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Social personality traits in chimpanzees: temporal stability and structure of behaviourally assessed personality traits in three captive populations

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Abstract Animals of many species show consistency in behaviour across time and contexts that differs from other individuals' behaviour in the same population. Such 'personality' affects fitness and has therefore become an increasingly relevant research topic in biology. However, consistent variation in social behaviour is understudied. In socially living species, behaviour occurs in a social environment and social interactions have a significant influence on individual fitness. This study addressed personality in social behaviour of 75 captive chimpanzees in three zoos by coding observed behaviour. Fifteen behavioural variables were significantly repeatable (range 0.21–0.93) in at least two of the three zoos. The behaviours showed considerable long-term stability across 3 years, which did not differ from the short-term repeatability. The repeatable behaviours were then analysed with factor analyses. They formed five independent factors, three of which consisted of social traits and were labelled 'sociability', 'positive affect' and 'equitability'. The two non-social behaviour factors were labelled 'anxiety' and 'activity'. The factor scores were analysed for sex and population differences. Males had higher factor scores in all traits except 'sociability'. The factor scores differed also between the zoos, implying

considerable external effects in trait expression. The results show that chimpanzees show personality in a broad range of social and non-social behaviours. The study highlights the importance of assessing personality in the social behaviour, especially in cohesive social species, as only then can we understand the consequences of personality in socially living species.

In many animal species, individuals show consistent differences in behaviour (Réale et al. 2007; Sih and Bell 2008). Such variation has been called 'personality' (Gosling 2001), 'behavioural type' (Sih and Watters 2005), 'coping style' (Koolhaas et al. 1999), 'behavioural syndrome' (Sih and Bell 2008) and 'temperament' (Réale et al. 2007). Each of these terms has a particular emphasis, but all share the feature that behaviour is more consistent temporally and contextually within than across individuals (Sih and Bell 2008). Animal personality is increasingly important in behavioural, evolutionary and theoretical ecology (e.g. Dall et al. 2004; McNamara et al. 2009; Réale et al. 2010; Sih et al. 2004), comparative psychology (Gosling 2001; Weiss et al. 2007; Uher 2008) and applied behavioural sciences (Ruis et al. 2000). Personality traits have moderate heritability (Bouchard and Loehlin 2001; Dingemanse et al. 2002) and they influence fitness (Smith and Blumstein 2008). This presents a challenge to explain how behavioural variation is maintained in a population (Dingemanse and Wolf 2010). Furthermore, given that behavioural flexibility should be more adaptive than consistency in an environment that varies unpredictably, the causal factors that underpin behavioural consistency and the fitness consequences that follow it are in

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the limelight of current research efforts (e.g. Bergmüller and Taborsky 2010).

Several personality traits have been described in vertebrates and invertebrates, but most studies have focused on only a few. Boldness, curiosity (or exploration tendency), activity and aggressiveness have attracted the most theoretical and empirical research. These personality traits occur in species from invertebrates to birds, reptiles, fish and mammals (Réale et al. 2007; Sih and Bell 2008). Furthermore, these traits may co-vary as syndromes, i.e. exhibit consistent correlations across different traits (Sih and Bell 2008; Dingemanse et al. 2010a), which suggests that they share proximate mechanisms. For example, boldness, activity and aggressiveness are correlated in many species (Dingemanse et al. 2010a; Sih and Bell 2008; Sih et al. 2004).

Personality variation in social behaviour other than aggression has received little research attention, so we know little about how inter-individual variation in social behaviour is attributable to personality (Bergmüller and Taborsky 2010; Krause et al. 2010; Schürch et al. 2010; cf. Virgin and Sapolsky 1997). However, personality in a social setting is gaining more attention for at least three reasons. First, in theoretical models that include "social environment" as an explanatory variable, it appears to maintain inter-individual variation in continuous behavioural traits (McNamara et al. 2009), thus shedding light on the evolutionary puzzles of personality. Second, personality influences how individuals interact in competitive, affiliative and cooperative social networks (Krause et al. 2010). For example, bold three-spined sticklebacks (*Gasterosteus aculeatus*) overall have fewer but more evenly distributed interactions with others, whilst shy individuals have more frequent but strongly skewed interactions with others (Pike et al. 2008). In a cooperatively breeding cichlid (*Neolamprologus pulcher*), curiosity, boldness and aggressiveness correlate positively as a syndrome, which also correlates with helping behaviour (Bergmüller and Taborsky 2007; Schürch and Heg 2010) and influences the number and quality of interactions in social networks (Schürch et al. 2010). Individuals also associate selectively according to personality; guppies (*Poecilia reticulata*) that leave the shoal to inspect predators prefer to associate with others of the same behavioural type (Croft et al. 2009). Third, sociability as a personality trait is likely to be an important factor in social interactions. Sociability, defined as an individual's reaction to the presence versus the absence of conspecifics and tendency to seek their proximity, has received only limited research attention. In common lizards (*Lacerta vivipara*), high social tolerance increases survival at high population density and dispersal at low density, whilst low social tolerance increases survival at low density and dispersal at high density (Cote and Clobert 2007; Cote et al. 2008, 2010). Sociability is likely to be especially relevant

in group-living species, in which individuals repeatedly interact within a network of relationships, and to have important repercussions on individual fitness and on population-level phenomena.

Altogether these studies suggest that personality affects the various aspects of social life, such as group composition (Croft et al. 2005), networking (Krause et al. 2010), dispersal (Cote et al. 2010), niche specialisation (Bergmüller and Taborsky 2010), social learning (Reader 2003), cooperation (Bergmüller et al. 2010; Fishman et al. 2001), group stability (Flack et al. 2006) and disease and parasite spread (Barber and Dingemanse 2010; Capitanio et al. 1999).

However, we know little of which types of social behaviour are personality traits in various species. Sociability is a broad trait category that encompasses a range of behaviours, from tolerance to the presence of an unfamiliar conspecific (lizards; Cote and Clobert 2007) to the tendency to actively seek proximity with others (guppies; Budaev 1997) and to form close bonds with frequent interactions across contexts and over the years (baboons, *Papio* sp.; Silk et al. 2009). Consistent variation may exist at all these levels of sociability and correlate with other personality traits as syndromes. For example, affinitive network size may correlate with the frequency of other kinds of affinitive behaviour (van Hooff 1973), boldness (Pike et al. 2008), calmness (Weinstein and Capitanio 2008) or activity (Konečná et al. 2008).

Addressing sociability in species with cohesive, individualised social networks, such as diurnal primates, should be informative. Primate social relationships form networks of qualitatively and quantitatively different histories of interactions that can be categorised in various ways (e.g. dominance, kinship and 'friendship': Cords and Aureli 2000; Silk 2002). Social relationships may last for years or even decades (Silk et al. 2010; Mitani 2009). Longevity and differential qualities of social relationships make primate social networks complex, and so personality can have substantial effects on behaviour and, potentially, on fitness.

The importance of sociability is suggested by several primate studies (Freeman and Gosling 2010). In chacma and yellow baboons (*Papio hamadryas ursinus* and *P. h. cynocephalus*), the quality of social relationships increases the survival of the females and their offspring (Silk et al. 2009, 2010). In rhesus macaques (*Macaca mulatta*), sociability influences the immune function (Capitanio et al. 1999). In chimpanzees (*Pan troglodytes*), alpha males have consistent individual differences in grooming and aggression patterns (Foster et al. 2009). Finally, in humans (*Homo sapiens*), sociability and its higher-level personality construct extraversion (Costa and McCrae 1992) predict the likelihood of having children (Jokela et al. 2009), initiation of social contacts (Buchanan et al. 2005), size of social networks (Swickert et al. 2002) and sexual activity (Nettle 2005; Schmitt 2004). Taken together, sociability figures

consistently in many primate species and has significant fitness consequences. Therefore, studies of social personality traits will shed light on the magnitude of personality variation in the social domain, allow the assessment of the interactions between social behaviour and other personality traits and enhance the understanding of the evolutionary significance of personality in a social environment.

In this study, I assessed personality in a large number ($N=75$) of captive chimpanzees. Earlier behavioural research on chimpanzee personality has assessed only youngsters (Anestis 2005), few individuals (Uher et al. 2008) or males only (Foster et al. 2009; Anestis 2006). Much research has been done on great ape personality with a 'psychological approach' that relies upon human subjective evaluations of animal personality (King and Figueredo 1997; Weiss et al. 2002, 2007; Murray 1998). These studies yield no data on individual variation at the behavioural level (Uher 2008; Koski 2011). Thus, the present study is the first to provide basic data on personality differences in a large number of chimpanzees of both sexes and from multiple captive facilities.

I quantified within-individual consistency and between-individual variation in a range of ecologically and evolutionarily relevant social behavioural patterns (Table 1). The first aim was to test if the sampled behaviours were repeatable (Lessells and Boag 1987) and thus agreed with the definition of personality. Repeatability assesses the proportion of variation in behaviour that is due to inter-individual variation, as compared to intra-individual variation, and thus measures an individual's behavioural consistency. Second, I addressed the trait correlation structure to understand which social behavioural patterns are expressed as broader trait categories and whether social behaviours form syndromes with non-social behaviours, including general activity and self-directed behaviours (SDBs) that can be considered as indicators of anxiety (Leavens et al. 2001; Maestripieri et al. 1992; Schino et al. 1996). I expected to find personality traits in the realms of grooming and aggression (Anestis 2005; Foster et al. 2009; Uher et al. 2008) but refrained from predictions concerning other potential personality traits or their structural organisation. I further assessed sex differences in personality scores. Based on chimpanzee socioecology (Pepper et al. 1999; Gilby and Wrangham 2008), I predicted that males are more sociable than females. Finally, I assessed whether different captive groups differed regarding individual personality scores.

Methods

Study subjects and data collection

The study consists of observational data of 75 adult and adolescent individuals' behaviour. The data were collected in 2002–2009 at three zoos: Burgers Zoo (AR) in Arnhem, The Netherlands, in 2002–2005; Chester Zoo (CH) in Chester, UK, in 2008; and Beekse Bergen Safaripark (BB) in Hilvarenbeek, The Netherlands in 2009.

The chimpanzee group of AR was established in 1971. During the study, the group had 5 adult or adolescent males, 17 adult or adolescent females and 7–9 infants and juveniles (not observed). All but four founding (wild-caught) individuals were born and reared in the group, and no new individuals were introduced during the study. Four individuals were transferred elsewhere before the end of the study but remained long enough to yield a sufficient amount of data (see below). The group lived in a combination of outdoor island (7,000 m^2), indoor enclosure (378 m^2) and adjacent off-exhibit feeding and sleeping cages.

The chimpanzee group of CH was established in 1956. The group had 5 adult and 1 adolescent male, 18 adult or adolescent females and 6 juveniles (not observed). All study subjects had been in the group since at least 1992 or born into the group later. The housing consisted of outdoor island (2,000 m^2), indoor enclosure (143 m^2) and adjacent off-exhibit feeding and sleeping cages.

The BB chimpanzee group was relatively newly established; the individuals were transferred from the Biomedical Primate Research Centre, Rijswijk, The Netherlands, to BB in 2006. The chimpanzees were divided into two groups, BBa and BBb. Both groups were formed by combining individuals from previously existing social groups; BBa was formed in 2003 and BBb in 2006. All individuals had been used in medical research until 2003, had varying rearing histories (i.e. mother or peer rearing) and past housing conditions (always socially but in varying group sizes). BBa had five adult males and 13 adult females and BBb had five adult males and six adult females. Neither group had infants or juveniles. Each group was housed in a combination of outdoor area (BBa, 2,786 m^2; BBb, 2,240 m^2), indoor enclosure (173 m^2) and adjacent off-exhibit cages. The groups had visual and auditory but no physical contact with each other.

In all facilities, the chimpanzees were fed three to four times daily and water was always available. The chimpanzees had regular enrichment with various toys and hidden, extractable or frozen food items, and the living quarters were furnished with climbing structures, logs, tyres, nets and straw or wood wool as nesting material. All zoos are in the European Association of Zoos and Aquaria and comply fully with the regulations for animal keeping and welfare. The study was purely observational and adhered to the national and international ethical requirements for animal welfare (Animal Behaviour Society Guidelines 2006).

Data were collected by myself and several students under my supervision. Before starting the data collection, the students trained at least for a month, after which their

Table 1 Behavioural variables sampled for repeatability

Variable	Definition	Calculated as
Activity	Time spent not resting or autogrooming (%)	Focal sample activity at each minute summed per category; observations spent resting or autogrooming subtracted from total (%)
Submission	Frequency of submissive behaviours (crouch, pant grunt)	Frequency/h submissions given
Aggression given	Frequency of aggression given (chase, hunch-over or physical aggression)	Frequency/h aggression given (ad lib. data, corrected to total group observation time)
Aggression received	Frequency of aggression received (chase, hunch-over or physical aggression)	Frequency/h aggression received (ad lib. data, corrected to total group observation time)
Number of neighbours	Number of individuals within 2 m	Average number of individuals in proximity, sampled once per focal observation
Approach others	Frequency of focal subject approaching others (not aggressively)	Frequency/h of focal subject approaching and staying in 2 m proximity of others
Being approached	Frequency of focal subject being approached by others (not aggressively)	Frequency/h of focal subject being approached with a neutral or positive response by the subject
Grooming density	Number of individuals the focal subject grooms	Total number of individuals focal subject gives grooming to divided by all available grooming partners
Grooming diversity	Skew of grooming given	Shannon–Wiener diversity index corrected to group size effect (see text for the formula)
Grooming initiated	Frequency of grooming given	Frequency/h of grooming given by focal subject, so that each grooming partner is counted only once/focal observation
Grooming received	Frequency of grooming received	Frequency/h of grooming received by focal subject, so that each grooming partner is counted only once/focal observation
Point affinitive behaviours	Frequency of short duration affinitive behaviours (kiss, kiss-bite, gentle touch, embrace, sexual inspection, genital touch, mount, mate, hand- or fingers-to-mouth)	Frequency/h of point affinitive behaviour by focal subject
Play initiated	Frequency of play initiated	Frequency/h of play initiated by focal subject
Play received	Frequency of play received	Frequency/h of play initiations accepted by focal subject
Scratching	Frequency of self-scratching (rough and gentle)	Frequency/h of self-scratching. Counted separately when separated by 5-s interval or the scratched body part changed
Auto-grooming	Duration autogroom	Frequency/h focal autogrooms. Recorded as durations to the nearest second

All frequency measures are corrected by the individual observation time, except aggressive conflicts (corrected by summed group observation time following the ad libitum recording)

inter-observer reliability was tested against my observations. Their inter-observer reliability had to meet the minimum criterion of 90% similarity before data were considered as reliable.

In each zoo, chimpanzees were observed at least 4 days a week, all day. Data were obtained by focal animal sampling (Martin and Bateson 1993) of 15-min (AR) or 10-min (CH and BB) duration, during which we recorded the focal individual's main activity at 1-min intervals and all social interactions and self-directed behaviours continuously. In addition, aggressive conflicts were recorded ad libitum. In each zoo, each animal usually was observed only once, occasionally twice, a day. The order of individuals was randomised at the beginning of the study and thereafter kept consistent but varying the first focal individual each day. By

the end of the study period, all individuals in a group had been observed for the same amount at each time of the day.

The data collection periods and the obtained observation hours were: AR, September 2002–October 2005, 1,541 h of focal observations (X=70 h/individual); CH, June–September 2008, 86 h of focal observations (X=3.6 h/individual); BB, May–September 2009, 93 h (group BBa, X=5 h/individual) and 154 h (group BBb, X=14 h/individual) of focal observations. (BBa was observed less than BBb due to a management decision that prohibited further observations.)

Behavioural variable extraction

From the focal observation data, I extracted the individual scores of behavioural variables. Originally, I selected 23

behaviours based on their relevance to chimpanzee socio-ecology and frequent expression in both captivity and the wild (van Hooff 1973; Nishida et al. 2010). However, the lack of sufficient data for all or the majority of the individuals forced me to exclude some behaviours (e.g. female submissive behaviour to other females; dominance displays) and combine others into larger categories (e.g. mild and severe aggression). Table 1 gives the final set of 16 variables sampled as potential personality behaviours.

Most of the behavioural variables were calculated as frequency per hour, corrected by the focal observation time per individual. Activity was calculated from time-budget data, derived from the focal sampling main activity per minute, and reported as the proportion of time spent not resting (i.e. walk, run, groom, play, forage, etc., but not rest or autogroom). The number of neighbours was the average number of individuals within 2 m of a focal subject at the beginning of the focal observation (sampled once/day). Grooming density was the proportion of grooming partners of all available partners (grooming partner was defined as a binary value of yes/no grooming given by a focal subject during the whole observation period; only adults and adolescents were considered). Grooming diversity index (GDI) was calculated with the Shannon–Wiener diversity index corrected for the group size effects (Cheney 1992; Di Bitetti 2000), as follows:

$$\text{Grooming diversity index} = H/H_{\max}$$
$$H = -SUM(p_i x \ln(p_i))$$

in which p_i is the proportion of individual's grooming effort given to the ith individual

$$H_{\max} = \ln(N - 1)$$

in which N is the number of individuals in the group. GDI results are in a value between 0 (representing perfect skew, i.e. all subject's grooming effort is directed to one individual) and 1 (representing perfect equality).

Data analyses

First, the data were divided into time periods to test repeatability (Lessells and Boag 1987). Data from AR covered nearly 3 years, allowing division into six periods based on the predominance of indoor and outdoor observations. The periods were: winter 1 (Oct 2002–April 2003, 74% observations indoors), summer 1 (May–September 2003, 100% observations outdoors), winter 2 (October 2003–January 2004, 91% observations indoors), summer 2 (June–October 2004, 100% observations outdoors), winter 3 (October 2004–April 2005, 56% observations indoors), summer 3 (May–August 2005, 98% observations outdoors). Data of CH and BB were divided into two periods: CH time 1 (June–mid-July 2008), time 2 (mid-July–September 2008); BB time 1 (May–mid-July 2009), time 2 (mid-July–September 2009). As the CH and BB studies were short-term studies, data could not be divided according to the indoor/outdoor observation context.

I calculated separately the individual behaviour scores for the 16 variables for each period. The repeatability of these individual behaviour scores was tested by intraclass correlation (ICC) with a two-way mixed model, with the period as fixed and the individual as a random factor (McGraw and Wong 1996). ICC analyses were run separately for each zoo. Repeatability analyses of the CH and BB data contained two behaviour scores per individual (i.e. time 1 and time 2) per behaviour. The individuals of BBa and BBb were pooled in the analysis. AR data allowed repeatability calculations of both short-term and long-term data. The short-term ICC was calculated on the individual behaviour scores from two consecutive winter observation periods (i.e. two scores per individual; winter 1 and winter 2), and the long-term ICC was calculated on the individual behaviour scores from all six periods (i.e. six scores per individual; from winter 1 to summer 3). Fewer individuals were included in the data set for the long-term ICC because four individuals were transferred to another zoo before the study was finished. Long- and short-term repeatability, respectively, were compared by testing the 16 variables' ICC values pairwise with Wilcoxon signed-rank test (given the non-normal distribution of the data). In addition, AR data allowed the comparison of the repeatability scores between different housing conditions; the ICC (model as above) of the variables was calculated for outdoor and indoor observations, respectively. The outdoor ICC consisted of individual behaviour scores from summer 1, summer 2 and summer 3 periods (i.e. three behaviour scores per individual). The procedure was repeated for the individual trait scores of winter 1, winter 2 and winter 3, representing indoor observations (again, three behaviour scores per individual). The indoor and outdoor ICC values were tested against each other with a Wilcoxon signed-rank test.

Secondly, I calculated the overall behaviour scores for each individual from the total observation time of those behaviours that were repeatable in at least two of the three zoos. There were two missing values of GDI (i.e. two individuals never groomed anyone during the study), which were replaced by the group mean GDI value. These scores were subjected to a Factor Analysis (FA). FA is a data reduction tool used to assess an unobservable latent construct that accounts for correlations amongst variables; it is preferable to principal components analysis when the aim is to interpret and label the emerging factors (Budaev 2010). The Kaiser–Meyer–Olkin Measure of Sampling Adequacy (KMO) and Bartlett's test of sphericity tests assured passable adequacy (KMO=0.66; Bartlett's sphericity

$\chi^2 = 484.4$, $df = 91$, $p < 0.0001$). FA was done using the correlation matrix and principal axis factoring; the factors were extracted based on eigenvalue >1 and scree-plot. The solution was Varimax rotated with Kaiser normalization. The analysis was repeated with an oblique (direct Oblimin) rotation.

Thirdly, I calculated the factor scores for the individuals with the regression method based on the final FA solution. These scores were compared across the zoos with one-way ANOVA or Kruskal–Wallis (K–W) tests, depending on the data distribution. Factor scores were also compared between males and females with independent samples t tests or Mann–Whitney U tests, depending on the data distribution. Analyses were done with SPSS 16.0 and 19.0.

Results

Nearly all tested potential personality variables were moderately or highly repeatable across all zoos (Table 2). Only one variable (frequency of aggression received) failed to show repeatability in two of the three zoos. Nine variables were repeatable in all three zoos and in both long-term and short-term AR data. Six additional variables were repeatable in all three zoos, but this was true only for the long-term data in AR (frequency of being approached, frequency of play invitations accepted and grooming diversity), or were repeatable in two out of the three zoos (activity, frequency of grooming received and frequency of play initiated). Thus, 15 behaviour variables were deemed repeatable based on sufficiently high scores in at least two out of the three zoos.

There were no consistent differences in repeatability values of indoor and outdoor observations of AR data (Wilcoxon signed ranks (WSR), $z = 1.48$, $p = 0.14$, $N = 16$; data not presented). There was also no temporal difference in the repeatability of AR data. The long-term repeatability that covered nearly continuous observations across 3 years had repeatability that were similar overall to data from two consecutive winter observation periods (WSR, $z = 1.89$, $p = 0.059$, $N = 16$). Long-term repeatability was higher than short-term repeatability for some variables, whilst short-term repeatability was higher than long-term repeatability for others (Table 2).

The 15 variables that were repeatable in at least two of the three zoos were included in the factor analysis of intercorrelational structure. The frequency of received aggression was excluded as an unrepeatable variable. After the initial run, the frequency of submissive behaviour was excluded due to poor loading in any factor (maximum loading 0.26) and poor communality (0.15). The remaining 14 variables were analysed again with FA, and 5 factors that explained 77.3% of variance were extracted. These were orthogonally rotated, and the solution is presented in Table 3.

The first factor explained 25.0% of the variance. It included strong loadings of the frequency of grooming given and received, the number of individuals in close proximity and the frequency of being approached with a neutral or positive response by a focal subject. These behaviours are sociopositive, reflecting relationship maintenance and sociability. Consequently, this factor was labelled *sociability*. The second factor explained 17.2% of the variance. Variables that loaded on this factor were the frequency of approaching others (non-aggressively), frequency of initiating and receiving play and frequency of short duration affinitive behaviours such as kiss, embrace and sexual behaviours. Therefore, this factor was labelled *positive affect*. The third factor explained 15.2% of the variance and had loadings from the two grooming indices, diversity and density. As they both loaded positively on the factor, and higher GDI indicates more equitable distribution of grooming given, this indicates that a high number of grooming partners correlated with a more equal distribution of grooming effort amongst them. Therefore I labelled this factor *equitability*. The fourth factor, which explained 11.4% of the variance, had high loadings from SDB. As SDBs are considered indicators of anxiety, I labelled this factor as *anxiety*. Finally, the fifth factor explained 8.4% of the variance and had loadings of activity, the frequency of aggression and (negatively) the frequency of proximity initiated. However, this factor has to be treated with caution because aggression and proximity initiation had relatively weak loadings (Budaev 2010) (Table 2). I labelled the factor *activity* but consider it less reliable than the first four factors.

Reanalysis with an oblique (direct Oblimin) rotation did not change much the solution; correlations between the factors did not exceed ±0.21 (range −0.01–0.209) (Table 4). Three variables loaded > ±0.40 on an additional factor (indicated as footnote "a" in Table 3).

The factor scores of individuals differed between males and females in all but the first factor (sociability, Mann-Whitney U test (MWU) $N_{females} = 55$, $N_{males} = 20$; $z = 0.61$, $p = 0.541$) (Fig. 1). In positive affect, equitability, anxiety and activity, the male scores were significantly higher than female scores (in all analyses $N_{females} = 55$, $N_{males} = 20$, positive affect, MWU, $z = 2.40$, $p = 0.017$; equitability t test, $F = 2.11$, $t = -3.33$, $p = 0.001$; anxiety, MWU, $z = 2.42$, $p = 0.016$; activity t test, $F = 0.23$, $t = -2.46$, $p = 0.016$).

The factor scores of individuals differed between the zoos in all but the fourth factor (sociability, K–W test $H(2) = 36.8$, $p < 0.000001$; positive affect, K–W $H(2) = 9.35$, $p = 0.009$; equitability, ANOVA $F(74) = 14.48$, $p < 0.00001$; anxiety, K–W $H(2) = 2.32$, $df = 2$, $p = 0.31$; activity, ANOVA $F(74) = 40.43$, $p < 0.00001$) (Fig. 2). Post-hoc assessment of the differences between the zoos in sociability and positive affect scores were done with MWU (with a Bonferroni

Table 2 Repeatability (intra-class correlation coefficient) of the 16 variables reported for each zoo

Variable	AR long	95% CI (lower, upper) F, p	AR short	95% CI (lower, upper) F, p	CH	95% CI (lower, upper) F, p	BB	95% CI (lower, upper) F, p
Submission	0.36	(0.18, 0.61) 4.42, <0.001	0.41	(−0.01, 0.70) 2.34, 0.027	0.34	(−0.06, 0.65) 2.05, 0.046	0.48	(0.14, 0.72) 2.83, 0.004
Aggression given	0.57	(0.38, 0.77) 8.94, <0.001	0.48	(0.08, 0.74) 2.83, 0.010	0.52	(0.15, 0.76) 3.15, 0.004	0.74	(0.51, 0.87) 6.5, <0.001
Aggression received	0.33	(0.15, 0.58) 3.92, <0.001	0.33	(−0.10, 0.65) 1.99, 0.062	−0.004	(−0.40, 0.40) 0.99, 0.507	−0.15	(−0.49, 0.23) 0.75, 0.78
No. neighbours	0.38	(0.19, 0.63) 4.71, <0.001	0.64	(0.31, 0.83) 4.57, <0.001	0.93	(0.84, 0.97) 26.0, <0.001	0.49	(0.16, 0.72) 2.92, 0.003
Approaching	0.21	(0.05, 0.46) 2.61, 0.002	0.50	(0.10, 0.75) 2.96, 0.008	0.92	(0.81, 0.96) 22.6, <0.001	0.53	(0.21, 0.75) 3.23, 0.001
Being approached	0.32	(0.14, 0.57) 3.85, <0.001	0.22	(−0.21, 0.58) 1.58, 0.153	0.86	(0.71, 0.94) 13.4, <0.001	0.46	(0.12, 0.70) 2.68, 0.006
Play initiate	0.43	(0.24, 0.67) 5.55, <0.001	0.52	(0.14, 0.77) 3.17, 0.005	0.87	(0.73, 0.94) 14.7, <0.001	0.19	(−0.18, 0.52) 1.48, 0.154
Play receive	0.26	(0.09, 0.52) 3.15, <0.001	0.25	(−0.18, 0.60) 1.68, 0.121	0.49	(0.11, 0.74) 2.88, 0.007	0.65	(0.38, 0.82) 4.74, <0.001
Groom given	0.47	(0.28, 0.70) 6.38, <0.001	0.62	(0.28, 0.63) 4.32, 0.001	0.47	(0.08, 0.73) 2.74, 0.010	0.39	(0.03, 0.66) 2.25, 0.018
Groom received	0.36	(0.17, 0.60) 4.31, <0.001	0.41	(−0.00, 0.71) 2.40, 0.025	0.71	(0.43, 0.86) 5.81, <0.001	0.30	(−0.07, 0.59) 1.84, 0.056
Point affinitive	0.78	(0.64, 0.90) 22.6, <0.001	0.82	(0.61, 0.92) 9.97, <0.001	0.53	(0.17, 0.77) 3.26, 0.003	0.66	(0.40, 0.83) 4.95, <0.001
Groom density	0.50	(0.30, 0.72) 6.95, <0.001	0.61	(0.26, 0.82) 4.13, 0.001	0.50	(0.12, 0.75) 2.96, 0.006	0.71	(0.48, 0.86) 6.00, <0.001
Groom divers.	0.48[a]	(0.27, 0.72) 6.47, <0.001	0.26	(−0.17, 0.61) 1.71, 0.113	0.38	(−0.01, 0.68) 2.25, 0.029	0.42[b]	(0.02, 0.71) 2.44, 0.020
Scratch	0.58	(0.39, 0.78) 9.23, <0.001	0.72	(0.44, 0.88) 6.24, <0.001	0.70	(0.42, 0.86) 5.70, <0.001	0.55	(0.23, 0.76) 3.43, 0.001
Autogroom	0.41	(0.21, 0.65) 5.09, <0.001	0.83	(0.64, 0.93) 10.8, 0.001	0.71	(0.43, 0.86) 5.83, <0.001	0.40	(0.05, 0.67) 2.34, 0.014
Activity	0.37	(0.18, 0.62) 4.54, <0.001	0.45	(0.04, 0.73) 2.61, 0.016	0.26	(−0.19, 0.57) 1.58, 0.140	0.91	(0.81, 0.95) 20.2, <0.001
$N=$	18		22		24		29	

ICC (3,1) values are given as consistency agreement and as single correlation. Bold values indicate statistical deviation from zero by F test. Each zoo was tested separately, but in BB the two groups (BBa and BBb) were pooled

AR Arnhem, *CH* Chester, *BB* Beekse Bergen, *AR long* repeatability analysis includes all six Arnhem sampling periods (six behaviour scores per individual), *AR short* repeatability analysis includes two consecutive Arnhem winter sampling periods (two behaviour scores per individual), *CI* confidence interval

[a] Due to missing values by two individuals (no grooming in one data period) $N=16$

[b] Due to missing values by six individuals (no grooming in one or both data periods) $N=23$

Table 3 Varimax rotated solution of factor analysis. Factor loadings>0.30, <−0.30 and communalities (h^2) are reported. [x] shows the additional loadings following an oblique rotation

Behaviour	Sociability	Positive affect	Equitability	Anxiety	Activity	h^2
Grooming initiated	0.887					0.869
Grooming received	0.802					0.664
No. neighbours	0.811				[−0.54][a]	0.841
Being approached	0.701				[−0.41][a]	0.565
Approach others		0.597			−0.399	0.575
Play initiated		0.829				0.715
Play received		0.708				0.525
Point-affinitive behaviour		0.855				0.771
Grooming diversity			0.837			0.742
Groom density			0.825			0.751
Scratch				0.911		0.856
Autogroom				0.658		0.463
Activity			[−0.43][a]		0.626	0.533
Aggression given					0.344	0.193
% variance explained	24.98	17.23	15.21	11.44	8.43	
Eigenvalue	3.5	2.41	2.13	1.60	1.18	

Analysis on correlation matrix, $N=75$

[a] Indicates the additional variable loadings that exceeded ±0.40 after oblique (direct Oblimin) rotation

correction; critical alpha set at $p=0.0167$). Sociability scores were significantly higher in CH than in BB and AR, whilst AR and BB did not differ from each other. Positive affect scores were also highest in CH, differing significantly from BB but not from AR. Post-hoc tests of equitability and activity scores were done with Gabriel's procedure following the unequal sample sizes and checked with Games–Howell procedure (Field 2005). Equitability scores were significantly higher in AR than in CH and BB, whilst CH and BB did not differ from each other. Activity scores were significantly lower in AR than in BB and CC, which did not differ from each other.
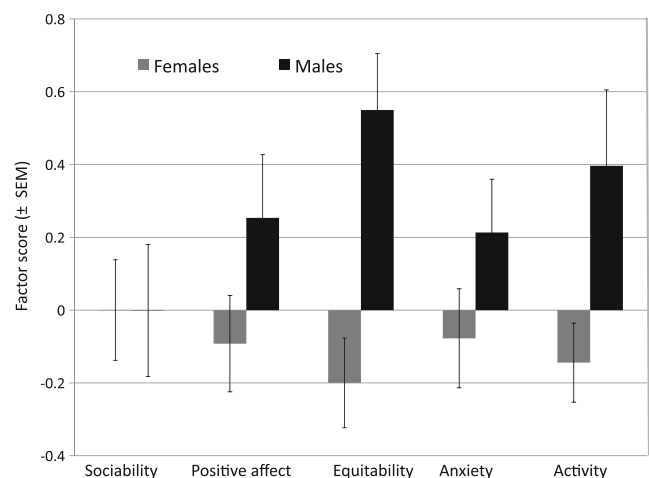
Discussion

This study aimed to identify personality traits in 75 captive chimpanzees from a broad base of ecologically relevant observable behaviours, with an emphasis on

Table 4 Intercorrelations of the factors (Oblimin rotation)

Factor	1	2	3	4	5
1	1.0	0.129	−0.025	−0.072	−0.113
2		1.0	−0.038	−0.011	−0.105
3			1.0	0.143	−0.209
4				1.0	0.025
5					1.0

social behaviour. All but one of the 16 behaviours were repeatable in at least two out of the three study populations, and most of them were repeatable in all three populations. Repeatability ranged between 0.21 and 0.93, which is within the values reported for most animal species (Bell et al. 2009). Thus, chimpanzees exhibited personality variation in several social behaviours. In addition, two commonly found personality traits, activity and aggressiveness, were confirmed to be repeatable in chimpanzees. The results support earlier, more limited behavioural personality studies on chimpanzees (Anestis

Fig. 1 Factor scores of males and females (all zoos combined). *Error bars* indicate±SEM. Males differed significantly from females in all factors (from $p<0.001$ to $p=0.017$), except sociability ($p=0.541$)
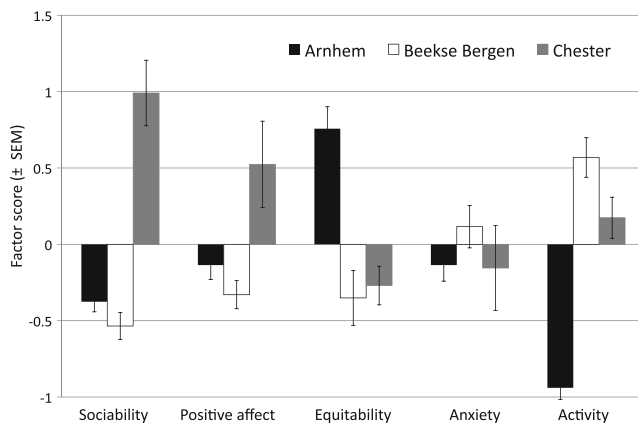
Fig. 2 Factor scores of the three study populations. *Error bars* indicate±SEM. Zoos differed significantly from each other in all factors (from $p<0.009$ to $p<0.000001$) except anxiety ($p=0.31$)

2005; Foster et al. 2009; Uher et al. 2008). However, direct comparisons are difficult, as to my knowledge only one study has formally tested trait repeatability (Uher et al. 2008), and that study included very few individuals ($N=5$) and had a very short time span (2 weeks between the obtained behaviour scores). The results given here on the diversity of social personality traits are novel and the number of individuals is much larger than in the previous studies. The identification of social personality traits is important in species that operate in complex social environments, as only then can we address the consequences of consistent individual variation on interaction patterns within a social system.

One of the key criteria of personality is consistency over time. The long-term repeatability, assessed across 3 years of observations, was similar to short-term repeatability. This indicates that the measured traits were truly personality traits in the sense of temporal consistency. However, due to the fact that social behaviour is always, by definition, a function of interactions, temporal consistency might result from particular social circumstances that create social niches for the individuals—subject to change should the circumstances alter. Temporal consistency would then be an artefact of unchanging social networks rather than a consequence of individual internal dispositions to certain behavioural patterns. Whilst this possibility cannot be ruled out, consistency over several years is likely to reflect more than situational effects on social behaviour. Furthermore, personality can be seen as behavioural reaction norms, so that behavioural phenotypes result from a combination of internal dispositions and extrinsic effects (Dingemanse et al. 2010b; Nettle and Penke 2010). Internal dispositions depend on genetic or other proximate-level mechanisms, whilst extrinsic effects can shape individual behaviour in time and across contexts. Thus, inter-individual variation in behaviour is an outcome of variation in the intercept

(individual's mean level of behaviour) and slope (individual's response to environmental variation) of a behavioural reaction norm (Dingemanse et al. 2010b). If behaviour is repeatable in time or across contexts within a population, the reaction norm curves have largely similar slopes but different intercepts between individuals. Behavioural reaction norms in social traits, thus, acknowledge the influence of a particular social environment as setting the affordances within which an individual operates, as dictated by its intrinsic personality dispositions. The result of high long-term repeatability suggests that the measured traits resulted from consistent differences amongst individual reaction norms. The next challenge is to address the shapes of the behavioural reaction norms as a function of various social environments.

I also investigated correlation patterns amongst the repeatable behaviours, which give insights into the potential behavioural syndromes. The traits formed five orthogonal factors, three of which included socio-positive behaviour. The independence of the factors was confirmed by the low correlations between factors and very similar solutions by orthogonal and oblique rotations. The first factor was named *sociability* following the loadings of given and received grooming, others approaching the focal subject and the average number of others in close proximity. Thus, behaviours essential in chimpanzee social relationship formation and maintenance, e.g. grooming, and those that reflect a general social tendency of seeking and accepting proximity were positively correlated. Independent of this general sociability factor, short-term affinitive behaviours, such as kissing, gentle touching and embracing, play activity and a tendency to approach others were correlated, forming the *positive affect* or playfulness factor. A third dimension to socio-positive behaviour was the positive correlation of the spread and the skew of grooming given, named *equitability*. I stress that this measure concerned only grooming given and, thus, is not indicative of dyadic grooming reciprocity. The positive correlation indicates that a larger number of grooming partners received more equitably divided grooming efforts, whilst grooming given to a few partners was skewed in distribution. This is somewhat surprising, as it could be expected that more grooming partners result in a stronger skew due to time and effort constraints (Dunbar 1993; Watts 2000). The result indicates that at least in these groups, constraints were relaxed to allow grooming efforts to be distributed equally amongst several grooming partners. Moreover, as there was a strong sex difference in equitability (see below), the pattern of grooming given equally to many partners appeared to be especially a male feature, whilst females groomed fewer individuals, amongst whom some were favoured relatively more often.

The assessed social behaviours formed three traits (factors) rather than a single category of sociability. Congruent findings were reported in a population of captive young chimpanzees, where socio-positive behaviours formed five orthogonal factors (Anestis 2005). Also in rhesus macaques, socio-positive behavioural traits correlate with two (subjectively rated) personality factors (Capitanio 1999). It appears that at least in primates, sociability is not a single trait, but social behaviours form several traits in a hierarchical organisation (cf. Réale et al. 2007). Multiple social traits might be typical in species with extensive and complex sociality, as in this study, and multiple dimensions to social behaviour might be a general function of increased social cohesion, complexity and possibly behaviour repertoire size, all of which are high in e.g. primates, cetaceans and social carnivores. Conversely, in species with less complex or cohesive social networks, sociability may encompass a single trait of proximity seeking and tolerance.

The fourth factor included SDBs, which are generally accepted indicators of short-term arousal, e.g. after aggressive conflicts and cognitive challenge (Leavens et al. 2001; Maestripieri et al. 1992) and the baseline anxiety (Schino et al. 1996). Some primate and bird studies have found covariation between anxiety and social behaviour (*Papio anubis*, Virgin and Sapolsky 1997; *P. troglodytes*, Anestis 2006) and exploration tendency (*Parus major*, Fucikova et al. 2009). In contrast, anxiety is encompassed by an independent construct, namely neuroticism, in the Five-Factor Model of human personality. Neuroticism includes the proneness to long-term anxiety and an easily triggered short-term stress response (Gunthert et al. 1999; Muris et al. 2004). The current study seems to support similar independence in chimpanzees (cf. Anestis 2005), suggesting that in this respect human and chimpanzee personality traits show structural similarity (cf. King and Figueredo 1997; Weiss et al. 2007).

The fifth factor included positive loadings of activity and aggressiveness and a negative loading of the frequency to approach others. Aggressiveness, thus, formed a syndrome with activity. Such a syndrome is described in many species, including three-spined sticklebacks, field crickets (*Gryllus integer*) and Hanuman langurs (*Semnopithecus entellus*) (Bell 2005; Kortet and Hedrick 2007; Konečná et al. 2008). However, due to the weak loadings of the aggression and (negatively) approach frequency, these interpretations remain tentative.

Behaviour correlations can be assumed to depend on shared proximate mechanisms and, thus, to reflect latent traits (Dingemanse et al. 2010a; Réale et al. 2007). For example, the correlation between initiated and accepted play was likely due to a mechanism influencing general playfulness. This in turn was connected to affinitive behaviours such as kissing and embracing, possibly due to

a latent trait of general positive affect. In humans, the similar personality construct, agreeableness, is correlated with cognitive processing of other's emotions (Nettle and Liddle 2008). It is tempting to speculate that individual differences in cognitive performance (Herrmann et al. 2010) may underpin the differences in positive affect also in chimpanzees.

Alternatively, behaviour correlations may result from similar influence by external factors. For example, kissing and playing might have been exchanged in the same context more often than in other contexts. Similarly, the possible syndrome between grooming and a number of individuals in close proximity may reflect a genuine latent trait of sociability, but may also occur because having many individuals in close proximity increases the likelihood of initiating and receiving grooming. At present, it is not possible to separate the effects of shared mechanisms and situational co-occurrence. The current results merely say that inter-individual variation in the measured behaviours is consistent, and consistent correlations exist amongst some behaviours.

The personality structure found in this study reflects only the behaviours that I chose to sample. This self-evident point is meaningful in that two of the most frequently sampled personality traits—boldness and exploration tendency—were not included, because I did not use experiments, and novel environments or objects rarely occur in captive environments. Boldness and exploration tendency are thus best addressed with targeted experimental research. Considering the generality of these personality traits across animals, including humans (Beaton et al. 2008; Gosling 2001; Réale et al. 2007; Sih et al. 2004), it is likely that chimpanzees show consistent variation in boldness and exploration. Whether boldness and exploration tendency also follow the general animal pattern of forming syndromes with other traits, such as aggression and activity, it remains to be investigated. Based on the evidence from a range of species, an activity-(aggression-) boldness syndrome is predicted to exist in chimpanzees.

Sex and population differences in personality scores

I also addressed sex and population differences in the personality scores of the five factors. Males had higher scores of positive affect, equitability, anxiety and activity, but not of sociability, than females. This suggests differential selection pressures on personality traits between males and females. Chimpanzee males form long-lasting, strong and equitable bonds amongst each other, whilst females are more solitary, even when cross-site variation in female association patterns is considered (Pepper et al. 1999; Gilby and Wrangham 2008; Langergraber et al. 2009; Lehmann and Boesch 2008; Mitani 2009). Furthermore, the higher anxiety score in males may reflect the stressors of a male-

dominated society with strong resource competition. Chimpanzee males compete heavily over rank position and reproduction, resulting in an intricate network of relationships managed by conflict, grooming and cooperation (Muller and Mitani 2005; Watts 2000). Therefore, directional selection probably favours higher personality trait levels on socio-positive and aggressive behaviour in males than females. Males in several other species have higher levels of aggressiveness and risk taking than females, whilst consistent intra-individual variation within sex is nevertheless maintained (Schuett et al. 2010). A growing body of evidence supports sex-specific effects of natural and sexual selection on personality traits (Dingemanse et al. 2002; Garamszegi et al. 2008; Schuett and Dall 2009; Schuett et al. 2010). Therefore, I hypothesize that the sex differences in personality scores in chimpanzees found in this study are a replicable pattern and found to be connected to selection pressures acting differently on the sexes.

Unfortunately, I could not assess the relationship between dominance rank and personality scores, because in CH and BB, the pattern of submissive behaviours did not yield a clear hierarchy within males or within females. In AR, the number of males ($N = 5$) was too small to reliably test the connection of rank position and personality.

The only factor that did not show sex differences was sociability, which was incongruent with my prediction. However, this may be due to the captive environment rather than reflecting a general chimpanzee pattern. Captive conditions result in increased gregariousness and atypical group compositions including the presence of matrilines (which is uncommon in the male-philopatric chimpanzees). This leads to increased familiarity and bonding amongst resident females (Baker and Smuts 1994) compared to wild chimpanzees (Langergraber et al. 2009; Gilby and Wrangham 2008). Such conditions are likely to favour increased sociability in females. In two of the study populations, female relationships are indeed described as valuable and strong, and females have a considerable role in the group social dynamics (de Waal 1994; Fraser et al. 2008).

Overall, captivity may increase the levels of some traits and decrease those of others. Limited possibilities to fission may increase aggression rates and, especially in crowded conditions, grooming and anxiety (Nieuwenhuijsen and de Waal 1982). Individuals may also respond differently to such stressors, depending on their personality. Conversely, some behaviours are less frequently expressed in captivity; travelling and foraging take up ca. 50–60% of time budget in the wild (e.g. Matsumoto-Oda and Oda 2001; Doran 1997) but considerably less in captivity. Furthermore, individual differences may be more emphasised in captivity. Wild chimpanzees are more constrained by ecological conditions than captive chimpanzees, which consequently may limit the expression of individual differences in e.g.

activity patterns. Comparable data from wild chimpanzees is crucial to address such aspects.

The groups differed in all personality factors except anxiety. This indicates that whilst the traits were similarly consistent across all populations (i.e. had largely similar repeatability values), the trait expression differed significantly. Two possible explanations could account for such differences. First, they may follow from genetic differences in the trait regulation amongst the zoo groups. However, this is unlikely because the majority of the chimpanzees were of the same subspecies (*Pan troglodytes verus*), and they have been breeding only for one or two generations at most. Second, different zoo environments may shape trait expression sufficiently differently. Several factors, including environmental enrichment (Wood 1998), current social dynamics such as the stability of male rank hierarchy and the age–sex ratio of the group, could have such effects. Behavioural variation amongst chimpanzees, both wild and captive, reflects the combined effects of internal dispositions and social and ecological environmental effects. The challenge is to understand how internal and external effects shape behaviour in different environments (Dingemanse et al. 2010b; Nettle and Penke 2010; Penke et al. 2007).

Conclusions and future directions

This study provides insights into personality in the social domain of a highly social primate that has complex social networks and a rich behavioural repertoire. The results confirm the existence of several social personality traits in chimpanzees. This is the first, necessary step that allows further research into the consequences of social personality traits in chimpanzees. Crucial aspects to investigate include the effects of personality on network patterns, population dynamics and fitness. For example, more equitable males may incur cooperative benefits from their grooming partners also in other contexts, such as food-sharing and mating (Mitani et al. 2000; Duffy et al. 2007). Decoupling current rank and consistently assertive behaviour as a result of personality (cf. King and Figueredo 1997) is also important, as rank position may mediate the personality's effect on fitness, and vice versa (Boesch et al. 2006; Pusey et al. 1997). For example, highly affiliative or sociable subordinate males may achieve higher reproductive success than expected by their rank if they are favoured by females or by dominant males as alliance partners. Alternatively, aggressive, non-sociable 'bullies' may achieve high rank and/or frequent matings by intimidation. If sociability, playfulness, equitability and activity-aggressiveness are truly general chimpanzee personality characteristics, I expect to find alternative reproductive and networking strategies employed by not only dominant (Foster et al. 2009) but by subordinate males according to their personality types. Only

long-term studies can reveal their consequences for realised fitness. In a broader framework, the study stresses the importance of addressing social behaviour in the animal personality research. Social personality traits are highly relevant, especially in species that live in an environment of individualised relationships and repeated interactions. Understanding the effects of various social personality traits both at the individual and the group level is crucial for understanding the mechanisms maintaining and consequences following personality. Furthermore, the results highlight the interplay of internal personality dispositions and the environment in shaping their expression, calling for research to reveal their underlying causalities.

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