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4 **Common Marmoset (*Callithrix jacchus*) Personality**

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30 **Abstract**

31 Increasing evidence suggests that personality structure differs between species, but the
32 evolutionary reasons for this variation are not fully understood. We built on earlier research
33 on New World monkeys to further elucidate the evolution of personality structure in
34 primates. We therefore examined personality in 100 family-reared adult common marmosets
35 (*Callithrix jacchus*) from three colonies on a 60-item questionnaire. Principal components
36 analyses revealed five domains that were largely similar to those found in a previous study on
37 captive, ex-pet, or formerly laboratory-housed marmosets that were housed in a sanctuary.
38 The interrater reliabilities of domain scores were consistent with the interrater reliabilities of
39 domain scores found in other species, including humans. Four domains---conscientiousness,
40 agreeableness, inquisitiveness, and assertiveness---resembled personality domains identified
41 in other nonhuman primates. The remaining domain, patience, was specific to common
42 marmosets. We used linear models to test for sex and age differences in the personality
43 domains. Males were lower than females in patience, and this difference was smaller in older
44 marmosets. Older marmosets were lower in inquisitiveness. Finally, older males and younger
45 females had higher scores in agreeableness than younger males and older females. These
46 findings suggest that cooperative breeding may have promoted the evolution of social
47 cognition and influenced the structure of marmoset prosocial personality characteristics.

48

49 Keywords: marmoset, personality, primates, cooperative breeding

50 **Introduction**

51 Individuals of a species can be described by personality traits associated with
52 dispersal, survival, offspring survival, cooperation, and cognitive ability (Sih & Del Giudice,
53 2012; Wolf & Weissing, 2012; Smith & Blumstein, 2008). Correlations among these traits
54 are known as behavioral syndromes (Sih et al., 2004), evolutionary characters (Araya-Ajoy &
55 Dingemanse, 2013), or personality components, factors, dimensions, or domains (Weiss &
56 Adams, 2013). These correlations suggest that personality traits are manifestations of one or
57 more underlying, latent processes. The species-specific personality structures defined by
58 traits are then products of natural selection and mechanistic links that maintain the
59 associations at species or population levels (e.g. Garamszegi et al., 2012; Dochtermann &
60 Dingemanse, 2013). Comparing personality structures across species can reveal ecological
61 and phylogenetic patterns of trait associations that hint at the functional bases of the traits
62 (Gosling & Graybeal, 2007; Weiss & Adams, 2013).

63 Unfortunately, many animal personality studies focus on a small number of traits,
64 such as aggression and boldness, and so an understanding of personality structure evolution is
65 limited (Koski, 2014). Research on nonhuman primate personality bucks this trend (e.g.,
66 Koski, 2011a; Massen et al., 2013; Neumann et al., 2013; Konečná et al., 2008, 2012; Morton
67 et al., 2013; Garai et al., 2016; Weiss et al., 2006, 2007, 2009, 2011, 2012a,b, 2015; Eckardt
68 et al., 2015; Neumann et al., 2013; Adams et al., 2015; Uher & Visalberghi, 2016).

69 Differences among species that are assessed on overlapping sets of traits are informative with
70 respect to the evolution of personality structure (Gosling & Graybeal, 2007; Weiss & Adams,
71 2013). For example, in macaque species (Weiss et al., 2011; Adams et al., 2015), brown
72 capuchin monkeys (Morton et al., 2013), and in mountain gorillas (Eckardt et al., 2015), traits
73 related to gregariousness and sociopositive behavior define one factor, whereas they define
74 two factors in chimpanzees (King & Figueredo, 1997), orangutans (Weiss et al., 2006), and in

75 humans (Costa & McCrae, 1992). On the other hand, in bonobos, most traits related to
76 gregariousness and sociopositive behavior define a single factor, but a few related to
77 gregariousness define a small additional factor (Weiss et al., 2015). These findings suggest
78 that traits related to sociopositive behavior and gregariousness were fused in the common
79 ancestor of platyrrhines and catarrhines, that the pattern in orangutans, chimpanzees,
80 bonobos, and humans is derived, and that the bonobo pattern possibly represents a
81 transitional form, ancestral to African apes.

82 Personality studies of New World monkeys are a new direction for primate
83 personality research (see, however, Byrne & Suomi, 2002), and have largely focused on
84 capuchin monkeys (Morton et al., 2013; Manson & Perry, 2013; but see Santillan-Doherty et
85 al., 2010 for spider monkeys, and Iwanicki & Lehmann, 2015; Šlipogor et al., 2016; and
86 Koski & Burkart, 2015 for common marmosets). One reason for the burgeoning interest in
87 studying New World monkey personality is that doing so helps to identify evolutionary
88 scenarios that led to the emergence of personality structures. For example, by studying
89 common marmosets, a cooperatively breeding species, one can determine whether and how
90 cooperative breeding might influence the evolution of personality structure. Among
91 cooperatively breeding species, some adults forgo breeding for several years and remain in
92 the natal group to help carry, groom, and provision their infant siblings (Digby, 2007;
93 Yamamoto et al., 2014). In primates, cooperative breeding has been associated with
94 behavioral and cognitive characteristics, including increased social tolerance and proactive
95 prosociality (Burkart et al., 2014; Schaffner & Caine, 2000), which facilitate performance in
96 socio-cognitive tasks (Burkart & van Schaik, 2010, 2016). For example, like great apes and
97 brown capuchin monkeys (Brosnan & de Waal, 2014; Anderson et al., 2013), common
98 marmosets appear to be able to detect fairness in reciprocal third-party acts (Kawai et al.,
99 2014). Moreover, although high reproductive skew leads to competition and occasionally

100 escalated aggression in Callitrichids (Schaffner & Caine, 2000; Digby et al., 2007;
101 Yamamoto et al., 2014), aggression and conflict among individuals is infrequent and tends to
102 not damage social relationships (Schaffner et al., 2005).

103 We assessed personality in common marmosets (*Callithrix jacchus*). Ours is not the
104 first study of personality in a cooperatively breeding primate species. For one, humans are
105 believed to be a cooperatively breeding species (Hrdy, 2009; Kramer, 2015), and have been
106 the focus of the vast majority of personality research. One feature of human personality
107 models, such as the Five-Factor Model (Costa & McCrae, 1992), is the absence of an
108 independent personality domain related to competitive prowess. Instead, traits related to
109 competitive prowess are found in the Five-Factor domains of extraversion, agreeableness,
110 and neuroticism (Costa & McCrae, 1992; cf. Gosling & John, 1999). In contrast, traits related
111 to assertiveness and competitive prowess form an independent personality domain in
112 humans' closest living nonhuman relatives, chimpanzees (King & Figueredo, 1997) and
113 bonobos (Weiss et al., 2015). Another feature of human personality is that agreeableness is
114 defined by positive associations with traits related to helpfulness and prosociality and
115 negative associations with traits related to aggression and competitiveness (Costa & McCrae,
116 1992). Its counterparts in chimpanzees (King & Figueredo, 1997; Freeman et al., 2013),
117 bonobos (Weiss et al., 2015; Garai et al., 2016), orangutans (Weiss et al., 2006), and gorillas
118 (Gold & Maple, 1994), on the other hand, are defined only by traits related to sociopositivity.
119 These differences between the personality structures of humans and great apes suggest that a
120 combination of high assertiveness and aggressiveness may be disadvantageous in cooperative
121 breeders, and that combinations of sociopositive tendencies and low aggressiveness may be
122 advantageous in cooperative breeders.

123 A recent study of common marmosets lent support to the possibility that certain
124 combinations of traits may be selected for or against specifically due to cooperative breeding,

125 while other combinations may be due to a more general primate heritage. Iwanicki and
126 Lehmann (2015) used ratings and behavioral observations to study marmoset personality. The
127 ratings revealed an extraversion domain that resembled domains labeled confidence,
128 dominance, or assertiveness that have been found in other nonhuman primate species
129 (Freeman & Gosling, 2010), and conscientiousness and openness domains that resembled
130 like-named domains in chimpanzees (King & Figueredo, 1997), humans (Costa & McCrae,
131 1992; Digman, 1990), and bonobos (Weiss et al., 2015). Additionally, they found an
132 agreeableness domain that resembled its human counterpart, as it included positive loadings
133 of prosocial traits and negative loadings of aggression. Moreover, Iwanicki and Lehmann's
134 behavioral observations that revealed agreeableness, neuroticism, and perceptual sensitivity
135 domains, showed that aggressive behavior was negatively correlated with agreeableness.

136 The identification of a conscientiousness domain in common marmosets is intriguing.
137 To date, conscientiousness and similar domains, such as attentiveness, have only been
138 identified in humans (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997),
139 bonobos (Weiss et al., 2015), and brown capuchin monkeys (Morton et al. 2013), all known
140 for their advanced cognitive abilities. This finding is thus consistent with the hypothesis that
141 cooperative breeding favored an increase of marmosets' cognitive skills, at least in the social
142 domain, perhaps by selecting for increased social attentiveness (Burkart & van Schaik, 2016).

143 Our main aim was to further examine personality structure in common marmosets. To
144 achieve this, we tested whether ratings of common marmosets on a broad questionnaire
145 would yield evidence for domains resembling those uncovered by Iwanicki and Lehmann's
146 (2015) study. Our sample differed from that of Iwanicki and Lehmann. The common
147 marmosets in our sample were adults who had been parent-reared. Iwanicki and Lehmann's
148 sample were former pets or former laboratory animals that were living in a sanctuary, and,
149 furthermore, many had been hand- or foster-reared (35/63), and the sample included juveniles

150 (5/63) as well as adults. These differences are important. Pet monkeys often have abnormal
151 rearing histories and hand-rearing is known to affect behavior (Soulsbury et al., 2009).
152 Moreover, the curiosity and playfulness of juveniles may skew the personality profiles. As
153 such, this study will show the degree to which the personality domains found by Iwanicki and
154 Lehmann are not specific to their sample.

155 Our second aim was to examine sex- and age-differences in personality. Sex
156 differences in mean trait level or syndrome structure are found in many species (e.g. Schuett
157 & Dall, 2009; Michelangeli et al., 2016; Fresnau et al., 2014), including non-human primates
158 (King et al., 2008) and humans (McCrae et al., 2005). Previous research has not found any
159 differences between male and female common marmosets in experimentally assessed
160 personality traits (Koski & Burkart, 2015; Šlipogor et al., 2016). However, females of this
161 species have been described to be more responsive in contexts involving food (Box et al.,
162 1997) and to explore novel objects in a foraging paradigm faster and more efficiently than
163 males (Yamamoto et al., 2004). Moreover, the patterns of prosocial behavior differ between
164 male and female helpers: in males, but not females, prosociality is higher in older, more
165 experienced individuals (Burkart, 2015). This suggests that the previous studies may have
166 failed to capture sex differences or that these differences are not reflected in repeatable
167 personality traits.

168 **Methods**

169 **Subjects**

170 The subjects were 100 common marmosets that ranged in age from 2 to 14 years ($M =$
171 6.36 , $SD = 3.05$). Of these subjects, 51 were males that ranged in age from 2 to 14 years ($M =$
172 6.02 , $SD = 3.03$) and 49 females that ranged in age from 2 to 14 years ($M = 6.71$, $SD = 3.06$).

173 **Housing and Husbandry**

174 Subjects were housed at Dstl. Salisbury, United Kingdom, the University of Vienna,

175 Department of Cognitive Biology, Austria, and the University of Zürich, Anthropological
176 Institute Primate Research Station, Switzerland. All subjects were born, reared, and housed in
177 social groups. The study was approved after review by the Stirling University Psychology
178 Ethics Committee and complies with legal and ethical requirements in the UK.

179 **United Kingdom.** This subsample included 51 subjects (25 males, 26 females) that
180 were born at the facility. Twins and singletons were reared in their natal group, while triplets
181 received supplementary feeding sessions for 2h twice per day for the first 8 weeks of life,
182 spending the remainder of their time with the group. This practice has been shown to have
183 little to no effect on neophobia, anhedonia, nor performance on cognitive bias tasks (Ash &
184 Buchanan-Smith, 2016). Breeding marmosets (in groups of 2-10 individuals) were housed in
185 one of three family rooms, each containing 8-12 groups of marmosets, in cages measuring
186 1.50m × 1.20m × 2.2m. Mixed-sex pairs were housed in one of three stock rooms, each
187 containing 10-18 pairs, in wire cages measuring 1.0m × 0.60m × 1.80m. Cages were
188 furnished with a nestbox, branches and logs, ropes, platforms, and perches, as well as
189 suspended toys, including ladders, buckets, tea towels, hanging baskets, and food devices.
190 Each family/pair also had access to a veranda. Temperature was thermostatically controlled at
191 23-24°C and humidity at 55% (range 45-65%), with lighting provided on a 12:12 h light:dark
192 cycle. All marmosets had *ad libitum* access to water. Primate pellets were given between
193 08:00-09:00, and a variety of fruit was provided between 13:30 and 14:30. Malt loaf, egg,
194 rusk, dates, peanuts, and bread were provided on alternate days. Gum arabic and banana
195 milkshake were both given twice a week. Mealworms and forage mix were also scattered
196 twice a week. Wet shavings were picked up each week, with a full cage clean every 8 weeks
197 in breeding rooms, and every 4 weeks in stock rooms. Each marmoset was weighed once a
198 month. New enrichment was provided once a week, including food parcels, boxes, and
199 mealworm feeders. Each family had access to a 'play cage' for 3 days each, while stock pairs

200 were provided with a 'bug box'. Every animal was syringe trained once a month, and human
201 socialization was carried out regularly. Housing and husbandry was in accordance with
202 relevant national legislation.

203 **The University of Vienna.** This subsample included 21 subjects (12 males, 9
204 females) housed in 3 social groups consisting of a breeding pair and their offspring. All
205 individuals were born in captivity and housed in their family groups. Every family group
206 lived in a wire mesh indoor enclosure connected with a passageway system of tunnels with
207 moveable doors to an outdoor enclosure (2.50 × 2.50 × 2.50 m indoors; 2.50 × 2.50 × 2.50 m
208 outdoors). All enclosures had enrichment objects (branches, ropes, platforms, blankets,
209 sleeping boxes, and tunnels), with wood shavings as floor bedding. An opaque plastic barrier
210 prevented visual contact between adjacent family groups, while the groups remained in
211 acoustic and olfactory contact. Daylight was the main source of lighting, but, because of the
212 low amount of natural light in winter, lamps were maintained on a stable 12:12h light:dark
213 cycle. In addition, one heating lamp per family group was always available on top of each
214 enclosure. Temperature was maintained at 24-26°C and humidity was kept at 40-60%. All
215 marmosets had *ad libitum* access to water and were fed every day at noon with a selection of
216 marmoset pellets, fruits, vegetables, grains, milk products, marmoset jelly, protein and
217 vitamin supplements, and insects. Several times per week monkeys received either a foraging
218 box with mealworms or marmoset gum on the branches. The housing conditions were in
219 accordance with Austrian legislation and the European Association of Zoos and Aquaria
220 husbandry guidelines for Callitrichidae.

221 **The University of Zurich.** This subsample included 28 subjects (14 males, 14
222 females) housed in 6 social groups consisting of a breeding pair and 1 to 4 adult offspring.
223 All individuals were born in the facility and reared by their natural parents in family groups.
224 Subjects were housed in large indoor-outdoor enclosures comprising one or several basic

225 units (2m × 1m × 2m indoors; 2.75m × 1.70m or 2.50m × 2.40m outdoors). The enclosures
226 included ropes, branches, and other enrichment devices, and were covered with natural
227 bedding material. Both indoor and outdoor enclosures had heating lamps. Subjects had almost
228 continuously free access to both enclosures, except during the necessary husbandry routines,
229 at outside temperature < 5°C, and at night. They were fed three times a day with a diet of
230 carbohydrate-rich mush enriched with vitamins and minerals, fruit, vegetables, gum, insects,
231 boiled egg, and nuts. Water was available *ad libitum*. The housing conditions were in
232 accordance with Swiss legislation and the European Association of Zoos and Aquaria
233 husbandry guidelines for Callitrichidae.

234 **Ratings**

235 Eighteen researchers or animal keepers (6 in the United Kingdom, 5 in Austria, and 7
236 in Switzerland) with one to thirteen years of familiarity with the subjects rated the marmosets
237 on a personality questionnaire. In the United Kingdom and in Switzerland, each subject was
238 rated by 2 people, and in Austria, each subject was rated by 5 people.

239 The personality questionnaire consisted of 60 items. Each item consisted of an
240 adjective paired with a brief definition that set it in the context of marmoset behavior (see
241 Table S1). For example, the item ‘helpful’ was defined as “Monkey is willing to assist,
242 accommodate to, or cooperate with other monkeys.” Because of a clerical error, one item
243 (unemotional) was included twice. For our analyses, we omitted ratings on the second
244 occurrence of this item. Of the 59 items, 47 were taken from the Hominoid Personality
245 Questionnaire^[1] (Weiss et al., 2009), which, together with its predecessors (King &
246 Figueredo, 1997; Weiss et al., 2006), and offshoots (Konečná et al., 2008, 2012; Iwanicki &
247 Lehman, 2015), has been used to assess personality in several nonhuman primate species
248 (Weiss, 2017). A further 12 items were taken from a questionnaire used to study Hanuman
249 langurs (Konečná et al., 2008) and Barbary macaque personality (Konečná et al., 2012).

250 The instructions on the questionnaire asked raters to judge subjects based on their
251 overall impressions of that monkey, to assign a rating of 1 (absence of a trait) to 7 (extreme
252 presence of a trait) for each trait, and to not discuss their ratings with other raters. To
253 minimize misunderstandings by German-speaking raters in Austria and Switzerland, we
254 translated the questionnaire into German and the raters had the forms available in both
255 languages at all times.

256 **Analyses**

257 We used two intraclass correlations (*ICCs*) to determine how consistent raters were in
258 their ratings of each item. The first of these, *ICC(3,1)*, indicates the reliability of ratings by
259 any single judge. The second, *ICC(3,k)*, measures the reliability of the mean rating of *k*
260 judges (Shrout & Fleiss, 1979).

261 As in previous studies (e.g. Morton et al., 2013), for reliable items, we used principal
262 components analysis to examine the personality structure of the mean ratings across all raters.
263 To determine how many components to extract, we inspected the scree plot and used parallel
264 analysis (Horn, 1965). We then subjected our components to an orthogonal (varimax) and
265 oblique (promax) rotation. If the varimax and promax rotations yielded similar components
266 and the interfactor correlations were modest, we interpreted the varimax rotation. If the two
267 rotations yielded different components or the inter-factor correlations were moderate to large,
268 we interpreted the promax rotation.

269 We then computed unit-weighted component scores (Gorsuch, 1984) to be used in our
270 final analyses. This involved our assigning weights of 0 to component loadings less than |0.4|,
271 weights of +1 to component loadings greater than or equal to 0.4, and weights of -1 to
272 component loadings that were less than or equal to -0.4. In the event that an item had multiple
273 loadings greater than or equal to |0.4| we assigned the weight to the component on which the
274 item had the highest absolute loading. We then transformed these raw unit-weighted scores

275 into z-scores (mean = 0, SD = 1). In the first of the two final analyses we ascertained the
276 interrater reliabilities of the domains, again using $ICC(3,1)$ and $ICC(3,k)$. In the second of
277 these analyses we used five multiple regressions (one for each personality domain) to test for
278 sex and age effects. Here the component score was the dependent variable and the
279 independent variables were sex (-1 for females, +1 for males), age (mean centered), and a
280 product term representing the sex \times age interaction.

281 We conducted all analyses using version 3.3.2 of R (R Core Team, 2016). Parallel
282 analysis and principal components analysis were conducted using the `fa.parallel` and `principal`
283 functions from the `psych` package (Revelle, 2015), respectively. Multiple regressions were
284 conducted using the `lm` function.

285 Results

286 Out of Range and Missing Data

287 One rater of one marmoset in Austria assigned a “0” to a single item and 5 raters of 24
288 marmosets in the United Kingdom assigned a “0” to up to 12 ratings, each. Combined, across
289 25 marmosets, 90 items were assigned a rating of “0”. We assigned a “1” to these ratings. In
290 addition, for the marmosets housed in the United Kingdom, one rater did not rate two
291 marmosets on a single trait, each, a second did not rate one marmoset on a single trait, and a
292 third did not rate three marmosets on a single trait, each, and one marmoset on two traits. For
293 the marmosets housed in Austria, one rater did not rate two marmosets on a single trait, each.
294 For the marmosets housed in Switzerland, one rater did not rate one marmosets on two traits.
295 In all 12 of these cases we substituted the mean value of the trait across all marmosets in the
296 study.

297 Item Interrater Reliabilities

298 The interrater reliabilities for all the items are available in Table S2. The interrater
299 reliabilities of the items ‘manipulative’ and ‘conventional’ were below 0. $ICC(3,1)$ estimates

300 for the remaining items ranged from 0.01 for ‘popular’ to 0.37 for ‘gentle’, and the mean and
301 standard deviation of the $ICC(3,1)$ estimates for these items were 0.20 and 0.09, respectively.
302 The interrater reliabilities of single ratings were lower but within the range of those in studies
303 of humans and other species (Morton et al., 2013; Weiss et al., 2011, 2015; Möttus et al.,
304 2017) and considered as acceptable (e.g. Möttus et al., 2014). $ICC(3,k)$ estimates for the items
305 with reliabilities greater than 0 ranged from 0.03 for ‘popular’ to 0.60 for ‘gentle’ and the
306 mean and standard deviation of the $ICC(3,k)$ estimates for these items were 0.38 and 0.14,
307 respectively. Note, that $ICC(3,k)$ estimates are not typically compared between studies
308 because they will, in part, vary as a function of how many raters there were per subject
309 whereas $ICC(3,1)$ estimates do not.

310 **Personality Structure**

311 Parallel analysis and examination of the scree plot indicated that there were five
312 components with eigenvalues equal to 16.09, 8.04, 4.84, 4.13, and 2.71, which accounted for
313 63% of the variance. To be certain that the five-component solution was best we also
314 extracted six components (see Tables S3 and S4). The sixth component had an eigenvalue of
315 1.84. After applying a varimax rotation, only the items ‘selective’ and ‘stingy’ had unique,
316 salient loadings on that component (0.50 and 0.49, respectively). After applying a promax
317 rotation, only the items ‘selective’, ‘stingy’, and ‘alert’ had unique, salient loadings on that
318 component (0.53, 0.52, and -0.40, respectively). The sixth component was thus
319 uninterpretable and so we retained a five-component solution.

320 For the five-component solution, because there were only minor differences between
321 varimax and promax solutions (all congruence coefficients ≥ 0.97) and the absolute
322 correlations between components were modest (range = 0.03 to 0.39, $M = 0.13$, $SD = 0.12$),
323 we retained the varimax-rotated solution (see Table S5 for the promax-rotated solution and
324 the correlations between components). Finally, we compared the five varimax-rotated

325 components to five varimax-rotated factors (see Table S6). The component and factor
326 structures were virtually identical (all congruence coefficients ≥ 0.99).

327 The five varimax-rotated components are presented in Table 1. For ease of
328 interpretation, we reflected the first, third, and fifth components by multiplying loadings by -
329 1. The first component resembled conscientiousness domains found in common marmosets
330 (Iwanicki & Lehmann, 2015), chimpanzees (King & Figueredo, 1997; Weiss et al., 2007;
331 Weiss et al., 2009; King et al., 2005), and bonobos (Weiss et al., 2015), though it was broader
332 than the chimpanzee and bonobo conscientiousness domains as it also encompassed traits
333 related to play behavior. This component thus described differences in low antagonism, high
334 self-control, and low playfulness, and we therefore named it ‘conscientiousness’.

335 The second component described high levels of sociopositive and prosocial traits, and
336 thus was a mix of traits related to the extraversion and agreeableness domains in humans
337 (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et
338 al., 2006). Similar to the agreeableness domain found by Iwanicki and Lehmann (2015), this
339 component included negative loadings of socio-negative traits such as ‘aggressive’ and
340 ‘irritable’. Thus, it differed from bonobo agreeableness (Weiss et al., 2015), brown capuchin
341 monkey sociability (Morton et al., 2013), and the friendliness domain found in various
342 macaque species (Adams et al., 2015; Weiss et al., 2011). In light of these comparisons, we
343 named this component ‘agreeableness’.

344 The third component was defined by loadings on items related to assertiveness,
345 dominance, such as a positive loading of ‘dominant’ and a negative loading of ‘submissive’,
346 but also by negative loadings on traits related to anxiety, vulnerability, and vigilance, such as
347 ‘fearful’ and ‘cautious’. This component was thus similar to the extraversion domain found in
348 the previous study of marmosets (Iwanicki & Lehmann, 2015) and domains labeled
349 dominance, confidence, and assertiveness in other nonhuman primate species (Freeman &

350 Gosling, 2010). We thus named this component ‘assertiveness’.

351 The fourth component was characterized by items related to attentiveness in brown
352 capuchin monkeys (Morton et al., 2013) and in bonobos (Weiss et al., 2015). For example,
353 ‘patient’ had a positive loading on this component and ‘distractible’ had a negative loading
354 on this component. It also included positive loadings from items related to sociopositive
355 behaviors, such as ‘sensitive’ and ‘sympathetic’, and problem solving, such as ‘inventive’
356 and ‘intelligent’. This component is thus different from the domains identified by Iwanicki
357 and Lehmann (2015) and appears to not have been found in other nonhuman primates. We
358 tentatively named this component ‘patience’.

359 The fifth component was characterized by positive and negative loadings of traits
360 related to activity, such as ‘active’ and ‘lazy’, respectively, positive loadings on traits related
361 to exploratory behavior, such as ‘inquisitive’, a negative loading on ‘solitary’, and a positive
362 loading on a trait related to vigilance (‘alert’). It thus strongly resembled the openness
363 domain identified by Iwanicki and Lehmann (2015). It also resembles the orangutan
364 extraversion domain (Weiss et al., 2006), which was characterized by traits related to
365 gregariousness and exploratory behavior. We named this component ‘inquisitiveness’.

366 **Component Interrater Reliabilities**

367 The interrater reliabilities of individual ratings for conscientiousness, sociability,
368 assertiveness, patience, and inquisitiveness were 0.41, 0.44, 0.32, 0.39, and 0.26,
369 respectively, and thus comparable to those derived in humans (McCrae & Costa, 1987) and in
370 nonhuman primates (Weiss et al., 2011, 2015). The interrater reliabilities of mean ratings for
371 these components were 0.65, 0.68, 0.56, 0.63, and 0.48, respectively.

372 **Sex and Age Effects**

373 The effects of sex, age, and the sex \times age interaction are presented in Table 2. For
374 conscientiousness, males were lower than females, but this effect was negligible and not

375 significant. Moreover, older subjects were lower in conscientiousness, but this effect was not
376 significant. The sex \times age interaction was also not significant.

377 For agreeableness, males were slightly higher than females and older subjects were
378 higher in sociability, but neither of these effects was significant. There was a significant sex \times
379 age interaction: among males, older subjects were higher in agreeableness whereas among
380 females, younger individuals were higher in agreeableness ($b = 0.07$, 95% CI = 0.03, 0.01, p
381 = 0.029). However, given the number of statistical tests and the non-significant sex and age
382 effects, this effect may be a false positive and should be treated with caution.

383 For assertiveness, males and older subjects scored lower than females and younger
384 subjects, respectively, but neither of these effects were significant. The sex \times age interaction
385 was also not significant.

386 For patience, males scored significantly lower than females ($b = -0.30$, 95% CI = -
387 0.48, -0.11, $p = 0.002$). Although older subjects were lower in patience, the effect of age was
388 not significant. There was, however, a significant sex \times age interaction indicating that the
389 difference between males and females was smaller among older subjects ($b = 0.07$, 95% CI =
390 0.01, 0.14, $p = 0.020$).

391 For inquisitiveness, males and older subjects were lower, but only the effect of age
392 was significant ($b = -0.13$, 95% CI = -0.19, -0.07, $p < 0.001$). The sex \times age interaction was
393 not significant.

394 Discussion

395 We asked individuals familiar with 100 common marmosets to rate them on 59
396 personality traits. Their ratings revealed five domains---conscientiousness, agreeableness,
397 assertiveness, patience, and inquisitiveness---that resembled domains found in a previous
398 study of common marmosets (Iwanicki & Lehmann, 2015).

399 Conscientiousness resembled domains found in humans (Digman, 1990; Costa &

400 McCrae, 1992) and in cognitively advanced nonhuman primates, such as chimpanzees (King
401 & Figueredo, 1997), brown capuchin monkeys (Morton et al., 2013), and bonobos (Weiss et
402 al., 2015). As such, this finding supports Iwanicki and Lehmann's (2015) finding in
403 marmosets, and indicates that marmosets have relatively advanced cognitive skills.
404 Particularly social cognition is advanced in marmosets. It may be favored due to the need for
405 increased social attentiveness and tolerance, as cooperative breeding requires an ability to
406 coordinate cooperative actions and to pay attention to others' actions and needs (Burkart &
407 van Schaik, 2010, 2016).

408 Assertiveness resembled domains found in several nonhuman primate species
409 (Freeman & Gosling, 2010) and corroborated Iwanicki and Lehmann's (2015) earlier finding
410 of a personality domain related to dominance in common marmosets. This finding lends
411 further support to the notion that domains like dominance, confidence, or assertiveness are
412 universal features of personality in nonhuman primates (see, e.g., Freeman & Gosling, 2010).
413 Apparently, the association of traits related to assertiveness and boldness is not selected
414 against in marmosets. Thus, cooperative breeding has perhaps not been the main driver of the
415 human pattern, where traits associated with assertiveness are found within the extraversion,
416 agreeableness, and neuroticism domains.

417 Inquisitiveness captured an association of curiosity, activity, exploration, and
418 vigilance. It was thus like the openness domain in the study of marmosets by Iwanicki and
419 Lehmann (2015), and resembled the openness domain in brown capuchin monkeys (Morton
420 et al., 2013). Similar domains that capture the association of activity and exploratory
421 tendency have been identified in Old World monkeys, including vervet monkeys (McGuire et
422 al., 1994) and rhesus macaques (Weiss et al., 2011), and in great apes, including chimpanzees
423 (King & Figueredo, 1997; Weiss et al., 2007, 2009) and bonobos (Weiss et al. 2015). As
424 such, it is likely that this domain may also be a universal primate personality domain. In

425 contrast, we did not find anything resembling the perceptual sensitivity domain, which
426 captured activity, vigilance, and time spent foraging relative to feeding, that was identified
427 using behavioral data (Iwanicki & Lehmann, 2015). Interestingly, in the Iwanicki &
428 Lehmann's (2015) study the items vigilance and activity were captured by the openness
429 domain, as was the case in our study, but openness did not correlate with perceptual
430 sensitivity. This suggests that the behavioral measures of activity and vigilance are not
431 assessing the same constructs as are ratings of those items. Therefore, in the future studies it
432 would be useful to assess the criterion validity of the openness and vigilance related items
433 and behaviors (see below) and address the implication of such differences between the
434 methods.

435 Of the remaining domains, agreeableness encompassed mostly prosocial personality
436 characteristics and, negatively, loadings on traits related to aggression. This finding supports
437 further the similarity in marmoset and human agreeableness identified earlier by Iwanicki and
438 Lehmann (2015), and implies that sociopositive traits of gregariousness and prosociality
439 associated with low aggressiveness may be adaptive in cooperative breeders.

440 Finally, the patience domain appeared to be unique to common marmosets. It included
441 characteristics related to a socio-positive orientation, attentiveness, inventiveness, and focus.
442 The existence of this domain, then, suggests that there was selection for a positive correlation
443 between prosocial traits and traits related to persistence and cognitive performance. However,
444 the agreeableness domain also captured prosocial traits, thus, socio-positive and helpful
445 characteristics are not unidimensional in marmosets. One possibility is that the patience
446 domain is akin to the "helping syndrome", i.e., the positive association of repeatable
447 prosocial behaviors directed to offspring, found in mongooses (*Mungos mungo*) and meerkats
448 (*Suricata suricatta*). However, in marmosets, the prosocial characteristics in patience are not
449 those related to actual helping, which are found in agreeableness, but those related to

450 discerning others' needs and responding to them kindly.

451 Another possibility is that feeding ecology may have led to the emergence of a
452 patience domain. Feeding ecology has proven an important driver of behavioral and brain
453 evolution in nonhuman primates (e.g. DeCasien et al., 2017; MacLean et al., 2014). For
454 marmosets, one possibility is that the evolution of the patience domain was favored by gum
455 feeding, namely as gum is an embedded food source and takes time and effort to extract.
456 Such a foraging strategy may promote cognition and curiosity (Burkart et al, 2016; Schuppli
457 et al., 2016, Stevens et al. 2005). Extractive foraging is suggested to favor an association of
458 exploration tendency and persistence (Massen et al., 2013). In our study we found that,
459 although inquisitiveness and patience domains were not correlated (Table S5), two traits that
460 defined inquisitiveness, 'exploratory' and 'inquisitive', had strong loadings on patience, too.
461 Another possibility is that the patience domain emerged in response to insectivory. Flushing
462 out insects and capturing fast moving prey presumably requires inquisitiveness and patience,
463 respectively. To test which of these hypotheses is supported requires a phylogenetic analysis
464 of primate and non-primate species that differ in their socioecologies and feeding ecologies,
465 that have been assessed on a large number of traits. However, the proposed hypotheses need
466 not be mutually exclusive, as marmoset prosociality entails proactive food sharing (Burkart et
467 al., 2007, 2014), so both obtaining and provisioning food items may favor the positive
468 associations of traits found in the patience domain.

469 In sum, the present findings mostly resemble those in a previous study of common
470 marmosets (Iwanicki & Lehmann, 2015), despite the marmosets in the current study having
471 different rearing histories and being rated by a somewhat different and much longer
472 questionnaire. Although there were also differences in cage size and complexity in the current
473 study, which may affect behavior (Kitchen & Martin, 1995: common marmosets), it is
474 unlikely that the smaller cages of the UK colony influenced personality significantly, as these

475 were still relatively large, enriched enclosures allowing opportunities for natural behavior. As
476 such, this study supports the generalizability of personality structure in humans (McCrae et
477 al., 2005) and in chimpanzees (Dutton, 2008; King et al., 2005; Weiss et al., 2007, 2009;
478 Freeman et al., 2013) across different samples. We also found that cooperative breeding may
479 have led to a conscientiousness-like domain in common marmosets, which may be related to
480 cooperative breeding affecting the evolution of increased social attention and cognition.
481 Further, we hypothesize that cooperative breeding may have promoted an inverse association
482 between aggression and prosociality in humans, as we found a similar pattern in marmosets.
483 Finally, we hypothesize that cooperative breeding may have led to the emergence of a unique
484 patience domain in common marmosets. To test these hypotheses, further, comparative
485 studies of callitrichids and more generally, cooperatively breeding primates, are warranted. It
486 would be particularly beneficial if the studies would also include behavioral measures and
487 experiments to complement the questionnaires.

488 Iwanicki and Lehmann (2015) found evidence of agreement between behavioral and
489 rated measures, most strongly concerning rated agreeableness and the behavioral measures of
490 prosociality and aggression. In contrast, openness and assertiveness, which were obtained
491 from ratings, were not correlated with any behavioral measures, bar play and self-grooming.
492 Several studies on other primate species have assessed the construct validity of questionnaires
493 (Pederson et al., 2005; Morton et al., 2013; Konečná et al., 2012; Uher & Asendorpf, 2008;
494 Freeman et al., 2013), and the results are mixed with some, but not all, constructs showing
495 correlations between conceptually similar behavioral measures of the same animals.
496 Correspondence of rated components and measured behaviors tends to be better in studies on
497 ape personality (Eckardt et al., 2015; Pederson et al., 2005; Freeman et al., 2013). As has
498 been discussed elsewhere (e.g., Uher, 2008; Uher et al., 2008; Koski, 2011b), this may be
499 because the rating method depends on the degree to which people can intuitively aggregate

525 suggest that the selection pressures related to cooperative breeding may have influenced
526 personality evolution in this species.

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References

537

Adams, M. J., Majolo, B., Ostner, J., Schülke, O., De Marco, A., Thierry, B., Engelhardt, A., Widdig,

538

A., Gerald, M.S., & Weiss, A. (2015). Personality structure and social style in macaques. *Journal of*

539

Personality and Social Psychology, 109, 338-353.

540

Anderson, J. R., Takimoto, A., Kuroshima, H., & Fujita, K. (2013). Capuchin monkeys judge third-party

541

reciprocity. *Cognition*, 127, 140-146.

542

Anestis, S. F. (2005). Behavioral style, dominance rank, and urinary cortisol in young chimpanzees (*Pan*

543

trogodytes). *Behaviour*, 142, 1251-1274.

544

Araya-Ajoy, Y. G., & Dingemanse, N. J. (2014). Characterizing behavioural “characters”: an evolutionary

545

framework. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132645-20132645.

546

Ash, H., & Buchanan-Smith, H. M. (2016). The long-term impact of infant rearing background on the affective

547

state of adult common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science*, 174, 128-136.

548

Box, H. O. (1997). Foraging strategies among male and female marmosets and tamarins (Callitrichidae): New

549

perspectives in an underexplored area. *Folia Primatologica*, 68, 296-306.

550

Brosnan, S. F., & de Waal, F. B. M. (2014). Evolution of responses to (un)fairness. *Science*, 346, 1251776-

551

1251776.

552

Burkart, J. (2015). Opposite effects of male and female helpers on social tolerance and proactive prosociality in

553

callitrichid family groups. *Scientific Reports*, 5, 1-9.

554

Burkart, J. M., & van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates?

555

Animal Cognition, 13 1-19.

556

Burkart, J. M., & Van Schaik, C. P. (2016). Revisiting the consequences of cooperative breeding. *Journal of*

557

Zoology, 299, 77-83.

558

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human

559

primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of*

560

Sciences, 104, 19762-19766.

561

Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler, K., Kosonen, Z.K.,

562

Martins, E., Meulman, E.J., Richiger, R. Rueth, K., Spillmann, B., Wiesendange, S., & van Schaik, C.P.

563

(2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, 5, 4747.

564

Byrne, G., & Suomi, S. J. (2002). Cortisol reactivity and its relation to homeage behavior and personality

565

ratings in tufted capuchin (*Cebus paella*) juveniles from birth to six years of age.

- 566 *Psychoneuroendocrinology*, 27, 139-154.
- 567 Carter, A. J., English, S., & Clutton-Brock, T. H. (2014). Cooperative personalities and social niche
568 specialization in female meerkats. *Journal of Evolutionary Biology*, 27, 815-825.
- 569 Costa, P. T., Jr. & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual
570 Differences*, 13, 653-665.
- 571 DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not
572 sociality. *Nature Ecology & Evolution*, 1, 1–7. <http://doi.org/10.1038/s41559-017-0112>
- 573 Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). *Callitrichines: the role of competition in cooperatively
574 breeding species*. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M.A., Bearder, S.K. (Eds.),
575 *Primates in Perspective* (pp. 85–105). New York: Oxford University Press.
- 576 Digman, J. M. (1990). Personality structure: Emergence of the Five-Factor Model. *Annual Review of
577 Psychology*, 41, 417-440.
- 578 Dochtermann, N. A., & Dingemans, N. J. (2013). Behavioral syndromes as evolutionary constraints.
579 *Behavioral Ecology*, 24, 806-811.
- 580 Dutton, D. M. (2008). Subjective assessment of chimpanzee (*Pan troglodytes*) personality: Reliability and
581 stability of trait ratings. *Primates*, 49, 253-259.
- 582 Eckardt, W., Steklis, H. D., Steklis, N. G., Fletcher, A. W., Stoinski, T. S., & Weiss, A. (2015). Personality
583 dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*).
584 *Journal of Comparative Psychology*, 129, 26-41.
- 585 English, S., Nakagawa, S., & Clutton-Brock, T. H. (2010). Consistent individual differences in cooperative
586 behaviour in meerkats (*Suricata suricatta*). *Journal of Evolutionary Biology*, 23, 1597-1604.
- 587 Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past
588 research. *American Journal of Primatology*, 71, 1-19.
- 589 Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013).
590 Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using
591 a simultaneous top-down/bottom-up design. *American Journal of Primatology*, 75, 1042-1053.
- 592 Fresneau, N., Kluehn, E., & Brommer, J. E. (2014) A sex-specific behavioral syndrome in a wild passerine.
593 *Behavioural Ecology* 25, 359–367.
- 594 Garai, C., Weiss, A., Arnaud, C., & Furuichi, T. (2016). Personality in wild bonobos (*Pan paniscus*). *American
595 Journal of Primatology*, 78, 1178-1189.

- 596 Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with
597 implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role
598 of mediator variables. *Evolutionary Ecology*, *26*, 1213-1235.
- 599 Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool.
600 *Zoo Biology*, *13*, 509-522.
- 601 Gorsuch, R. L. (1984). *Factor analysis*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- 602 Gosling, S. D., & Graybeal, A. (2007). Tree thinking: A new paradigm for integrating comparative data in
603 psychology. *The Journal of General Psychology*, *134*, 259-277.
- 604 Horn, J. L. (1965). A rationale and test for the number of factors in factor analysis. *Psychometrika*,
605 *30*, 179-185.
- 606 Hrdy, S. B. (2009). *Mothers and others. The evolutionary origins of mutual understanding*. Cambridge MA:
607 Belknap Press.
- 608 Iwanicki, S., & Lehmann, J. (2015). Behavioral and trait rating assessments of personality in common
609 marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, *129*, 205-217.
- 610 Kawai, N., Yasue, M., Banno, T., & Ichinohe, N. (2014). Marmoset monkeys evaluate third-party reciprocity.
611 *Biology Letters*, *10*, 20140058–20140058.
- 612 King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality.
613 *Journal of Research in Personality*, *31*, 257-271.
- 614 King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national
615 generalization of personality structure: Zoological parks and an African sanctuary. *Journal of Personality*,
616 *73*, 389-410.
- 617 Kitchen, A. M., & Martin, A. A. (1995). The effects of cage size and complexity on the behavior of captive
618 common marmosets (*Callithrix jacchus jacchus*). *Laboratory Animals*, *30*, 317-326.
- 619 Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., & Pluháček, J. (2008). Personality in free-
620 ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. *Journal*
621 *of Comparative Psychology*, *122*, 379-389.
- 622 Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in Barbary macaques (*Macaca sylvanus*):
623 Temporal stability and social rank. *Journal of Research in Personality*, *46*, 581-590.
- 624 Koski, S. E. (2011a). Social personality traits in chimpanzees: Temporal stability and structure of behaviourally
625 assessed personality traits in three captive populations. *Behavioral Ecology and Sociobiology*, *65*, 2161-

- 626 2174.
- 627 Koski, S. E. (2011b). How to measure animal personality and why does it matter? Integrating the psychological
628 and biological approaches to animal personality. In M. Inoue-Murayama., S. Kawamura. & A. Weiss (Eds.)
629 From Genes to Animal Behavior (pp. 115–136). Tokyo: Springer.
- 630 Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, 2, 1-
631 6.
- 632 Koski S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in
633 personality. *Scientific Reports*, 5, 8878.
- 634 Kramer, K. L. (2015). Cooperative breeding and human evolution. *Emerging Trends in Social and Behavioral*
635 *Sciences: An interdisciplinary, searchable, and linkable resource*. 1-13.
- 636 MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of
637 self-control. *Proceedings of the National Academy of Sciences*, 111, E2140–E2148.
- 638 Manson, J. H., & Perry, S. (2013). Personality structure, sex differences, and temporal change and stability in
639 wild white-faced capuchins, *Cebus capucinus*. *Journal of Comparative Psychology*, 127, 299-311
- 640 Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on
641 chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with
642 group experiments. *American Journal of Primatology*, 75, 947-958.
- 643 McCrae, R. R., & Costa, P. T., Jr. (1987). Validation of the five-factor model of personality across instruments
644 and observers. *Journal of Personality and Social Psychology*, 52, 81-90.
- 645 McCrae, R. R., Terracciano, A., & 78 members of the personality profiles of cultures project. (2005). Universal
646 features of personality traits from the observer's perspective: Data from 50 cultures. *Journal of Personality*
647 *and Social Psychology*, 88, 547-561.
- 648 McGuire, M. T., Raleigh, M. J., & Pollack, D. B. (1994). Personality features in vervet monkeys: The effects of
649 sex, age, social status, and group composition. *American Journal of Primatology*, 33, 1–13.
- 650 Michelangeli, M., Chapple, D. G., & Wong, B. B. M. (2016). Are behavioural syndromes sex specific?
651 Personality in a widespread lizard species. *Behavioral Ecology and Sociobiology*, 70, 1911-1919.
- 652 Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., de Waal, F. B.
653 M., Widness, J., Essler, J. L., & Weiss, A. (2013). Personality structure in brown capuchin monkeys
654 (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus
655 macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, 127, 282-298.

- 656 Möttus, R., Kandler, C., Bleidorn, W., Riemann, R., & McCrae, R. R. (2017). Personality traits below facets:
657 The consensual validity, longitudinal stability, heritability, and utility of personality nuances. *Journal of*
658 *Personality and Social Psychology*, *112*, 474-490.
- 659 Möttus, R., McCrae, R. R., Allik, J., & Realo, A. (2014). Cross-rater agreement on common and specific
660 variance of personality scales and items. *Journal of Research in Personality*, *52*, 47–54.
- 661 Neumann, C., Agil, M., Widdig, A., & Engelhardt, A. (2013). Personality of wild male crested macaques
662 (*Macaca nigra*). *PloS One*, *8*: e69383.
- 663 Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts
664 behavior. *Journal of Research in Personality*, *39*, 534-549.
- 665 Revelle, W. (2015). Package ‘psych’. Retrieved 7th November 2016 from [https://cran.r-](https://cran.r-project.org/web/packages/psych/psych.pdf)
666 [project.org/web/packages/psych/psych.pdf](https://cran.r-project.org/web/packages/psych/psych.pdf)
- 667 Roberts, B. W., Walton, K. E., & Viechtbauer, W. (2006). Patterns of mean-level change in personality traits
668 across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin*, *132*, 1–25.
- 669 Sanderson, J. L., Stott, I., Young, A. J., Vitikainen, E. I. K., Hodge, S. J., & Cant, M. A. (2015). The origins of
670 consistent individual differences in cooperation in wild banded mongooses, *Mungos mungo*. *Animal*
671 *Behaviour*, *107*(C), 193-200.
- 672 Santillán-Doherty, A. M., Cortés-Sotres, J., Arenas-Rosas, R. V., Márquez-Arias, A., Cruz, C., Medellín, A.,
673 Aguirre, M., Muñoz-Delgado, J., & Díaz, J. L. (2010). Novelty-seeking temperament in captive stump-tail
674 macaques (*Macaca arctoides*) and spider monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology*,
675 *124*, 211-218.
- 676 Schaffner, C. M., & Caine, N. G. (2000). The peacefulness of cooperatively breeding partners. In F. Aureli & F.
677 B. M. de Waal (Eds.) *Natural Conflict Resolution* (pp155-169). Berkeley: University of California Press.
- 678 Schaffner, C. M., Aureli, F., & Caine, N. G. (2005). Why small groups of tamarins do not reconcile conflicts.
679 *Folia Primatologica*, *76*, 67-76.
- 680 Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches,
681 *Taeniopygia guttata*. *Animal Behaviour*, *77*, 1041–1050.
- 682 Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews*,
683 *85*(2), 217–246.
- 684 Schuppli, C., Graber, S. M., Isler, K., & van Schaik, C. P. (2016). Life history, cognition and the evolution of
685 complex foraging niches. *Journal of Human Evolution*, *92*(C), 91–100.

- 686 Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological*
687 *Bulletin, 86*, 420-428.
- 688 Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology
689 perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 2762-2772.
- 690 Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview.
691 *Trends in Ecology and Evolution, 19*, 372 - 378.
- 692 Šlipogor, V., Gunhold-de Oliveira, T., Tadić, Z., Massen, J. J. M., & Bugnyar, T. (2016). Consistent inter-
693 individual differences in common marmosets (*Callithrix jacchus*) in Boldness-Shyness, Stress-Activity, and
694 Exploration-Avoidance. *American Journal of Primatology, 78*, 1–13.
- 695 Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral*
696 *Ecology, 19*, 448-455.
- 697 Soulsbury, C. D., Iossa, G., Kennell, S. & Harris, S. (2009). The welfare and suitability of primates kept as pets.
698 *Journal of Applied Animal Welfare Science, 12*, 1-20.
- 699 Stevens, J. R., Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New
700 World monkeys. *Biology Letters, 1*(2), 223-226.
- 701 Uher, J. (2008). Comparative personality research: Methodological approaches. *European Journal of*
702 *Personality, 22*, 427-455.
- 703 Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the Great Apes: Comparing ecologically valid
704 behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality, 42*, 821–838.
- 705 Uher, J., & Visalberghi, E. (2016). Observations versus assessments of personality: A five-method multi-species
706 study reveals numerous biases in ratings and methodological limitations of standardised assessments.
707 *Journal of Research in Personality, 61*, 61-79.
- 708 Uher, J., Asendorpf, J. B., & Call, J. (2008). Personality in the behaviour of Great Apes: Temporal stability,
709 cross-situational consistency and coherence in response. *Animal Behaviour, 75*, 99-112.
- 710 Weiss, A. (2017). Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire.
711 In J. Vonk, A. Weiss, & S. Kuczaj (Eds.), *Personality in Nonhuman Animals*. Springer.
- 712 Weiss, A., & Adams, M. J. (2013). Differential behavioral ecology: The structure, life history, and evolution of
713 animal personality. In C. Carere & D. Maestriperi (Eds.) *Animal Personalities. Behavior, physiology, and*
714 *evolution* (pp. 96-123). Chicago: University of Chicago Press, Chicago.
- 715 Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living

- 716 fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology*, *125*, 72-83.
- 717 Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2012a). Extraversion predicts longer survival in
718 gorillas: An 18-year longitudinal study. *Proceedings of the Royal Society B: Biological Sciences*, *280*,
719 20122231–20122231.
- 720 Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Usono, T., Ochiai, T., Matsuzawa, T., Hirata, S., &
721 King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal*
722 *of Primatology*, *71*, 283-292.
- 723 Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012b). All too human?
724 Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour*, *83*, 1355-
725 1365.
- 726 Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo*
727 *pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, *90*, 501-511.
- 728 Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*)
729 personality structure and development: Zoological parks and Yerkes National Primate Research Center.
730 *American Journal of Primatology*, *69*, 1264-1277.
- 731 Weiss, A., Staes, N., Pereboom, J. J. M., Inoue-Murayama, M., Stevens, J. M. G., & Eens, M. (2015).
732 Personality in Bonobos. *Psychological Science*, *26*, 1430-1439.
- 733 Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in*
734 *Ecology & Evolution*, *27*, 1-10.
- 735 Yamamoto, M. E., Araujo, A., de Fatima Arruda, M., Lima, A. K. M., de Oliveira Siqueira, J., & Hattori, W. T.
736 (2014). Male and female breeding strategies in a cooperative primate. *Behavioural Processes*, *109*, 27-33.
- 737 Yamamoto, M.E., Domeniconi, C. & Box, H. (2004). Sex differences in common marmosets (*Callithrix*
738 *jacchus*) in response to an unfamiliar food task. *Primates*, *45*, 249-254.

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740 ^[1] Available at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf

741

742 Table 1
 743 *Varimax-Rotated Component Loadings*
 744

Item	Con*	Agr	Ass*	Pat	Inq*	h^2
Thoughtless	-0.81	-0.15	-0.20	-0.07	-0.01	0.72
Bullying	-0.80	-0.32	0.16	-0.02	-0.04	0.78
Clumsy	-0.80	-0.08	-0.23	0.04	-0.26	0.77
Eccentric	-0.79	-0.14	-0.09	0.16	-0.15	0.71
Reckless	-0.76	-0.39	0.13	-0.07	0.12	0.77
Disorganized	-0.72	0.02	-0.11	-0.07	-0.22	0.59
Imitative	-0.70	-0.01	-0.27	-0.11	0.17	0.61
Erratic	-0.69	-0.28	-0.25	-0.01	-0.11	0.63
Jealous	-0.69	-0.36	0.14	0.13	0.08	0.64
Aggressive	-0.68	-0.51	-0.02	0.03	-0.05	0.74
Irritable	-0.67	-0.56	0.00	0.05	-0.05	0.77
Impulsive	-0.66	-0.45	0.09	-0.04	0.09	0.65
Excitable	-0.63	-0.55	-0.15	-0.03	-0.01	0.72
Unperceptive	-0.61	-0.09	0.00	-0.30	-0.24	0.53
Socially playful	-0.58	0.16	-0.46	0.10	0.34	0.71
Depressed	-0.56	-0.12	-0.44	0.21	-0.43	0.75
Stingy	-0.53	-0.32	0.30	0.02	0.05	0.48
Playful	-0.51	0.02	-0.45	0.21	0.40	0.67
Assertive	-0.48	-0.29	0.46	0.03	0.15	0.55
Friendly	0.20	0.84	-0.08	0.10	0.07	0.76
Equable	0.25	0.74	0.18	-0.01	-0.08	0.65
Affectionate	0.23	0.73	0.00	0.14	0.04	0.61
Permissive	0.47	0.68	0.03	-0.08	-0.10	0.70
Gentle	0.56	0.67	0.00	0.05	-0.06	0.76
Sociable	0.00	0.63	0.04	-0.12	0.36	0.54
Popular	0.10	0.62	0.41	-0.08	0.09	0.59
Helpful	0.14	0.62	-0.17	0.24	-0.12	0.50
Predictable	0.00	0.55	0.16	-0.09	-0.11	0.35
Unemotional	0.18	0.54	0.17	-0.20	-0.08	0.39
Protective	0.21	0.50	0.02	0.12	-0.13	0.32
Cautious	0.02	0.07	-0.76	-0.03	-0.31	0.68
Dependent	-0.15	-0.01	-0.75	-0.15	0.06	0.61
Dominant	-0.33	-0.06	0.75	-0.03	-0.03	0.67
Independent	-0.09	0.22	0.73	0.15	-0.07	0.62
Confident	0.08	0.24	0.72	0.15	0.28	0.69
Timid	-0.25	-0.31	-0.71	-0.08	-0.29	0.76
Submissive	-0.23	0.10	-0.71	0.10	-0.11	0.58
Fearful	-0.30	-0.41	-0.68	-0.08	-0.13	0.75
Tense	-0.26	-0.44	-0.57	-0.12	-0.27	0.67
Anxious	-0.42	-0.37	-0.57	0.03	-0.39	0.79

Vulnerable	-0.56	-0.21	-0.56	0.16	-0.31	0.79
Selective	-0.39	-0.03	0.44	0.17	-0.09	0.38
Sympathetic	0.09	0.35	-0.43	0.40	-0.23	0.52
Distractible	-0.22	0.05	-0.22	-0.78	0.02	0.71
Quitting	-0.26	0.08	-0.23	-0.76	-0.09	0.71
Intelligent	-0.07	0.01	0.02	0.75	0.22	0.62
Inventive	-0.23	-0.19	-0.23	0.66	0.27	0.65
Sensitive	-0.11	0.34	-0.14	0.66	-0.13	0.60
Persistent	-0.40	0.02	0.18	0.65	0.11	0.63
Patient	0.32	0.47	0.10	0.50	-0.04	0.59
Lazy	-0.16	0.36	-0.05	-0.02	-0.68	0.62
Exploratory	0.08	-0.01	0.18	0.38	0.67	0.64
Inquisitive	0.02	0.00	0.29	0.39	0.65	0.66
Active	-0.09	-0.46	-0.17	-0.10	0.61	0.63
Opportunistic	-0.25	-0.21	0.34	0.31	0.53	0.60
Solitary	-0.21	-0.25	-0.15	0.01	-0.49	0.36
Alert	0.05	0.00	0.33	-0.02	0.43	0.30
Proportion of variance	0.20	0.14	0.14	0.08	0.07	

745 *Note.* Con = Conscientiousness, Agr = Agreeableness, Ass = Assertiveness, Pat = Patience,
746 Inq = Inquisitiveness, h^2 = communality. Bold typeface indicates loadings \geq than $|.4|$.
747 *Loadings of this factor were reflected.

748

749 Table 2
 750 *The linear effects of sex and age on the component scores*
 751

	<i>b</i>	<i>SE</i>	95% <i>CI</i>		<i>t</i>	<i>p</i>
			2.5%	97.5%		
Conscientiousness						
Intercept	0.01	0.10	-0.19	0.21	0.14	.889
Sex	-0.01	0.10	-0.21	0.19	-0.07	.941
Age	-0.04	0.03	-0.11	0.02	-1.28	.204
Sex × Age	0.04	0.03	-0.03	0.11	1.21	.229
Agreeableness						
Intercept	0.02	0.10	-0.17	0.22	0.23	.817
Sex	0.11	0.10	-0.09	0.30	1.09	.277
Age	0.05	0.03	-0.02	0.11	1.49	.140
Sex × Age	0.07	0.03	0.01	0.14	2.21	.029
Assertiveness						
Intercept	0.01	0.10	-0.19	0.21	0.11	.909
Sex	-0.11	0.10	-0.31	0.09	-1.09	.277
Age	-0.03	0.03	-0.09	0.04	-0.76	.449
Sex × Age	0.03	0.03	-0.04	0.09	0.81	.421
Patience						
Intercept	0.03	0.09	-0.16	0.22	0.33	.740
Sex	-0.30	0.09	-0.48	-0.11	-3.13	.002
Age	-0.05	0.03	-0.11	0.01	-1.50	.136
Sex × Age	0.07	0.03	0.01	0.14	2.36	.020
Inquisitiveness						
Intercept	0.01	0.09	-0.18	0.19	0.06	.952
Sex	-0.15	0.09	-0.34	0.04	-1.59	.115
Age	-0.13	0.03	-0.19	-0.07	-4.11	< .001
Sex × Age	0.01	0.03	-0.05	0.07	0.25	.802

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