying	-0.04	**0.85**	0.00	0.11	0.07	0.77
Dominant	-0.09	**0.79**	0.06	0.01	-0.07	0.80
Manipulative	0.21	**0.72**	-0.10	0.04	-0.33	0.57
Aggressive	-0.12	**0.69**	0.15	-0.05	-0.17	0.80
Defiant	-0.09	**0.65**	0.20	-0.01	-0.20	0.78
Irritable	0.00	**0.50**	**0.48**	-0.18	-0.11	0.74
Excitable	-0.02	0.16	**0.78**	-0.08	-0.06	0.78
Unemotional	-0.10	0.15	**-0.77**	0.00	0.26	0.52
Impulsive	-0.10	0.06	**0.75**	0.13	0.13	0.76
Cool	0.18	-0.05	**-0.66**	-0.06	0.01	0.65
Fearful	0.23	-0.10	**0.62**	**-0.42**	0.28	0.51
Distractible	-0.11	-0.05	**0.53**	0.23	0.10	0.40
Disorganized	-0.10	0.15	**0.52**	0.18	0.12	0.51
Stable	0.21	-0.19	**-0.46**	0.07	-0.38	0.64
Thoughtless	-0.22	-0.03	**0.41**	0.38	0.02	0.45
Predictable	0.12	-0.08	**-0.40**	0.04	0.02	0.27
Erratic	-0.20	0.32	0.35	-0.06	0.20	0.54
Curious	0.14	0.13	0.08	**0.73**	0.02	0.61
Inquisitive	0.17	0.11	0.06	**0.72**	0.09	0.55
Inventive	0.27	0.18	-0.05	**0.68**	0.11	0.51
Playful	0.23	-0.12	0.32	**0.65**	-0.04	0.60
Cautious	**0.47**	0.08	0.24	**-0.59**	0.21	0.53
Active	0.28	0.18	**0.41**	**0.52**	-0.13	0.69
Autistic	0.03	-0.13	0.09	0.19	**0.68**	0.45

Timid	0.14	0.00	0.34	-0.18	**0.65**	0.58
Depressed	-0.17	0.07	-0.27	-0.04	**0.64**	0.51
Clumsy	-0.04	0.17	-0.05	0.00	**0.58**	0.33
Vulnerable	-0.02	-0.19	-0.02	0.04	**0.57**	0.39
Lazy	-0.23	-0.05	**-0.45**	-0.17	**0.50**	0.59
Submissive	0.33	-0.20	-0.18	-0.01	**0.48**	0.61
Proportion of variance	0.20	0.14	0.13	0.08	0.08	

	Factor Correlations				
Factor	Soc	Dom	Imp	Opn	Neg
Soc	1.00				
Dom	-0.53	1.00			
Imp	-0.45	0.57	1.00		
Opn	0.06	0.15	0.18	1.00	
Neg	-0.06	-0.19	-0.04	-0.38	1.00

Note. N = 128. Soc = Sociability, Dom = Dominance, Imp = Impulsiveness, Opn = Openness, Neg = Negative Affect, h^2 = communalities. Factors extracted using a maximum likelihood estimation and rotated using the promax procedure. Factor loadings greater than or equal to |0.4| are in bold.

Table 3

Pattern Matrix from the Second-Order Factor Analysis of Personality Factors

	Promax Rotation		Varimax Rotation		
First-Order Factor	Pro-sociality	Boldness	Pro-sociality	Boldness	h^2
Dominance	**-0.79**	0.15	**-0.80**	0.21	0.68
Sociability	**0.72**	0.21	**0.70**	0.15	0.51
Impulsiveness	**-0.67**	0.08	**-0.68**	0.13	0.48
Negative affect	-0.01	**0.62**	0.04	**-0.61**	0.38
Openness	-0.01	**-0.61**	-0.06	**0.61**	0.38
Proportion of variance	0.32	0.17	0.32	0.17	

Note. $N = 128$. h^2 = communalities. Factors extracted from the factor correlation matrix from Table 2 using a maximum likelihood estimation and rotated using the promax and varimax procedures. The Pro-Social factor for both structures were reflected, that is, the loadings were multiplied by -1. The promax-rotated factors correlated -0.15. Factor loadings greater than or equal to |0.4| are in bold.

Table 4

Results from Factor Analysis of the Subjective Well-Being Scale

Item	Loading	h^2
Be marmoset	0.98	0.97
Balance of moods	0.86	0.73
Ability to achieve goals	0.82	0.67
Pleasure from social interactions	0.55	0.30

Note. $N = 128$. h^2 = communalities.

Table 5

Correlations Between Unit-Weighted Factor Scores Based on Factor Loadings in the Present Study and Factor Loadings from Three Previous Studies of Common Marmoset Personality

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Iwanicki and Lehman (2015)			
Extraversion			
Sociability	-0.50	-0.62	-0.36
Dominance	**0.82**	**0.75**	**0.87**
Impulsiveness	0.50	0.36	0.62
Openness	0.54	0.40	0.65
Negative affect	**-0.70**	**-0.78**	**-0.60**
Agreeableness			
Sociability	**0.86**	**0.81**	**0.90**
Dominance	**-0.84**	**-0.88**	**-0.77**
Impulsiveness	-0.76	-0.82	-0.67
Openness	-0.07	-0.24	0.11
Negative affect	0.25	0.08	0.41
Conscientiousness			
Sociability	**0.83**	**0.77**	**0.88**
Dominance	-0.47	-0.59	-0.32
Impulsiveness	-0.63	-0.73	-0.51
Openness	0.00	-0.17	0.18
Negative affect	0.05	-0.13	0.22
Openness			
Sociability	0.11	-0.07	0.28
Dominance	0.34	0.18	0.49
Impulsiveness	0.27	0.10	0.42
Openness	**0.96**	**0.94**	**0.97**
Negative affect	-0.40	-0.53	-0.24
Koski et al. (2017)			
Conscientiousness			
Sociability	0.62	0.51	0.72
Dominance	**-0.89**	**-0.92**	**-0.84**
Impulsiveness	**-0.84**	**-0.89**	**-0.79**
Openness	-0.39	-0.53	-0.23
Negative affect	0.19	0.01	0.35
Agreeableness			
Sociability	**0.95**	**0.92**	**0.96**
Dominance	-0.68	-0.77	-0.58
Impulsiveness	-0.72	-0.79	-0.62
Openness	0.03	-0.14	0.20
Negative affect	0.13	-0.05	0.29
Assertiveness			

	Sociability	**-0.67**	**-0.76**	**-0.57**
	Dominance	**0.67**	**0.57**	**0.76**
	Impulsiveness	0.33	0.16	0.47
	Openness	0.32	0.15	0.47
	Negative affect	**-0.64**	**-0.73**	**-0.53**
Patience				
	Sociability	**0.74**	**0.65**	**0.81**
	Dominance	-0.37	-0.51	-0.21
	Impulsiveness	-0.59	-0.69	-0.47
	Openness	0.21	0.04	0.37
	Negative affect	-0.03	-0.21	0.14
Inquisitiveness				
	Sociability	0.34	0.18	0.48
	Dominance	0.21	0.04	0.37
	Impulsiveness	0.17	-0.01	0.33
	Openness	**0.82**	**0.76**	**0.87**
	Negative affect	-0.56	-0.67	-0.43
Inoue-Murayama et al. (2018)				
Dominance				
	Sociability	-0.71	-0.79	-0.62
	Dominance	**0.94**	**0.91**	**0.96**
	Impulsiveness	0.83	0.77	0.88
	Openness	0.34	0.18	0.49
	Negative affect	-0.38	-0.52	-0.22
Sociability				
	Sociability	**0.93**	**0.90**	**0.95**
	Dominance	-0.40	-0.54	-0.25
	Impulsiveness	-0.39	-0.52	-0.23
	Openness	0.40	0.24	0.54
	Negative affect	-0.12	-0.29	0.05
Neuroticism				
	Sociability	-0.30	-0.45	-0.14
	Dominance	-0.03	-0.20	0.14
	Impulsiveness	0.35	0.19	0.49
	Openness	-0.34	-0.49	-0.18
	Negative affect	**0.82**	**0.75**	**0.87**

Note. $N = 128$. The highest correlation between the five factors found in this study and each factor found in a previous study are highlighted in bold. In cases where the confidence intervals of two or more of the highest correlations overlapped, we highlighted both correlations.

Table 6

Correlations Between Unit-Weighted Factor Scores Based on Loadings from the Second-Order Factor Analysis in the Present Study and Factor Loadings from Three Previous Studies of Common Marmoset Personality

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Iwanicki and Lehman (2015)			
Extraversion			
Pro-sociality	**-0.72**	**-0.80**	**-0.63**
Boldness	**0.73**	**0.64**	**0.80**
Agreeableness			
Pro-sociality	**0.95**	**0.93**	**0.97**
Boldness	-0.18	-0.35	-0.01
Conscientiousness			
Pro-sociality	**0.73**	**0.64**	**0.81**
Boldness	-0.02	-0.20	0.15
Openness			
Pro-sociality	-0.20	-0.36	-0.03
Boldness	**0.83**	**0.76**	**0.87**
Koski et al. (2017)			
Conscientiousness			
Pro-sociality	**0.91**	**0.88**	**0.94**
Boldness	-0.35	-0.49	-0.19
Agreeableness			
Pro-sociality	**0.90**	**0.87**	**0.93**
Boldness	-0.05	-0.22	0.12
Assertiveness			
Pro-sociality	**-0.67**	**-0.76**	**-0.56**
Boldness	**0.56**	**0.43**	**0.67**
Patience			
Pro-sociality	**0.64**	**0.53**	**0.73**
Boldness	0.15	-0.02	0.32
Inquisitiveness			
Pro-sociality	-0.02	-0.19	0.16
Boldness	**0.84**	**0.78**	**0.88**
Inoue-Murayama et al. (2018)			
Dominance			
Pro-sociality	**-0.97**	**-0.98**	**-0.95**
Boldness	0.43	0.28	0.56
Sociability			
Pro-sociality	**0.66**	**0.55**	**0.75**
Boldness	0.32	0.16	0.47
Neuroticism			
Pro-sociality	-0.21	-0.37	-0.04
Boldness	**-0.68**	**-0.76**	**-0.57**

Note. $N = 128$. The highest correlation between the five factors found in this study and each factor found in a previous study are highlighted in bold. In cases where the confidence intervals of two or more of the highest correlations overlapped, we highlighted both correlations.

Table 7

Correlations Between Subjective Well-Being Scale Items and Factor and Personality Factors

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Moods			
Sociability	**0.42**	**0.26**	**0.55**
Dominance	-0.18	-0.34	< -0.01
Impulsiveness	**-0.27**	**-0.43**	**-0.11**
Openness	**0.38**	**0.22**	**0.52**
Negative affect	-0.14	-0.30	0.04
Pro-sociality	**0.33**	**0.16**	**0.48**
Boldness	**0.31**	**0.15**	**0.46**
Social			
Sociability	**0.53**	**0.40**	**0.65**
Dominance	-0.22	-0.38	-0.05
Impulsiveness	-0.24	-0.40	-0.07
Openness	0.14	-0.03	0.31
Negative affect	-0.11	-0.27	0.07
Pro-sociality	**0.38**	**0.22**	**0.52**
Boldness	0.15	-0.03	0.31
Goals			
Sociability	**0.39**	**0.24**	**0.53**
Dominance	-0.08	-0.25	0.10
Impulsiveness	-0.22	-0.38	-0.05
Openness	0.25	0.08	0.40
Negative affect	-0.22	-0.38	-0.05
Pro-sociality	0.26	0.09	0.41
Boldness	**0.28**	**0.11**	**0.43**
Be marmoset			
Sociability	**0.45**	**0.30**	**0.58**
Dominance	-0.18	-0.34	< -0.01
Impulsiveness	**-0.28**	**-0.43**	**-0.11**
Openness	**0.33**	**0.16**	**0.48**
Negative affect	**-0.27**	**-0.42**	**-0.10**
Pro-sociality	**0.34**	**0.18**	**0.49**
Boldness	**0.36**	**0.20**	**0.50**
Subjective well-being			
Sociability	**0.53**	**0.39**	**0.65**
Dominance	-0.19	-0.36	-0.02
Impulsiveness	**-0.30**	**-0.45**	**-0.13**
Openness	**0.32**	**0.15**	**0.47**
Negative affect	-0.21	-0.37	-0.04
Pro-sociality	**0.39**	**0.23**	**0.53**
Boldness	**0.32**	**0.16**	**0.47**

Note. $N = 128$. Estimates in bold are significant at $P < 0.05$ after adjustment using Holm's method. 95% confidence intervals are based on the nominal (unadjusted) significance level.

Figure 1

Personality domains found in previous studies and grouped by the psychological construct they represent. From left to right, the first two columns are domains found by Iwanicki and Lehmann (2015) in two datasets, the third refers to domains found by Koski et al. (2017), the fourth to domains found by Inoue-Murayama et al. (2018), and the fourth refers to domains found by Yokoyama et al. (2011). Domains in the same 'box' measure the same construct. Constructs separated by dotted lines are related constructs.

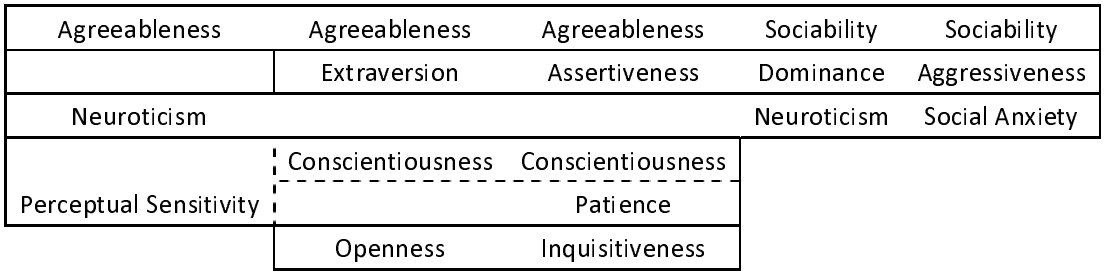


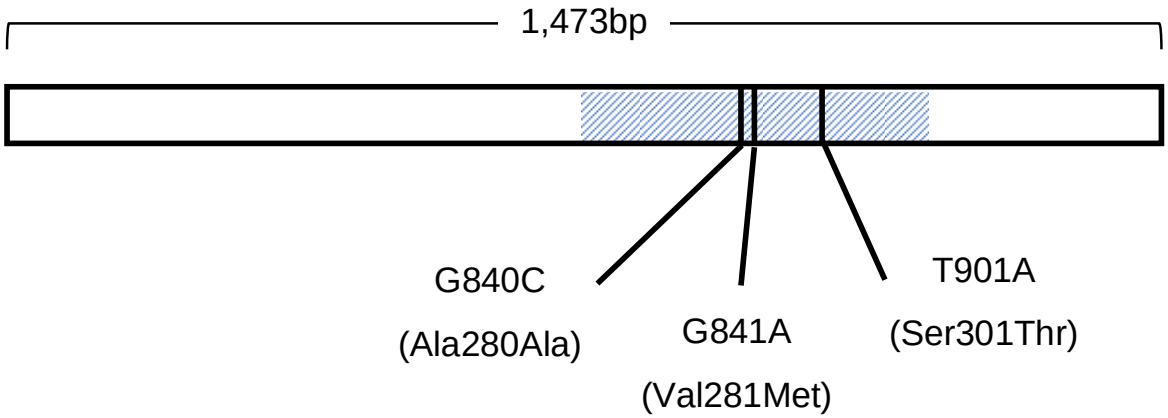
Figure 2

The sequence is based on NC_013897. Primer sequences are underlined. Start and stop codon sequences are in boxes. The third intracellular region is enclosed in the parentheses. Nucleotide substitutions are shown in capital and bold letters; G840C (A280A), G841A (V281M), T901A (S301T).

tggattcccttcctccgaaacttccttggagactgggcggaagaccccaggggaaggggcgaaaggga
tcttcgctctgctttttcttccttcctctttcccgcgcggggctcacaggcatggatgtgctcagccc
tggtcagggcaacaataccacatcatccccgggtccctttgagaccgccagcaacactactggtatct
ccgacgtgaccttcggctaccaagtgatcacctctctgctgttgggcacgctcatcttctgtgcggtg
ctgggcaatgcctgcgtggtggctgccatcgccctggagcgctccctgcagaacgtggccaattatct
tattggctctttggcggtcaccgacctcatggtgtcggtgttggtgctgcccatggccgcgctgtatc
aggtgctcaacaagtggactctgggccaggtcacctgcgacctgttcatagccctcgacgtgctgtgc
tgtacctcatccatcctgcacctgtgcgccatcgcgctggacaggtactgggccatcacggaccccat
cgactacgtgaacaagaggacgccccggcgcgctgctgcgctcatctcgctcacttggcttattggct
tcctcatctccatcccgcccatgctgggctggcgcaccccggaagaccgctcggaccccgacgcatgc
accattagcaaggaccacggctacactatctactccaccttcggcgctttctacatcccgctgctgct
catgctggttctctatgggcgcatattccgagctgcgcgcttccgcattcgcaagacagtgaaaaagg
tggagaagaccggagcggacacccgccgtggagcatctccggccccgcagcccaagaagagcgtgaat
ggagaatcggggagcaggaactggagactgagcgtggagagcaagtcagagagtgctctgtgcgccaa
tggcgcGGtgaggcaaggtgacgacggcgccgccctggaggtgatcgaggtgcaccgggtgggcaacT
ccaaagagcacttgcctctgcccagcgaggctggtgctacccccttgtgcccccgcctctttcgagagg
aaaaatgagcgcaacgccgaggcgaagcgcaagatggccctggcccgagagaggaagacagtgaagac
gctgggcattatcatgggtactttcatcctctgctggctgcccttcttcatcgtggctcttgttctgc
ctttctgtgagagcagttgccacatgcccaccctgttgggcgctataatcaattggctgggctactcc
aactctctgcttaaccccgtcatttacgcatacttcaacaaggactttcaaaacgcgtttaagaagat
ctttaagtgtaagttctgccgccaatgatgatggaggagtagccggccagtgcgggggttacaggatc
cgccccattcactatgcttggaccaaccctagggaatcaacacct

Figure 3

Locations of the single nucleotide polymorphisms on the single exon of the common marmoset serotonin receptor 1a gene



Note. The shaded region corresponds to the third intracellular region.

References

1. Rylands AB, Coimbra-Filho AF, Mittermeier RA. Systematics, geographic distribution, and some notes on the conservation status of the Callitrichidae. In: Rylands AB, editor. Marmosets and tamarins: Systematics, behaviour, and ecology. New York: Oxford University Press; 1993. p. 11–77.

2. Rylands AB, de Faria DS. Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: Rylands AB, editor. Marmosets and tamarins: Systematics, behaviour, and ecology. New York: Oxford University Press; 1993. p. 262-72.

3. Servick K. Why are U.S. neuroscientists clamoring for marmosets? Science. 2018:383-4.

4. Preuss TM. Critique of pure marmoset. Brain Behav Evol. 2019;93(2-3):92-107. doi: 10.1159/000500500.

5. Burkart JM, Fehr E, Efferson C, van Schaik CP. Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. Proc Natl Acad Sci U S A. 2007;104(50):19762-6. doi: 10.1073/pnas.0710310104.

6. Burkart JM, Allon O, Amici F, Fichtel C, Finkenwirth C, Heschl A, et al. The evolutionary origin of human hyper-cooperation. Nature Communications. 2014;5. doi: 10.1038/ncomms5747.

7. Kawai N, Yasue M, Banno T, Ichinohe N. Marmoset monkeys evaluate third-party reciprocity. Biology Letters. 2014;10(5). doi: 10.1098/rsbl.2014.0058.

8. Burkart JM, van Schaick CP. Cognitive consequences of cooperative breeding in primates? Anim Cogn. 2010;13:1-19. doi: 10.1007/s10071-009-0263-7.

9. Digby LJ, Ferrari SF, Saltzman W. Callitrichines: The role of competition in cooperatively breeding species. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK,

Stumpf RM, editors. Primates in Perspective. 2nd ed. Oxford: Oxford University Press; 2010. p. 91-107.

10. Šlipogor V, Gunhold-de Oliveira T, Tadić Z, Massen JJM, Bugnyar T. Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in Boldness-Shyness, Stress-Activity, and Exploration-Avoidance. Am J Primatol. 2016;78(9):961-73. doi: 10.1002/ajp.22566.

11. Martin JS, Massen JJM, Šlipogor V, Bugnyar T, Jaeggi AV, Koski SE. The EGA+GNM framework: An integrative approach to modelling behavioural syndromes. Methods in Ecology and Evolution. 2019;10(2):245-57. doi: 10.1111/2041-210x.13100.

12. Koski SE, Burkart JM. Common marmosets show social plasticity and group-level similarity in personality. Scientific Reports. 2015;5. doi: 10.1038/srep08878.

13. Inoue-Murayama M, Yokoyama C, Yamanashi Y, Weiss A. Common marmoset (*Callithrix jacchus*) personality, subjective well-being, hair cortisol level, and *AVPR1a*, *OPRM1*, and *DAT* genotypes. Scientific Reports. 2018. doi: 10.1038/s41598-018-28112-7.

14. Tomassetti D, Caracciolo S, Manciocco A, Chiarotti F, Vitale A, De Filippis B. Personality and lateralization in common marmosets (*Callithrix jacchus*). Behavioural Processes. 2019;167. doi: 10.1016/j.beproc.2019.103899.

15. Yokoyama C, Kawasaki A, Hayashi T, Onoe H. Linkage between the midline cortical serotonergic system and social behavior traits: positron emission tomography studies of common marmosets. Cereb Cortex. 2013;23:2136-45. doi: 10.1093/cercor/bhs196.

16. Šlipogor V, Burkart JM, Martin JS, Bugnyar T, Koski SE. Personality method validation in common marmosets (*Callithrix jacchus*): Getting the best of both worlds. J Comp Psychol. 2020;134(1):52-70. doi: 10.1037/com0000188.

17. Iwanicki S, Lehmann J. Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). J Comp Psychol. 2015;129(3):205-17. doi: 10.1037/a0039318.

18. Gosling SD, Graybeal A. Tree thinking: A new paradigm for integrating comparative data in psychology. J Gen Psychol. 2007;134:259-77. doi: 10.3200/GENP.134.2.259-278.

19. Harvey PH, Pagel MD. The comparative method in evolutionary biology. Oxford, England: Oxford University Press; 1991.

20. Gorsuch RL. Factor analysis. 2nd ed. Hillsdale, NJ: Lawrence Erlbaum Associates; 1983.

21. Araya-Ajoy YG, Dingemanse NJ. Characterizing behavioural 'characters': an evolutionary framework. P R Soc B. 2014;281(1776). doi: 10.1098/Rspb.2013.2645.

22. McCrae RR, John OP. An introduction to the Five-Factor Model and its applications. J Pers. 1992;60:175-215. doi: 10.1111/j.1467-6494.1992.tb00970.x.

23. Digman JM. Personality structure: Emergence of the Five-Factor Model. Annu Rev Psychol. 1990;41:417-40. doi: 10.1146/annurev.ps.41.020190.002221.

24. Adams MJ, Majolo B, Ostner J, Schuelke O, De Marco A, Thierry B, et al. Personality structure and social style in macaques. J Pers Soc Psychol. 2015;109(2):338-53. doi: 10.1037/pspp0000041.

25. Weiss A, Staes N, Pereboom JJM, Inoue-Murayama M, Stevens JMG, Eens M. Personality in bonobos. Psychol Sci. 2015;26(9):1430-9. doi: 10.1177/0956797615589933.

26. Wilson VAD, Inoue-Murayama M, Weiss A. A comparison of personality in the common and bolivian squirrel monkey (*Saimiri sciureus* and *Saimiri boliviensis*). J Comp Psychol. 2018;132(1):24-39. doi: 10.1037/com0000093.

27. Robinson LM, Morton FB, Gartner MC, Widness J, Paukner A, Essler JL, et al. Divergent personality structures of brown and white-faced capuchins. J Comp Psychol. 2016;130(4):305-12. doi: 10.1037/com0000037.

28. Morton FB, Lee PC, Buchanan-Smith HM, Brosnan SF, Thierry B, Paukner A, et al. Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). J Comp Psychol. 2013;127:282-98. doi: 10.1037/a0031723.

29. Fernández-Bolaños M, Delval I, de Oliveira RS, Izar P. Assessing the personality structure of wild capuchin monkeys (*Sapajus xanthosternos*) using trait rating and behavioral coding. J Comp Psychol. 2020;134(3):349-60. doi: 10.1037/com0000219.

30. Masilkova M, Šlipogor V, Weiss A, Konečná M. Comparative assessment of behaviorally derived personality structures in golden-handed tamarins (*Saguinus midas*), cotton-top tamarins (*Saguinus oedipus*), and common marmosets (*Callithrix jacchus*). J Comp Psychol. 2020;Advance online publication. doi: 10.1037/com0000226.

31. Koski SE, Buchanan-Smith H, Ash H, Burkart J, Bugnyar T, Weiss A. Common marmoset (*Callithrix jacchus*) personality. J Comp Psychol. 2017;131(4):326-36. doi: 10.1037/com0000089.

32. Yokoyama C, Onoe H. Molecular brain imaging of personality traits in nonhuman primates: A study of the common marmoset. In: Inoue-Murayama M, Kawamura S, Weiss A, editors. From Genes to Animal Behavior: Social Structures, Personalities, Communication by Color. Tokyo: Springer Japan; 2011. p. 389-406.

33. Weiss A. Personality traits: A view from the animal kingdom. J Pers. 2017. doi: 10.1111/jopy.12310.

34. Delgado MM, Sulloway FJ. Attributes of conscientiousness throughout the animal kingdom: An empirical and evolutionary overview. Psychol Bull. 2017;143(8):823-67. doi: 10.1037/bul0000107.

35. MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, et al. The evolution of self-control. Proc Natl Acad Sci U S A. 2014;111(20):E2140-E8. doi: 10.1073/pnas.1323533111.

36. McCrae RR, Terracciano A, 78 Members of the Personality Profiles of Cultures Project. Universal features of personality traits from the observer's perspective: Data from 50 cultures. J Pers Soc Psychol. 2005;88(3):547-61. doi: 10.1037/0022-3514.88.3.547. PubMed PMID: ISI:000227310400009.

37. Weiss A, King JE, Hopkins WD. A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological parks and Yerkes National Primate Research Center. American Journal of Primatology. 2007;69(11):1264-77. doi: 10.1002/ajp.20428.

38. King JE, Weiss A, Farmer KH. A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. Journal of Personality. 2005;73(2):389-410. doi: 10.1111/j.1467-6494.2005.00313.x.

39. King JE, Figueredo AJ. The Five-Factor Model plus Dominance in chimpanzee personality. J Res Pers. 1997;31(2):257-71. doi: 10.1006/jrpe.1997.2179.

40. Weiss A, Inoue-Murayama M, Hong K-W, Inoue E, Udono S, Ochiai T, et al. Assessing chimpanzee personality and subjective well-being in Japan. American Journal of Primatology. 2009;71(4):283-92. doi: 10.1002/ajp.20649.

41. Freeman HD, Brosnan SF, Hopper LM, Lambeth SP, Schapiro SJ, Gosling SD. Developing a comprehensive and comparative questionnaire for measuring personality in

chimpanzees using a simultaneous top-down/bottom-up design. Am J Primatol. 2013;75(10):1042-53. doi: 10.1002/ajp.22168.

42. Dutton DM. Subjective assessment of chimpanzee (*Pan troglodytes*) personality: Reliability and stability of trait ratings. Primates. 2008;49(4):253-9. doi: 10.1007/s10329-008-0094-1.

43. Shrout PE, Fleiss JL. Intraclass correlations: Uses in assessing rater reliability. Psychol Bull. 1979;86(2):420-8. doi: 10.1037/0033-2909.86.2.420.

44. Šlipogor V, Massen JJM, Schiel N, Souto A, Bugnyar T. Temporal consistency and ecological validity of personality structure in common marmosets (*Callithrix jacchus*): A unifying field and laboratory approach. Am J Primatol. 2021;83(2). doi: 10.1002/ajp.23229.

45. DeNeve KM, Cooper H. The happy personality: A meta-analysis of 137 personality traits and subjective well-being. Psychological Bulletin. 1998;124(2):197-229. doi: 10.1037/0033-2909.124.2.197.

46. Steel P, Schmidt J, Shultz J. Refining the relationship between personality and subjective well-being. Psychol Bull. 2008;134(1):138-61. doi: 10.1037/0033-2909.134.1.138.

47. King JE, Landau VI. Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? Journal of Research in Personality. 2003;37(1):1-15. doi: 10.1016/S0092-6566(02)00527-5.

48. Robinson LM, Altschul D, Wallace E, Úbeda Y, Llorente M, Machanda Z, et al. Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. Appl Anim Behav Sci. 2017;191:90-7. doi: 10.1016/j.applanim.2017.02.008.

49. Weiss A, King JE, Perkins L. Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). J Pers Soc Psychol. 2006;90(3):501-11. doi: 10.1037/0022-3514.90.3.501.

50. Weiss A, Adams MJ, Widdig A, Gerald MS. Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. J Comp Psychol. 2011;125(1):72-83. doi: 10.1037/a0021187.

51. Robinson LM, Waran NK, Leach MC, Morton FB, Paukner A, Lonsdorf E, et al. Happiness is positive welfare in brown capuchins (*Sapajus apella*). Appl Anim Behav Sci. 2016;181:145-51. doi: 10.1016/j.applanim.2016.05.029. PubMed PMID: WOS:000381171300019.

52. Wilt J, Revelle W. Extraversion. In: Widiger TA, editor. The Oxford Handbook of the Five Factor Model. New York: Oxford University Press; 2017. p. 57-82.

53. Tackett JL, Lahey BB. Neuroticism. In: Widiger TA, editor. The Oxford Handbook of the Five Factor Model. New York: Oxford University Press; 2017. p. 39-56.

54. Staes N, Sherwood CC, Freeman H, Brosnan SF, Schapiro SJ, Hopkins WD, et al. Serotonin Receptor 1A Variation Is Associated with Anxiety and Agonistic Behavior in Chimpanzees. Mol Biol Evol. 2019;36(7):1418-29. doi: 10.1093/molbev/msz061.

55. Hayashi T, Hou Y, Glasser MF, Autio JA, Knoblauch K, Inoue-Murayama M, et al. The nonhuman primate neuroimaging and neuroanatomy project. Neuroimage. 2021;229:117726. doi: https://doi.org/10.1016/j.neuroimage.2021.117726.

56. Weiss A. Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire. In: Vonk J, Weiss A, Kuczaj S, editors. Personality in Nonhuman Animals. Cham, Switzerland: Springer; 2017. p. 19-38.

57. Goldberg LR. An alternative "description of personality": the Big-Five factor structure. Journal of Personality and Social Psychology. 1990;59(6):1216-29. doi: 10.1037/0022-3514.59.6.1216. PubMed PMID: 2283588.

58. McCrae RR, Costa PT, Jr. Updating Norman's “adequate taxonomy”: Intelligence and personality dimensions in natural language and in questionnaires. J Pers Soc Psychol. 1985;49(3):710-21. doi: 10.1037/0022-3514.49.3.710.

59. Costa PT, Jr., McCrae RR. Revised NEO Personality Inventory (NEO-PI-R) and NEO Five-Factor Inventory (NEO-FFI) professional manual. Odessa, FL: Psychological Assessment Resources; 1992.

60. Diener E, Suh EM, Lucas RE, Smith HL. Subjective well-being: Three decades of progress. Psychological Bulletin. 1999;125(2):276-302. doi: 10.1037/0033-2909.125.2.276.

61. Diener E, Emmons RA. The independence of positive and negative affect. J Pers Soc Psychol. 1984;47(5):1105-17. doi: 10.1037//0022-3514.47.5.1105.

62. Pavot W, Diener E, Colvin CR, Sandvik E. Further validation of the Satisfaction with Life Scale - Evidence for the cross-method convergence of well-being measures. Journal of Personality Assessment. 1991;57(1):149-61. doi: 10.1207/s15327752jpa5701_17.

63. Campbell A. The sense of well-being in America: Recent patterns and trends. New York: McGraw-Hill; 1981.

64. Cantor N, Sanderson CA. Life task participation and well-being: The importance of taking part in daily life. In: Kahneman D, Diener E, Schwarz N, editors. Well-being: The foundations of hedonic psychology. New York: Russell Sage Foundation; 1999. p. 230-43.

65. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2020.

66. Revelle W. psych: Procedures for psychological, psychometric, and personality research. 1.9.12 ed. Evanston, IL: Northwestern University; 2019.

67. Navarro-Gonzalez D, Lorenzo-Seva U. EFA.MRFA: Dimensionality assessment using minimum rank factor analysis. 1.0.9 ed2020.

68. de Winter JCF, Dodou D, Wieringa PA. Exploratory factor analysis with small sample sizes. Multivariate Behavioral Research. 2009;44(2):147-81. doi: 10.1080/00273170902794206.

69. MacCallum RC, Widaman KF, Zhang S, Hong S. Sample size in factor analysis. Psychological Methods. 1999;4(1):84-99. doi: 10.1037/1082-989X.4.1.84.

70. Mundfrom DJ, Shaw DG, Ke TL. Minimum sample size recommendations for conducting factor analyses. International Journal of Testing. 2005;5(2):159-68. doi: 10.1207/s15327574ijt0502_4.

71. Horn JL. A rationale and test for the number of factors in factor analysis. Psychometrika. 1965;30:179-85. doi: 10.1007/BF02289447.

72. Auerswald M, Moshagen M. How to determine the number of factors to retain in exploratory factor analysis: a comparison of extraction methods under realistic conditions. Psychol Methods. 2019;24(4):468-91. doi: 10.1037/met0000200.

73. Schwarz G. Estimating the dimension of a model. Annals of Statistics. 1978;6(2):461-4. doi: 10.1214/aos/1176344136.

74. Ceulemans E, Kiers HAL. Selecting among three-mode principal component models of different types and complexities: A numerical convex hull based method. Br J Math Stat Psychol. 2006;59(1):133-50. doi: 10.1348/000711005X64817.

75. Lorenzo-Seva U, Timmerman ME, Kiers HA. The Hull method for selecting the number of common factors. Multivar Behav Res. 2011;46(2):340-64. doi: 10.1080/00273171.2011.564527.

76. Wainer H. Estimating coefficients in linear models: It don't make no nevermind. Psychol Bull. 1976;83:213-7.

77. Holm S. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics. 1979;6(2):65-70.

78. Costa PT, Jr., McCrae RR. Manual supplement for the NEO-4. Odessa, FL: Psychological Assessment Resources; 1998.

79. Bäckström M, Björklund F, Larsson MR. Five-factor inventories have a major general factor related to social desirability which can be reduced by framing items neutrally. J Res Pers. 2009;43(3):335-44.

80. Freeman HD, Gosling SD. Personality in nonhuman primates: A review and evaluation of past research. Am J Primatol. 2010;72(8):653-71. doi: 10.1002/ajp.20833.

81. Costa PT, Jr., McCrae RR. Cross-sectional studies of personality in a national sample: I. Development and validation of survey measures. Psychology and Aging. 1986;1(2):140-3. doi: 10.1037/0882-7974.1.2.140.

82. Digman JM. Higher-order factors of the Big Five. J Pers Soc Psychol. 1997;73(6):1246-56. doi: 10.1037/0022-3514.73.6.1246.

83. Musek J. A general factor of personality: Evidence for the Big One in the Five-Factor Model. J Res Pers. 2007;41(6):1213–33. doi: 10.1016/j.jrp.2007.02.003.

84. Revelle W, Wilt J. The general factor of personality: A general critique. J Res Pers. 2013;47(5):493-504. doi: 10.1016/j.jrp.2013.04.012.

85. Ferguson E, Chamorro-Premuzic T, Pickering A, Weiss A. Five into one doesn't go: A critique of the General Factor of Personality. In: Chamorro-Premuzic T, von Stumm S, Furnham A, editors. The Wiley-Blackwell Handbook of Individual Differences. West Sussex, UK: Wiley-Blackwell; 2011. p. 162-86.

86. Mutch C. Higher-order factors of the Big Five model of personality: A reanalysis of Digman (1997). Psychol Rep. 2005;96(1):167-77. doi: 10.2466/pr0.96.1.167-177.

87. Weiss A, Bates TC, Luciano M. Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. Psychol Sci. 2008;19:205-10. doi: 10.1111/j.1467-9280.2008.02068.x.

88. Weiss A, Baselmans BML, Hofer E, Yang J, Okbay A, Lind PA, et al. Personality polygenes, positive affect, and life satisfaction. Twin Res Hum Genet. 2016;19(5):407-17. doi: 10.1017/thg.2016.65.

89. Hahn E, Gottschling J, König CJ, Spinath FM. The heritability of job satisfaction reconsidered: only unique environmental influences beyond personality. Journal of Business and Psychology. 2016;31(2):217-31. doi: 10.1007/s10869-015-9413-x.

90. Hahn E, Johnson W, Spinath FM. Beyond the heritability of life satisfaction – The roles of personality and twin-specific influences. Journal of Research in Personality. 2013;47(6):757-67. doi: 0.1016/j.jrp.2013.07.003.

91. Adams MJ, King JE, Weiss A. The majority of genetic variation in orangutan personality and subjective-well being is nonadditive. Behav Genet. 2012;42:675-86. doi: 10.1007/s10519-012-9537-y.

92. Weiss A, King JE, Enns RM. Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). J Pers Soc Psychol. 2002;83:1141-9. doi: 10.1037//0022-3514.83.5.1141.

93. Munafò MR, Freimer NB, Ng W, Ophoff R, Veijola J, Miettunen J, et al. 5-HTTLPR genotype and anxiety-related personality traits: A meta-analysis and new data. Am J Med Genet B Neuropsychiatr Genet. 2009;150B(2):271-81. doi: 10.1002/ajmg.b.30808.