



Fig. 2 Factor scores of the three study populations. Error bars indicate \pm 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 affiliative 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.