

## Marmoset Personality

1

- 1 This is a post-peer-review, pre-copyedit version of an article published in Journal of
- 2 Comparative Psychology, vol. 131, issue 4. The final authenticated version is available online
- 3 at: <https://doi.org/10.1037/com0000089>.

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

5

6

Sonja E. Koski

7

University of Helsinki

8

Hannah M. Buchanan-Smith and Hayley Ash

9

University of Stirling

10

Judith M. Burkart

11

University of Zurich

12

Thomas Bugnyar

13

University of Vienna

14

Alexander Weiss

15

University of Edinburgh

16

17

Author Note

18

Sonja E. Koski, Department of Anthropology, University of Zurich; Hannah M.

19

Buchanan-Smith and Hayley Ash, Behaviour and Evolution Research Group and Scottish

20

Primate Research Group, Psychology, Faculty of Natural Sciences, University of Stirling;

21

Judith M. Burkart, Department of Anthropology, University of Zurich; Thomas Bugnyar,

22

Department of Cognitive Biology, University of Vienna; Alexander Weiss, Scottish Primate

23

Research Group, School of Philosophy, Psychology and Language Sciences, Department of

24

Psychology, The University of Edinburgh.

25

26

27

Please address correspondence concerning this article to: Sonja E. Koski, Centre of

28

Excellence in Intersubjectivity in Interaction, Department of Social Sciences, University of

29

Helsinki. Unioninkatu 35, 00014 Helsinki, Finland. E-mail: [sonja.koski@helsinki.fi](mailto:sonja.koski@helsinki.fi).

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<sup>[1]</sup> (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  $\geq 0.97$ ) 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  $\geq 0.99$ ).

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.

527 **Acknowledgements**

528 We thank the staff at the three facilities (Dstl. Salisbury, UK; Zurich University  
529 Primate Station, Switzerland, and Vienna University Cognitive Biology primate facility,  
530 Austria) for their assistance with the research and dedicated care of the marmosets. We are  
531 grateful to all those who completed the questionnaires, namely: Michèle Schubiger, Christa  
532 Finkenwirth, Eloisa Martins, Heinz Galli, Thomas Bischof, Alexandra Christian, Caecilia  
533 Faltin, Martina Schiestl, Tina Gunhold, and Vedrana Šlipogor. We are grateful to Doree  
534 Fragazy and the three anonymous reviewers for their helpful comments that greatly improved  
535 the manuscript. HA was funded by a studentship awarded by the NC3Rs.

536

**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 homecage 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 7<sup>th</sup> 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.

739

740 <sup>[1]</sup> Available at [http://extras.springer.com/2011/978-1-4614-0175-9/weiss\\_monkey\\_personality.pdf](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	<b>-0.81</b>	-0.15	-0.20	-0.07	-0.01	0.72
Bullying	<b>-0.80</b>	-0.32	0.16	-0.02	-0.04	0.78
Clumsy	<b>-0.80</b>	-0.08	-0.23	0.04	-0.26	0.77
Eccentric	<b>-0.79</b>	-0.14	-0.09	0.16	-0.15	0.71
Reckless	<b>-0.76</b>	-0.39	0.13	-0.07	0.12	0.77
Disorganized	<b>-0.72</b>	0.02	-0.11	-0.07	-0.22	0.59
Imitative	<b>-0.70</b>	-0.01	-0.27	-0.11	0.17	0.61
Erratic	<b>-0.69</b>	-0.28	-0.25	-0.01	-0.11	0.63
Jealous	<b>-0.69</b>	-0.36	0.14	0.13	0.08	0.64
Aggressive	<b>-0.68</b>	<b>-0.51</b>	-0.02	0.03	-0.05	0.74
Irritable	<b>-0.67</b>	<b>-0.56</b>	0.00	0.05	-0.05	0.77
Impulsive	<b>-0.66</b>	<b>-0.45</b>	0.09	-0.04	0.09	0.65
Excitable	<b>-0.63</b>	<b>-0.55</b>	-0.15	-0.03	-0.01	0.72
Unperceptive	<b>-0.61</b>	-0.09	0.00	-0.30	-0.24	0.53
Socially playful	<b>-0.58</b>	0.16	<b>-0.46</b>	0.10	0.34	0.71
Depressed	<b>-0.56</b>	-0.12	<b>-0.44</b>	0.21	<b>-0.43</b>	0.75
Stingy	<b>-0.53</b>	-0.32	0.30	0.02	0.05	0.48
Playful	<b>-0.51</b>	0.02	<b>-0.45</b>	0.21	<b>0.40</b>	0.67
Assertive	<b>-0.48</b>	-0.29	<b>0.46</b>	0.03	0.15	0.55
Friendly	0.20	<b>0.84</b>	-0.08	0.10	0.07	0.76
Equable	0.25	<b>0.74</b>	0.18	-0.01	-0.08	0.65
Affectionate	0.23	<b>0.73</b>	0.00	0.14	0.04	0.61
Permissive	<b>0.47</b>	<b>0.68</b>	0.03	-0.08	-0.10	0.70
Gentle	<b>0.56</b>	<b>0.67</b>	0.00	0.05	-0.06	0.76
Sociable	0.00	<b>0.63</b>	0.04	-0.12	0.36	0.54
Popular	0.10	<b>0.62</b>	<b>0.41</b>	-0.08	0.09	0.59
Helpful	0.14	<b>0.62</b>	-0.17	0.24	-0.12	0.50
Predictable	0.00	<b>0.55</b>	0.16	-0.09	-0.11	0.35
Unemotional	0.18	<b>0.54</b>	0.17	-0.20	-0.08	0.39
Protective	0.21	<b>0.50</b>	0.02	0.12	-0.13	0.32
Cautious	0.02	0.07	<b>-0.76</b>	-0.03	-0.31	0.68
Dependent	-0.15	-0.01	<b>-0.75</b>	-0.15	0.06	0.61
Dominant	-0.33	-0.06	<b>0.75</b>	-0.03	-0.03	0.67
Independent	-0.09	0.22	<b>0.73</b>	0.15	-0.07	0.62
Confident	0.08	0.24	<b>0.72</b>	0.15	0.28	0.69
Timid	-0.25	-0.31	<b>-0.71</b>	-0.08	-0.29	0.76
Submissive	-0.23	0.10	<b>-0.71</b>	0.10	-0.11	0.58
Fearful	-0.30	<b>-0.41</b>	<b>-0.68</b>	-0.08	-0.13	0.75
Tense	-0.26	<b>-0.44</b>	<b>-0.57</b>	-0.12	-0.27	0.67
Anxious	<b>-0.42</b>	-0.37	<b>-0.57</b>	0.03	-0.39	0.79

Vulnerable	<b>-0.56</b>	-0.21	<b>-0.56</b>	0.16	-0.31	0.79
Selective	-0.39	-0.03	<b>0.44</b>	0.17	-0.09	0.38
Sympathetic	0.09	0.35	<b>-0.43</b>	<b>0.40</b>	-0.23	0.52
Distractible	-0.22	0.05	-0.22	<b>-0.78</b>	0.02	0.71
Quitting	-0.26	0.08	-0.23	<b>-0.76</b>	-0.09	0.71
Intelligent	-0.07	0.01	0.02	<b>0.75</b>	0.22	0.62
Inventive	-0.23	-0.19	-0.23	<b>0.66</b>	0.27	0.65
Sensitive	-0.11	0.34	-0.14	<b>0.66</b>	-0.13	0.60
Persistent	<b>-0.40</b>	0.02	0.18	<b>0.65</b>	0.11	0.63
Patient	0.32	<b>0.47</b>	0.10	<b>0.50</b>	-0.04	0.59
Lazy	-0.16	0.36	-0.05	-0.02	<b>-0.68</b>	0.62
Exploratory	0.08	-0.01	0.18	0.38	<b>0.67</b>	0.64
Inquisitive	0.02	0.00	0.29	0.39	<b>0.65</b>	0.66
Active	-0.09	<b>-0.46</b>	-0.17	-0.10	<b>0.61</b>	0.63
Opportunistic	-0.25	-0.21	0.34	0.31	<b>0.53</b>	0.60
Solitary	-0.21	-0.25	-0.15	0.01	<b>-0.49</b>	0.36
Alert	0.05	0.00	0.33	-0.02	<b>0.43</b>	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  $|\cdot 4|$ .

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	<b>0.07</b>	<b>0.03</b>	<b>0.01</b>	<b>0.14</b>	<b>2.21</b>	<b>.029</b>
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	<b>-0.30</b>	<b>0.09</b>	<b>-0.48</b>	<b>-0.11</b>	<b>-3.13</b>	<b>.002</b>
Age	-0.05	0.03	-0.11	0.01	-1.50	.136
Sex × Age	<b>0.07</b>	<b>0.03</b>	<b>0.01</b>	<b>0.14</b>	<b>2.36</b>	<b>.020</b>
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	<b>-0.13</b>	<b>0.03</b>	<b>-0.19</b>	<b>-0.07</b>	<b>-4.11</b>	<b>&lt; .001</b>
Sex × Age	0.01	0.03	-0.05	0.07	0.25	.802

752