



## Growing into the self: the development of personality in rhesus macaques



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Although personality has been widely studied among animal species, only a few studies have investigated the long-term development of personality during early ontogeny. In fact, no study of nonhuman primates has consistently mapped personality development from birth to adulthood. Our study aimed at closing this gap by examining the development of personality among free-ranging rhesus macaques, *Macaca mulatta*, using longitudinal behavioural data of 24 subjects (3758 h) collected from birth to 7 years of age on the island of Cayo Santiago, Puerto Rico, U.S.A. In our analyses we combined different frameworks of animal personality research to discuss behavioural differences in terms of latent personality models, behavioural syndromes and behavioural characters. The results showed that a core model of rhesus macaque personality, comprising three latent factors (Fearfulness, Aggression, Sociability), can already be established over the course of the first 7 years of life. However, only Fearfulness emerged consistently throughout development. While the factor of Sociability diffused during maturation, Aggression stabilized towards adulthood after having inconsistent loadings during infancy. When assessing correlations among behaviours separately on the within- and between-individual level, again only Fearfulness showed significant results averaged over the entire study period and can therefore be classified as behavioural syndrome or behavioural character. We discuss differences in correlations, interactions between sex and age and the effect of maternal rank as potential source of differences in stability of latent traits. Furthermore, we assessed plasticity of behaviour with regard to first maternity in females and natal dispersal of males. While the latter was accompanied by an increase of fearful behaviour and decrease of physical aggression, first maternity was marked by a mixed pattern of changes. Overall, our results suggest that rhesus macaques are not born into their personality, but grow into it.

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Over the last few decades it has become very popular to measure an animal's personality, applying this concept to a variety of different taxa (Gosling, 2001). Given the plurality of distinct research fields and traditions that investigate the nature of personality, only a broad definition seems widely accepted: personality reflects individual characteristics that are stable over time (Gosling, 2001). In humans, personality is a well-established construct and commonly described by the Big Five, a personality model that captures a person's characteristics in five different dimensions: Agreeableness, Extraversion, Openness, Neuroticism

and Conscientiousness (Digman, 1990). These five dimensions have been supported in both genders and across different cultures (Digman, 1990; Schmitt, Realo, Voracek, & Allik, 2008). Personality research in nonhuman primates (hereafter referred to as primates) has commonly adopted the methodological framework of human psychology by establishing multivariate personality models, where sets of related behaviours are statistically summarized into latent personality dimensions, which together define an individual's personality (Freeman & Gosling, 2010; Uher, 2011). Consequently, the Big Five Model could, at least to some extent, be transferred to different primate species. For example, models of chimpanzee, *Pan troglodytes*, personality fully include the Big Five dimensions alongside an additional dimension of Dominance (King & Figueredo, 1997), while other primate species (e.g. orang-utans, *Pongo pygmaeus*, rhesus macaques, *Macaca mulatta*) incorporate

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at least parts of the original human model (Freeman & Gosling, 2010; Weiss, Adams, Widdig, & Gerald, 2011).

However, the adoption of the human personality methodology is only one way of studying animal personality. Studies of animal personality other than primates often define personality as stable individual differences in a single behaviour, also defined as behavioural type (Jandt et al., 2014; Sih, Bell, & Johnson, 2004). Such single behaviour dimensions may cover traits such as aggression, activity, exploration or boldness (Bell & Stamps, 2004; Smith & Blumstein, 2008). An associated multivariate perspective of stable behavioural differences is furthermore pursued by investigating behavioural syndromes, which denote stable between-individual correlations between behaviours (Dingemanse, Dochtermann, & Nakagawa, 2012; Sih et al., 2004). While these different terminological frameworks tend to neglect each other, it should be stressed that they actually share some major similarities. In fact, between-individual correlations underlying behavioural syndromes could be used as building blocks of a latent personality model. Hence, both frameworks can not only coexist, but also be combined in their different methodological strengths. While latent personality models offer the manageability of large sets of related behaviours and can model personality dimensions (i.e. factors) as statistically independent representations, linear mixed-model approaches in behavioural syndrome research allow us to decompose phenotypic correlations into within- and between-individual correlations and therefore, for example, control for potential environmental influences on the correlation between the respective behaviours (Dingemanse & Dochtermann, 2013; Dingemanse et al., 2012; Garamszegi et al., 2015). An integration of latent models and covariance decomposition has already been introduced by modelling a 'behavioural character' of Aggressiveness in the great tit, *Parus major* (Araya-Ajoy & Dingemanse, 2013). In short, a behavioural character relates behavioural differences to an evolutionarily selected latent unit that influences correlations between behaviours on both the between- and the within-individual level and across different environments. In conclusion, the time seems ripe to further integrate the strengths of different approaches into the same study of animal personality, while attention needs to be paid to differences in terminology. In our case, to maintain consistency with previous studies on primate personality, relative stability in a single behaviour will not be defined as personality, but as differential behavioural repeatability (Putnam, 2011) or rank order stability.

A common aspect of animal personality research, regardless of the framework used, is that most studies have focused on adult or adolescent animals (cf. Freeman & Gosling, 2010; Smith & Blumstein, 2008; Stamps & Groothuis, 2010). Consequently, we are lacking knowledge of how personality develops during early ontogeny. The focus of our analysis is therefore to provide more information on this matter, by studying the personality development of rhesus macaques, which have been studied more often with regard to personality than any other primate species (Freeman & Gosling, 2010). Accordingly, they already provide information about the personality structure of mature and immature individuals (see below). However, in contrast to the broad consent of the human Big Five Personality Model (Digman, 1990), studies of adult rhesus macaques differ considerably in their number and labelling of the proposed personality dimensions ranging from three to six latent factors (cf. Brent et al., 2014; Capitanio, 1999; Stevenson-Hinde & Zunz, 1978; Weiss et al., 2011). While these differences match evidence for intraspecific personality variation across populations (e.g. Bell, 2004; Dingemanse et al., 2007) or within the same sample across time and fluctuating environment (e.g. Dingemanse, Both, Drent, & Tinbergen, 2004; Garamszegi et al., 2015), an obvious explanation of such heterogeneity stems

also from considerable differences in the choice of data acquisition across studies. These differences may lie, for example, in the assessment of variables (questionnaire ratings versus coding of behavioural observations), the use of different questionnaires or coding of different sets of behaviour, or living conditions of the animals (captive versus free-ranging). Despite such differences, Neumann, Agil, Widdig, and Engelhardt (2013) recently noted that the three factors Fearfulness (or Excitability), Sociability and Aggression are relatively consistent across rhesus macaque studies, whereby Aggression is in some studies integrated into factors labelled Confidence or Dominance. These three personality dimensions are also the most commonly assessed dimensions within all present studies of primate personality (Freeman & Gosling, 2010) and stable in adult rhesus macaques (Brent et al., 2014; Suomi, Novak, & Well, 1996; Weiss et al., 2011).

Nevertheless, the question remains how personality emerges and develops during early ontogeny. Are individuals born with a stable personality or do they grow into it as they mature? In fact, individual differences during early ontogeny of rhesus macaques appear less elaborated than in adults, but in most cases already reflect the core dimensions of primate personality as outlined above (Clarke & Snipes, 1998; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Weinstein & Capitanio, 2008). With regard to stability, the few existing studies of early personality development in rhesus macaques lack comparable results. Rank order stability between 1 and 4 years of age has only been reported for Confidence/Aggression (Stevenson-Hinde et al., 1980) and absolute changes have been described in various behavioural domains, e.g. early increases in sociable and active behaviour (Clarke & Snipes, 1998) or decreasing confidence and activity towards adulthood (Bolig, Price, O'Neill, & Suomi, 1992). Although these first results of interindividual differences during ontogeny are promising, no study has consistently mapped personality development of rhesus macaques from birth up to adulthood or investigated such development under naturalistic field conditions. Hence, we cannot explain how the stability of adult personality evolves during development, nor how such development could be influenced by important life history events. In their review of the development of animal personality, Stamps and Groothuis (2010), however, suggest the influence of major physiological (e.g. sexual maturation) or environmental changes (e.g. dispersal) on the stability of personality. Specific changes that affect the development of personality could therefore be the first maternity of females and the natal dispersal of males. Earlier studies of rhesus macaques have already found personality changes during sexual maturation for both males and females (Bolig et al., 1992) and personality differences between mothers and non-mothers (Klepper-Kilgore, 1999). Furthermore, many studies have investigated the influence of personality as a predictor of natal dispersal (reviewed by Cote, Clobert, Brodin, Fogarty, & Sih, 2010; in rhesus macaques e.g. Mehlman et al., 1995; Trefilov, Berard, Krawczak, & Schmidtke, 2000). However, we lack studies that in turn have examined the influence of dispersal on the developing personality.

The present study aimed to investigate the development of personality in rhesus macaques using a study design that allowed us to compare the same individuals with the same methods throughout their first 7 years of life and therefore covering all developmental life stages to the onset of adulthood (see below). Given the evidence that the three most consistent dimensions of the adult rhesus personality model (Fearfulness, Aggression, Sociability) can be already detected during infancy or early childhood (Clarke & Snipes, 1998; Stevenson-Hinde et al., 1980; Weinstein & Capitanio, 2008), we focused on the development of this core model. The study was especially motivated to provide close-to-naturalistic data, building upon behavioural coding of free-

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