

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 matriline (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