Personality in wild bonobos (Pan paniscus)

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ABSTRACT

To understand the evolution of personality structure requires examining personality dimensions in multiple species using a common set of traits. Little research has been conducted on personality in wild populations of nonhuman primates. Using behavioral observations and questionnaire ratings, we examined factors influencing personality in 16 wild bonobos (*Pan paniscus*) at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo. We extracted five factors from 31 of the items from the Hominoid Personality Questionnaire (HPQ) and three factors from observed behaviors. The HPQ factors were labeled Unemotionality_Q, Friendliness_Q, Aggressiveness_Q, Irritability_Q, and Activity_Q. The behavioral factors were labeled Grooming_B, Playfulness_B, and Introversion_B. We established the convergent and divergent validity of these factors by obtaining correlations between the HPQ and behavioral factors. We tested for sex differences and found that males were significantly higher on Introversion_B and significantly lower in Irritability_Q. We then tested for age differences and found that Friendliness_Q was lower and Aggressiveness_Q was higher in older individuals. Finally, we found that, among males, hierarchical rank was associated with higher Aggressiveness_Q. These findings contrast with findings in chimpanzees in ways consistent with known species differences. For one, consistent with the more egalitarian structure of bonobo society, we did not identify a clear Dominance factor. Also, the results related to sex differences were consistent with previous findings that reveal closer bonds between female bonobos than female chimpanzees. These findings highlight the importance of studying personality in closely related species and the need to consider species' socioecology when studying personality.

Keywords: personality; bonobo; questionnaire; observation

INTRODUCTION

Darwin proposed that behavior and underlying psychological dispositions in animals are subject to natural selection [Darwin, 1998/1872]. We know now that these dispositions, commonly known as personality traits [Réale et al., 2007], are manifested as behavioral, affective and cognitive differences among individuals that are stable over time and consistent across situations. Studies have revealed variation in personality in multiple species, including invertebrates [Gyuris et al., 2010], fish [Bell and Sih, 2007], birds [Dingemanse et al., 2002], and nonhuman primates [Freeman and Gosling, 2010]. Personality traits in these and other species are heritable [Weiss et al., 2000; Dingemanse et al., 2002; Brent et al., 2013] and have fitness consequences [Capitanio et al., 1999; Dingemanse et al., 2004; Dingemanse and Réale, 2005; for a review see Smith and Blumstein, 2008; Weiss et al., 2012a].

Theories proposed to explain the evolution of personality, include spatial or temporal fluctuation in selection (i.e. whether certain traits are related to greater fitness changes in space or time), frequency-dependent selection (i.e. traits' fitness are related to how common or rare that trait is in the population), and sexually antagonistic selection (i.e. traits related to greater fitness in males are related to poorer fitness in females and vice versa) [Penke et al., 2007; Réale et al., 2007; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010; Dall and Griffith, 2014]. One approach to understanding what mechanisms drive the evolution of personality is to compare related species [Gosling and Graybeal 2007. However, measuring personality in nonhuman animals in an ecologically relevant and comparable way is difficult [Carter et al., 2013].

Methods used to study animal personality can roughly be divided into behavioral coding studies and rating studies [Gosling, 2001; Itoh, 2002; Uher, 2008; Uher and Asendorpf, 2008; Freeman and Gosling, 2010]. Personality traits derived from behavioral coding studies are comparable across species or populations. But behavioral coding is time consuming, and makes it difficult to account for variability due to noise, especially when the sample size is small, and thus may not capture rarely occurring but important behaviors [Freeman et al., 2011]. Rating studies involve providing a questionnaire to raters who know the subjects well, and also provide data that are comparable across species or populations. Moreover, rating studies enable rapid collection of data. However, ratings rely upon the accumulated knowledge by raters of individuals in many different situations and contexts, a resource that is not always available [Freeman et al., 2011]. A growing body of literature focuses on the reliability and validity of ratings [Gosling and Vazire, 2002]. However, the use of ratings is sometimes criticized, because of its reliance on rater-based impressions [Uher, 2008].

The methodological differences between coding and rating studies make it difficult to compare their results [Gosling, 2008; Uher, 2008]. Other factors also hinder progress in animal personality research. In the case of primates, most studies have been on captive animals [Freeman and Gosling, 2010; see, however, Weiss et al., 2011; Konečná et al., 2008; Seyfarth et al., 2012; Carter et al., 2014; Manson and Perry, 2013; Neumann et al., 2013]. Animal personality research would therefore benefit from more studies of wild populations, because captivity may increase or decrease the expression of some personality traits [Koski, 2011]. Another hindering factor is that for practical reasons most researchers do not study variation and covariation in a broad suite of traits [Sih et

al., 2004; Réale et al., 2007; Sih and Bell, 2008]. For example, social behaviors other than aggression should be emphasized more because complex social systems also contribute to personality evolution [Koski, 2011].

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are the species most closely related to humans. Assessing their personalities in the wild therefore provides insights into human personality evolution. Although some studies of chimpanzee and bonobo personality have been undertaken, most of the chimpanzee research and all of the bonobo research has been in captive settings [Uher and Asendorpf, 2008; Uher et al., 2008; Freeman and Gosling, 2010; Herrmann et al., 2011; Murray, 2011; Massen et al., 2013; Massen and Koski, 2014; Weiss et al., 2015].

Bonobos and chimpanzees live in fission-fusion social systems and are male-philopatric [Kano, 1982; Goodall, 1983]. However, unlike female chimpanzees, female bonobos have prolonged estrous periods, have high social status, and maintain strong social bonds [Furuichi, 1989; Kano, 1992; Parish, 1996; Furuichi, 1997; Parish and de Waal, 2000; Furuichi, 2011; Surbeck et al., 2011]. Furthermore, unlike chimpanzees, there are no recorded incidents of infanticide in bonobos, group encounters are peaceful, and competition among males for females is not marked by physical aggression [Furuichi and Hashimoto, 2004; Furuichi, 2009; Paoli, 2009; Furuichi, 2011]. Given these differences and similarities between chimpanzees and bonobos, studying bonobo personality and comparing it to that of chimpanzees can highlight important species-specific, ecological factors that may have played a role in personality evolution.

Our study had two goals. We first wanted to reveal personality dimensions in wild bonobos for the first time, using ratings and observational methods. We then wanted to test whether sex, age, and rank were associated with bonobo personality factors.

We made four predictions based on the aforementioned differences between chimpanzees and bonobos. The first was that, given the neotenous traits of bonobos compared to chimpanzees [Hare et al., 2012], playfulness would be a key component of bonobo personality. The second and third were that, given the lower level of aggression in bonobos compared to chimpanzees, their personality structure would not include a Dominance dimension like that found in chimpanzees [King and Figueredo, 1997; Weiss et al., 2007; 2009] and that correlations between personality traits and dominance rank would be low. The fourth was that, given the strong social bonds among female bonobos, and weak social bonds among male bonobos compared to chimpanzees resulting in frequent social interactions among female bonobos but not female chimpanzees [Parish, 1996; Furuichi, 1997; Furuichi, 2011; Surbeck et al., 2011], for personality traits related to sociability, sex differences in bonobos will be opposite those in chimpanzees. The fifth was that, given the high social status of female bonobos compared to female chimpanzees [Furuichi, 2011; Surbeck et al., 2011], unlike chimpanzees, sex differences in aggression-related personality traits would favor females.

METHODS

This research was noninvasive and complied with the legal requirements of the Democratic Republic of the Congo and the ethical requirements of the American Society of Primatologists.

Study Site and Subjects

Fieldwork took place in Wamba (0°11'08" N, 22°37'58" E) in the Luo Scientific Reserve, Democratic Republic of the Congo, between May and November 2013. Detailed information about the field site has been described elsewhere [Kano, 1992; Hashimoto et al., 2008].

Subjects were members of the eastern subgroup of a non-provisioned wild bonobo group (P-group). All individuals of the study group were habituated to humans and could be individually recognized. During the observation period the subgroup consisted of 28 individuals. Exact ages were unknown, and so we classified individuals as infants and juveniles (estimate age of less than 7 years), adolescents (age 7-14 years), adults (age 15-30 years), and old adults (aged 30 years or older) based on their body size and proportions, the condition of their teeth and, in the case of females, sexual swelling patterns and nipple length. For our study we observed all of the adult and adolescent males and females (N = 16): 2 male and 2 female adolescents, 3 male and 4 female adults, and 2 male and 3 female old adults.

Behavioral Observations

The first author (CG) collected behavioral observations using focal animal sampling. Sessions were 30 minutes long. During each session, behavioral status was recorded by

instantaneous sampling at 5-minute intervals and behavioral events and social interactions together with the identity of the partner were recorded continuously throughout the session [Altmann, 1974; Martin and Bateson, 1993]. We chose to record behaviors that we thought would be tied to personality in some way and that were comparable to previous coding studies of personality in nonhuman primates [e.g. Koski, 2011; Neumann et al., 2013; Massen and Koski, 2014]. CG also recorded the context for each focal observation – i.e., the behavior that the majority of individuals in sight were engaged in (grooming, resting, feeding or moving). A total of 316.28 hours of focal data were collected from the 16 individuals (mean observation time per subject = 19.8 ± SD 0.98 hours). For each subject, the aim was to collect focal observations evenly throughout the study period – after the randomly chosen first focal observations CG observed the individual present with the smallest observation time. If a focal subject was lost within 15 minutes from the start of the focal observation, we discarded the data. One subject was observed at most twice a day.

We extracted 15 behavioral indices from behavioral observations (Table I). The aggression rate was so low that we could not include this behavior.

Dominance Rank

In addition to focal sampling, we recorded all aggressive interactions *ad libitum* [Altmann, 1974] to establish the social hierarchy. We could not determine female rank due to the low frequency of aggressive interactions. We therefore could only examine associations between rank and personality in males. To do so we constructed a dominance matrix and ranked individuals so that the alpha male had a rank of 1 [Borries

et al., 1991]. However, make rank did not appear to be linear as there were several undecided aggressive interactions. Hence, following the beta male, who was assigned a rank of 2, three males were assigned a rank of 4, and the two lowest ranking males were assigned a rank of 6.5 (because of ties). Because the two lowest ranking males were adolescents, associations between age and rank should be interpreted with caution. For ease of interpretation, we multiplied rank by -1.

Questionnaire Ratings

We asked 2 Japanese researchers and 3 Congolese field assistants to fill out the Japanese and French translation of Hominoid Personality Questionnaire [HPQ; Weiss et al., 2009], respectively. Raters knew the bonobos they rated for between 7 months and 5 years.

The HPQ is an expanded version of a questionnaire developed for chimpanzee personality assessment with 54 personality descriptive items, each consisting of an adjective and a one to three sentence definition in the context of behavior [Weiss et al., 2009]. Each item is rated on a 7-point scale with 1 defined as "Displays either total absence or negligible amounts of the trait" and 7 defined as "Displays extremely large amounts of the trait". The HPQ instructs raters to not discuss their ratings with each other, and to rely on their judgment when rating individual animals. The HPQ is available at: http://goo.gl/bXOlrC.

Data Reduction

To select HPQ items to be entered into the factor analysis we assessed the interrater reliabilities of the individual items using two intraclass correlation coefficients (*ICC*s): *ICC*(3,1) estimates the reliability of ratings by one individual (two-way mixed single measures) and *ICC*(3,*k*) calculates the reliability on the basis of the mean of *k* independent raters (*k* = 5 in this study) per bonobo (two-way mixed average measures) [Shrout and Fleiss, 1979]. Due to our small sample size, and also to ensure a high degree of interrater reliability, we chose to be conservative and to omit items with an *ICC*(3,*k*) < 0.6. We used the remaining items for factor analysis. For the behavioral indices we did not have interrater reliabilities and so we used all 15 behavioral indices.

We used factor analyses to identify the structure underlying the correlations among the HPQ items and among the behavioral indices. For the personality ratings, the scores were aggregated across the raters. The number of factors for ratings and behaviors was determined by parallel analysis of all individual ratings [Horn, 1965]. Because preliminary analyses indicated that the varimax- (orthogonal) and promax-rotated (oblique) factors did not differ substantially, we interpreted the varimax-rotated factors, similarly as in other nonhuman primate studies [King and Figueredo, 1997; Weiss et al., 2006; 2011]. Factor loadings on items were defined as salient if they had the highest absolute loading that exceeded 0.4. Factor scores were obtained using the regression method. We also conducted factor analyses using regularized exploratory factor analysis (REFA), which is designed for small sample sizes [Jung and Lee, 2011; Jung, 2013]. Because REFA provides more conservative factor loadings, we defined factor loadings on items as salient if they had absolute loadings exceeding 0.3 and were the highest of the factor loadings. We examined the replicability of the factor structures based on

behavioral observations and questionnaire ratings by estimating the factor congruence coefficients between factors derived from the two factor extraction methods.

Analyses of Factors Derived from Ratings and Observation

We used Pearson's product-moment correlations to examine the associations of factors derived from the HPQ with the factors derived from behavioral observations. To test for sex differences, we used independent samples t-tests or Mann–Whitney U tests, depending on whether the data were normally distributed. To analyze the effects of age, we compared mean levels of factor scores of adolescents, adults, and old adults using either a one-way analysis of variance or a Kruskal–Wallis (K–W) test, again depending on whether the data were normally distributed. We used Pearson's product-moment correlations to examine associations between factor scores and dominance rank in males.

With the exception of the REFA we conducted our statistical analyses using version 3.1.2 of R [R Core Team, 2014]. We conducted the REFA using MATLAB code developed by Jung and Lee [Jung and Lee, 2011]. All tests were two-tailed and α was set to 0.05 unless otherwise specified.

RESULTS

Interrater Reliability of Questionnaire Ratings

Interrater reliabilities of the questionnaire items are presented in Table II. We excluded 7 items with negative ICC values and 16 items with $ICC(3,k)$ estimates below 0.6 from further analyses. The $ICC(3,1)$ values of these same items ranged from 0.24

(*affectionate*) to 0.71 (*clumsy*). The *ICC*(3,*k*) values of the remaining 31 items ranged between 0.62 (*affectionate*) to 0.92 (*clumsy*).

Personality Structures

Using the fa.parallel function of the 'psych' package [Revelle, 2014], we conducted two parallel analyses to determine how many factors we could extract from the ratings and the observed behaviors. In both cases we extracted these factors using the fa function of the package 'psych' [Revelle, 2014].

Parallel analysis of the 31 items suggested retaining 5 factors. We labeled these factors Unemotionality$_Q$, Friendliness$_Q$, Aggressiveness$_Q$, Irritability$_Q$ and Activity$_Q$ (Table III). Subscript 'Q' indicates that the factors were derived from the HPQ ratings. The items *dependent/follower*, *sensitive*, *unperceptive*, *vulnerable*, *submissive* and *protective* had salient loadings on two factors. The items *disorganized* and *imitative* had no salient loadings. The interrater reliabilities of the factors are presented in Table IV.

Parallel analysis of the 15 behavioral indices suggested extracting 3 factors (Table V). We labeled these factors Grooming$_B$, Playfulness$_B$, and Introversion$_B$. The subscript 'B' indicates that these factors were derived from behavioral observations. The indices *activity* and *playing evenness* had salient loadings on two factors. Because we could not test whether these factors or behavioral indices were repeatable, we refer to these factors as behavioral tendencies.

Regulatory Exploratory Factor Analysis

The parallel analysis for REFA yielded only two factors from the ratings. However, we extracted five factors to compare the factor structures from the two factor analysis methods (Table S.I). Factor congruence coefficients $\geq |0.85|$ are considered as indicators of replicability [Haven and ten Berge, 1977]. The factor congruence coefficients (Table S.II) revealed that only Unemotionality$_Q$ and Friendliness$_Q$ were found using factor analysis and REFA. The parallel analysis for REFA suggested extracting three behavioral factors (Table S.III), and these were highly comparable with the varimax-rotated factors (Table S.IV).

Correlations between Ratings and Behavioral Observations

Table VI shows the correlation matrix of factors derived from questionnaire ratings and from the behavioral observations. The only significant correlation indicated that higher Friendliness$_Q$ was associated with higher Playfulness$_B$. There was also a non-significant trend indicating that higher Unemotionality$_Q$ was associated with higher Introversion$_B$. Finally, although not statistically significant, the directions of some of the larger remaining correlations were in the direction that would be expected based on the meaning of the questionnaire- and behaviorally-based factors (e.g. Aggressiveness$_Q$ correlated negatively with Grooming$_B$ and Playfulness$_B$, Irritability$_Q$ correlated negatively with Introversion$_B$).

Sex Differences

Males had significantly higher Introversion$_B$ scores than females ($t = -2.85$, $df = 14$, $P = 0.013$), while females had significantly higher Irritability$_Q$ scores than males ($t = 4.55$, $df = 14$, $P = 0.0005$).

Age Differences

Age was significantly associated with Friendliness$_Q$ (K–W test: $H(2) = 7.84$, $df = 2$, $P = 0.020$) and Aggressiveness$_Q$ (ANOVA: $F_{2.0, 7.6} = 18.68$, $P = 0.001$). Post-hoc tests of the factor score differences among the age categories were conducted via Mann-Whitney U tests. To adjust for multiple tests, we used a Bonferroni correction (adjusted $\alpha = 0.0167$). Adolescents scored higher on Friendliness$_Q$ than old adults ($N_Y = 4$, $N_O = 5$, $U = 20$, $P = 0.016$) and adults ($N_Y = 4$, $N_A = 7$, $U = 27$, $P = 0.012$). Adolescents also scored lower on Aggressiveness$_Q$ than adults ($N_Y = 4$, $N_A = 7$, $U = 0$, $P = 0.006$).

Rank Differences

We did not find any significant correlation between rank and factors derived from behavioral indices. We did, however, find a statistically significant correlation between rank and Aggressiveness$_Q$; higher-ranking males were rated as more aggressive ($R = 0.88$, $P = 0.008$).

DISCUSSION

In 16 wild bonobos, five factors explained the correlations among 31 questionnaire items and three factors explained the correlations among 15 behavioral indices. The interrater reliabilities of the questionnaire-derived factors were comparable to or exceeded those found in human and animal personality studies [Funder et al., 1995; Gosling, 2001; Freeman and Gosling, 2010]. Personality dimensions similar to the Unemotionality$_Q$, Friendliness$_Q$, Aggressiveness$_Q$, Irritability$_Q$ and Activity$_Q$ have been found in other nonhuman primate species [for a review see Freeman and Gosling, 2010].

The behavioral factors were labeled Grooming$_B$, Playfulness$_B$, and Introversion$_B$. There was some evidence for convergent validity [Campbell and Fiske, 1959] in that Friendliness$_Q$ was significantly correlated with Playfulness$_B$. None of the other correlations achieved significance, probably due to our small sample size. However, the direction and size of some of the other correlations were in the expected direction based on the definitions of the questionnaire- and behavior-based factors, and within the range of validity correlations found in studies of humans [for a review see Meyer et al., 2001] and nonhuman primates [for a review see Freeman and Gosling, 2010]. The only exception to this was that Grooming$_B$ had a very low and non-significant correlation with Friendliness$_Q$. However, this may be because bonobos differ in chimpanzees in their grooming habits in that bonobos engage mainly in dyadic grooming interactions as opposed to polyadic grooming [Sakamaki, 2013], which suggests that grooming may serve different functions in bonobos and chimpanzees.

Unemotionality$_Q$ loaded on items such as *anxious* and *vulnerable* – which are usually markers of Neuroticism in other great apes [Fearful in Gold and Maple, 1994; Neuroticism in Weiss et al., 2006; 2009; 2012] – but also *individualistic*, *lazy* and *unemotional*, which, in other studies, load on Openness [Eckardt et al., 2014] or Extraversion [Weiss et al., 2006; 2009]. The only personality study that contained a large sample size of bonobos found six personality dimensions [Weiss et al., 2015]. Unemotionality$_Q$ was similar to the inverse of Extraversion in captive bonobos [Weiss et al., 2015]. The fact that we did not find a clear Neuroticism factor, but a mixed factor with items related to Openness or Extraversion suggests that there may have been less selective pressure for the evolution of a dimension similar to Neuroticism in wild

bonobos. This is consistent with the less competitive nature of bonobo society compared to other great apes [Parish and de Waal, 2000; Paoli, 2009; Furuichi, 2011]. Although it is possible that this factor did not emerge because of our small sample size or because of the conservative inter-rater reliability cut-point, a recent large study of captive bonobos that used a liberal interrater reliability cut-point also did not find a factor resembling Neuroticism [Weiss et al. 2015].

A clear Neuroticism dimension was also absent in Hanuman langurs [Konečná et al., 2008] and Barbary macaques [Konečná et al., 2012] leading the authors of these studies to suggest that Neuroticism may not evolve in species where aggression is not followed by severe consequences. However, the causality is not clear. An alternative hypothesis offered by Eckardt et al. [2014] who, after not finding any Neuroticism-like dimension in wild mountain gorillas, is that Neuroticism may not evolve in species living in relatively stable environments where competition over food resources is low.

Friendliness$_Q$ was made up of items that loaded on Extraversion or Agreeableness (*friendly*, *affectionate*) and Openness (*inventive*, *impulsive*) in other nonhuman primate species [Gold and Maple, 1994; King and Figueredo, 1997; Weiss et al., 2006; Konečná et al., 2008; Weiss et al., 2009; 2011] and also in humans [Goldberg, 1990]. Friendliness$_Q$ is also similar to Friendliness in rhesus macaques [Weiss et al., 2011] and to factors labeled Sociability in gorillas [Eckardt et al., 2014], brown capuchin monkeys [Morton et al., 2013], and rhesus macaques [Stevenson-Hinde et al., 1980; Capitanio, 1999], and it was similar to Openness and Agreeableness in captive bonobos [Weiss et al., 2015].

Aggressiveness$_Q$ loaded on the items *bullying*, *decisive* and *aggressive*. This factor is similar to components or factors labeled Confidence in other nonhuman primates that were related to rank [Capitanio, 1999; Konečná et al., 2008; Konečná et al., 2012]. This factor was similar to the Dominance dimension found in chimpanzees [King and Figueredo, 1997; Weiss et al., 2012b], orangutans [Weiss et al., 2006; 2012b], and gorillas [Gold and Maple, 1994; Kuhar et al., 2006; Eckardt et al., 2014; Schaefer and Steklis, 2014]. However, the loading of *submissive* on this factor was lower than its loading on Unemotionality$_Q$. This loading was also markedly weaker than it is in other great apes. Aggressiveness$_Q$ was the only factor associated with rank. Though based on the lack of a correlation we cannot establish that there is no Dominance factor in bonobos, these results partially support our prediction that Dominance does not play a major role in bonobo personality. Moreover, although the item *dominant* often has one of the highest interrater reliabilities in other great apes [e.g., King and Figueredo, 1997], its interrater reliability in this study was low, *ICC*(3,1) = 0.06. Similarly to our findings, in captive bonobos the factor Assertiveness was not as clearly an indicator of dominance traits as was the chimpanzees Dominance factor [Weiss et al., 2015].

Irritability$_Q$ comprised the items *irritable*, *protective*, (not) *sociable*, and (not) *playful*. As such, it partly resembled the inverse of Extraversion but it also contained items related to high and low Agreeableness in humans [Goldberg, 1990]. In chimpanzees the first two loadings are indicative of low Conscientiousness and high Agreeableness, respectively, and the latter two are indicative of low Extraversion [King and Figueredo, 1997; Weiss et al., 2009]. In other nonhuman primate species, these associations are

similar, though *irritable* is associated with high Dominance [orangutans in Weiss et al., 2006; rhesus macaques in Weiss et al., 2011] or high Confidence [Hanuman langurs in Konečná et al., 2008]. This, again, may reflect the reduced importance or salience of a Dominance factor in wild bonobos.

As in free-ranging rhesus macaques [Weiss et al., 2011], $Activity_Q$ comprised a separate factor in wild bonobos. This pattern differs from other nonhuman primates where items such as *active* or *activity* load with items related to exploratory behavior (*curious*, *inventive*, *innovative*, *inquisitive*), resulting in factors labeled Excitability [Stevenson-Hinde et al., 1980], Activity/Excitability [Konečná et al., 2012], Extraversion [Weiss et al., 2006], or Openness [Eckardt et al., 2014]. Items associated with the tendency to explore the environment are difficult to recognize in bonobos probably due to their low level of tool use [Hohmann and Fruth, 2003; Gruber et al., 2010; Furuichi et al., 2014]. Other species that did not have an Openness factor were Hanuman langurs [Konečná et al., 2008] and Barbary macaques [Konečná et al., 2012]. This led the authors of these studies to hypothesize that Openness might be selected for in fluctuating environments. The present findings support this hypothesis, namely as bonobos evolved in an environment with smaller seasonal changes in food availability [Furuichi, 2009; Hare et al., 2012]. However, because of our conservative reliability criterion we omitted items related to exploratory behavior, and so the present findings offer only weak support for this hypothesis. It is worth noting that $Activity_Q$ is not to be confused with overall locomotion, i.e. it is not a factor that would predict the calories burnt.

Only the factors Unemotionality$_Q$ and Friendliness$_Q$ replicated when analyzed using REFA. Thus, results related to Aggressiveness$_Q$, Irritability$_Q$ and Activity$_Q$ should be viewed with caution. Comparing the last three factors with those derived from captive bonobos, we found that the pattern of salient loadings of Aggressiveness$_Q$ suggested that it was similar to the inverse of Conscientiousness, while Activity$_Q$ was similar to Openness, and Irritability$_Q$ resembled the inverse of Openness [Weiss et al., 2015].

Factor analysis of the behavioral indices revealed dimensions labeled Grooming$_B$, Playfulness$_B$ and Introversion$_B$. Unfortunately, we could not test whether these factors were repeatable, and thus verify that they were personality factors. Similar behavioral factors have been found to be repeatable in captive chimpanzees [Koski, 2011] and wild crested macaques [Neumann et al., 2013]. Future studies of wild bonobo personality are necessary to verify that these behaviors are repeatable.

Grooming$_B$ was similar to the behaviorally-derived Sociability factor (both contained items related to grooming time and initiation), Playfulness$_B$ was similar to Positive affect (both were associated with play initiation and play time), and Introversion$_B$ to Anxiety (both had items scratching and self-grooming) in captive chimpanzees [Koski, 2011; Massen and Koski, 2014]. Given that two of these behaviorally-derived factors are related to social behavior (Grooming$_B$ and Playfulness$_B$), our results support the idea that in primates, and probably other species with complex social systems, sociability is not a single trait [see, e.g., Anestis, 2005; Koski, 2011]. The emergence of Playfulness$_B$ supported our prediction that play has an important role in bonobo personality, but studies in wild chimpanzees applying similar methods are needed to verify if this is a

true species difference. When we analyzed the behavioral indices by using REFA, we found three similar factors indicating that the small sample size did not reduce the factor stability.

In addition to determining the structure of personality in wild bonobos, we found that males were more introverted than females, and that females were more irritable than males. These findings are consistent with our prediction that sex differences in bonobo personality traits related to sociability would be opposite to what they are in chimpanzees [Buirski et al., 1978; King et al., 2008]. Our prediction that sex differences are opposite in the *Pan* species regarding traits related to aggression was therefore not supported. However, we did not find sex differences in Aggressiveness$_Q$, which differs from previous reports in chimpanzees [Buirski et al., 1978; King et al., 2008].

Adolescents had higher scores on Friendliness$_Q$ and lower scores on Aggressiveness$_Q$, than adults and old adults. These findings are consistent with findings in chimpanzees [King et al., 2005; Weiss et al., 2009] and gorillas [Kuhar et al., 2006; Eckardt et al., 2014] as older individuals in both species are higher in dimensions related to Dominance and lower in dimensions related to Extraversion.

Our prediction that the correlation between personality and rank is low in bonobos was not supported. However, we found a correlation only for one factor, in contrast with wild chimpanzees, where more correlations have been found [Buirski et al., 1978]. Higher male rank was associated with higher Aggressiveness$_Q$. This is consistent with studies in wild chimpanzees [Buirski et al., 1978] and other nonhuman primates

[Capitanio, 1999; Konečná et al., 2008; Konečná et al., 2012]. However, because age is associated with Aggressiveness$_Q$ and rank in our subjects, the association between rank and Aggressiveness$_Q$ may be confounded by age.

Although our study is the first to examine personality in wild bonobos, it is not without its limitations. For one, we cannot rule out the possibility that differences between chimpanzees and bonobos are population differences and not species differences [Doran et al., 2002]. To be sure that the differences we identified reflect species differences will require additional studies of personality in several wild populations of both bonobos and chimpanzees. Another limitation of this study is that we only selected questionnaire items with high interrater reliabilities. We were thus unable to directly compare the wild bonobo factor structure to factor structures derived in previous nonhuman primate personality studies. Furthermore, the reduced item set, and thus lower factor saturation, combined with the small sample size, may have reduced the stability of the factor structure [Velicer and Fava, 1998; MacCallum et al., 1999]. However, for both the behavioral and questionnaire data analysis, we met the minimum criteria suggested by simulation studies [de Winter et al., 2009], and using REFA we found that the three behavioral factors replicable and that two ratings-derived factors were replicable. Moreover, the rating based factors were similar to those derived in a captive population [Weiss et al., 2015]. However, future studies with larger sample sizes are thus needed to confirm the factor structures derived in the present study.

In conclusion, questionnaire ratings can be used to study personality in wild bonobos (and probably other wild nonhuman primates) in that the interrater reliabilities were

comparable to those found in other personality studies [Meyer et al., 2001; Freeman and Gosling, 2010]. Furthermore, these results supported some of our predictions based on the differences between chimpanzees and bonobos: play had an important role in bonobo personality, there was no Dominance factor, sex differences in traits related to sociability were opposite in direction to those in chimpanzees, and we did not find sex differences in aggression-related traits, unlike in chimpanzees. These findings were consistent with differences between chimpanzee and bonobo social systems identified in behavioral studies, e.g. female bonobos aggregating more and having high social status compared to female chimpanzees, and lower level of aggression in bonobo societies compared to chimpanzees [Goodall, 1983; Kano, 1992; Parish and de Waal, 2000; Furuichi, 2011]. Our study of personality in wild bonobos provides insights into the evolution of personality and the social systems of primates, and aids in our understanding of the evolution of individual differences in behavior.

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