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## Personality Dimensions and Their Behavioral Correlates in Wild Virunga Mountain Gorillas (*Gorilla Beringei Beringei*)

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1 **Personality Dimensions and Their Behavioral Correlates in Wild Virunga Mountain**

2 **Gorillas (*Gorilla beringei beringei*)**

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11

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### Abstract

Studies of animal personality improve our understanding of individual variation in measures of life-history and fitness, such as health and reproductive success. Using a 54 trait personality questionnaire developed for studying great apes and other nonhuman primates, we obtained ratings on 116 wild mountain gorillas (*Gorilla beringei beringei*) monitored by the Dian Fossey Gorilla Fund's Karisoke Research Center in Rwanda. There were eight raters who each had more than 1.5 years of working experience with the subjects. Principal component analyses identified four personality dimensions with high inter-rater reliabilities --- Dominance, Openness, Sociability, and Proto-Agreeableness --- that reflected personality features unique to gorillas and personality features shared with other hominoids. We next examined the associations of these dimensions with independently collected behavioral measures derived from long-term records. Predicted correlations were found between the personality dimensions and corresponding behaviors. For example, Dominance, Openness, Sociability, and Proto-Agreeableness were related to gorilla dominance strength, time spent playing, rates of approaches and rates of interventions in intra-group conflicts, respectively. These findings enrich the comparative-evolutionary study of personality and provide insights into how species differences in personality are related to ecology, social systems, and life history.

Keywords: Personality, mountain gorillas, wild, evolution, behavior

## 44 **Personality Dimensions and Their Behavioral Correlates in Wild Virunga Mountain**

### 45 **Gorillas (*Gorilla beringei beringei*)**

#### 46 **Comparative Personality Research**

47 The study of animal personality, that is stable individual differences in behavior within  
48 populations (Freeman & Gosling, 2010), has become a growing area of research in behavioral  
49 ecology (Réale, Dingemanse, Kazem, & Wright, 2010) and comparative psychology (Gosling,  
50 2001). This increased interest stems largely from a desire to understand the adaptive significance  
51 of behavioral phenotypes in numerous animal populations (Réale et al., 2010; Kralj-Fiser &  
52 Schuett, 2014). More specifically, for those studying the adaptive function of personality, there is  
53 a need to address the vexing question of why additive genetic variation in personality persists in  
54 spite of the fact that personality dimensions are associated with fitness-related outcomes (Penke,  
55 Denissen, & Miller, 2007)? A related question concerns why individual differences in  
56 behavioral, affective, and cognitive dispositions can be described by a few broad species-typical  
57 dimensions in humans (Goldberg, 1990), nonhuman great apes, and other primates (Freeman &  
58 Gosling, 2010).

59 Examining which traits make up the smaller number of personality dimensions in  
60 different species is useful for understanding the phylogeny of personality (Gosling & Graybeal,  
61 2007). For instance, studies of chimpanzees (King & Figueredo, 1997) and orangutans (Weiss,  
62 King, & Perkins, 2006) have been used to trace the origins of human dimensions—Openness,  
63 Conscientiousness, Extraversion, Agreeableness, and Neuroticism—known as the “Big-Five” or  
64 “Five-Factor Model” (Digman, 1990; Goldberg, 1990). From the study of chimpanzee  
65 personality structure, which resembled the human Big-Five with the addition of a dimension  
66 related to dominance and competitive prowess (King & Figueredo, 1997), the most parsimonious

67 **explanation** is that the five human factors were present in the common ancestor of humans and  
68 chimpanzees ~4-6 million years ago. Likewise, the study of orangutan personality indicated that  
69 Neuroticism, Extraversion, and Agreeableness can be traced to the common ancestor of great  
70 apes ~15-16 million years ago, and that dimensions describing the common ancestor of great  
71 apes also included a dimension related to competitive prowess and one that included tendencies  
72 towards decisiveness, intelligence, and competence (Weiss et al., 2006).

73 Comparing dimensions that describe multiple personality traits across species requires **the**  
74 **assessment of** these dispositions using comparable methods. One approach is to obtain ratings of  
75 **personality traits** from knowledgeable judges. The validity of this method is well-accepted **as**  
76 **ratings** are consistent across independent judges (**Gosling, 2001**), stable over time **and contexts**  
77 (Capitanio, 1999; King, Weiss, & Sisco, 2008; Weiss, Adams, Widdig, & Gerald, 2011),  
78 associated with physiological characteristics and health (Blatchley & Hopkins, 2010; Capitanio,  
79 Mendoza, & Bentson, 2004; Capitanio, Mendoza, & Cole, 2011; Locurto, 2007; Weiss, Gartner,  
80 Gold, & Stoinski, 2012), well-being (King & Landau, 2003; Weiss et al., 2006; Weiss, Adams,  
81 Widdig, & Gerald, 2011), and observed behaviors (**Gold & Maple, 1994; Gosling & Vazire,**  
82 **2002; Konečná et al., 2008; Konečná, Weiss, Lhota, & Wallner, 2012; Kuhar, Stoinski, Lukas, &**  
83 **Maple, 2006; Morton, Buchanan-Smith, Brosnan, Thierry, & Paukner, 2013; Pederson, King, &**  
84 **Landau, 2005; Schaefer & Steklis, 2014**). Moreover, chimpanzee personality dimensions  
85 described by raters from different cultures on different populations of the same species reveal  
86 highly **similar dimensions** (King, Weiss, & Farmer, 2005; Weiss et al., 2009; Weiss, King, &  
87 Hopkins, 2007), and there is mounting evidence that these dimensions are genetically-based  
88 (Adams, King, & Weiss, 2012; Hong et al., 2011; Hopkins, Donaldson, & Young, 2012; Weiss,

89 King, & Figueredo, 2000), and not the products of rater biases, including anthropomorphic  
90 projection (Weiss et al., 2012).

### 91 **Study objectives**

92       The first two goals of this study were to describe wild mountain gorilla personality and to  
93 compare it to the personalities of chimpanzees (King & Figueredo, 1997), orangutans (Weiss,  
94 King, & Perkins, 2006), rhesus macaques (Weiss et al., 2011), and brown capuchin monkeys  
95 (Morton et al., 2013), all of which were assessed using the Hominoid Personality Questionnaire  
96 (HPQ; Weiss et al., 2009). To these ends, while previous studies of gorilla personality (Gold &  
97 Maple, 1994; Kuhar et al., 2006) used the Gorilla Behavioral Index, a modified version of the  
98 Madingley Questionnaire (Stevenson-Hinde & Zunz, 1978), we used a modified version of the  
99 HPQ so that we could directly compare the dimensions of mountain gorillas to those of the other  
100 species.

101       The third goal of this study was to examine sex and age differences in mountain gorilla  
102 personality. Gorillas are the most sexually dimorphic great ape (Taylor, 1997) as a result of  
103 strong sexual selection among males who compete for access to reproductive females (Harcourt  
104 & Stewart, 2007). We hypothesize that such high sexual dimorphism in gorillas leads to sex  
105 differences in personality, which become more evident in adulthood when sexual differentiation  
106 has complete.

107       The fourth goal of this study was to examine the association between gorilla personality  
108 dimensions and naturally occurring behaviors. A previous study of 25 captive gorillas, using the  
109 Gorilla Behavioral Index (Kuhar et al., 2006), found modest correlations between behaviors and  
110 personality dimensions labeled extroverted, dominant, fearful, and understanding. More recently,  
111 in six captive male gorillas, Schaefer and Steklis (2014) found associations between behaviors

112 and personality dimensions labeled Dominance, Extraversion/Agreeableness, and  
113 Conscientiousness that were obtained from ratings on the HPQ in ways consistent with the  
114 definitions of these dimensions. Because these previous gorilla studies were constrained by  
115 behaviors observed in zoo settings, we aimed to test predictions for a large sample of wild  
116 gorillas on the relationship between specific naturally occurring gorilla behaviors and the  
117 personality dimensions that emerged from the HPQ.

### 118 **Which dimensions characterize mountain gorilla personality?**

119 We used multiple approaches for predicting personality features of the Virunga mountain  
120 gorillas. Specifically, we focused on gorilla-specific and population-specific ecology and social  
121 system. We also considered existing findings in great apes (Weiss et al., 2011) and the 14 most  
122 commonly identified personality categories in primates across 18 comprehensive studies (see  
123 Table II in Freeman & Gosling, 2010).

124 Among great apes and within gorillas, the Virunga mountain gorillas comprise the most  
125 folivorous population (Harcourt & Stewart, 2007). Their high-altitude habitat represents an  
126 extreme for the genus and is characterized by low fruit availability but dense **terrestrial**  
127 **vegetation** that is spatially and temporally abundant (Fossey & Harcourt, 1977; Schaller, 1963;  
128 Vedder, 1984; Watts, 1984). These environmental conditions translate into low levels of intra-  
129 and inter-group food competition (Robbins, Robbins, Gerald-Steklis, & Steklis, 2007), which **is**  
130 **reflected in** relatively low levels of intra-group aggression and large home range overlaps  
131 between groups (Caillaud et al., 2014; Fossey & Harcourt, 1977; Harcourt & Stewart, 2007).  
132 This pattern differs considerably **from** other great ape populations (Harcourt & Stewart, 2007).  
133 We hypothesize that living in such a stable and predictable environment with limited food  
134 competition results in low vulnerability to stress, low aggressiveness, high emotional stability,

135 and very low neurotic tendencies. This hypothesis is further supported by the general nature of  
136 gorillas which is commonly described as calm, introverted and emotionally stable (Parker &  
137 Mitchel, 1999).

138 In addition, in a stable environment such as the Virunga habitat, curiosity, creativity and  
139 exploratory tendencies may not be as necessary as in environments with seasonal food shortages.  
140 As a consequence, mountain gorillas may not have experienced strong selection to explore  
141 alternative food sources and food extraction techniques, such as hunting and termite fishing in  
142 chimpanzees, to ensure their survival (Boesch & Boesch, 1989, 1990). This has been offered as  
143 an explanation for why Openness is absent in Hanuman langurs (Konečná et al., 2008, though  
144 see Konečná et. al., 2012). Thus, from an ecological perspective, we expect mountain gorillas to  
145 lack a personality dimension incorporating curiosity, creativity, and exploration, such as  
146 Openness in humans (Goldberg, 1990) and chimpanzees (King & Figueredo, 1997). On the other  
147 hand, Openness may be important in adult gorilla personality from a social standpoint. Dispersal  
148 pattern strategies to avoid inbreeding and to increase breeding opportunities set gorillas apart  
149 from other great apes because emigration from the natal group is common for both sexes  
150 (Robbins, 1995; Watts, 1990). Females transfer during inter-group encounters, whereas males  
151 become solitary after leaving their natal group and then attempt to recruit females from existing  
152 groups. Both situations require individuals to be socially curious and open, and thus from a  
153 social perspective adult gorillas should have a dimension reflecting Openness.

154 Gorillas live in hierarchically structured societies with adult males clearly dominant over  
155 females (Harcourt & Stewart, 2007). Dominance hierarchies within the sexes also exist, although  
156 female-female relationships are generally considered more egalitarian than in other primates as a  
157 result of the lower levels of feeding competition (Robbins, 1996; Robbins, Robbins, Gerald-



158 Steklis, & Steklis, 2005). Accordingly, we predict that mountain gorilla personality will be  
159 characterized by a Dominance dimension and that adult males score higher than adult females on  
160 such a dimension, with stronger sex differences in adulthood. Dimensions categorized as  
161 Confidence, Independence and Intelligence (Freeman & Gosling, 2010) complement qualities  
162 associated with dominance in mountain gorillas and thus should be closely tied to gorilla  
163 Dominance in a similar fashion to that shown in other nonhuman great apes (Gold & Maple,  
164 1994; King & Figueredo, 1997; Kuhar et al. 2006; Schaefer & Steklis, 2014).

165 The social role of male and female gorillas is also distinct (Harcourt & Stewart, 2007).  
166 Silverbacks, in particular dominant males, act as group leaders, mediate within-group social  
167 conflicts, and protect infants from infanticide (Schaller, 1963; Harcourt & Stewart, 2007; Watts,  
168 1989). This role requires supportive attitudes that are commonly part of an Agreeableness  
169 dimension in humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss et  
170 al., 2009; Weiss et al., 2006). Females, on the other hand, are compliant and rely on male  
171 protection and leadership. Females also cooperate with each other in contests by supporting  
172 subordinate parties (Harcourt & Stewart, 2007). Thus, gorillas are expected to show an  
173 Agreeableness dimension.

174 Compared to other great apes, gorillas form cohesive social groups without regular  
175 fission-fusion dynamics (Harcourt & Stewart, 2007). In addition, between- rather than within-sex  
176 relationships form the core of gorilla society (Harcourt, 1979; Watts, 1992, 1996) as females  
177 establish and maintain bonds with males (Harcourt & Stewart, 2007; Watts, 1992). Thus, a  
178 distinct Sociability dimension on which adult females score higher than males is expected in  
179 gorilla personality structure. Table 1 summarizes our predictions for the personality structure of  
180 the Virunga mountain gorilla based on key ecological and social features.

181 -----

182 Insert Table 1 about Here

183 -----

## 184 **Methods**

### 185 **Subjects**

186 Subjects were 116 wild habituated Virunga mountain gorillas (60 females and 56 males;  
187 **Table 2**) monitored by the **Dian Fossey Gorilla Fund's** Karisoke Research Center in the  
188 Volcanoes National Park, Rwanda. The mean age of subjects was 13.5 years ( $SD = 9.7$ ). Female  
189 and male gorillas had a mean age of 15.4 years ( $SD = 10.5$ ) and 11.1 years ( $SD = 8.2$ ),  
190 respectively.

191 -----

192 Insert Table 2 about Here

193 -----

### 194 **Ratings**

195 **Questionnaire.** **Personality was assessed using a version of the HPQ (Weiss et al., 2009)**  
196 **modified for studying wild mountain gorillas (HPQ<sub>GO</sub>) (see supplemental questionnaire).** For the  
197 purpose of **this** study, the HPQ<sub>GO</sub> was provided in English and French. The HPQ<sub>GO</sub> includes 54  
198 traits selected from measures and taxonomies of the human Five-Factor **Model** (Goldberg, 1990)  
199 **and later additions (see supplemental Table 1).** Each trait was paired with a brief description that  
200 **set** it in the context of wild mountain gorilla behavior. **The HPQ<sub>GO</sub> instructs raters to base their**  
201 **ratings on whether a gorilla scores above, below, or average for a trait on their “own subjective**  
202 **judgement of typical gorilla behavior” (see supplemental questionnaire) rather than on estimated**  
203 **frequencies of particular behaviors.** Raters **were instructed** to avoid discussing their **ratings and**

204 to rate each trait on a 7-point scale, ranging from trait displayed “either total absence or  
205 negligible amounts” (1) to “extremely large amounts” (7).

206 **Raters and Rating Procedure.** There were eight raters, each with more than 1.5 years of  
207 working experience with this population ( $M = 9.6$  years) and training in collecting long-term  
208 behavioral data. This led to a total of 556 ratings of the 116 gorillas ( $M = 4.8$  raters per gorilla).  
209 Ratings took place between June 2007 and January 2008. Raters completed the HPQ<sub>GO</sub> for  
210 individual gorillas they had known for at least one year. Thus, infants younger than one year  
211 were excluded from the study.

212 Six Rwandan raters used the French translation of the HPQ<sub>GO</sub> and two international  
213 researchers used the English version. Completion of the questionnaire differed slightly between  
214 English- and Rwandan-speaking raters. English-speaking raters completed the questionnaire  
215 individually, whereas Rwandan raters met as a group and rated each gorilla in assistance of a  
216 professional Rwandan translator with a Bachelor’s degree in French and English. The group  
217 setting allowed brief clarifications of the rating concept and French trait definitions in their  
218 native language, Kinyarwanda, to ensure that potential language barriers had a minimal influence  
219 on the understanding of each trait. During those meetings, raters were not allowed to discuss  
220 their rating decisions and experiences related to the gorillas.

221 **Behavioral Data Collection.** Ten researchers at the Karisoke Research Center, including  
222 four who rated gorilla personality, collected long-term behavioral data (see Table 3). Before  
223 researchers started collecting behavioral data, inter-observer reliability tests were conducted with  
224 occasional follow-ups to ensure the reliability of these data. The data set incorporates behavioral  
225 records from up to two years prior to subjects’ rating age; for example, ratings on an eight year-  
226 old gorilla would be validated with behavior collected between the gorilla’s sixth and eighth year

227 of life. Data from focal animal samples provided a mean of 23 hours ( $SD = 17$ ) of observation  
228 time per gorilla and a total of 2,691 hours. The majority of behavioral data were recorded  
229 continuously (see Table 3). Activity patterns of the focal animal and social group, as well as  
230 proximity data (number of individuals within 5 m distance) of the focal animal were recorded  
231 using instantaneous sampling with 5-min or 10-min sampling intervals. We distinguished group  
232 resting from group non-resting states (feeding, feed-travel, and travel).

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234

Insert Table 3 about Here

235

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## 236 Analyses

237 **Missing Data.** One rater omitted five trait ratings across three gorillas. Those missing  
238 values were substituted with the mean ratings for those traits over all other raters.

239 **Trait Inter-rater Reliabilities.** Because we were only interested in the reliabilities of  
240 those raters who were familiar with these gorillas, inter-rater reliabilities of ratings were  
241 determined using two intraclass correlations (*ICCs*) that treat raters as a fixed effect (Shrout &  
242 Fleiss, 1979). The first, *ICC(3,1)*, indicates the reliability of individual ratings of the raters. The  
243 second, *ICC(3,k)*, indicates the reliability of mean ratings across raters.

244 These *ICCs* were computed using mean squares derived from a general linear model in  
245 which the score assigned to a particular trait is the dependent variable. The predictors in this  
246 model include categorical variables representing the target (gorilla), the judge (rater), and the  
247 Target  $\times$  Judge interaction. The mean square for the first predictor term is the between targets  
248 mean square (BMS) and indicates the amount of variance contributed by the target. The mean  
249 square for the second predictor term is the error mean square (EMS) and indicates the amount of

250 variance contributed by the error.  $ICC(3,1)$  is equal to the ratio of the difference between BMS  
251 and EMS to the sum of BMS and the product of EMS and  $(k-1)$  where  $k$  equals the mean number  
252 of raters per subject.  $ICC(3,k)$  is equal to the ratio of the difference between BMS and EMS to  
253 BMS.

254 We excluded traits with  $ICCs \leq 0$  from further analyses. This liberal cut-off point was  
255 chosen to be consistent with prior studies and recommendations (Gosling & Vazire, 2002; Weiss  
256 et al., 2009), and because, for any measure of reliability, single traits have markedly lower  
257 reliabilities than scales (see Nakagawa & Schielzeth, 2010, equation 37 or Nunnally & Bernstein,  
258 1994, equations 6-18).

259 **Identifying Personality Structure.** For each gorilla we took the mean trait scores across  
260 raters for all reliable traits and analyzed these scores using principal-components analysis (PCA).  
261 We used Horn's (1965) parallel analysis to determine the number of components that had  
262 eigenvalues exceeding the eigenvalue expected under chance at the 95th percentile. We rotated  
263 components using orthogonal (varimax) and oblique (promax) procedures. If the oblique rotation  
264 produced components that were highly intercorrelated or noticeably different from those derived  
265 using the orthogonal rotation, we retained the components from the oblique solution. We  
266 otherwise retained the components from the orthogonal solution.

267 We next tested whether the dimensions identified were affected by the fact that the mean  
268 age of this sample was lower than that of the sample of chimpanzees ( $M = 18.7$  years;  $SD = 12.0$ ;  
269 King & Figueredo, 1997) and the sample of orangutans ( $M = 21.4$ ;  $SD = 11.5$ ; Weiss et al.,  
270 2006), both of which have comparable lifespans to gorillas. We first conducted two additional  
271 PCAs. The first was based on a subsample of 100 gorillas that were not infants (age  $> 3.5$  years).  
272 The second was based on a subsample of 86 gorillas that included only subadults and adults (age

273 > 6 years). In both cases, as before, we used the same procedure to determine the number of  
274 components to select between the varimax- or promax-rotated components. We then compared  
275 the structures derived from these subsamples to that of the full sample using targeted orthogonal  
276 Procrustes rotations (McCrae, Zonderman, Bond, Costa, & Paunonen, 1996).  
277 Finally, like previous studies that used this questionnaire (Morton et al., 2013; Weiss et al., 2006,  
278 Weiss et al., 2009, Weiss et al., 2011), trait loadings  $\geq .4$  were defined as salient. In cases where  
279 two or more components had salient loadings on a trait, the trait was assigned to the component  
280 with the higher loading. We used these definitions to generate unit-weighted component scores  
281 (Gorsuch, 1983) in which traits with salient and positive loadings were assigned a weight of +1,  
282 traits with salient and negative loadings were assigned a weight of -1, and all other loadings were  
283 assigned a weight of 0. Unit weighted component scores were converted into z-scores.

284 **Cross-species Comparisons.** To identify, describe, and label personality dimensions, we  
285 compared the gorilla personality dimensions derived in this study to those derived in studies of  
286 other species that used the HPQ or one of its antecedents (see supplemental Table 1), i.e. the  
287 Chimpanzee Personality Questionnaire (King & Figueredo, 1997) or the Orangutan Personality  
288 Questionnaire (Weiss et al., 2006). We first computed unit-weighted scores for our sample based  
289 on the personality structures of chimpanzees (King & Figueredo, 1997; Weiss et al., 2009),  
290 orangutans (Weiss et al., 2006), rhesus macaques (Weiss et al., 2011), and brown capuchin  
291 monkeys (Morton et al., 2013). We then obtained correlations between these unit-weighted  
292 scores and those based on the gorilla structure identified in this study.

293 **Component Reliabilities.** We estimated  $ICC(3,1)$  and  $ICC(3,k)$  for each gorilla  
294 personality component in the same manner as we did for the traits. For each component, we also  
295 computed Cronbach's alpha, a measure of internal consistency reliability.

296 **Age and Sex Differences.** To investigate sex and age effects on mountain gorilla  
297 personality, we conducted individual linear regression models for each gorilla personality  
298 dimension (z-scores) with sex, age, and Sex  $\times$  Age being entered as independent variables. Age  
299 was mean centered to facilitate the interpretation of interactions.

300 **Behavioral Correlations.** We used two-tailed Spearman's rank correlations to examine  
301 whether those mountain gorilla personality dimensions derived from ratings were associated with  
302 predicted behavioral observations (see Table 3). Construct validity was tested by linking  
303 behavior with personality dimensions to understand the functional bases of personality  
304 dimensions.

305 Since social behavior can be influenced by the predominant group activity (Harcourt,  
306 1978), where appropriate, behaviors were analyzed separately by group activity (see Table 3).  
307 This approach accounts for unequal proportions of group resting and non-resting periods during  
308 focal sampling. For example, grooming occurs more frequently during group resting periods in  
309 mountain gorillas (Harcourt, 1978). Also, food-stealing is expected to occur more frequently  
310 when the majority of the group is feeding or feed-traveling. Similarly, our analysis of "time spent  
311 resting" and "number of individuals within 5 m" was restricted to group resting periods since a  
312 bias in data collection towards group non-resting periods is likely to translate into less time  
313 resting and fewer individuals in proximity, respectively.

314 We also calculated frequencies of each continuously collected behavior (except  
315 displacement and grooming) per total observation time (in hours). In the case of instantaneously  
316 collected proximity data, we calculated the mean number of individuals within 5 m over all scans  
317 for each gorilla. Instantaneous data on grooming, playing, and resting were transformed into the  
318 percentage of scans a gorilla spent in each of the activities. In addition, we counted the number

319 of grooming recipients of each gorilla as a measure of social network strength. To account for  
320 the availability of potential grooming partners, we used the **number** of group members each  
321 gorilla groomed, **calculated as a percentage of total partners**, for further statistical tests.  
322 **Furthermore, the suitability of a behavior as an indicator** of a given personality dimension can  
323 change with gorilla age. For example, grooming indicates sociability in adult gorillas better than  
324 in immature gorillas because **social grooming of others is not common in mountain gorillas until**  
325 **adolescence** (Fletcher, 1994). **Hence, age effects on behaviors such as playing, grooming,**  
326 **aggression, and intervening in social conflicts, were taken into account by limiting the analyses**  
327 **to gorillas within the appropriate age range for those behaviors (see Table 3). Also, if** a behavior  
328 was analyzed by group activity, we split the dataset by group activity before calculating  
329 frequencies, means, or percentages.

330 **The** dominance strength of adult gorillas was calculated **from** displacement events using  
331 the Wittemyer and Getz (2006) method, which is particularly appropriate for dominance matrices  
332 with unknown dyadic relationships. **As a** first step, matrices of adult female and adult male  
333 dominance relationships (established through displacements) for each study group (Pablo,  
334 Beetsme, and Shinda) were rearranged by minimizing the number of inconsistencies (I) and the  
335 strength of these inconsistencies **(SI)** using an iterative procedure ('I & SI method') following de  
336 Vries (1998), provided by Matman<sup>TM</sup> software version 1.0 (Noldus Information Technology,  
337 1998). The order of two individuals, A and B, in a matrix is defined as inconsistent when A  
338 dominates B but A is below B. The strength of the inconsistency would be the distance between  
339 the ranks of A and B. Second, all unknown values  $a_{ij}$  for dyad  $i - j$  with  $i$  and  $j$  referring to  
340 reordered ranks (first step) were replaced with interpolated values  $\hat{a}_{ij}$ , calculated by **equation 1**  
341 where N is the total number of males / females in a given hierarchy **matrix:**



$$\hat{a}_{ij} = (1 - \hat{a}_{ji}) = 0.5 - ((i - j) / 2N) \quad (1)$$

342 The interpolation is thus built upon the assumption that, the greater the separation in  
343 ranks between two individuals with an unknown relationship, the more likely the higher-ranking  
344 individual is to dominate the lower-ranking individual (Bradley & Terry, 1952; Crow, 1990). As  
345 a final step, to obtain a unique rank order for adult males and adult females in each study group,  
346 the relative dominance strength for each individual  $i$  was generated by subtracting the column  
347 sum (sum of losses) from the row sum (sum of wins) in the interpolated hierarchy matrix. Once  
348 the gorilla personality structure was described, we made predictions about the relationships  
349 between behavior measures and dimensions to evaluate convergent validity between both  
350 measures (see Results section).

## 351 Results

### 352 Inter-Rater Reliabilities of Traits

353 The  $ICC(3,1)$  and  $ICC(3,k)$  for each trait are presented in supplemental Table 2. One trait,  
354 *unperceptive*, was not reliable.  $ICC(3,1)$ s of the remaining traits ranged from .03 for *predictable*  
355 to .72 for *dominant* ( $M = .26, SD = .16$ ).  $ICC(3,k)$ s of the remaining traits ranged from .14 for  
356 *predictable* to .92 for *dominant* ( $M = .58, SD = .20$ ).

### 357 Principal Component Analyses

358 Parallel analyses indicated that there were four components in the full data set, five  
359 components in the subsample that did not include infants, and four components in the subsample  
360 that only included subadults and adults. To determine whether to retain a four or five component  
361 solution, we conducted an Everett (1983) test. This involved obtaining four and five component  
362 solutions from the full data set and the two subsamples. These solutions were then compared  
363 using targeted orthogonal Procrustes rotations (McCrae et al., 1996).

364 The four component solutions for the two subsamples were nearly equivalent to those  
365 derived from the full data set (see top panel of Table 4). However, while the five component  
366 solution for the subsample that did not include infants was nearly equivalent to the full data set,  
367 the fifth component from the sample that included subadults and adults was notably lower (see  
368 bottom panel of Table 4). These results indicate that including infants and juveniles did not  
369 influence the component structure, and that the four component solution was the most stable. We  
370 therefore retained the four component solution of the full data set for further analyses.

371 -----

372 Insert Table 4 about Here

373 -----

374 Most communalities were high ( $> .6$ ), only a few communalities were low ( $< .5$ ), and the  
375 ratio of traits to dimensions was high. Therefore, our sample size was sufficient to guarantee a  
376 stable structure (de Winter, Dodou, & Wieringa, 2009; MacCallum, Widaman, Zhang, & Hong,  
377 1999). The fact that all dimensions have at least four traits with loadings greater than  $|.6|$  also  
378 indicates that the structure is stable (Guadagnoli & Velicer, 1988).

379 The correlations among dimensions were modest with a range of .02 to .41 and a mean of  
380 .22, and there were only minor differences between the varimax- (see Table 5) and promax-  
381 rotated dimensions (see supplemental Table 3). We thus interpreted the varimax solution. The  
382 dimensions explained 68% of the variance.

383 -----

384 Insert Table 5 about Here

385 -----

386 **Cross-Species Comparison**



410 into Openness. In humans and great apes, this facet is commonly found in Extraversion  
411 (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006).  $O_{GO}$  also includes traits reflecting  
412 impulsiveness and emotional instability (not *unemotional*, *impulsive*, *excitable*, not *stable*,  
413 *erratic*, not *predictable*, and not *cool*) which load on Neuroticism across humans and other great  
414 apes (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2006).

415 The third dimension describes *social*, *affectionate*, *gentle*, and *sympathetic* gorillas who  
416 were not *solitary*, not *depressed*, not *defiant*, and not *individualistic*. Six out of nine traits  
417 matched those defining Extraversion or Agreeableness in humans and other great apes  
418 (Goldberg, 1990; King & Figueredo, 1997; Weiss et al., 2006; Weiss et al., 2009) (see Table 5).  
419 A combination of Extraversion and Agreeableness dimensions also emerged in the personality of  
420 rhesus macaques (Weiss et al., 2011) and brown capuchin monkeys (Morton et al., 2013), named  
421 Friendliness and Sociability, respectively (see Table 6). Given the closest resemblance of this  
422 gorilla dimension to the brown capuchin monkey Sociability dimension, and the absence of an  
423 activity facet tied to Sociability in gorillas as in the Extraversion dimension of other great apes,  
424 we labeled the third dimension Sociability ( $S_{GO}$ ).

425 Likely on account of its high negative loadings on traits related to aggressive behavior  
426 and hostile emotions, the final gorilla dimension most closely resembles the inverse of the  
427 orangutan (Weiss et al., 2006) and rhesus macaque Dominance (Weiss et al., 2011) and was the  
428 mirror image of brown capuchin Assertiveness (Morton et al., 2013) (see Table 6). This  
429 dimension also marks traits capturing low Agreeableness in humans (Goldberg, 1990) and shares  
430 trait loadings of Conscientiousness in chimpanzees (Weiss et al., 2009) (see Table 5). The last  
431 gorilla dimension thus describes content, emotionally stable, and friendly gorillas. Since key

432 traits from human Conscientiousness such as *organized, cautious, thoughtful*, and *persistent* were  
433 missing **in** this dimension, we **labeled** it ‘Proto-Agreeableness’ (**P-A<sub>GO</sub>**).

#### 434 **Component Inter-Rater Reliabilities and Internal Consistency Reliabilities**

435 The inter-rater reliabilities of components ranged from moderate to substantial. The  
436 internal consistency reliabilities were all high (see Table 7).

437 -----

438 Insert Table 7 about Here

439 -----

#### 440 **Age and Sex Differences**

441 The parameter estimates of the regression model (see Table 8) for the examination of age  
442 and sex effects on each gorilla personality dimension (see Figure 1) **show** that male gorillas **had**  
443 higher Dominance scores than female gorillas from approximately the age of 8 years with a  
444 significantly steeper age-related increase on  $D_{GO}$  in males compared to females. Males were also  
445 more open than females in particular until the age of 20 years but also **displayed** a steeper age-  
446 related decrease in Openness. Female gorillas, on the other hand, were more social than males.  
447 This sex difference was consistent across all ages. No sex differences occurred in the gorilla  
448 variant of Agreeableness which declined with age.

449 -----

450 Insert Table 8 and Figure 1 about Here

451 -----

#### 452 **Behavioral Validation**

453 **Predictions.** Based on the gorilla personality structure, we made predictions for  
454 associations between behavioral measures (see Table 3) and each of the personality dimensions.

455 We predicted  $D_{GO}$  would be related to the dominance strength in adult gorillas. We also expected  
456 a positive association between rates of interventions (per hour) and  $D_{GO}$  because a supportive  
457 facet characterizes this dimension.

458 Exploratory and investigative tendencies, as well as activity, are key facets of  $O_{GO}$  and  
459 thus this dimension should be positively associated with rates of staring (per hour) and playing  
460 (percentage of scans) and whilst negatively associated with resting (percentage of scans).

461 Moreover, because staring and playing imply close proximity to interaction partners, we  
462 predicted a direct association between  $O_{GO}$  and rates of approach and the number of gorillas  
463 within 5 m.

464  $S_{GO}$  is comprised of traits characterizing a social, agreeable, and peaceful gorilla, and is  
465 expected to correspond to social behavior such as staring, grooming (percentage of scans), and  
466 rate of touching (per hour). In addition, an inverse relationship was predicted between  $S_{GO}$  and  
467 rates of aggression (per hours). Because of the lack of an activity facet in  $S_{GO}$ , we did not expect  
468 a correlation between this dimension and playing. Also, like  $O_{GO}$ , gorillas high on Sociability  
469 should have high rates of approach and high numbers of gorillas within 5 m to maintain an  
470 environment for social interaction.

471 We predicted a negative relationship between  $P-A_{GO}$ , which has negative loadings on the  
472 traits *manipulative* and *aggressive*, and both rates of aggression and rates of interventions, which  
473 usually involve aggressive elements. Low jealousy and stinginess that characterize higher scores  
474 on this dimension should be reflected in low rates of food-stealing (per hour).

475 **Correlations Between Gorilla Behavior and Personality Dimensions.** As expected,  
476  $D_{GO}$  correlated positively with dominance strength in adult gorillas (see Figure 2) and rates of  
477 interventions (by subadults and adults) (see Table 9). We conducted an additional test with rates

478 of interventions for males and females separately which showed a significant relationship  
479 between rates of interventions and  $D_{GO}$  scores in males ( $N = 39, r_s = .53, p < .001$ ) but not in  
480 females ( $N = 47, r_s = .25, p = .09$ ).  $D_{GO}$  was also associated with other behaviors beyond our  
481 predictions. Gorillas scoring high on Dominance spent more time resting than gorillas scoring  
482 low on this dimension, and rates of staring and approaches were lower in gorillas scoring high on  
483 Dominance.

484 -----  
485 Insert Figure 2 about Here  
486 -----

487 Consistent with key traits of  $O_{GO}$  and our predictions, gorillas scoring high on this  
488 dimension had higher rates of staring and spent less time resting and immatures also spent more  
489 time playing. We also expected a positive correlation between  $O_{GO}$  and approach rates as well as  
490 the number of individuals within 5m but there was no association found. Instead,  $O_{GO}$  was  
491 negatively related to dominance strength of adult gorillas. Finally, the rate of touching was  
492 positively correlated with  $O_{GO}$ .

493 In line with our predictions, gorillas high on  $S_{GO}$  had more individuals in close proximity  
494 and higher approach rates. The rate of touching was not significantly correlated with  $S_{GO}$ . Also  
495 as expected, sociable subadult and adult gorillas spent more time grooming and had more  
496 grooming partners. Lastly, sociable gorillas spent less time resting during group resting periods.

497 As predicted, the fourth gorilla personality dimension,  $P-A_{GO}$ , was negatively related to  
498 rates of interventions. Contrary to our predictions, rates of aggression and rates of food stealing  
499 in subadult and adult gorillas were not significantly related to  $P-A_{GO}$ . Similar to more sociable

500 gorillas, gorillas high on P- $A_{GO}$  also spent less time resting, stared more frequently at other  
501 gorillas and had higher approach rates.

## 502 Discussion

503 Our main goal was to describe the personality structure of a wild habituated mountain  
504 gorilla population. The structure of wild mountain gorilla's personality included the dimensions  
505 Dominance, Openness, Sociability, and Proto-Agreeableness. These dimensions are associated  
506 with observed behaviors and had characteristics unique to gorillas and characteristics shared with  
507 other hominoids.

508 The inter-rater and internal consistency reliabilities of these dimensions and their traits  
509 are comparable to those found in studies of captive, semi-free, and free ranging nonhuman  
510 primates (Capitanio, 1999; King & Farmer, 2005; King & Figueredo, 1997; Konečná et al.,  
511 2008; Morton et al., 2013; Uher & Asendorpf, 2008; Weiss et al., 2007; Weiss et al., 2009,  
512 Weiss et. al., 2011), and also to those of facets (Costa & McCrae, 1992) or items (Kenrick &  
513 Stringfield, 1980) found in studies of humans. Yet, we cannot exclude rating biases due to  
514 previous discussions between about the animals, which is a possible problem of all personality  
515 studies based on ratings (Cicchetti, 1994).

## 516 Dominance

517 Like other primates (Freeman & Gosling, 2010), wild mountain gorillas possess a  
518 dimension associated with competitive prowess ( $D_{GO}$ ). However, the gorilla variant differs from  
519 those of other apes and rhesus macaques in two respects. First,  $D_{GO}$  lacks an aggressive facet, a  
520 finding underpinned by a lack of an association between this dimension and rates of aggression.  
521 This suggests that aggressive features are not necessarily attributes of a dominant mountain  
522 gorilla. Secondly,  $D_{GO}$  incorporates traits (*protective*, *helpful*, and *sensitive*) that loaded on



523 Agreeableness in other hominoids (Goldberg, 1990; King & Figueredo, 1997; Weiss et al.,  
524 2006). This ‘supportive’ facet may be specific to Virunga mountain gorillas or it may be specific  
525 to gorillas more generally. This facet can be explained in terms of species-typical social  
526 organization and the role of dominant males in gorilla social groups, which includes group  
527 protection and the mediation of within-group social conflicts (Schaller, 1963; Watts, 1996). Such  
528 an interpretation is further supported by clear links between  $D_{GO}$  and behavioral measures such  
529 as dominance strength and rates of interventions. Our findings also indicate that high-ranking  
530 females intervene more often than low-ranking females. Thus, high-ranking females may play a  
531 role similar to males in mediating within-group conflicts. However, the relationship between  
532 female dominance and female’s social role within mountain gorilla groups is not well-understood  
533 and needs to be addressed in future studies. Our findings also revealed lower scores on  $D_{GO}$  in  
534 females than in males, as might be expected in the male-dominated mountain gorilla society. The  
535 absence of a ‘supportive’ facet in captive western lowland gorillas (Gold & Maple, 1994; Kuhar  
536 et al., 2006; Schaefer & Steklis, 2014) may be due to the lack of key circumstances in captivity,  
537 such as external threats from inter-group encounters or it may reflect the smaller number of traits  
538 assessed by the GBI.

539 Gorillas high on  $D_{GO}$  also stare less at other gorillas, have lower approach rates, spend  
540 more time resting and groom fewer group members. Although these associations were not  
541 predicted, they are consistent with certain aspects of mountain gorilla socio-ecology. In  
542 particular, staring in mountain gorillas has multiple functions and tends to be directed up the  
543 hierarchy (Yamagiwa, 1992). Also, given that dominant gorillas are responsible for group  
544 protection, resting may allow dominant individuals to monitor the group and environment.  
545 Finally, dominant gorillas are group leaders and are used as a reference to the group’s center

546 (Watts, 1985). Establishing strong bonds with the protectors of the group through close  
547 interactions is important for group members and may be reflected in higher approach rates and  
548 grooming efforts towards dominant gorillas rather than vice versa (Harcourt & Stewart, 2007;  
549 Watts, 1992).

550 Our findings also indicate that among great apes, the absence of a broadly defined,  
551 distinct, dominance-like dimension (Digman, 1990; Goldberg, 1990) remains a unique feature of  
552 human personality (de Waal, 1995). This is not to say that narrowly defined lower-order  
553 dimensions or facets (Cattell & Mead, 2008; Costa & McCrae, 1995; Morrone-Strupinsky &  
554 Depue, 2004; Patrick, Fowles, & Krueger, 2009; Tellegen, 1982) related to dominance do not  
555 exist or cannot be found in humans. Indeed, studies have found elements related to agency,  
556 boldness, assertiveness, social dominance, ambition, and achievement in humans (Benning,  
557 Patrick, Blonigen, Hicks, and Iacono, 2005; McCrae, 1995; Morrone-Strupinsky & Depue, 2004;  
558 Patrick et al., 2009). However, these are specific to the particular instrument used in personality  
559 assessment and generally do not emerge in principal component or exploratory factor analyses of  
560 large batteries of items (Goldberg, 1990). Assessing humans using a version of the HPQ will rule  
561 out the possibility that the Dominance dimension is specific to the HPQ and not the species being  
562 rated. If such a study fails to identify a dominance-like dimension in humans, this would suggest  
563 that the lack of such a dimension is a unique feature of human personality.

564 There is growing evidence that differences between hierarchical societies of nonhuman  
565 great apes and humans reflect our evolutionary past as hunter-gatherers, including strong  
566 egalitarian tendencies, with social coalitions and alliances that span across a network of groups  
567 (Gavrilets, Duenez-Guzman, & Vose, 2008). Studies of personality structure in the more  
568 egalitarian bonobos (de Waal, 1995) are needed to determine whether the lack of Dominance, a

569 seemingly unique feature of human personality, evolved through the selection of increasingly  
570 cooperative-egalitarian societies (Boehm, 1999; Weiss et al., 2011).

### 571 **Openness**

572 Consistent with our predictions, mountain gorilla personality structure includes an  
573 Openness dimension.  $O_{GO}$  was most similar to Openness found in brown capuchin monkeys  
574 (Morton et al., 2013) and rhesus macaques (Weiss et al., 2011), and to a lesser extent to the  
575 narrower variants in humans (Goldberg, 1990) and chimpanzees (King & Figueredo, 1997;  
576 Weiss et al., 2009) and to orangutan Extraversion. Orangutans are semi-solitary (Galdikas, 1985)  
577 and lack an Openness dimension (Weiss et al., 2006). Thus, these findings suggest that Openness  
578 benefits group-living primates with complex social systems.

579 The relatively stronger similarity of  $O_{GO}$  to brown capuchin monkeys (Morton et al.,  
580 2013) compared to phylogenetically closer related great apes and rhesus macaques is difficult to  
581 explain. The activity facet in  $O_{GO}$  may play a role therein as it is a key part of a distinct Activity  
582 dimension in rhesus macaques, which are believed to represent the common ancestor of  
583 catarrhines, and combines with sociability-related traits to create an Extraversion dimension in  
584 orangutans (Weiss et al., 2006), chimpanzees (King & Figueredo, 1997; Weiss et al., 2009), and  
585 humans (Goldberg, 1990). Mountain gorillas and brown capuchins lack a distinct Extraversion  
586 dimension, and traits describing activity merge with a facet that captures Openness (*curious,*  
587 *innovative, inquisitive, and inventive*) across primates.

588 The question remains as to why Activity is part of  $O_{GO}$  and not part of  $S_{GO}$  or  
589 Extraversion as in chimpanzees, humans, and orangutans? Activity combined with sociability  
590 may be a key feature of primates living in societies with high degrees of fission-fusion dynamics  
591 where group/party size and composition vary frequently (Aureli et al., 2008). Considering that

592 our knowledge of orangutan personality is based on a captive population composed of Sumatran  
593 and Bornean orangutan species which exhibit different degrees of fission-fusion dynamics in the  
594 wild (van Schaik, 1999), it would be valuable to investigate personality separately for each  
595 species. We predict that with increasing fission-fusion dynamics and complexity of social  
596 systems, Openness and extraverted Sociability (Extraversion) would become more distinct  
597 dimensions.

598 As predicted,  $O_{GO}$  combines three traits *curiosity*, *playful*, and *active*. Open gorillas had  
599 relatively high rates of staring and allocated less time to resting and more time to playing.  
600 Staring reflects curiosity but can also function as play solicitation in mountain gorillas  
601 (Yamagiwa, 1992). Furthermore, our findings demonstrate that  $O_{GO}$  captures behavioral  
602 variability among mountain gorillas even when excluding immature gorillas who are more active  
603 and playful and show greater curiosity within their environment. Playing, a key trait of  $O_{GO}$ , may  
604 remain important into early adulthood because of its role in developing social competence and  
605 forming long-term social bonds (Baldwin & Baldwin, 1974; Thompson, 1996), refining the  
606 neuromuscular system (Byers & Walters, 1995), and developing flexible kinematic and  
607 emotional responses to cognitively demanding situations (Spinka et al., 2001).

608 The predicted relationships between  $O_{GO}$  and rates of approach and proximity patterns  
609 were not supported. The lack of evidence for those relationships suggests that open gorillas  
610 socialize more opportunistically rather than actively seeking out social partners and/or that  $O_{GO}$   
611 encompasses behaviors that do not require social interactions, including the exploration of new  
612 objects in the environment. An open gorilla may also frequently transfer between groups without  
613 developing close associations with group members.

614 **Sociability**

615 As predicted, mountain gorilla personality encompasses a dimension related to  
616 Sociability ( $S_{GO}$ ) on which females score higher than males, reflecting the females' role in  
617 establishing bonds with males and caring for offspring (Fletcher, 1994; Harcourt & Stewart,  
618 2007; Watts, 1992). Also consistent with our predictions,  $S_{GO}$  was directly related to time spent  
619 grooming, number of grooming partners, proximity pattern, and rates of approach. In contrast to  
620 humans and other great apes (Goldberg, 1990; King & Figueredo, 1997; Weiss, King & Perkins,  
621 2006), mountain gorillas lack distinct Agreeableness and Extraversion dimensions. Instead, they  
622 possess a blend of these dimensions. The same pattern is found in rhesus and Barbary macaques  
623 whose personality structures may be representative of the common ancestor of catarrhines  
624 (Konečná et al., 2012; Weiss, Adams, & Perkins, 2006), and also in brown capuchin monkeys  
625 (Morton et al., 2013).

626 This pattern of hominoid personality dimensions raises intriguing questions. For example,  
627 what selection pressures favor separate Extraversion and Agreeableness dimensions?  
628 Independent Agreeableness and Extraversion dimensions may be favoured in primate species  
629 living in social systems with fission-fusion dynamics such as humans, chimpanzees, and  
630 orangutans (Aureli et al., 2008). The potential for spatio-temporal variation in cohesion and  
631 individual membership in groups of primates with fission-fusion dynamics may require more  
632 complex and flexible social and cognitive abilities (Aureli et al., 2008). The independence of  
633 Agreeableness and Extraversion offers more behavioral strategies to respond and adapt to  
634 varying ecological and social environments affecting costs and benefits of living in groups. This  
635 is supported by a study in humans showing that individual differences in Extraversion and  
636 Agreeableness are linked to variation in cooperative behaviour across different situations (Koole,  
637 Jager, van den Berg, Vlek, & Hofstee, 2001). For examples, extraverted and disagreeable

638 participants followed a strategy that maximized their gain from collective sources across  
639 situations, while introverted and agreeable participants were more cooperative and sensitive to  
640 situational changes in the social environment and in collective resource availability. However,  
641 fission-fusion dynamics may not be the only evolutionary driver of independent Agreeableness  
642 and Extraversion dimensions in primates as a blend of both dimensions was also found in brown  
643 capuchin monkeys (Morton et al., 2013) of which some populations live in a society with lower  
644 fission-fusion dynamics (Aureli et al., 2008).

#### 645 **Proto-Agreeableness**

646 The reverse (multiply trait loadings by “-1”) of gorilla ‘Proto-Agreeableness’ (P- $A_{GO}$ )  
647 captured traits that are part of the negative pole of human Agreeableness (Goldberg, 1990) and of  
648 the positive pole of orangutan Dominance (Weiss et al., 2006). This dimension may stem from  
649 the lost aggressive-selfish facet in  $D_{GO}$  that is attached to Dominance in rhesus macaques and  
650 orangutans (Weiss et al., 2006; Weiss et al., 2011). The lack of covariance between aggressive-  
651 selfish behavioral tendencies and traits describing Dominance may highlight the relatively low  
652 importance of aggressive tendencies, particularly given the degree of sexual dimorphism,  
653 compared to supportive tendencies for gorilla dominance.

654 With the exception of dominance strength, the behaviors associated with P- $A_{GO}$  are the  
655 same, though in the opposite direction, as those related to  $D_{GO}$ . In other words, the correlations  
656 suggest that gorillas high on ‘Proto-Agreeableness’ share behaviors with low-ranking gorillas,  
657 but they are not necessarily low in the social hierarchy. Similar findings in humans show that  
658 high prominence, respect, and being influential are not related to Agreeableness (Anderson,  
659 John, Keltner, & Kring, 2001; Savin-Williams, 1979).

660           **Similar** to the orangutan (Weiss et al., 2006) and rhesus macaque (Weiss et al., 2011)  
661 personality structure, and indeed the personality structure of most non-primate species (Gosling  
662 & John, 1999), mountain gorilla personality lacks a dimension like human Conscientiousness  
663 (Goldberg, 1990). There is **some** indication that captive western lowland gorillas **possess a**  
664 **dimension like** Conscientiousness (Schaefer & Steklis, 2014), but given the small sample size (8  
665 individuals), additional data are needed to confirm **those findings**. To date, the hypothesis holds  
666 that Conscientiousness evolved recently within **Homininae** (Gosling & John, 1999). This does  
667 not mean that other primates and animals do not **differ in** behavioral tendencies **that underpin**  
668 Conscientiousness, such as determination, planning, order, and discipline (Gosling & John,  
669 1999). Rather, it indicates that these tendencies are not as central in most animals' personalities  
670 and behavioral repertoires **so as** to be captured **by** a separate dimension. **Selection for**  
671 **Conscientiousness within Homininae** may be the emergence of cooperative hunting **behavior,**  
672 which **takes** a central role in hominid evolution and involves high levels of organization, timing,  
673 control, and, to some extent, delayed gratification (Boesch & Boesch, 1989). **Alternatively,**  
674 **societies with strong reliance on social learning, tool use, and with distinct "cultural" traditions**  
675 **may play an important role in the evolution of Conscientiousness in primates (Morton et al.,**  
676 **2013) which is supported by close resemblances of Conscientiousness in organutan Intellect**  
677 **(Weiss et al., 2006) and in brown capuchin Attentiveness (Morton et al., 2013).**

678           In line with our predictions that neurotic tendencies are less **evident** in species that live in  
679 stable and predictable **environments**, Neuroticism, which captures fearfulness, emotional  
680 reactivity, vulnerability to stress and excitability (Gosling & John, 1990), is absent in mountain  
681 gorillas. **This contrasts with findings in humans and other great apes (Costa & McCrae, 1992;**  
682 **Digman, 1990; Goldberg, 1990; Weiss et al., 2009; Weiss et al., 2006).** Studying personality of

683 gorilla species along a gradient of increasing seasonal variation in food availability would be a  
684 strong test of this prediction.

### 685 **Conclusions**

686 Our findings highlight the insights into the proximate and ultimate bases of personality  
687 by merging approaches hailing from behavioral, ecology, personality psychology, and  
688 comparative psychology. Future studies, applying similar methods to study primates that span a  
689 range of social systems and ecological niches, are needed to understand the evolution of primate  
690 personality and its relationship with social and environmental factors. Studying personality  
691 variation across well-studied wild gorilla species and populations (Sousa & Casanova,  
692 2005/2006) will open up new opportunities to better understand the interplay of behavior,  
693 ecology, social systems, and personality that is only partially elucidated by captive populations.  
694 Future comparative personality studies also have the potential to provide further insight into  
695 speciation processes and the role that personality plays in these processes (Uher, 2008; Weiss &  
696 Adams, 2013).



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1002 Table 1

1003 **Predictions** for dimension categories (see Freeman & Gosling, 2010) in Virunga mountain gorilla  
 1004 personality structure based on gorilla-/population-specific ecology and society ('+' expected, '-'  
 1005 not expected, 'empty' no prediction).

Ecological & social feature	Sociability	Confidence	Aggression	Fearfulness	Curiosity	Anxiousness	Playfulness	Activity	Excitability	Impulsivity	Dominance	Agreeableness	Irritability	Intelligence	Independence
Stable environment			-	-	-			-	-				-		
Low food competition / no territorial defence			-												
Cohesive social groups / lack of fission-fusion	+							-							
Strong male-female bonds	+														
Social role of males and females												+			
Hierarchical social system (dominance)		+									+			+	+
Male and female dispersal					+										

1006

1007 Table 2

1008 Distribution of 116 study gorillas over all age-sex classes (see Table II in Breuer et al., 2009)

1009 with modified age-range of infants.

Age category	Age-range (year)	N females	N males	N Total
Full-grown silverback	>15	0	18	18
Young silverback	>12-15	0	6	6
Blackbacks	>8-12	0	8	8
Adult female	> 8.0	40	-	40
Sub-adult	> 6.0 – 8.0	7	7	14
Juvenile	> 3.5 – 6.0	9	6	15
Infant	1.0 – 3.5	4	11	15

1010



1011 Table 3

1012 Behavioral categories and rules for recording each behavior.

Behavior	Definition	Recording rules	Data restricted to:
Aggression	An individual successfully or unsuccessfully tries to hit, shove, drag, kick, grab, chase or bite another individual in an agonistic manner often associated with a threatening face, such an open-mouth.	Continuous	Sub-/adults
Staring	An individual looks intently at another individual (or vice versa) at very close range between > 0-1 m.	Continuous	
Intervention	During an agonistic encounter, a previously uninvolved individual (the third party) ends a conflict between the two individuals engaged in an agonistic interaction by supporting any one individual or being neutral. This also includes intervention during food-stealing.	Continuous	Sub-/adults
Displacement	One individual moves away from another approaching individual when the approaching individual is within 2 m proximity. The retreat is in direct response to the approaching individual. This may include physical contact which should be recorded as a separate behavioral event. Actor and recipient are recorded.	Continuous	Adults
Food-stealing	An individual takes or tries to take a food item either directly from the hands or mouth of another or from a pile of food collected by another individual.	Continuous	Non-resting & Sub-/adults
Touching	An individual gently puts hands, fingers (not bent) or feet on another individual in an affiliate manner.	Continuous	
Approach	One individual moves to within 2 m of another individual and either remains within 2m for a minimum duration of 1 min or engages in an affiliative behavior. This behavior is not recorded during group travel periods.	Continuous	
Grooming	An individual picks through the hair of another individual with fingers or lips, removing dry skin, dirt, insects, etc. Actor and recipient are recorded.	Continuous / Instant	Resting & Sub-/adults
Playing	An individual engages in wrestling, chasing, sparring, and/or mock-biting with another individual. This category also includes infants playing on mother's body.	Instant	Immatures
Resting	The focal is inactive in one spot without actively engaging in social interactions.	Instant	Resting
Individuals within 5 m	Sum of group members within 0-5 m distance to the focal.	Instant	Resting

1013

1014 Table 4

1015 Everett (1983) test of robustness of the four- and five dimension solutions.

	I	II	III	IV		Congruence
Infants excluded	0.98	0.99	0.99	0.99		0.99
Infants & Juveniles excluded	0.96	0.97	0.98	0.95		0.99
	I	II	III	IV	V	Congruence
Infants excluded	0.98	0.99	0.99	1.00	0.99	0.99
Infants & Juveniles excluded	0.97	0.98	0.97	0.99	0.86	0.96

1016

1017 Table 5

1018 Traits loading on gorilla personality **dimensions** (R reflected) derived from a PCA with varimax

1019 rotation including 116 gorillas compared to other great apes.

Trait	Gorilla							$h^2$
	HU	CH	OR	D <sub>R</sub>	O	S	P-A <sub>R</sub>	
<i>Intelligent</i>	+O <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	<b>0.91</b>	-0.09	0.05	-0.17	0.86
<i>Decisive</i>	+C <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	<b>0.81</b>	-0.22	-0.13	-0.20	0.77
<i>Protective</i>	+A <sup>b</sup>	+A <sup>d</sup>	+A <sup>f</sup>	<b>0.81</b>	-0.16	-0.07	-0.39	0.83
<i>Timid</i>	-E <sup>a,c</sup>	-D <sup>d</sup>	+N <sup>f</sup>	<b>-0.80</b>	-0.36	0.05	0.07	0.78
<i>Anxious</i>	+N <sup>a,c</sup>	-D <sup>e</sup>	+N <sup>f</sup>	<b>-0.78</b>	-0.36	0.04	-0.24	0.79
<i>Independent</i>	-N <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	<b>0.77</b>	-0.25	-0.37	-0.24	0.84
<i>Dominant</i>	+E <sup>a,c</sup>	+D <sup>d</sup>	+D <sup>f</sup>	<b>0.75</b>	-0.25	-0.14	<b>-0.45</b>	0.85
<i>Fearful</i>	+N <sup>a</sup>	-D <sup>d</sup>	+N <sup>f</sup>	<b>-0.73</b>	0.03	0.05	-0.21	0.58
<i>Sensitive</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	<b>0.72</b>	-0.36	0.27	-0.08	0.73
<i>Distractible</i>	----	----	----	<b>-0.71</b>	<b>0.44</b>	0.35	0.10	0.83
<i>Helpful</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	<b>0.68</b>	-0.31	0.29	-0.32	0.75
<i>Bullying</i>	-A <sup>b</sup>	+D <sup>d</sup>	+D <sup>f</sup>	<b>0.64</b>	0.15	-0.29	-0.57	0.83
<i>Dependent</i>	+N <sup>a</sup>	-D <sup>d</sup>	-I <sup>f</sup>	<b>-0.63</b>	0.33	<b>0.40</b>	0.25	0.73
<b>Disorganized</b>	-C <sup>a</sup>	-C <sup>d</sup>	-I <sup>f</sup>	<b>-0.62</b>	<b>0.55</b>	-0.05	0.07	0.68
<i>Submissive</i>	-E <sup>c</sup> /+N <sup>a</sup>	-D <sup>d</sup>	-D <sup>f</sup>	<b>-0.61</b>	-0.19	0.32	0.28	0.59
<i>Imitative</i>	-O <sup>b</sup>	+E <sup>d</sup>	+E <sup>f</sup>	<b>-0.60</b>	<b>0.53</b>	0.39	0.26	0.87
<i>Persistent</i>	+C <sup>a</sup>	+D <sup>d</sup>	+D <sup>f</sup>	<b>0.55</b>	0.22	-0.16	<b>-0.47</b>	0.60
<i>Clumsy</i>	----	-C <sup>e</sup>	+I <sup>f</sup>	<b>-0.54</b>	0.09	-0.03	-0.02	0.30
<i>Vulnerable</i>	+N <sup>c</sup>	-D <sup>e</sup>	+N <sup>f</sup>	<b>-0.53</b>	0.31	-0.16	0.15	0.42
<i>Active</i>	+E <sup>a</sup>	+E <sup>d</sup>	+E <sup>f</sup>	-0.10	<b>0.83</b>	0.21	0.27	0.81
<i>Cool</i>	-E <sup>a</sup>	-N <sup>e</sup>	-N <sup>f</sup>	0.23	<b>-0.77</b>	0.27	0.22	0.77
<i>Thoughtless</i>	-C <sup>c</sup> /-A <sup>a</sup>	-C <sup>e</sup>	----	-0.20	<b>0.77</b>	-0.15	-0.12	0.66
<i>Unemotional</i>	-N <sup>a,c</sup>	-N <sup>d</sup>	-E <sup>f</sup>	-0.08	<b>-0.76</b>	-0.11	-0.05	0.60
<i>Playful</i>	+E <sup>a</sup>	+E <sup>d</sup>	+E <sup>f</sup>	-0.40	<b>0.75</b>	0.35	0.27	0.91
<i>Impulsive</i>	+E <sup>a</sup>	-C <sup>d</sup>	+N <sup>f</sup>	-0.07	<b>0.74</b>	-0.07	-0.35	0.68
<i>Lazy</i>	-C <sup>a</sup>	-E <sup>d</sup>	-E <sup>f</sup>	-0.23	<b>-0.73</b>	-0.12	-0.25	0.67
<i>Curious</i>	+O <sup>a</sup>	+O <sup>e</sup>	+E <sup>f</sup>	-0.38	<b>0.73</b>	0.36	0.07	0.81
<i>Inventive</i>	+O <sup>a</sup>	+O <sup>d</sup>	+E <sup>f</sup>	-0.08	<b>0.70</b>	0.22	-0.21	0.59
<i>Excitable</i>	+N <sup>a</sup>	+N <sup>d</sup>	+N <sup>f</sup>	-0.12	<b>0.70</b>	-0.11	-0.37	0.64
<i>Inquisitive</i>	+O <sup>a</sup>	+O <sup>d</sup>	+E <sup>f</sup>	-0.31	<b>0.68</b>	0.36	0.05	0.69
<i>Reckless</i>	-C <sup>a</sup>	-C <sup>d</sup>	+D <sup>f</sup>	-0.09	<b>0.63</b>	-0.25	<b>-0.50</b>	0.72
<i>Innovative</i>	+O <sup>a</sup>	+O <sup>e</sup>	----	0.14	<b>0.62</b>	0.08	-0.22	0.46
<i>Stable</i>	-N <sup>a</sup>	-N <sup>d</sup>	-N <sup>f</sup>	0.27	<b>-0.61</b>	0.31	0.13	0.56
<i>Conventional</i>	-O <sup>c</sup> /-C <sup>a</sup>	+A <sup>e</sup>	-E <sup>f</sup>	0.05	<b>-0.60</b>	0.36	0.19	0.53
<i>Quitting</i>	-C <sup>c</sup>	-C <sup>e</sup>	----	-0.48	<b>0.60</b>	0.14	0.14	0.64
<i>Erratic</i>	-C <sup>a</sup>	-C <sup>d</sup>	+N <sup>f</sup>	-0.25	<b>0.57</b>	-0.38	-0.27	0.60
<i>Predictable</i>	+C <sup>a</sup>	+C <sup>d</sup>	-N <sup>f</sup>	-0.24	<b>-0.48</b>	0.41	0.03	0.46
<i>Cautious</i>	+C <sup>a</sup>	-D <sup>d</sup>	+N <sup>f</sup>	0.07	-0.37	-0.14	-0.32	0.26
<i>Friendly</i>	+A <sup>a</sup>	+E <sup>d</sup>	+A <sup>f</sup>	-0.21	0.12	<b>0.87</b>	0.22	0.86
<i>Sociable</i>	+E <sup>a,c</sup>	+E <sup>d</sup>	+A <sup>f</sup>	-0.01	0.27	<b>0.85</b>	-0.17	0.82
<i>Affectionate</i>	+A <sup>a</sup>	+E <sup>d</sup>	+A <sup>f</sup>	0.03	-0.04	<b>0.82</b>	0.03	0.68
<i>Solitary</i>	-E <sup>b</sup>	-E <sup>d</sup>	-E <sup>f</sup>	0.15	-0.12	<b>-0.81</b>	-0.07	0.70
<i>Depressed</i>	-E <sup>b</sup>	-E <sup>d</sup>	-E <sup>f</sup>	-0.08	-0.33	<b>-0.76</b>	-0.18	0.72
<i>Gentle</i>	+A <sup>b</sup>	+A <sup>d</sup>	-D <sup>f</sup>	-0.14	-0.22	<b>0.68</b>	<b>0.43</b>	0.70
<i>Sympathetic</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	0.38	-0.36	<b>0.63</b>	-0.06	0.68
<i>Defiant</i>	-A <sup>b</sup>	-C <sup>e</sup>	+D <sup>f</sup>	0.31	0.23	<b>-0.61</b>	<b>-0.51</b>	0.77

<i>Individualistic</i>	-N <sup>a</sup>	-E <sup>e</sup>	----	0.34	0.03	<b>-0.55</b>	<b>-0.48</b>	0.64
<i>Jealous</i>	-A <sup>a</sup> /+N <sup>a,c</sup>	-C <sup>d</sup>	+D <sup>f</sup>	0.15	0.12	-0.12	<b>-0.85</b>	0.77
<i>Irritable</i>	-A <sup>a,c</sup>	-C <sup>e</sup>	+D <sup>f</sup>	0.17	0.18	<b>-0.42</b>	<b>-0.75</b>	0.81
<i>Aggressive</i>	-A <sup>a</sup>	-C <sup>d</sup>	+D <sup>f</sup>	0.35	0.11	<b>-0.48</b>	<b>-0.71</b>	0.87
<i>Stingy</i>	-A <sup>a,c</sup>	+D <sup>d</sup>	+D <sup>f</sup>	0.45	-0.07	-0.23	<b>-0.68</b>	0.72
<i>Manipulative</i>	-A <sup>a</sup>	+D <sup>e</sup>	+D <sup>f</sup>	0.31	-0.27	0.28	<b>-0.53</b>	0.53
<i>Autistic</i>	----	nl	nl	-0.01	0.13	-0.05	-0.29	0.11
% variance				21	21	15	11	

1020 *Note.* Boldface = salient loadings; nl = no loading; '----' = trait (or included term) not assessed; '+' = positive  
1021 loadings; '-' = negative loadings;  $h^2$  communality; E = Extraversion (facets: sociability, assertiveness, activity,  
1022 positive emotions<sup>§</sup>); C = Conscientiousness (facets: deliberation, self-discipline, dutifulness, order<sup>§</sup>); O = Openness  
1023 (facets: ideas/intellect, imagination, creativity, curiosity<sup>§</sup>); N = Neuroticism (facets: anxiety, depression,  
1024 vulnerability to stress, moodiness<sup>§</sup>); A = Agreeableness (trust, tender-mindedness, cooperation, lack of aggression<sup>§</sup>);  
1025 D = Dominance (nonhuman great apes); I = Intellect (orangutan); HU = human, CH = chimpanzee, OR = orangutan.  
1026 <sup>a</sup> traits (or synonyms of traits) and classification (Goldberg, 1990)  
1027 <sup>b</sup> traits and their classification (Goldberg, 1990) as described in Table 1 (King & Figueredo, 1997)  
1028 <sup>c</sup> traits and their classification (McCrae & Costa, 1987)  
1029 <sup>d</sup> traits and their classification (King & Figueredo, 1997)  
1030 <sup>e</sup> traits and their classification (Weiss et al., 2008)  
1031 <sup>f</sup> traits and their classification (Weiss et al., 2006)  
1032 <sup>§</sup> for more details see John (1990) and Costa & McCrae (1992)  
1033

1034 Table 6

1035 **Correlations** between unit-weighted scores as defined by the mountain gorilla, chimpanzee (1:  
 1036 King & Figueredo, 1997; 2: Weiss et al., 2008), orangutan (Weiss et al., 2006), rhesus macaque  
 1037 (Weiss et al., 2010), brown capuchin monkey (Morton et al., 2013) personality structure.

	<i>Gorilla</i>			
	I	II	III	IV
<i>Chimpanzee1</i>				
Dominance	<b>0.97 (0.96, 0.98)</b>	-0.23 (-0.40, -0.05)	<b>-0.36 (-0.51, -0.19)</b>	<b>-0.65 (-0.75, -0.53)</b>
Extraversion	<b>-0.54 (-0.66, -0.39)</b>	<b>0.52 (0.38, 0.64)</b>	<b>0.84 (0.78, 0.89)</b>	<b>0.48 (0.32, 0.61)</b>
Conscientiousness	0.18 (-0.01, 0.35)	<b>-0.78 (-0.01, -0.35)</b>	<b>0.40 (-0.84, -0.70)</b>	<b>0.44 (0.28, 0.58)</b>
Agreeableness	<b>0.62 (0.49, 0.72)</b>	<b>-0.56 (-0.67, -0.42)</b>	<b>0.35 (0.18, 0.01)</b>	-0.13(-0.30, 0.06)
Neuroticism	-0.20 (-0.37, -0.02)	<b>0.82 (0.75, 0.87)</b>	-0.18 (-0.35, 0.01)	-0.23 (-0.39, -0.05)
Openness	<b>-0.41 (-0.55, -0.24)</b>	<b>0.86 (0.81, 0.90)</b>	0.27 (0.09, 0.43)	0.16 (-0.02, 0.34)
<i>Chimpanzee2</i>				
Dominance	<b>0.97 (0.95, 0.98)</b>	-0.22 (-0.39, -0.04)	<b>-0.42 (-0.56, -0.26)</b>	<b>-0.66 (-0.75, -0.54)</b>
Extraversion	<b>-0.51 (-0.63, -0.36)</b>	<b>0.57 (0.43, 0.68)</b>	<b>0.81 (0.74, 0.87)</b>	<b>0.44 (0.28, 0.57)</b>
Conscientiousness	-0.21 (-0.37, -0.02)	<b>-0.53 (-0.65, -0.39)</b>	<b>0.61 (0.48, 0.71)</b>	<b>0.73 (0.63, 0.81)</b>
Agreeableness	<b>0.67 (0.55, 0.76)</b>	<b>-0.49 (-0.61, -0.33)</b>	<b>0.31 (0.13, 0.47)</b>	-0.18 (-0.35, 0.00)
Neuroticism	-0.21 (-0.38, -0.03)	<b>0.82 (0.75, 0.87)</b>	-0.11 (-0.29, 0.07)	-0.17 (-0.34, 0.01)
Openness	<b>-0.39 (-0.53, -0.22)</b>	<b>0.81 (0.74, 0.87)</b>	<b>0.26 (0.08, 0.42)</b>	0.14 (-0.14, 0.31)
<i>Orangutan</i>				
Extraversion	<b>-0.53 (-0.65, -0.39)</b>	<b>0.85 (0.79, 0.89)</b>	<b>0.51 (0.36, 0.64)</b>	<b>0.33 (0.16, 0.49)</b>
Dominance	<b>0.72 (0.62, 0.80)</b>	0.04 (-0.14, 0.22)	<b>-0.62 (-0.72, -0.49)</b>	<b>-0.93 (-0.95, -0.90)</b>
Neuroticism	<b>-0.54 (-0.65, -0.39)</b>	<b>0.67 (0.56, 0.76)</b>	-0.25 (-0.42, -0.07)	-0.11 (-0.28, 0.08)
Agreeableness	<b>0.40 (0.23, 0.54)</b>	<b>-0.24 (-0.40, -0.06)</b>	<b>0.64 (0.52, 0.74)</b>	-0.06 (-0.24, 0.12)
Intellect	<b>0.96 (0.94, 0.97)</b>	<b>-0.47 (-0.60, -0.32)</b>	<b>-0.36 (-0.51, -0.19)</b>	<b>-0.50 (-0.63, -0.35)</b>
<i>Rhesus macaque</i>				
Confidence	<b>0.93 (0.89, 0.95)</b>	<b>-0.47 (-0.60, -0.31)</b>	-0.25 (-0.41, -0.07)	<b>-0.42 (-0.56, -0.26)</b>
Openness	<b>-0.49 (-0.62, -0.34)</b>	<b>0.92 (0.89, 0.95)</b>	0.23 (0.05, 0.39)	0.17 (-0.01, 0.34)
Dominance	<b>0.74 (0.64, 0.81)</b>	0.02 (-0.16, 0.20)	<b>-0.68 (-0.77, -0.57)</b>	<b>-0.91 (-0.94, -0.87)</b>
Friendliness	<b>0.50 (0.35, 0.63)</b>	-0.16 (-0.33, 0.02)	<b>0.59 (0.46, 0.70)</b>	-0.15 (-0.32, 0.04)
Activity	<b>-0.34 (-0.49, -0.16)</b>	<b>0.90 (0.86, 0.93)</b>	<b>0.18 (0.00, 0.35)</b>	0.20 (0.02, 0.37)
Anxiety	<b>-0.41 (-0.55, -0.24)</b>	<b>0.81 (0.73, 0.86)</b>	-0.17 (-0.34, 0.01)	-0.25 (-0.41, -0.07)
<i>Brown Capuchin</i>				
Assertiveness	<b>0.87 (0.81, 0.91)</b>	-0.10 (-0.28, 0.09)	<b>-0.55 (-0.67, -0.41)</b>	<b>-0.86 (-0.90, -0.80)</b>
Openness	<b>-0.34 (-0.49, -0.17)</b>	<b>0.94 (0.92, 0.96)</b>	0.18 (-0.01, 0.35)	0.10 (-0.08, 0.28)
Neuroticism	<b>-0.38 (-0.53, -0.21)</b>	<b>0.86 (0.80, 0.90)</b>	<b>-0.22 (-0.38, -0.03)</b>	-0.11 (-0.28, 0.08)
Sociability	-0.20 (-0.37, -0.02)	0.19 (0.00, 0.36)	<b>0.93 (0.90, 0.95)</b>	<b>0.34 (0.17, 0.50)</b>
Attentiveness	<b>0.76 (0.67, 0.83)</b>	<b>-0.77 (-0.84, -0.69)</b>	-0.01 (-0.19, 0.17)	-0.25 (-0.42, -0.07)

1038 *Note.* Significant effects at  $p < .05$ . (boldface). 95% confidence intervals in brackets.

1039

1040 Table 7

1041 Inter-rater reliabilities of gorilla personality dimensions.

Dimension	<i>ICC(3,1)</i>	<i>ICC(3,k)</i>	Cronbach's $\alpha$
I	0.69	0.92	0.95
II	0.41	0.77	0.94
III	0.45	0.80	0.92
IV	0.42	0.78	0.88

1042

1043 Table 8

1044 Output of regressions examining age and sex effects on mountain gorilla personality dimensions

1045 using z-scores.

Dimension	Predictors	<i>b</i>	<i>SE<sub>b</sub></i>	<i>t</i>	<i>p</i>
Dominance	Age	0.449	0.105	4.284	<0.001
	Sex	0.050	0.007	7.377	<0.001
	Age x Sex	0.079	0.011	7.064	<0.001
Openness	Age	0.489	0.147	3.323	0.001
	Sex	-0.040	0.010	-4.216	<0.001
	Age x Sex	-0.035	0.016	-2.263	0.026
Sociability	Age	-0.597	0.167	-3.582	<0.001
	Sex	-0.046	0.011	-4.289	<0.001
	Age x Sex	-0.006	0.018	-0.344	0.732
Proto-Agreeableness	Age	-0.154	0.164	-0.936	0.351
	Sex	-0.049	0.011	-4.604	<0.001
	Age x Sex	-0.015	0.017	-0.854	0.395

1046

1047 Table 9

1048 Spearman's rank correlations between behavioral measures and trait dimensions.

Behavioral measure	<i>n</i>	Dominance	Openness	Sociability	Proto-Agreeableness
Dominance strength	58	0.65*	-0.45*	0.02	-0.01
Intervention per hour	86	0.32*	-0.14	0.04	-0.35*
Staring per hour	116	-0.57*	0.39*	0.43*	0.35*
% Playing	30	-0.26	0.60*	0.27	0.26
% Resting	116	0.58*	-0.28*	-0.51*	-0.37*
% Grooming	86	-0.12	-0.29	0.33*	0.00
N Grooming Partners	86	-0.07	0.01	0.41*	0.15
Mean N Gorillas $\leq 5$ m	116	-0.04	-0.10	0.28*	-0.07
Touching per hour	116	-0.10	0.27*	0.17	0.15
Approaches per hour	116	-0.66*	0.18	0.55*	0.36*
Aggression per hour	86	0.18	-0.31	0.22	-0.10
Food-stealing per hour	86	0.09	-0.02	0.06	-0.10

1049 Notes. \* Correlations significant at  $p < .004$ .

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1051 Figure 1

1052 Score distribution of female (circle) and male (triangle) gorillas on each mountain gorilla

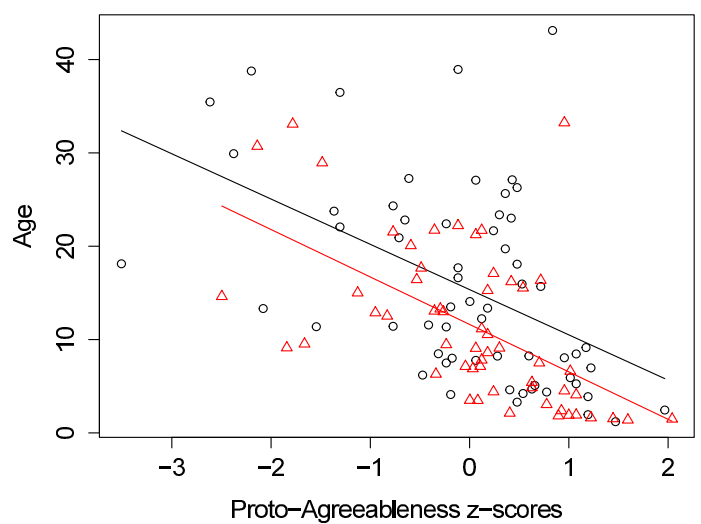
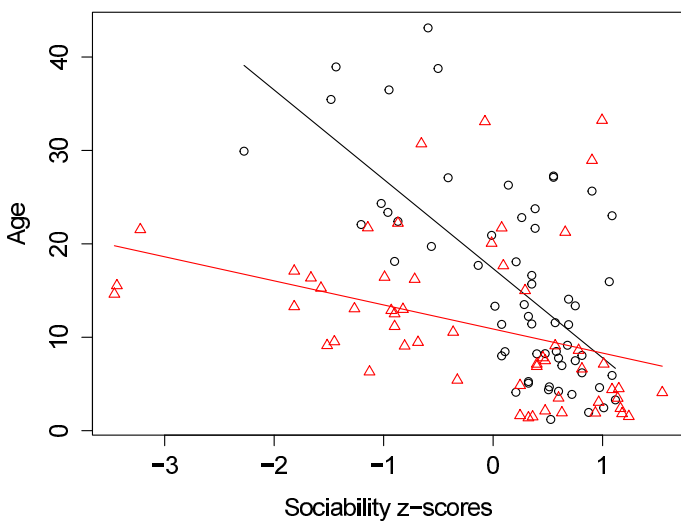
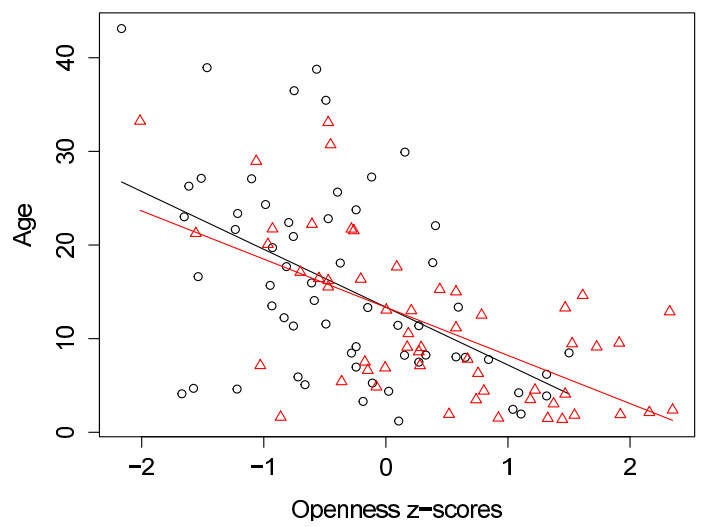
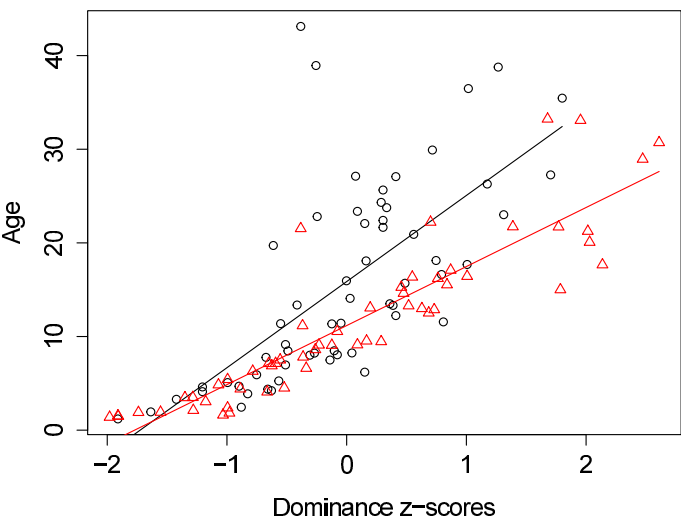
1053 personality dimension presented by gorilla age.

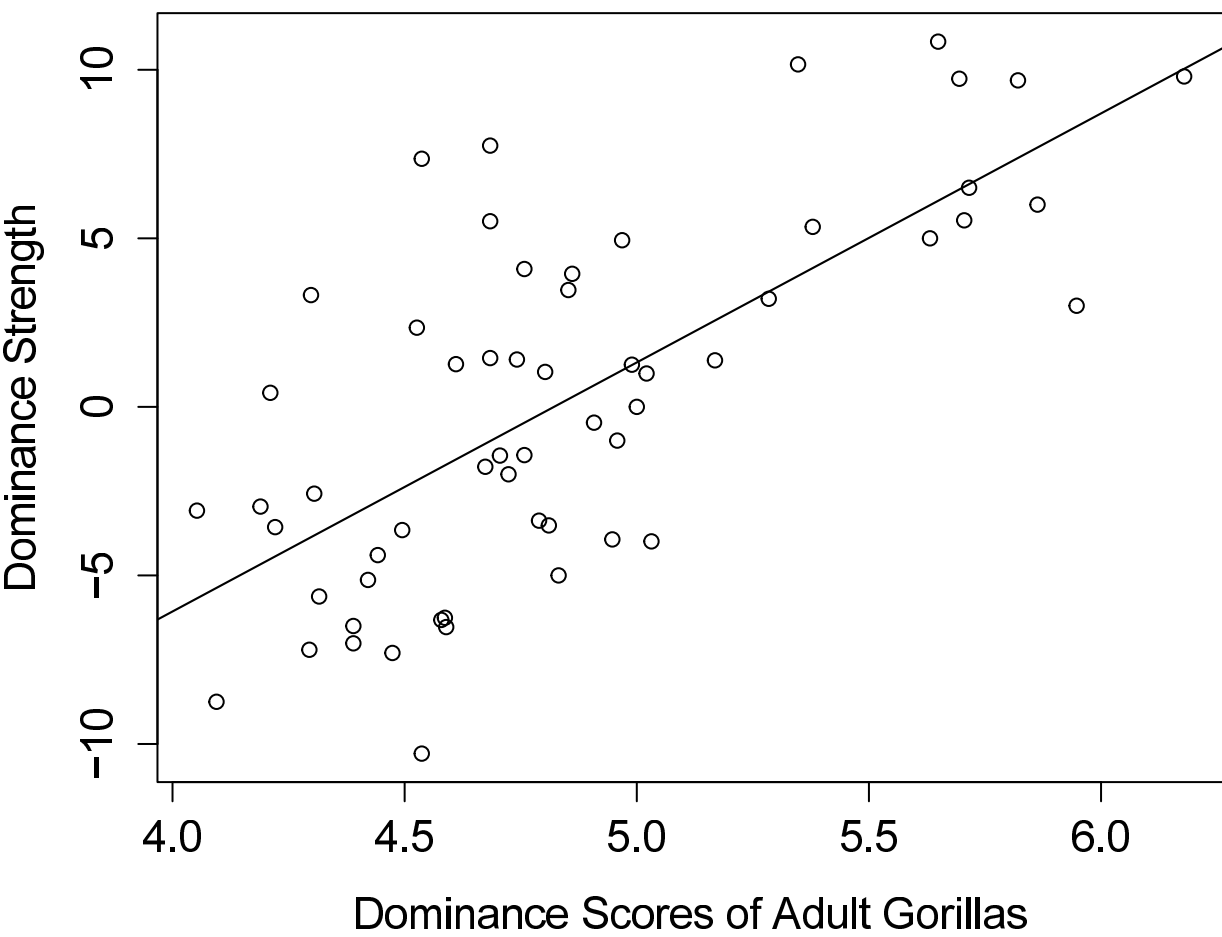
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1055 Figure 2

1056 **Relationship** between gorilla Dominance scores and dominance strength.

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1 Supplemental table 1  
2 Modification of great ape personality questionnaires from the human Five-Factor Model (FFM)  
3 to the Hominoid Personality Questionnaire (HPQ).

Questionnaire	N traits	FFM plus
Human Five-Factor Model FFM (Goldberg, 1990)	75	
Chimpanzee Personality Questionnaire CPQ (King & Figueredo, 1997)	43 of 75 (FFM)	clumsy, autistic
Orangutan Personality Questionnaire OPQ (Weiss et al., 2006)	48 (43 from CPQ)	anxious, vulnerable, cool, curious, conventional
Hominoid Personality questionnaire HPQ (Weiss et al., 2009)	54	thoughtless, distractible, quitting, individualistic, innovative, unperceptive

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20 Supplemental table 2

21 Inter-rater reliabilities of traits.

Trait	<i>ICC(3,1)</i>	<i>ICC(3,k)</i>
Fearful	0.31	0.69
Dominant	0.72	0.92
Persistent	0.24	0.61
Cautious	0.14	0.44
Stable	0.18	0.52
Autistic	0.15	0.47
Curious	0.32	0.69
Thoughtless	0.27	0.64
Stingy	0.23	0.59
Jealous	0.17	0.49
Individualistic	0.26	0.63
Reckless	0.15	0.46
Sociable	0.37	0.73
Distractible	0.39	0.75
Timid	0.17	0.49
Sympathetic	0.18	0.51
Playful	0.66	0.90
Solitary	0.50	0.83
Vulnerable	0.12	0.39
Innovative	0.05	0.21
Active	0.37	0.74
Helpful	0.33	0.70
Bullying	0.43	0.78
Aggressive	0.43	0.78
Manipulative	0.20	0.55
Gentle	0.31	0.68
Affectionate	0.17	0.50
Excitable	0.16	0.47
Impulsive	0.10	0.35
Inquisitive	0.24	0.61
Submissive	0.09	0.31
Cool	0.34	0.71
Dependent	0.25	0.62
Irritable	0.32	0.69
Unperceptive	-0.02	-0.13
Predictable	0.03	0.14

Decisive	0.36	0.73
Depressed	0.29	0.66
Conventional	0.13	0.42
Sensitive	0.24	0.60
Defiant	0.24	0.60
Intelligent	0.33	0.70
Protective	0.48	0.82
Quitting	0.16	0.47
Inventive	0.13	0.42
Clumsy	0.10	0.34
Erratic	0.07	0.26
Friendly	0.29	0.67
Anxious	0.14	0.43
Lazy	0.22	0.58
Disorganized	0.12	0.40
Unemotional	0.14	0.43
Imitative	0.54	0.85
Independent	0.57	0.86

22 *Note. ICC(3,1) = reliability of individual ratings; ICC(3,k) = reliability of mean ratings*

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Supplemental table 3

Traits loading on gorilla personality dimension derived from a PCA with promax rotation including 116 gorillas compared to other great apes.

**Comment [u1]:** Must make this landscape

Trait	Promax-rotated components							$h^2$
	HU	CH	OR	O	D <sub>R</sub>	S	P-A <sub>R</sub>	
<i>Intelligent</i>	+O <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	0.02	<b>0.92</b>	0.15	-0.07	0.86
<i>Decisive</i>	+C <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	-0.14	<b>0.78</b>	-0.04	-0.10	0.77
<i>Protective</i>	+A <sup>b</sup>	+A <sup>d</sup>	+A <sup>f</sup>	-0.08	<b>0.74</b>	0.07	-0.32	0.83
<i>Timid</i>	-E <sup>a,c</sup>	-D <sup>d</sup>	+N <sup>f</sup>	-0.47	<b>-0.92</b>	-0.03	-0.05	0.78
<i>Anxious</i>	+N <sup>a,c</sup>	-D <sup>e</sup>	+N <sup>f</sup>	-0.48	<b>-0.96</b>	0.04	-0.39	0.79
<i>Independent</i>	-N <sup>a</sup>	+D <sup>d</sup>	+I <sup>f</sup>	-0.20	<b>0.71</b>	-0.29	-0.10	0.84
<i>Dominant</i>	+E <sup>a,c</sup>	+D <sup>d</sup>	+D <sup>f</sup>	-0.19	<b>0.64</b>	0.01	-0.39	0.85

<i>Fearful</i>	+N <sup>a</sup>	-D <sup>d</sup>	+N <sup>f</sup>	-0.06	<b>-0.83</b>	0.07	-0.36	0.58
<i>Sensitive</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	-0.26	<b>0.70</b>	0.34	-0.04	0.73
<i>Distractible</i>	----	----	----	0.41	<b>-0.64</b>	0.33	-0.05	0.83
<i>Helpful</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	-0.22	<b>0.60</b>	0.43	-0.33	0.75
<i>Bullying</i>	-A <sup>b</sup>	+D <sup>d</sup>	+D <sup>f</sup>	0.20	<b>0.56</b>	-0.11	-0.50	0.83
<i>Dependent</i>	+N <sup>a</sup>	-D <sup>d</sup>	-I <sup>f</sup>	0.31	<b>-0.54</b>	0.34	0.13	0.73
<i>Disorganised</i>	-C <sup>a</sup>	-C <sup>d</sup>	-I <sup>f</sup>	0.49	<b>-0.54</b>	-0.08	0.01	0.68
<i>Submissive</i>	-E <sup>c</sup> /+N <sup>a</sup>	-D <sup>d</sup>	-D <sup>f</sup>	-0.24	<b>-0.61</b>	0.22	0.17	0.59
<i>Imitative</i>	-O <sup>b</sup>	+E <sup>d</sup>	+E <sup>f</sup>	0.51	<b>-0.47</b>	0.34	0.16	0.87
<i>Persistent</i>	+C <sup>a</sup>	+D <sup>d</sup>	+D <sup>f</sup>	0.28	<b>0.51</b>	0.01	-0.43	0.60
<i>Clumsy</i>	----	-C <sup>e</sup>	+I <sup>f</sup>	0.02	<b>-0.57</b>	-0.06	-0.09	0.30
<i>Vulnerable</i>	+N <sup>c</sup>	-D <sup>e</sup>	+N <sup>f</sup>	0.24	<b>-0.48</b>	-0.22	0.13	0.42
<i>Active</i>	+E <sup>a</sup>	+E <sup>d</sup>	+E <sup>f</sup>	<b>0.87</b>	0.12	0.19	0.26	0.81
<i>Cool</i>	-E <sup>a</sup>	-N <sup>e</sup>	-N <sup>f</sup>	<b>-0.75</b>	0.16	0.20	0.23	0.77
<i>Thoughtless</i>	-C <sup>c</sup> /-A <sup>a</sup>	-C <sup>e</sup>	----	<b>0.76</b>	-0.10	-0.10	-0.12	0.66
<i>Unemotional</i>	-N <sup>a,c</sup>	-N <sup>d</sup>	-E <sup>f</sup>	<b>-0.81</b>	-0.25	-0.15	-0.06	0.60
<i>Playful</i>	+E <sup>a</sup>	+E <sup>d</sup>	+E <sup>f</sup>	<b>0.76</b>	-0.21	0.31	0.20	0.91
<i>Impulsive</i>	+E <sup>a</sup>	-C <sup>d</sup>	+N <sup>f</sup>	<b>0.75</b>	-0.03	0.06	-0.39	0.68
<i>Lazy</i>	-C <sup>a</sup>	-E <sup>d</sup>	-E <sup>f</sup>	<b>-0.81</b>	-0.45	-0.11	-0.31	0.67
<i>Curious</i>	+O <sup>a</sup>	+O <sup>e</sup>	+E <sup>f</sup>	<b>0.74</b>	-0.24	0.38	-0.03	0.81
<i>Inventive</i>	+O <sup>a</sup>	+O <sup>d</sup>	+E <sup>f</sup>	<b>0.74</b>	0.00	0.33	-0.28	0.59
<i>Excitable</i>	+N <sup>a</sup>	+N <sup>d</sup>	+N <sup>f</sup>	<b>0.69</b>	-0.09	0.01	-0.41	0.64
<i>Inquisitive</i>	+O <sup>a</sup>	+O <sup>d</sup>	+E <sup>f</sup>	<b>0.70</b>	-0.18	0.39	-0.04	0.69
<i>Reckless</i>	-C <sup>a</sup>	-C <sup>d</sup>	+D <sup>f</sup>	<b>0.61</b>	-0.11	-0.10	-0.53	0.72
<i>Innovative</i>	+O <sup>a</sup>	+O <sup>c</sup>	----	<b>0.67</b>	0.22	0.19	-0.23	0.46
<i>Stable</i>	-N <sup>a</sup>	-N <sup>d</sup>	-N <sup>f</sup>	<b>-0.58</b>	0.21	0.28	0.12	0.56
<i>Conventional</i>	-O <sup>c</sup> /-C <sup>a</sup>	+A <sup>e</sup>	-E <sup>f</sup>	<b>-0.59</b>	0.00	0.30	0.15	0.53
<i>Quitting</i>	-C <sup>c</sup>	-C <sup>e</sup>	----	<b>0.58</b>	-0.37	0.11	0.07	0.64
<i>Erratic</i>	-C <sup>a</sup>	-C <sup>d</sup>	+N <sup>f</sup>	<b>0.52</b>	-0.23	-0.33	-0.26	0.60
<i>Predictable</i>	+C <sup>a</sup>	+C <sup>d</sup>	-N <sup>f</sup>	<b>-0.50</b>	-0.33	0.39	-0.08	0.46
<i>Cautious</i>	+C <sup>a</sup>	-D <sup>d</sup>	+N <sup>f</sup>	-0.40	-0.08	-0.08	-0.33	0.26
<i>Friendly</i>	+A <sup>a</sup>	+E <sup>d</sup>	+A <sup>f</sup>	0.18	-0.12	<b>0.86</b>	0.07	0.86
<i>Sociable</i>	+E <sup>a,c</sup>	+E <sup>d</sup>	+A <sup>f</sup>	0.36	0.11	<b>0.87</b>	0.04	0.82
<i>Affectionate</i>	+A <sup>a</sup>	+E <sup>d</sup>	+A <sup>f</sup>	0.03	0.06	<b>0.87</b>	-0.11	0.68
<i>Solitary</i>	-E <sup>b</sup>	-E <sup>d</sup>	-E <sup>f</sup>	-0.18	0.10	<b>-0.84</b>	0.09	0.70
<i>Depressed</i>	-E <sup>b</sup>	-E <sup>d</sup>	-E <sup>f</sup>	-0.42	-0.21	<b>-0.79</b>	-0.09	0.72
<i>Gentle</i>	+A <sup>b</sup>	+A <sup>d</sup>	-D <sup>f</sup>	-0.17	-0.06	<b>0.59</b>	0.34	0.70
<i>Sympathetic</i>	+A <sup>a</sup>	+A <sup>d</sup>	+A <sup>f</sup>	-0.27	0.35	<b>0.70</b>	-0.13	0.68
<i>Defiant</i>	-A <sup>b</sup>	-C <sup>e</sup>	+D <sup>f</sup>	0.21	0.23	<b>-0.48</b>	-0.43	0.77
<i>Individualistic</i>	-N <sup>a</sup>	-E <sup>c</sup>	----	0.01	0.23	<b>-0.44</b>	-0.40	0.64



<i>Jealous</i>	-A <sup>a</sup> /+N <sup>a,c</sup>	-C <sup>d</sup>	+D <sup>f</sup>	0.12	-0.03	0.12	<b>-0.93</b>	0.77
<i>Irritable</i>	-A <sup>a,c</sup>	-C <sup>e</sup>	+D <sup>f</sup>	0.16	0.01	-0.22	<b>-0.76</b>	0.81
<i>Aggressive</i>	-A <sup>a</sup>	-C <sup>d</sup>	+D <sup>f</sup>	0.10	0.21	-0.29	<b>-0.68</b>	0.87
<i>Stingy</i>	-A <sup>a,c</sup>	+D <sup>d</sup>	+D <sup>f</sup>	-0.05	0.29	-0.03	<b>-0.68</b>	0.72
<i>Manipulative</i>	-A <sup>a</sup>	+D <sup>e</sup>	+D <sup>f</sup>	-0.23	0.16	0.45	<b>-0.61</b>	0.53
<i>Autistic</i>	----	nl	nl	0.12	-0.06	0.03	-0.33	0.11
% variance				21	21	14	12	

39 *Note.* Boldface = salient loadings; nl = no loading; '----' = trait (or included term) not assessed; '+' = positive loadings; '-' = negative loadings;  $h^2$  communality;  
40 E = Extraversion (facets: sociability, assertiveness, activity, positive emotions<sup>g</sup>); C = Conscientiousness (facets: deliberation, self-discipline, dutifulness, order<sup>g</sup>);  
41 O = Openness (facets: ideas/intellect, imagination, creativity, curiosity<sup>g</sup>); N = Neuroticism (facets: anxiety, depression, vulnerability to stress, moodiness<sup>g</sup>); A =  
42 Agreeableness (trust, tendermindedness, cooperation, lack of aggression<sup>g</sup>); D = Dominance (nonhuman great apes); I = Intellect (orangutan); HU = human, CH =  
43 chimpanzee, OR = orang-utan.

44 <sup>a</sup> traits (or synonyms of traits) and classification (Goldberg, 1990)

45 <sup>b</sup> traits and their classification (Goldberg, 1990) as described in Table 1 (King & Figueredo, 1997)

46 <sup>c</sup> traits and their classification (McCrae & Costa, 1987)

47 <sup>d</sup> traits and their classification (King & Figueredo, 1997)

48 <sup>e</sup> traits and their classification (Weiss et al., 2008)

49 <sup>f</sup> traits and their classification (Weiss et al., 2006)

50 <sup>g</sup> for more details see John (1990) and Costa & McCrae (1992)

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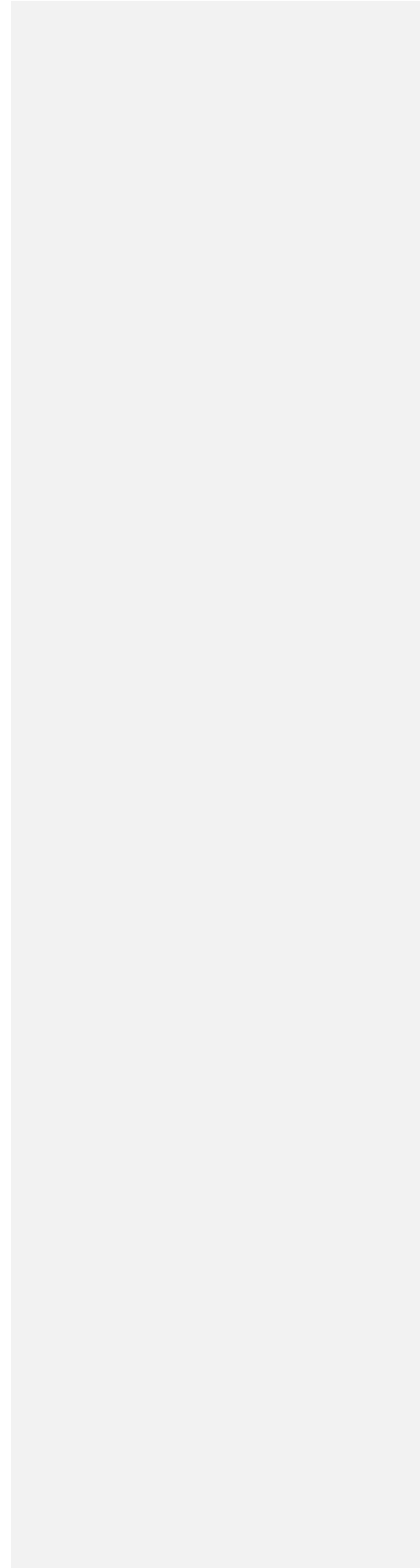
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## GORILLA PERSONALITY TRAIT ASSESSMENT

Gorilla personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed on the following pages. Make your judgments on the basis of your own understanding of the trait guided by the short clarifying definition following each trait. The gorilla's own behaviors and interactions with other gorillas should be the basis for your numerical ratings. Use your own subjective judgment of typical gorilla behavior to decide if the gorilla you are scoring is above, below, or average for a trait. The following seven point scale should be used to make your ratings.

1. **Displays either total absence or negligible amounts of the trait.**
2. **Displays small amounts of the trait on infrequent occasions.**
3. **Displays somewhat less than average amounts of the trait.**
4. **Displays about average amounts of the trait.**
5. **Displays somewhat greater than average amounts of the trait.**
6. **Displays considerable amounts of the trait on frequent occasions.**
7. **Displays extremely large amounts of the trait.**

Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the gorilla and you are somewhat unsure about it. Indicate your rating by placing a cross in the box underneath the chosen number.

**Finally, do not discuss your rating of any particular gorilla with anyone else. As explained in the handout accompanying this questionnaire, this restriction is necessary in order to obtain valid reliability coefficients for the traits.**

## GORILLA PERSONALITY TRAIT ASSESSMENT

Gorilla's full name: \_\_\_\_\_

Rater's full name: \_\_\_\_\_

Date (Mon/Day/Yr): \_\_\_\_\_

---

**FEARFUL:** Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**DOMINANT:** Subject is able to displace, threaten, or take food from other gorillas. Or subject may express high status by decisively intervening in social interactions.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**PERSISTENT:** Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**CAUTIOUS:** Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviors.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**STABLE:** Subject reacts to its environment including the behavior of other gorillas in a calm, equable, way. Subject is not easily upset by the behaviors of other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**AUTISTIC:** Subject often displays repeated, continuous, and stereotyped behaviors such as rocking or self claspings.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**CURIOUS:** Subject has a desire to see or know about objects or other gorillas. This includes a desire to know about the affairs of other gorillas that do not directly concern the subject.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**THOUGHTLESS:** Subject often behaves in a way that seems imprudent or forgetful.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**STINGY/GREEDY:** Subject is excessively desirous or covetous of food, favored locations, or other resources in the environment. Subject is unwilling to share these resources with others.

least most

1      2      3      4      5      6      7

---

**JEALOUS:** Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged gorillas.

least most

1      2      3      4      5      6      7

---

**INDIVIDUALISTIC:** Subject's behavior stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.

least most

1      2      3      4      5      6      7

---

**RECKLESS:** Subject is rash or unconcerned about the consequences of its behaviors.

least most

1      2      3      4      5      6      7

**SOCIABLE:** Subject seeks and enjoys the company of other gorillas and engages in amicable, affable, interactions with them.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**DISTRACTABLE:** Subject is easily distracted and has a short attention span.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**TIMID:** Subject lacks self confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**SYMPATHETIC:** Subject seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**PLAYFUL:** Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviors with or without other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**SOLITARY:** Subject prefers to spend considerable time alone not seeking or avoiding contact with other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**VULNERABLE:** Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behavior, aggression, or attack by another gorilla.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**INNOVATIVE:** Subject engages in new or different behaviors that may involve the use of objects or materials or ways of interacting with others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**ACTIVE:** Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behavior.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**HELPFUL:** Subject is willing to assist, accommodate, or cooperate with other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>



**BULLYING:** Subject is overbearing and intimidating towards younger or lower ranking gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**AGGRESSIVE:** Subject often initiates fights or other menacing and agonistic encounters with other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**MANIPULATIVE:** Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Gorilla seems able and willing to use others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**GENTLE:** Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**AFFECTIONATE:** Subject seems to have a warm attachment or closeness with other gorillas. This may entail frequently grooming, touching, embracing, or lying next to others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**EXCITABLE:** Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**IMPULSIVE:** Subject often displays some spontaneous or sudden behavior that could not have been anticipated. There often seems to be some emotional reason behind the sudden behavior.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**INQUISITIVE:** Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about other gorillas, objects, or persons within its view.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**SUBMISSIVE:** Subject often gives in or yields to another gorilla. Subject acts as if it is subordinate or of lower rank than other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**COOL:** Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**DEPENDENT/FOLLOWER:** Subject often relies on other gorillas for leadership, reassurance, touching, embracing and other forms of social support.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**IRRITABLE:** Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behavior.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**UNPERCEPTIVE:** Subject is slow to respond or understand moods, dispositions, or behaviors of others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**PREDICTABLE:** Subject's behavior is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioral routine.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**DECISIVE:** Subject is deliberate, determined, and purposeful in its activities.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**DEPRESSED:** Subject does not seek out social interactions with others and often fails to respond to social interactions of other gorillas. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**CONVENTIONAL:** Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**SENSITIVE:** Subject is able to understand or read the mood, disposition, feelings, or intentions of other gorillas often on the basis of subtle, minimal cues.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**DEFIANT:** Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavorable consequences or threats from others.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**INTELLIGENT:** Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**PROTECTIVE:** Subject shows concern for other gorillas and often intervenes to prevent harm or annoyance from coming to them.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**QUITTING:** Subject readily stops or gives up activities that have recently been started.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**INVENTIVE:** Subject is more likely than others to do new things including novel social or non-social behaviors. Novel behavior may also include new ways of using materials in the environment.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**CLUMSY:** Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**ERRATIC:** Subject is inconsistent, indefinite, and widely varying in its behavior and moods.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**FRIENDLY:** Subject often seeks out contact with other gorillas for amiable, genial activities. Subject infrequently initiates hostile behaviors towards other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**ANXIOUS:** Subject often seems distressed, troubled, or is in a state of uncertainty.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**LAZY:** Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**DISORGANIZED:** Subject is scatterbrained, sloppy, or haphazard in its behavior as if not following a consistent goal.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**UNEMOTIONAL:** Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

---

**IMITATIVE:** Subject often mimics, or copies behaviors that it has observed in other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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**INDEPENDENT:** Subject is individualistic and determines its own course of action without control or interference from other gorillas.

least most

1	2	3	4	5	6	7
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

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