

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 (Gunther 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 affiliative 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-