



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



Christoph von Borell ^{a, b, c, *}, Lars Kulik ^{a, b}, Anja Widdig ^{a, b}

^a Junior Research Group of Primate Kin Selection, Department of Primatology, Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany

^b Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany

^c Institute of Psychology, Biological Personality Psychology, University of Göttingen, Göttingen, Germany

ARTICLE INFO

Article history:

Received 5 January 2016

Initial acceptance 11 February 2016

Final acceptance 15 September 2016

MS. number: 16-00011R

Keywords:

animal personality
behavioural character
behavioural development
behavioural syndrome
first maternity
natal dispersal
nonhuman primate
rhesus macaques
temperament

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.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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

* Correspondence and present address: C. von Borell, Institute of Psychology, Biological Personality Psychology, University of Göttingen, Goßlerstraße 14, 37073, Göttingen, Germany.

E-mail address: christoph.borell@psych.uni-goettingen.de (C. von Borell).

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-

ranging rhesus macaques. In particular, we aimed to assess whether and at what age behaviours consistently load on a designated personality factor, whether correlations between behaviours correspond to the concepts of behavioural syndromes and behavioural characters, and how the development of latent personality traits is influenced by sex, rank and age, as well as the impact of life history events. Specifically, we hypothesized absolute changes depending on sex, with males expected to perform more fearful and less aggressive behaviour after their natal dispersal (in relation to the time prior to dispersal). In contrast, we expected no such differences for females after their first maternity (in relation to the prior time without a dependent infant). In addition, we predicted an influence of early differences in dominance rank on aggressive and fearful behaviour, corresponding to results in adult rhesus macaques (Bolig et al., 1992; Brent et al., 2014) and age-related effects on the development of absolute display of behaviour (according to Kulik, Amici, Langos, & Widdig, 2015a, 2015b).

METHODS

Study Species, Population and Subjects

Rhesus macaques live in multimale, multifemale groups, mate promiscuously (Manson, 1992) and females give birth to a single offspring during the breeding season (Rawlins & Kessler, 1986). Males disperse from their natal group between the ages of 3 and 5.5 years (Berard, 1990; Colvin, 1983; Lindburg, 1969), while females are philopatric and form stable matrilineal hierarchies (Gouzoules & Gouzoules, 1987). During the first 7 years of life, we may distinguish between infants (0–1 years of age), juveniles (from 1 year of age to sexual maturation; reached approximately by females at 2.5 years and by males at 3–3.5 years), adolescents (from being sexually mature to skeletal maturation; reached by females between 4 and 6 years, by males between 6 and 8 years) and adults (see Bercovitch & Goy, 1990; Kulik et al., 2015a, 2015b; Langos, Kulik, Ruiz-Lambides, & Widdig, 2015).

The study was conducted on the rhesus macaque population of Cayo Santiago, a 15.2 ha island offshore Puerto Rico (U.S.A.), which is managed by the Caribbean Primate Research Center (CPRC). Although the population is provisioned, it spends approximately 50% of its feeding time on natural vegetation (Marriott, Roemer, & Sultana, 1989). Since 1956, CPRC census takers have continuously recorded demographic data, including the date of birth and death of subjects, their sex, group membership, number of maternal kin and events of male dispersal.

From October 2004 to August 2011, we followed 55 focal subjects (29 males, 26 females) born into one cohort of our study troop (group R), which were part of a long-term study on the development of social relationships. We continuously collected data starting immediately after birth until the subjects reached 7 years of age. Over the course of the study, the sample size, however, diminished because 15 focal subjects (nine males, six females) died and 16 were removed (10 males, six females) by the CPRC due to colony management. Thus, about half of the sample, 14 females and 10 males, survived until the study was completed. We excluded all subjects that dropped out over the course of the study, because as important stages in the development of the variables are missing, mean values of behavioural observations would be systematically biased when aggregated over the whole study period and behavioural heterogeneity between different years could otherwise stem from differing samples. Hence, we used a sample size of 24 subjects in all analyses (except first maternity and dispersal). Details of the amount of data collected each year are given in Table 1. During the study period, 15 females (of which 14 were observed until the end of the study) gave birth to at least one offspring and 12 males (of

which eight were observed until the end of the study) migrated from their birth group, while two males stayed in the natal group until the study was completed. All group members, including focal subjects, were recognized on an individual basis using natural markings and individual tattoos.

Behavioural Data Collection

We recorded behavioural observations using a 20 min focal animal sampling protocol (Altmann, 1974). During each protocol, we coded interactions between the focal subject and all other group members, which could be affiliative (e.g. grooming, approaching, sharing spatial proximity; as defined in Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2002) or aggressive (either physically, such as pushing, hitting, grabbing, biting, attacking, or non-physically, such as staring, head bobbing, showing vocal/open mouth threats, lunging, charging, chasing, as also defined in Widdig et al., 2002). These focal observations were conducted not more than once per day and focal subject. They were evenly distributed over the day, balanced weekly among subjects, and sampled continuously throughout the year. Owing to their extremely close bonding, we excluded interactions between focal subjects and their mothers (and likewise when female focal subjects gave birth, we also excluded interactions with their own offspring) from data analysis to ensure unbiased measurements of the development of social and aggressive behaviour (as in Kulik et al., 2015a). Otherwise, results could be driven by mother–offspring interaction, masking more subtle differences in the interaction with other group members. Additionally, we took point time samples (PTS; Altmann, 1974) every 4 min within a focal protocol (resulting in six data points taken at minutes 0, 4, 8, 12, 16 and 20), comprising the current activity of the focal subject and the identity of all neighbours within a radius of 2.0 m of the focal subject. Finally, we collected ad libitum data (Altmann, 1974) on displacement, aggression or submission among all group members in order to construct dominance hierarchies (see below). The data were collected by A.W. and three field assistants. Interobserver reliability tests ranged between 90% and 97%, with subsequent assistants conducting simultaneous focal samples with the trainer (Kaufman & Rosenthal, 2009). We used Psion Workabout handhelds and processed the collected data with Observer software (version 5.0, Noldus Information Technology, Wageningen, Netherlands).

Maternal Kinship and Maternal Rank

We derived information on maternity from long-term field observations and confirmed the behaviourally assigned mother for all 24 focal subjects by genetic analyses (for details see Kulik et al., 2015b). Furthermore, a maternal family was defined for each focal subject including dyads related only over the maternal kin line, i.e. pairs of individuals that shared the same mother and/or maternal grandmother, as confirmed via genetic analysis including pedigree data up to the grandparent generation (Widdig et al., 2016). Specifically, the 24 focal subjects were assigned to 24 unique mothers, for which, in turn, 23 unique mothers (96%), i.e. the grandmothers of the focal subject, were confirmed genetically. In the remaining case, there was no genetic sample of the demographic grandmother available. Since the level of demographically misassigned mothers is generally low in the entire study population (approximately 2%; see Kazem & Widdig, 2013), we felt confident to assign the demographic grandmother without genetic confirmation.

The rank of all focal subjects was assigned according to the rank of their mother (hereafter maternal rank), with offspring of the same female ranking directly below their mother and inverse to

Table 1
Overview of data collected from the 24 surviving subjects (sum = 3757.67 h)

	Whole study	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7
Mean (SD) (h)	156.67 (9.69)	29.39 (4.21)	26.86 (2.31)	19.02 (1.55)	25.25 (1.29)	21.92 (1.84)	22.86 (6.92)	11.24 (1.82)
Range (h)	123.00–167.00	11.67–34.33	20.00–29.00	16.33–22.00	21.67–27.00	17.67–25.00	12.67–30.33	9.33–14.67

birth order (Chapais, 1992; Datta, 1988; Pereira, 1995). We applied maternal rank for the entire study period as we lacked detailed rank data, particularly after male subjects dispersed into different social groups. Maternal rank was taken from the adult female hierarchy, which is based on the outcome of dyadic agonistic interactions, collected via ad libitum and focal animal sampling, calculated using the I&SI method (de Vries, 1998; as used in Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001). The dominance relationships among sexually mature females were stable since 1998 as confirmed via ad libitum sampling over our entire study period. More information on these approaches are provided in Kulik et al. (2015b).

Variables of the Personality Model

Based on previous studies of behavioural personality assessment in macaques (Brent et al., 2014; Neumann et al., 2013), we selected 11 behaviours from our data set as variables that could potentially fit the three common personality dimensions of rhesus macaque personality, namely Aggression, Sociability and Fearfulness (see above). In our analysis, we included only interactions in which the focal animal was the initiator of the behaviour, except for submissive behaviour received by the focal animal. The interaction partner could be any group member except the focal mother (see above). The values of all variables represent the number of occurrences per day. Variables that encompass prosocial interactions ('Grooming', 'Affiliation', 'Diversity of Grooming Partners' and 'Diversity of Affiliation Partners') were further restricted to interactions outside the entire maternal kin line. The reasoning behind this is that in female philopatric societies, such as rhesus macaques, maternally related females, especially closely related family members, form strong and permanent social bonds with one another (Kapsalis & Berman, 1996; Schülke, Wenzel, & Ostner, 2013). A truly sociable individual, however, should also display frequent prosocial behaviour outside the maternal family. In line with our reasoning of excluding interactions with the mother for all variables, we hence excluded prosocial interactions between maternal kin to avoid results that are biased by family-centred interactions. Note that such bias towards close maternal kin has also been shown for aggressive behaviours, although not as pronounced and not consistently differing compared to other kin classes (Widdig et al., 2002). Therefore, we did not correct for a maternal kin bias in the variables assumed to be associated with aggressive behaviour (i.e. 'Nonphysical Aggression', 'Physical Aggression', 'Agonistic Approach'). The variables that could potentially fit a latent trait of Fearfulness were calculated in heterogeneous ways. As a first variable, we chose the daily number of friendly approaches initiated by the focal subject. The tendency to avoid the approach of novel stimuli or potential interaction partners is one of the most basic conceptualizations of Fearfulness found in both humans and animals (Putnam, 2011). The variable 'Resting' was taken from PTS data and thus represents the number of daily activity patterns (0–6) including focal resting. In previous studies, the association between resting behaviour and personality differed within and between macaque species. Some personality models of adult rhesus macaques included a distinct factor of activity (Stevenson-Hinde & Zunz, 1978; Weiss et al., 2011), while it has also

been assigned to a factor of excitability, alongside subordinate behaviour (Capitani, 1999). In a behavioural assessment of personality in male Sulawesi crested macaques, *Macaca nigra* (Neumann et al., 2013), as well as in questionnaire ratings of Barbary macaques, *Macaca sylvanus* (Konečná, Weiss, Lhota, & Wallner, 2012), measures of general activity likewise loaded negatively on the factor anxiety. Since it has also been shown that fearful human children (e.g. classified as behaviourally inhibited or highly reactive; see Kagan, 2003) appear hesitant, avoiding and inactive when encountering a novel (potentially fearful) situation, show inhibited motor activity, keep a safe distance and cease their play behaviour (Asendorpf, 1994; Fox, Henderson, Marshall, Nichols, & Ghera, 2005), we were confident about including 'Resting' as a potentially fearful behaviour in our study. The aspect of keeping a safe distance is further reflected in the variable 'Proximity'. Proximity represents the daily number of unique individuals within a 2 m range of the focal subject recorded during PTS. A fearful individual should tend to keep its distance from other individuals and thus tolerate fewer animals in close proximity. Finally, the variable 'Submissiveness' represents how often a focal animal showed a fear grin or left in any behavioural interaction. To correct for incomplete measurements, each daily count of all variables was divided by the number of actual PTS taken. As units of measurement, we aggregated the scores for each variable year-wise, matching the age of the respective focal subject. If necessary for statistical analysis, the variables were z-standardized to match the same scale. A detailed summary of all variables and their respective meaning are given in the Appendix (Table A1).

Statistical Analysis

All statistical computations were performed using the software R 3.1.1 (R Core Team, 2014); if a package did not support this release, an earlier version (R 3.0.2) was used. For specific hypotheses, we applied false discovery rate (FDR) correction to account for multiple testing (Benjamini & Hochberg, 1995) and, based on the FDR, corrected confidence intervals of estimates for false coverage rate (FCR), respectively (see Benjamini & Yekutieli, 2005).

Statistical Evaluation of the Personality Model

The evaluation of the personality model is based upon a dual multiple factor analysis (dual-MFA) which is an extension of principal component analysis that handles multiple data tables representing repeated observations on the same variables (Abdi, Williams, & Valentin, 2013) and is computed via principal axes factoring (Van Deun, Smilde, van der Werf, Kiers, & Van Mechelen, 2009). It is an exploratory and descriptive multivariate technique (Abdi et al., 2013) which aims to reduce the complexity of a set of repeatedly measured variables to common factors (and thus not subject to family-wise error rates). However, it does not allow the partitioning of covariance into between- and within-individual correlations, which we therefore pursued in a second step (see below). A dual-MFA provides an aggregated factor solution (also called compromise factor solution), which is a weighted average of the multiple data tables included (see Van Deun et al., 2009), and also partial factor

solutions for each table, respectively. For our analysis, we included year-wise repeated measures of the behavioural variables for all 24 subjects, i.e. seven data tables, which we z-standardized prior to analysis, as proposed by [Abdi et al. \(2013\)](#). As measures of appropriateness to perform a factor analysis we computed the Kaiser–Meyer–Olkin measure of sampling adequacy and Bartlett's test of sphericity using the R package 'rela' ([Chajewski, 2009](#)). To determine the appropriate number of factors we examined the scree plot, including a parallel analysis plot that compares actual to simulated data. The factor solution was orthogonally rotated using the varimax technique. To assess whether we can jointly analyse the development of the personality model in males and females, e.g. inspect partial factor solutions, we computed the congruency coefficient R_c ([Abdi, 2010](#)) of their year-wise mean values of absolute correlations between all variables designated to a common personality dimension.

Decomposing Phenotypic Correlations

Since phenotypically observed correlations may result solely from within-individual covariance of plasticity in behaviours ([Brommer, Karell, Ahola, & Karstinen, 2014](#); [Dingemanse et al., 2012](#); [Uher, 2011](#)), behavioural syndromes are specifically defined and calculated as between-individual correlations among them ([Dingemanse & Dochtermann, 2013](#)). To evaluate whether the phenotypic correlations underlying the factor analysis resemble between-individual correlations in terms of behavioural syndromes and to assess correlated changes within individuals, we fitted bivariate linear mixed models with random intercepts for the focal subjects and year-wise repeated measures for each behaviour and focal subject as response (resulting in seven values per subject and behaviour). These models allowed us to statistically decompose between- from within-individual covariation. We used the MCMCglmm R package ([Hadfield, 2010](#)) to fit the models and calculated between-individual correlations according to [Dingemanse and Dochtermann \(2013\)](#). Notably, we included the same data set as for the dual-MFA, i.e. where all behaviours were z-standardized for each year separately, which allowed us to also obtain measures of differential repeatability (also named rank order stability) from the same models (see below). For the estimation of parameters, we specified a noninformative inverse gamma prior with shape and scale parameters equal to 0.001 (following [Dingemanse & Dochtermann, 2013](#); [Garamszegi et al., 2015](#)). Each model was run for 1.3 million iterations, with a burn-in of 300 000 iterations and parameters estimated from a sample of 1000 iterations. Comparable estimates of average phenotypic correlations among behaviours were obtained using a within-study meta-analytical approach ([Nakagawa & Santos, 2012](#)). Instead of estimating a common effect size of different studies (as usually done in meta-analysis), we here calculated the common effect size of correlations from different years. The advantage of performing a within-study meta-analysis lies in enhanced statistical power, which leads to more precise estimates of an effect size ([Nakagawa & Santos, 2012](#)). The meta-analysis was calculated as a random-effects model, meaning that each year-wise correlation is allowed to vary around its own 'true' effect size, using the R package metafor ([Viechtbauer, 2010](#)). The estimates of common effect sizes for each correlation, in terms of Fisher's z-transformed correlations, were retransformed into Pearson correlation coefficients and corrected for nonindependence of the sample according to the correction formula in [Nakagawa and Santos \(2012\)](#), which was set to the most conservative measure as reasoned in [Davidson, Jennions, and Nicotra \(2011\)](#) and [Slatyer, Mautz, Backwell, and Jennions \(2012\)](#). For the

purpose of illustration, we summarized all bivariate correlations into average correlations between behavioural variables of a common personality factor.

Repeatability of Behaviour

The assessment of repeatability is important since it is a requirement for between-individual correlations ([Dingemanse et al., 2012](#)), while previous ontogenetic studies have in fact shown stable phenotypic correlations, but zero repeatability of behaviour ([Bell & Stamps, 2004](#)), conditions of zero repeatability of behaviour and zero between-individual correlations ([Urszán et al., 2015](#)), or zero repeatability of behaviour and changes in latent personality models ([Sussman & Ha, 2011](#)) across different species. Since absolute changes in behaviour during early ontogeny are likely to be part of maturation processes which do not necessarily deny the notion of a stable personality, we assessed differential repeatability, which states whether focal animals are comparatively stable in a behaviour, e.g. stay relatively aggressive over time compared to their peers, or not. As outlined above, we computed measures of differential repeatability from the bivariate linear mixed models specified in the section Decomposing Phenotypic Correlations, which are identical to LMM-based repeatability estimates described by [Nakagawa and Schielzeth \(2010\)](#). To assess the probability of pseudorepeatability ([Dingemanse & Dochtermann, 2013](#)) due to differing individual conditions related to the mother's dominance status, we additionally ran the same models including dominance rank as a fixed effect, i.e. computed adjusted repeatability estimates ([Nakagawa & Schielzeth, 2010](#)). Repeatability estimates may vary between 0 and 1 and a high repeatability estimate (i.e. close to 1) reflects a high ratio of between-subjects variance to the total variance and thus little within-subjects variance (see [Nakagawa & Schielzeth, 2010](#)).

Further Analysis of the Development of Personality

To gain a deeper understanding of the way personality develops, we conducted additional analyses that explore potential influences on the ontogeny of an individual's personality.

The influence of sex, age and maternal rank

Since previous research has shown a significant relationship between dominance rank and submissive or aggressive behaviour ([Bolíg et al., 1992](#); [Brent et al., 2014](#)), as well as quadratic age effects and sex differences in the development of affiliative and aggressive behaviours ([Kulik et al., 2015a, 2015b](#)), we assessed how these variables affect aggregated scores of latent personality dimensions. We fitted linear mixed models in the R package lme4 ([Bates, Maechler, Bolker, & Walker, 2015](#)), with the z-standardized factor weighted sum scores of all z-standardized behaviours of each respective latent dimension as response and included age (linear and quadratic term), maternal rank and sex as predictors. As the effects of maternal rank and sex could vary with age and, additionally, the effect of maternal rank could be influenced by the individual's sex, we also included as predictors all two-way interactions between these terms. Age and maternal rank were z-standardized prior to analysis (as reasoned in [Schielzeth, 2010](#)). Each full model was compared to a null model (containing only the random effects) via a likelihood ratio test (LRT; [Dobson, 2002](#)). If the comparisons between full and null model reached significance, we subsequently tested all interactions by comparing the full to a reduced model without the respective interaction by additional LRTs. Nonsignificant interactions were removed from the final model to reliably interpret the lower terms (i.e. main effects)

included (Engqvist, 2005). Interactions were only deemed significant after controlling for FDR due to multiple hypotheses testing (see above) and confidence intervals of estimates were corrected for FCR, respectively.

The influence of developmental milestones

As outlined above, two important milestones affect the lives of rhesus macaques during maturation: females experience their first maternity and males disperse from their natal group. To assess the potential influence of these events on the frequency and consistency of displayed behaviour, we compared data 1 year before and 1 year after the given event, individually timed to the day the subject gave birth or left the group. We chose a time frame of 1 year around an event to exclude other developmental influences (e.g. the time during infancy). Since this analysis was not focused on changes throughout the entire study period, we included all subjects that were observed 1 year before and after the respective event, which allowed us to increase the sample size to 12 males dispersing and 15 females giving birth. Changes in the consistency of behaviour were assessed via Pearson correlation coefficients between the frequency before and after a given event. Absolute changes are displayed as the mean differences of z-standardized frequencies before and after the event, revealing information on the direction and magnitude of changes (in the scale of z-scores, i.e. units of standard deviation). We computed 95% confidence intervals for all respective changes via bootstrapping. Following the suggestions for the effect size Cohen's *d* (Cohen, 1992), which is likewise measured in units of standard deviation, one could interpret changes above 0.8 as large and changes above 0.5 as medium effects.

Ethical Note

The study was conducted in accordance with the current laws and ethical standards of the countries in which it took place. Human intervention into behaviour of monkeys was limited to the annual trapping season (conducted by trained staff of the CPRC and assisted by A.W.), during which yearlings received tetanus immunization (Kessler et al., 2015), were marked with identification codes (tattoos), and DNA samples were collected for genetic analysis. For this purpose, individuals were anaesthetized by CPRC veterinarians using hydrochloride ketamine (10 mg/kg body weight), which aimed to last only 30 min. Animals were constantly monitored for their welfare; babies in addition were not anaesthetized, but allowed body contact with their mothers to minimize stress. Animals were kept in individual cages until complete recovery (decision taken by veterinarian only) and released to their own social group as soon as possible to ensure social integration. All of these procedures, including the behavioural observations, have been approved by the CPRC and the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol No. 4060105).

RESULTS

Statistical Evaluation of the Personality Model

As a first step, we found that the aggregated data of all 24 surviving focal subjects fulfilled the formal requirements of a factor analysis. The Kaiser–Meyer–Olkin measure of sampling adequacy was 0.69, which is above the minimum suggested threshold of 0.5, and Bartlett's test of sphericity was significant ($P < 0.001$), implying a significant deviation from the identity matrix and thus a sufficient basis of correlations. The parallel analysis suggested the extraction of three factors (see Fig. A1 in the Appendix), which matched our

theoretically expected framework. The compromise factor loadings of each variable are presented in Table 2. The results show that all behaviours load strongest on their theoretically designated personality factors, which may thus be named Fearfulness, Sociability and Aggression.

As the developmental pattern of trait-related correlations turned out to be significantly similar between both sexes (congruency coefficient R_c [95% confidence interval, CI] = 0.95 [0.85; 0.94], $P = 0.004$), we analysed the development of the latent personality model jointly for both sexes based on the results of the dual-MFA. Table 3 shows whether, in the year-wise partial factor solutions, all variables of a designated personality dimension have their highest loading on the same factor and with a theoretically plausible direction (plus or minus), as was established in the aggregated compromise factor solution above, or not. The results show that Fearfulness has consistent loadings throughout development, Aggression stabilizes during ontogeny and Sociability emerges from birth onwards but diffuses towards adulthood. More detailed results of all partial factor solutions are provided in the Appendix (Tables A2–A9), which additionally show that behavioural variables may have substantial loadings (>0.4) on more than one factor in a given year.

Decomposing Phenotypic Correlations

Fig. 1 shows how phenotypic correlations are decomposed into correlated differences between individuals and correlated changes within individuals. For clarity, we do not present the complexity of all bivariate relationships between behaviours, but summarize them by averaging respective estimates between behavioural variables of a common personality dimension based on the results of the dual-MFA, which serves as a proxy of inferential tests of behavioural syndromes on a higher hierarchical level. In Fearfulness, both between-individual and within-individual correlations were significant and showed overlapping confidence intervals. The pattern in Aggression was similar; however, the confidence intervals of between-individual and within-individual correlations both included the value 0 and

Table 2
Compromise factor loadings of the dual multiple factor analysis (dual-MFA)

Variable	Factor 1: Sociability	Factor 2: Aggression	Factor 3: Fearfulness
Nonphysical aggression	0.00	0.75	0.00
Physical aggression	−0.12	0.74	0.11
Agonistic approach	0.25	0.64	0.00
Grooming	0.71	−0.32	0.00
Affiliation	0.76	0.18	−0.11
Diversity of grooming partners	0.79	0.00	−0.18
Diversity of affiliation partners	0.76	0.00	0.00
Submissiveness	0.27	−0.14	− 0.75
Proximity	−0.16	0.00	0.88
Resting	−0.13	0.12	− 0.64
Friendly approach	−0.11	0.11	0.74

Data comprise all subjects surviving the entire study period (7 years, 24 subjects). The highest loading of a behaviour on a respective factor is marked in bold.

Table 3
Results of the year-wise partial factor solutions

Latent structure	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7
Aggression	No	No	Yes	Yes	Yes	Yes	Yes
Fearfulness	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Sociability	Yes	Yes	Yes	Yes	Yes	No	No

The table shows whether all variables of a designated personality dimension load consistently on the same factor in a given year of life ('yes') or not ('no').

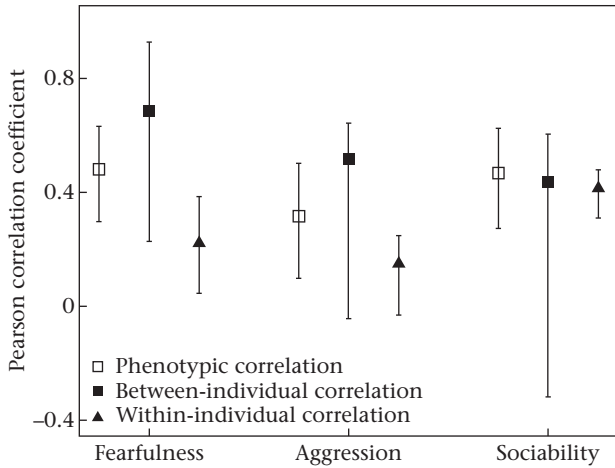


Figure 1. A comparison of average phenotypic, between-individual and within-individual correlations between variables of a designated personality factor (mean and 95% confidence intervals are shown).

were therefore not statistically significant. Sociability, in contrast, was marked by significant correlated changes within individuals, but did not show an average significant correlation between them. Therefore, when aggregated over the whole study period, only in Fearfulness did the phenotypic correlations underlying the dual-MFA resemble the notion of a behavioural syndrome. Notably, only fearful behaviours loaded consistently on the same latent factor during all stages of ontogeny in our study. When we adjusted the analysis to include only the years of consistent loadings in Aggression and Sociability, aggressive behaviours indeed showed significant correlations between individuals (Pearson correlation coefficient [95% CI]: $r = 0.54 [0.01, 0.67]$) and within individuals ($r = 0.29 [0.13, 0.39]$), while the pattern remained the same in Sociability (between individuals: $r = 0.48 [-0.26, 0.64]$; within individuals: $r = 0.48 [0.36, 0.56]$).

Repeatability of Behaviour

As evident from Table 4, all behaviours within the study showed significance in their differential repeatability estimates and were of mostly moderate magnitude. When we adjusted repeatability for dominance rank we obtained similar results that were highly correlated with unadjusted estimates ($r = 0.99, P < 0.001$) and did not differ significantly from them (mean difference = 0.014; $t_{10} = 2.1, P = 0.06$).

Table 4
Differential repeatability of behaviour

Variable	Repeatability for both sexes over the entire study
Diversity of grooming partners	0.26 [0.15, 0.47]
Diversity of affiliation partners	0.16 [0.07, 0.30]
Affiliation	0.24 [0.11, 0.39]
Grooming	0.33 [0.18, 0.48]
Physical aggression	0.22 [0.10, 0.36]
Nonphysical aggression	0.24 [0.14, 0.43]
Agonistic approach	0.35 [0.21, 0.55]
Submissiveness	0.47 [0.33, 0.66]
Proximity	0.58 [0.44, 0.76]
Resting	0.25 [0.12, 0.42]
Friendly approach	0.44 [0.30, 0.65]

The 95% confidence intervals are given in parentheses. Results that differ significantly from 0 are marked in bold.

Further Analysis of the Development of Personality

The influence of sex, age and maternal rank

The comparisons between full and null models were significant for all three personality dimensions (Fearfulness: $\chi^2_9 = 132.83, P < 0.001$; Aggression: $\chi^2_9 = 64.49, P < 0.001$; Sociability: $\chi^2_9 = 18.10, P = 0.034$). Specifically, we found a significant interaction between sex and age in Fearfulness and Aggression (Fearfulness: $\beta = 0.46 [0.34, 0.59], SE = 0.06, \chi^2_1 = 28.21, P < 0.001$, see Fig. 2; Aggression: $\beta = 0.44 [0.25, 0.73], SE = 0.14, \chi^2_1 = 8.07, P = 0.004$, see Fig. 3), implying sex differences in the absolute development of personality, while the correlations between behaviours were similar between males and females (see above). As is evident from Figs. 2 and 3, these absolute differences started to appear during the time of sexual maturation, when males showed both more fearful and aggressive behaviour than females. For both dimensions we also found a significant effect of maternal rank (Fearfulness: $\beta = -0.32 [-0.40, -0.25], SE = 0.04, \chi^2_1 = 28.97, P < 0.001$; Aggression: $\beta = 0.19 [0.08, 0.26], SE = 0.06, \chi^2_1 = 9.22,$



Figure 2. The interaction effect of sex and age on the z-standardized score of Fearfulness. Lines depict the estimated slope of the model. Year-wise mean frequencies are displayed together with their 95% confidence intervals.

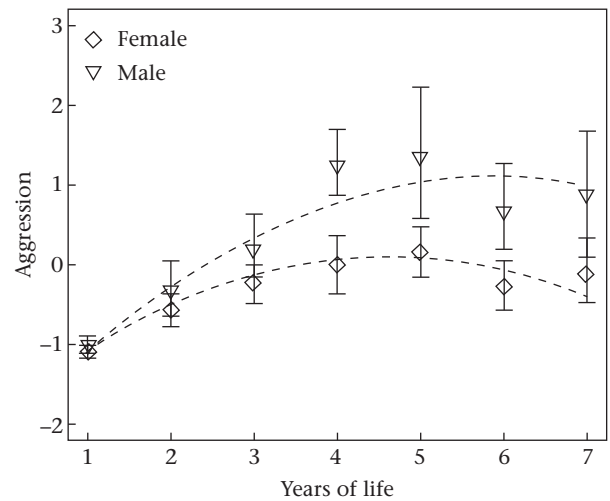


Figure 3. The interaction of sex and age on the z-standardized score of Aggression. Lines depict the estimated slope of the model. Year-wise mean frequencies are displayed together with their 95% confidence intervals.

Table 5
Mean differences in z-standardized frequencies of behaviours 1 year before and after important life history events

Variable	Before and after male migration	Before and after first maternity
Diversity of grooming partners	0.13 [−0.80, 1.03]	−0.79 [−1.61, −0.06]
Diversity of affiliation partners	0.19 [−0.74, 1.21]	0.02 [−0.83, 0.81]
Affiliation	−0.58 [−1.53, 0.14]	−0.83 [−1.71, −0.22]
Grooming	0.28 [−0.77, 1.06]	−0.17 [−1.00, 0.67]
Physical aggression	−1.40 [−2.05, −0.74]	−0.41 [−1.22, 0.34]
Nonphysical aggression	−0.84 [−1.66, 0.02]	−0.61 [−1.43, 0.11]
Agonistic approach	0.33 [−0.64, 1.08]	−0.05 [−0.80, 0.70]
Submissiveness	1.02 [0.18, 1.84]	−0.51 [−1.28, 0.27]
Proximity	−1.17 [−1.90, −0.46]	0.31 [−0.46, 1.18]
Resting	0.52 [0.01, 1.54]	0.84 [0.12, 1.56]
Friendly approach	−1.55 [−2.13, −0.95]	−0.75 [−1.43, 0.01]

Significant changes, i.e. FCR-corrected confidence intervals not containing the value of 0, are displayed in bold. A positive number indicates an increase and a negative number a decrease.

$P = 0.002$). Sociability, on the other hand, was not significantly related to any of the predictors. Note that the estimates of regression weights are reported together with 97% confidence intervals based on FCR correction.

The influence of developmental milestones

Table 5 displays the changes of z-standardized absolute frequencies of behaviours 1 year before and 1 year after the date of a given event. All changes are reported together with 97.5% confidence intervals based on FCR correction. Dispersing males became more fearful, changing significantly in all respective behaviours, while also initiating significantly less physical aggression. After first maternity, females showed a mixed pattern of changes. They tended to reduce sociable interactions outside their maternal kin line (significantly decreasing in two respective variables) and rested significantly more often. In the Appendix (Table A9) we additionally provide the Pearson correlation coefficients between frequencies of a behaviour before and after life history events. Similar to the pattern of absolute changes, males changed especially in their rank order of Fearfulness, whereas females showed significant repeatability in most fearful behaviours, but changed in the other dimensions.

DISCUSSION

In our study we have provided a link between the three most common personality dimensions of previous research in primates (Fearfulness, Sociability and Aggression), a framework of behavioural coding and a developmental perspective. Particularly, we assessed, for the first time, how personality in rhesus macaques develops from birth to the onset of adulthood. Compared to earlier studies, our model and approach are similar to the study of Stevenson-Hinde et al. (1980) who examined the development of the factors Confidence, Sociability and Excitability between 1- and 4-year-old rhesus macaques, using a rating assessment. Whereas the composition of our model was therefore a replication of earlier results based on a different methodological approach, one of our further objectives was to provide more evidence on the formation of stability of this basic model of rhesus personality. Herein, previous research still lacked consistent results. In the study of Stevenson-Hinde et al. (1980) only Confidence showed differential stability. Other studies of early personality development in rhesus macaques could not support or refute these results since they did not provide measures of differential stability and covered a different age range (Bolg et al., 1992; Clarke & Snipes, 1998; Weinstein & Capitanio, 2008). Our results now allowed us to approach the question of repeatability

consistently from birth to adulthood and on different scales or levels of interaction between behaviours. Overall, all behaviours within our study showed significant differential stability and matched repeatability estimates across different species and studies well (other studies have an average magnitude of 0.37, reviewed by Bell, Hankison, & Laskowski, 2009). However, the absolute display of behaviour could vary significantly throughout development, in our case denoted by significant interactions between sex and age in Fearfulness and Aggression. Such variation makes sense, since the process of maturation will change individuals with respect to, for example, body size, mobility, dependency on kin, environmental fluctuation or simply experience. Consequently, ontogenetic change in behaviour has been widely described across different species (e.g. Dingemans et al., 2004; Garamszegi et al., 2015; Herczeg, Ab Ghani, & Merilä, 2013; Kulik et al., 2015a, 2015b; Naguib, Flörcke, & van Oers, 2011; Santillán-Doherty, Mayagoitia, Muñoz Delgado, Kajihara, & Mendoza, 2002; Stevenson-Hinde et al., 1980; Sussman & Ha, 2011) or was even dependent on whether or not individuals had specific experiences (Urszán et al., 2015).

Apart from stability and change in single behaviours, personality research is, across disciplines, also interested in individual differences that lead to multivariate interactions of behaviour, commonly in terms of either behavioural syndromes or latent personality models. Recent studies of behavioural syndromes have shown that whether correlations between behaviours remain stable or change throughout development depends on demographic factors (Garamszegi et al., 2015) or differences in environment (Bell & Stamps, 2004; Urszán et al., 2015). Latent personality models, especially applied to personality in primates, have been most commonly reported to be stable during adulthood. It is, however, not well known how such stability evolves during ontogeny and how early personality development is affected by life history events. As our results now show, the emergence of related multivariate interindividual differences depends on the personality dimension in question. For example, consistent differences in multiple aggressive behaviours cannot be expected in infant rhesus macaques, while a general disposition of being fearful or sociable can be. Furthermore, only fearful behaviours appeared to have consistent loadings on a common factor throughout ontogeny. However, such a stable pattern of phenotypic correlations underlying a stable latent factor does not imply the same as a stable behavioural syndrome in terms of between-individual correlations (see above). Therefore, we also assessed whether the phenotypic correlations applied to factor analysis hold up when between-individual covariance is separated from within-individual covariance. This decomposition of the correlations between behaviours revealed that, averaged over ontogeny, fearful behaviours were significantly correlated between individuals and hence equivalent to a behavioural syndrome. Although we could not model it in depth, Fearfulness did in fact also match the characteristics of a 'behavioural character', as defined in Araya-Ajoy and Dingemans (2013). A behavioural character is proposed as an evolutionarily selected functional unit, given that it can be modelled as a latent factor influencing distinct but related behaviours that are significantly and similarly correlated between individuals and show within-individual plasticity, show nonzero repeatability, are similarly correlated in different environments (in this case e.g. before and after life history events) and are quasi-independent from other characters (e.g. other factors). Since Fearfulness was related to the maternal rank inherited by an individual at birth, however, we cannot, with the analyses conducted, separate the effect of evolutionary selection from the effect of the social system to which an individual is exposed. Stable interindividual differences could also be the result of an ontogenetic feedback process depending on an individual's state at birth, in this case the inherited rank (Sih et al., 2015). The personality dimensions of

Aggression and Sociability were less stable during ontogeny and also not as clearly related to the concepts of behavioural syndromes or behavioural characters. While we did find significant between-individual and within-individual correlations in Aggression when accounting for the fact that aggressive behaviours only loaded on a common factor from the third year onwards, sociable behaviours were in either case (over the whole study period or at times of consistent loadings) only significantly correlated on the within-individual level. The first finding could reflect that a latent personality trait is not necessarily bound to the same behaviours throughout development and hence that potential biological underpinnings of differences in Aggression may vary in how or even whether they can be observed on the phenotypic level at different stages of ontogeny. This phenomenon is well known from personality development in humans and termed heterotypic continuity of a latent trait (Putnam, 2011). This could also be the case for Sociability. However, our results imply that multivariate differences in being sociable might in fact not stem from a latent factor that reflects genetic differences between individuals, but that the association between sociable behaviours derives from systematic plasticity within individuals, i.e. a behavioural strategy employed flexibly due to environmental constraints. This could, in turn, explain a diffusion of the factor Sociability after adolescence, a time of behavioural reorganization due to important life history events in rhesus macaques. It has been already shown that male adolescent rhesus macaques with comparably low concentrations of CSF 5-hydroxyindoleacetic acid (5-HIAA) migrate earlier from their natal group than peers having higher concentrations of 5-HIAA (Mehlman et al., 1995; Trefilov et al., 2000). The same subjects also showed an inverse relationship of being less affiliative and sociable (Mehlman et al., 1995), while more aggressive (Mehlman et al., 1994) than their peers. These findings have contributed to the body of research that has discussed personality as influencing group dispersal (Cote et al., 2010). Our results, in turn, shed further light on how dispersal affects the development of personality.

As hypothesized, we could show that male migration was accompanied by a major decline in physical aggression and a pattern of becoming more fearful. This is a very plausible reaction to losing the security of familiar interaction partners and territory, which is consequently associated with an increase in stress and aggression received (Trefilov et al., 2000). In the case of female rhesus macaques, life history is strongly influenced by the birth of offspring. After first maternity, behavioural changes did not imply a consistent alteration of a personality dimension as a whole. Instead, we observed substantial increases in resting behaviour, as well as decreasing initiation of some sociable interactions outside the maternal kin line. This mixed pattern of changes in sociable behaviours matched our finding of a diffusion of the latent factor of Sociability during that time. A decrease in activity after childbirth has been similarly found in humans, with women becoming more relaxed and tolerant after birth (Wiklund, Edman, Larsson, & Andolf, 2006). Likewise, in a personality comparison between captive female rhesus macaques with and without dependent infants, it was shown that mothers are less playful and inquisitive, while being more depressed and irritable (Klepper-Kilgore, 1999). However, such changes in behaviour do not allow a causal interpretation, since we did not have a control group of subjects that did not migrate or give birth. Therefore, differential and absolute discontinuity around maternity or migration might just be an effect of general maturation. Bolig et al. (1992), for instance, reported a general decline in activity between adolescence and adulthood. Future studies could therefore compare personality change in a narrower, but intensely observed time frame between individuals that have already dispersed or given birth and those that trail behind.

In conclusion, we may infer that, in line with psychological theory (Rothbart, 2007), an individual rhesus macaque grows into its personality and is not born with it. The path leading from early differences at infancy to a stable personality appears to be influenced by multiple constraints on an individual's state, of which we have discussed maternal rank, sex, life history events or environmental change. Further studies are needed to extend and replicate these results by employing a bigger sample size and dynamic measures of environmental context and dominance hierarchy, which would allow for the assessment of developing situational profiles (behavioural reaction norms, see e.g. Dingemanse, Kazem, Réale, & Wright, 2010; Shoda, Mischel, & Wright, 1994), incorporate distinctive steps of our analysis in a single multilevel structural equation model, and test state–behaviour feedback loops (Sih et al., 2015) between dominance rank and individual differences in behaviour.

Acknowledgments

We are most grateful to the CPRC for their permission and support of this study. In particular, we thank the staff of the Cayo Santiago Field Station, and especially Edgar Davila, Julio Resto, Giselle Caraballo Cruz and Angelina Ruiz-Lambides, for their cooperation throughout the observational study and the collection of the DNA samples. We are also grateful to Doreen Langos, Joyce Moewius and Akie Yanagie for their enthusiasm during the collection of behavioural data, and to Klaus Leipholz, Constance Dubuc and Margaret Chiavetta for their cooperation during DNA sampling. We are especially grateful to Andrea Trefilov, Elisabeth Kirst, Peter Nürnberg, Petra Otremba, Marion Nagy, Laura Muniz and Stefanie Bley for their input and collaboration in improving and extending the genetic database, and to Linda Vigilant for laboratory access. We are grateful to Christof Neumann and Stefan Schumke for statistical advice and also thank the editor and referees of our paper for their useful comments. The population of Cayo Santiago was supported by grant number 8P40 OD012217 from the National Center for Research Resources (NCRR), the Office of Research Infrastructure Programs (ORIP) of the National Institutes of Health and the Medical Sciences Campus of the University of Puerto Rico. The content of this publication is solely the responsibility of the authors and does not necessarily represent the official views of NCRR or ORIP. This project was conducted within the Jr. Research Group of Primate Kin Selection, an Emmy-Noether Group funded by the German Research Foundation (DFG; grant numbers WI 1801/1-1, 1-2, 2-1, 3-1 awarded to A.W.). Additionally, funding was received through the University of Leipzig. We thank the Max-Planck Institute for Evolutionary Anthropology, Leipzig, for their logistic support and for hosting the Jr. Research Group of Primate Kin Selection.

References

- Abdi, H. (2010). Congruence: Congruence coefficient, RV coefficient, and mantel coefficient. In N. J. Salkind, D. M. Dougherty, & B. Frey (Eds.), *Encyclopedia of Research Design* (pp. 222–229). Thousand Oaks, CA: Sage.
- Abdi, H., Williams, L. J., & Valentin, D. (2013). Multiple factor analysis: Principal component analysis for multitable and multiblock data sets. *Wiley Interdisciplinary Reviews: Computational Statistics*, 5(2), 149–179. <http://dx.doi.org/10.1002/wics.1246>.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267. <http://dx.doi.org/10.1163/156853974X00534>.
- Araya-Ajoy, Y. G., & Dingemanse, N. J. (2013). Characterizing behavioural 'characters': An evolutionary framework. *Proceedings of the Royal Society B: Biological Sciences*, 281(1776). <http://dx.doi.org/10.1098/rspb.2013.2645>, 20132645–20132645.
- Asendorpf, J. B. (1994). The malleability of behavior inhibition: A study of individual developmental functions. *Developmental Psychology*, 30(6), 912–919. <http://dx.doi.org/10.1037/0012-1649.30.6.912>.

- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4, R package (Version 1.0-8)*. Retrieved from: <http://CRAN.R-project.org/package=lme4>.
- Bell, A. M. (2004). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*): Behavioural syndromes. *Journal of Evolutionary Biology*, 18(2), 464–473. <http://dx.doi.org/10.1111/j.1420-9101.2004.00817.x>.
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, 77(4), 771–783. <http://dx.doi.org/10.1016/j.anbehav.2008.12.022>.
- Bell, A. M., & Stamps, J. A. (2004). Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68(6), 1339–1348. <http://dx.doi.org/10.1016/j.anbehav.2004.05.007>.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300. <http://dx.doi.org/10.2307/2346101>.
- Benjamini, Y., & Yekutieli, D. (2005). False discovery rate—adjusted multiple confidence intervals for selected parameters. *Journal of the American Statistical Association*, 100(469), 71–81. <http://dx.doi.org/10.1198/016214504000001907>.
- Berard, J. D. (1990). *Life history patterns of male rhesus macaques on Cayo Santiago*. Eugene, OR: University of Oregon.
- Bercovitch, F. B., & Goy, R. W. (1990). The socioendocrinology of reproductive development and reproductive success in macaques. In T. E. Ziegler, & F. B. Bercovitch (Eds.), *Socioendocrinology of primate reproduction* (pp. 59–93). New York, NY: Wiley-Liss.
- Bolig, R., Price, C. S., O'Neill, P. L., & Suomi, S. J. (1992). Subjective assessment of reactivity level and personality of rhesus monkeys. *International Journal of Primatology*, 13, 287–306.
- Brent, L. J. N., Semple, S., MacLarnon, A., Ruiz-Lambides, A., Gonzalez-Martinez, J., & Platt, M. L. (2014). Personality traits in rhesus macaques *Macaca mulatta* are heritable but do not predict reproductive output. *International Journal of Primatology*, 35(1), 188–209. <http://dx.doi.org/10.1007/s10764-013-9724-6>.
- Brommer, J. E., Karell, P., Ahola, K., & Karstinen, T. (2014). Residual correlations, and not individual properties, determine a nest defense boldness syndrome. *Behavioral Ecology*, 25(4), 802–812. <http://dx.doi.org/10.1093/beheco/aru057>.
- Capitanio, J. P. (1999). Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology*, 47(4), 299–320. [http://dx.doi.org/10.1002/\(SICI\)1098-2345\(1999\)47:4<299::AID-AJP3>3.0.CO;2-P](http://dx.doi.org/10.1002/(SICI)1098-2345(1999)47:4<299::AID-AJP3>3.0.CO;2-P).
- Chajewski, M. (2009). *rela: Scale item analysis. (Version R package version 4.1)*. Retrieved from: <https://cran.r-project.org/web/packages/rela/index.html>.
- Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 29–59). Oxford, U.K.: Oxford University Press.
- Clarke, A. S., & Snipes, M. (1998). Early behavioral development and temperamental traits in mother- vs peer-reared rhesus monkeys. *Primates*, 39(4), 433–448. <http://dx.doi.org/10.1007/BF02557567>.
- Cohen, J. (1992). A power primer. *Psychological Bulletin*, 112(1), 155–159. <http://dx.doi.org/10.1037/0033-2909.112.1.155>.
- Colvin, J. (1983). Influences of the social situation on male emigration. In R. A. Hinde (Ed.), *Primate social relationship. An integrated approach* (pp. 160–171). Oxford, U.K.: Blackwell.
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4065–4076. <http://dx.doi.org/10.1098/rstb.2010.0176>.
- Datta, S. (1988). The acquisition of dominance among free-ranging rhesus monkey siblings. *Animal Behaviour*, 36(3), 754–772. [http://dx.doi.org/10.1016/S0003-3472\(88\)80159-3](http://dx.doi.org/10.1016/S0003-3472(88)80159-3).
- Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis: Invasive species have higher phenotypic plasticity. *Ecology Letters*, 14(4), 419–431. <http://dx.doi.org/10.1111/j.1461-0248.2011.01596.x>.
- Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology*, 41(1), 417–440. <http://dx.doi.org/10.1146/annurev.ps.41.020190.002221>.
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, 271(1541), 847–852. <http://dx.doi.org/10.1098/rspb.2004.2680>.
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54. <http://dx.doi.org/10.1111/1365-2656.12013>.
- Dingemanse, N. J., Dochtermann, N. A., & Nakagawa, S. (2012). Defining behavioural syndromes and the role of 'syndrome deviation' in understanding their evolution. *Behavioral Ecology and Sociobiology*, 66(11), 1543–1548. <http://dx.doi.org/10.1007/s00265-012-1416-2>.
- Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81–89. <http://dx.doi.org/10.1016/j.tree.2009.07.013>.
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, 76(6), 1128–1138. <http://dx.doi.org/10.1111/j.1365-2656.2007.01284.x>.
- Dobson, A. J. (2002). *An introduction to generalized linear models* (2nd ed.). Boca Raton, FL: CRC Press.
- Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, 70(4), 967–971. <http://dx.doi.org/10.1016/j.anbehav.2005.01.016>.
- Fox, N. A., Henderson, H. A., Marshall, P. J., Nichols, K. E., & Ghera, M. M. (2005). Behavioral inhibition: Linking biology and behavior within a developmental framework. *Annual Review of Psychology*, 56(1), 235–262. <http://dx.doi.org/10.1146/annurev.psych.55.090902.141532>.
- Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology*, 72(8), 653–671. <http://dx.doi.org/10.1002/ajp.20833>.
- Garamszegi, L. Z., Markó, G., Szász, E., Zsebök, S., Azcárate, M., Herczeg, G., et al. (2015). Among-year variation in the repeatability, within- and between-individual, and phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and Sociobiology*, 69(12), 2005–2017. <http://dx.doi.org/10.1007/s00265-015-2012-z>.
- Gosling, S. D. (2001). From mice to men: What can we learn from animal research? *Psychological Bulletin*, 127, 45–86.
- Gouzoules, S., & Gouzoules, H. (1987). Kinship. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 299–305). Chicago, IL: University of Chicago Press.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm package. *Journal of Statistical Software*, 33(2). <http://dx.doi.org/10.18637/jss.v033.i02>.
- Herczeg, G., Ab Ghani, N. I., & Merilä, J. (2013). Evolution of stickleback feeding behaviour: Genetics of population divergence at different ontogenetic stages. *Journal of Evolutionary Biology*, 26(5), 955–962. <http://dx.doi.org/10.1111/jeb.12103>.
- Jandt, J. M., Bengtson, S., Pinter-Wollman, N., Pruiitt, J. N., Raine, N. E., Dornhaus, A., et al. (2014). Behavioural syndromes and social insects: Personality at multiple levels: Behavioural syndromes and social insects. *Biological Reviews*, 89(1), 48–67. <http://dx.doi.org/10.1111/brv.12042>.
- Kagan, J. (2003). Biology, context, and developmental inquiry. *Annual Review of Psychology*, 54(1), 1–23. <http://dx.doi.org/10.1146/annurev.psych.54.101601.145240>.
- Kapsalis, E., & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). II. Testing predictions for three hypothesized organizing principles. *Behaviour*, 133(15/16), 1235–1263. <http://dx.doi.org/10.1163/156853996X00387>.
- Kaufman, A. B., & Rosenthal, R. (2009). Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. *Animal Behaviour*, 78(6), 1487–1491. <http://dx.doi.org/10.1016/j.anbehav.2009.09.014>.
- Kazem, A. J. N., & Widdig, A. (2013). Visual phenotype matching: Cues to paternity are present in rhesus macaque faces. *PLoS One*, 8(2), e55846. <http://dx.doi.org/10.1371/journal.pone.0055846>.
- Kessler, M. J., Hernández Pacheco, R., Rawlins, R. G., Ruiz-Lambides, A., Delgado, D. L., & Sabat, A. M. (2015). Long-term effects of tetanus toxoid inoculation on the demography and life expectancy of the Cayo Santiago rhesus macaques. *American Journal of Primatology*, 77(2), 211–221. <http://dx.doi.org/10.1002/ajp.22323>.
- King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, 31(2), 257–271. <http://dx.doi.org/10.1006/jrpe.1997.2179>.
- Klepper-Kilgore, N. (1999). Abstracts of presentations, twenty-second annual meeting, the American society of primatologists. *American Journal of Primatology*, 49(1), 55–70. [http://dx.doi.org/10.1002/\(SICI\)1098-2345\(1999\)49:1<55::AID-AJP4>3.0.CO;2-G](http://dx.doi.org/10.1002/(SICI)1098-2345(1999)49:1<55::AID-AJP4>3.0.CO;2-G).
- Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. *Journal of Research in Personality*, 46(5), 581–590. <http://dx.doi.org/10.1016/j.jrp.2012.06.004>.
- Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015a). Sex differences in the development of aggressive behavior in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 36(4), 764–789. <http://dx.doi.org/10.1007/s10764-015-9853-1>.
- Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015b). Sex differences in the development of social relationships in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 36(2), 353–376. <http://dx.doi.org/10.1007/s10764-015-9826-4>.
- Langos, D., Kulik, L., Ruiz-Lambides, A., & Widdig, A. (2015). Does male care, provided to immature individuals, influence immature fitness in rhesus macaques? *PLoS One*, 10(9), e0137841. <http://dx.doi.org/10.1371/journal.pone.0137841>.
- Lindburg, D. G. (1969). Rhesus monkeys: Mating season mobility of adult males. *Science*, 166, 1176–1178. <http://dx.doi.org/10.1126/science.166.3909.1176>.
- Manson, J. H. (1992). Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, 44, 405–416. [http://dx.doi.org/10.1016/0003-3472\(92\)90051-A](http://dx.doi.org/10.1016/0003-3472(92)90051-A).
- Marriott, B. M., Roemer, J., & Sultana, C. (1989). An overview of the food intake patterns of the Cayo Santiago rhesus monkeys (*Macaca mulatta*): Report of a pilot study. *Puerto Rico Health Sciences Journal*, 8(1), 87–94.
- Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., ... Linnoila, M. (1994). Low CSF 5-HIAA concentrations and severe aggression and impaired impulse control in nonhuman primates. *American Journal of Psychiatry*, 151(10), 1485–1491. <http://dx.doi.org/10.1176/ajp.151.10.1485>.

- Mehlman, P. T., Higley, J. D., Faucher, I., Lilly, A. A., Taub, D. M., Vickers, J., ... Linnoila, M. (1995). Correlation of CSF 5-HIAA concentration with sociality and the timing of emigration in free-ranging primates. *American Journal of Psychiatry*, 152, 907–913.
- Naguib, M., Flörcke, C., & van Oers, K. (2011). Effects of social conditions during early development on stress response and personality traits in great tits (*Parus major*). *Developmental Psychobiology*, 53(6), 592–600. <http://dx.doi.org/10.1002/dev.20533>.
- Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26(5), 1253–1274. <http://dx.doi.org/10.1007/s10682-012-9555-5>.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), 935–956. <http://dx.doi.org/10.1111/j.1469-185X.2010.00141.x>.
- Neumann, C., Agil, M., Widdig, A., & Engelhardt, A. (2013). Personality of wild male crested macaques (*Macaca nigra*). *PLoS One*, 8(8), e69383. <http://dx.doi.org/10.1371/journal.pone.0069383>.
- Pereira, M. E. (1995). Development and social dominance among group-living primates. *American Journal of Primatology*, 37(2), 143–175. <http://dx.doi.org/10.1002/ajp.1350370207>.
- Putnam, S. P. (2011). Stability and instability of childhood traits: Implications for personality development of animals. *Developmental Psychobiology*, 53(6), 510–520. <http://dx.doi.org/10.1002/dev.20578>.
- R Core Team. (2014). *R: A language and environment for statistical computing (Version 3.0.2)*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from: <http://www.R-project.org/>.
- Rawlins, R. G., & Kessler, M. J. (1986). *The Cayo Santiago macaques. History, behavior and biology*. Albany, NY: State University of New York Press.
- Rothbart, M. K. (2007). Temperament, development, and personality. *Current Directions in Psychological Science*, 16(4), 207–212. <http://dx.doi.org/10.1111/j.1467-8721.2007.00505.x>.
- Santillán-Doherty, A. M., Mayagoitia, L., Muñoz Delgado, J., Kajihara, K., & Mendoza, M. (2002). Estudio longitudinal de la personalidad en primates no humanos. *Revista Latinoamericana de Psicología*, 34(3), 241–249.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <http://dx.doi.org/10.1111/j.2041-210X.2010.00012.x>.
- Schmitt, D. P., Realo, A., Voracek, M., & Allik, J. (2008). Why can't a man be more like a woman? Sex differences in Big Five personality traits across 55 cultures. *Journal of Personality and Social Psychology*, 94(1), 168–182. <http://dx.doi.org/10.1037/0022-3514.94.1.168>.
- Schülke, O., Wenzel, S., & Ostner, J. (2013). Paternal relatedness predicts the strength of social bonds among female rhesus macaques. *PLoS One*, 8(3), e59789. <http://dx.doi.org/10.1371/journal.pone.0059789>.
- Shoda, Y., Mischel, W., & Wright, J. C. (1994). Intraindividual stability in the organization and patterning of behavior: Incorporating psychological situations into the idiographic analysis of personality. *Journal of Personality and Social Psychology*, 67(4), 674–687. <http://dx.doi.org/10.1037/0022-3514.67.4.674>.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378. <http://dx.doi.org/10.1016/j.tree.2004.04.009>.
- Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state-behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, 30(1), 50–60. <http://dx.doi.org/10.1016/j.tree.2014.11.004>.
- Slatyer, R. A., Mautz, B. S., Backwell, P. R. Y., & Jennions, M. D. (2012). Estimating genetic benefits of polyandry from experimental studies: A meta-analysis. *Biological Reviews*, 87(1), 1–33. <http://dx.doi.org/10.1111/j.1469-185X.2011.00182.x>.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, 19(2), 448–455. <http://dx.doi.org/10.1093/beheco/arm144>.
- Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews*, 85(2), 301–325. <http://dx.doi.org/10.1111/j.1469-185X.2009.00103.x>.
- Stevenson-Hinde, J., Stillwell-Barnes, R., & Zunz, M. (1980). Subjective assessment of rhesus monkeys over four successive years. *Primates*, 21, 66–82.
- Stevenson-Hinde, J., & Zunz, M. (1978). Subjective assessment of individual rhesus monkeys. *Primates*, 19(3), 473–482. <http://dx.doi.org/10.1007/BF02373309>.
- Suomi, S. J., Novak, M. A., & Well, A. (1996). Aging in rhesus monkeys: Different windows on behavioral continuity and change. *Developmental Psychology*, 32(6), 1116–1128. <http://dx.doi.org/10.1037/0012-1649.32.6.1116>.
- Sussman, A., & Ha, J. (2011). Developmental and cross-situational stability in infant pigtailed macaque temperament. *Developmental Psychology*, 47(3), 781–791. <http://dx.doi.org/10.1037/a0022999>.
- Trefilov, A., Berard, J. D., Krawczak, M., & Schmidtke, J. (2000). Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. *Behavior Genetics*, 30, 295–301.
- Uher, J. (2011). Individual behavioral phenotypes: An integrative meta-theoretical framework. Why 'behavioral syndromes' are not analogs of 'personality'. *Developmental Psychobiology*, 1–28. <http://dx.doi.org/10.1002/dev.20544>.
- Urszán, T. J., Garamszegi, L. Z., Nagy, G., Hettyey, A., Török, J., & Herczeg, G. (2015). No personality without experience? A test on *Rana dalmatina* tadpoles. *Ecology and Evolution*, 5(24), 5847–5856. <http://dx.doi.org/10.1002/ece3.1804>.
- Van Deun, K., Smilde, A. K., van der Werf, M. J., Kiers, H. A., & Van Mechelen, I. (2009). A structured overview of simultaneous component based data integration. *BMC Bioinformatics*, 10(246), 1–15. <http://dx.doi.org/10.1186/1471-2105-10-246>.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3). <http://dx.doi.org/10.18637/jss.v036.i03>.
- de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: A new procedure and review. *Animal Behaviour*, 55(4), 827–843. <http://dx.doi.org/10.1006/anbe.1997.0708>.
- Weinstein, T. A. R., & Capitanio, J. P. (2008). Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta*. *Animal Behaviour*, 76(2), 455–465. <http://dx.doi.org/10.1016/j.anbehav.2008.01.024>.
- Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology*, 125(1), 72–83. <http://dx.doi.org/10.1037/a0021187>.
- Widdig, A., Kessler, M. J., Bercovitch, F. B., Berard, J. D., Duggleby, C., Nürnberg, P., ... Schmidtke, J. (2016). Genetic studies on the Cayo Santiago rhesus macaques: A review of 40 years of research. *American Journal of Primatology*, 78(1), 44–62. <http://dx.doi.org/10.1002/ajp.22424>.
- Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences of the United States of America*, 98(24), 13769–13773. <http://dx.doi.org/10.1073/pnas.241210198>.
- Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2002). Affiliation and aggression among adult female rhesus macaques: A genetic analysis of paternal cohorts. *Behaviour*, 139, 371–391. <http://dx.doi.org/10.1163/156853902760102717>.
- Wiklund, I., Edman, G., Larsson, C., & Andolf, E. (2006). Personality and mode of delivery. *Acta Obstetrica et Gynecologica Scandinavica*, 85(10), 1225–1230. <http://dx.doi.org/10.1080/00016340600839833>.

Appendix

Table A1
Behavioural variables and their definition (as defined in Widdig et al., 2002)

Variable	Definition
Nonphysical aggression	Rate of focal aggression lacking body contact towards the opponents such as stare, head bobbing, vocal/open mouth threat, lunge, charge or chase
Physical aggression	Rate of focal aggression including body contact such as push, hit, grab, bite or attack
Agonistic approach	Rate of approaches initiated by the focal subject, where the recipient leaves by means of avoidance or displacement, shows signs of fear or aggression
Grooming	Focal subject picking through fur or over the skin of social partner, using hands and/or mouth for a minimum of 5 s
Affiliation	Rate of affiliative behaviour given to individuals, such as hug, hold, smelling mouth or lipsmack
Diversity of grooming partners	Number of different grooming partners
Diversity of affiliation partners	Number of different affiliation partners
Friendly approach	Rate of approaching other individuals, ranging from body contact up to 2.0 m and followed by affiliative interaction or shared spatial proximity
Submissiveness	Mean number of signs of fear (fear grin) or leaving when approached by another individual
Proximity	Mean number of group members observed in close distance (within 2 m) in PTS
Resting	Mean number of PTS where the focal subject was inactive

Note that in the present analysis we considered only interactions of the focal subject with social partners apart from the mother, or, in the case of prosocial behaviour, outside the maternal kin line of the respective focal subject.

Table A2
Varimax rotated partial factor solution for year 1

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.04	−0.11	0.62
	Physical aggression	−0.19	0.16	0.55
	Agonistic approach	0.25	0.48	0.40
Sociability	Grooming	0.76	−0.15	−0.28
	Affiliation	0.85	−0.10	0.02
	Diversity of grooming partners	0.96	0.08	−0.11
	Diversity of affiliation partners	1.05	−0.06	0.06
Fearfulness	Submissiveness	0.40	−0.46	0.04
	Proximity	−0.05	0.70	−0.17
	Resting	0.14	−0.50	−0.16
	Friendly approach	0.26	0.32	0.28

Table A3
Varimax rotated partial factor solution for year 2

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.01	−0.04	0.78
	Physical aggression	−0.37	−0.25	0.73
	Agonistic approach	−0.07	0.51	0.12
Sociability	Grooming	0.04	0.84	−0.49
	Affiliation	0.10	0.92	−0.08
	Diversity of grooming partners	0.01	0.97	−0.29
	Diversity of affiliation partners	0.01	0.95	−0.14
Fearfulness	Submissiveness	0.74	0.09	−0.16
	Proximity	−0.68	0.03	−0.01
	Resting	0.45	−0.33	0.23
	Friendly approach	−0.52	−0.05	0.26

Table A4
Varimax rotated partial factor solution for year 3

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.23	0.04	0.73
	Physical aggression	−0.11	0.31	0.70
	Agonistic approach	−0.03	0.15	0.60
Sociability	Grooming	0.28	0.93	−0.21
	Affiliation	0.15	0.84	0.15
	Diversity of grooming partners	0.15	0.96	−0.01
	Diversity of affiliation partners	0.22	0.87	−0.06
Fearfulness	Submissiveness	0.82	0.18	−0.04
	Proximity	−0.83	−0.32	0.15
	Resting	0.43	−0.40	0.42
	Friendly approach	−0.73	−0.21	0.30

Table A5
Varimax rotated partial factor solution for year 4

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.01	−0.03	0.87
	Physical aggression	0.01	0.06	0.80
	Agonistic approach	0.00	−0.30	0.75
Sociability	Grooming	0.76	0.07	−0.26
	Affiliation	0.76	−0.32	0.04
	Diversity of grooming partners	0.54	−0.11	0.31
	Diversity of affiliation partners	0.64	0.08	−0.01
Fearfulness	Submissiveness	0.31	−0.90	0.08
	Proximity	0.07	1.01	−0.14
	Resting	−0.14	−0.75	0.26
	Friendly approach	−0.14	0.89	0.15

Table A6

Varimax rotated partial factor solution for year 5

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.13	0.15	0.80
	Physical aggression	0.16	0.07	0.87
	Agonistic approach	0.28	−0.20	0.75
Sociability	Grooming	0.65	−0.07	−0.34
	Affiliation	0.65	−0.15	0.28
	Diversity of grooming partners	0.84	−0.20	−0.18
	Diversity of affiliation partners	0.62	−0.05	0.05
Fearfulness	Submissiveness	0.38	−0.87	−0.14
	Proximity	−0.29	0.93	−0.16
	Resting	−0.08	−0.57	−0.06
	Friendly approach	−0.14	0.96	0.00

Table A7

Varimax rotated partial factor solution for year 6

Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	−0.11	−0.07	0.82
	Physical aggression	−0.30	0.04	0.88
	Agonistic approach	0.31	0.31	0.87
Sociability	Grooming	0.19	0.55	−0.13
	Affiliation	0.17	0.55	0.58
	Diversity of grooming partners	0.55	0.62	0.16
	Diversity of affiliation partners	0.21	0.65	0.23
Fearfulness	Submissiveness	0.88	0.19	−0.35
	Proximity	−0.95	−0.19	−0.16
	Resting	0.72	−0.24	−0.12
	Friendly approach	−0.89	−0.13	−0.06

Table A8

Varimax rotated partial factor solution for year 7

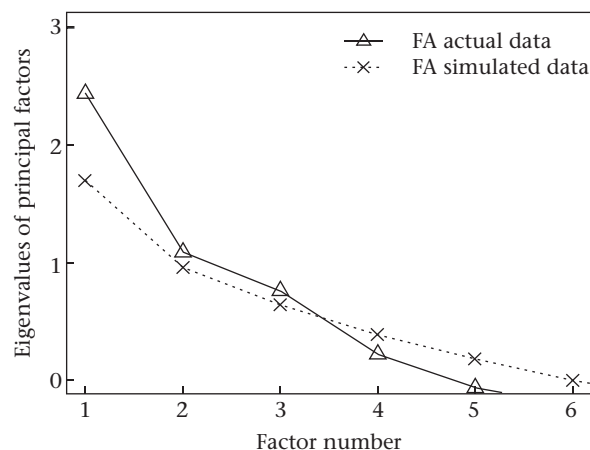
Latent structure	Variable	Standard factor loading F1	Standard factor loading F2	Standard factor loading F3
Aggression	Nonphysical aggression	0.09	0.22	0.67
	Physical aggression	0.05	0.13	0.66
	Agonistic approach	0.27	0.19	0.69
Sociability	Grooming	−0.06	0.33	0.59
	Affiliation	0.02	0.73	0.04
	Diversity of grooming partners	0.59	0.54	0.20
	Diversity of affiliation partners	0.17	0.54	0.14
Fearfulness	Submissiveness	0.66	0.14	−0.18
	Proximity	−1.10	−0.12	−0.30
	Resting	0.95	0.08	0.37
	Friendly approach	−1.01	−0.05	−0.21

Table A9

Pearson correlation coefficients between frequencies of a behaviour 1 year before and after life events

Variable	Correlations before and after male migration	Correlations before and after first maternity
Diversity of grooming partners	0.56 [−0.06, 0.87]	−0.02 [−0.54, 0.52]
Diversity of affiliation partners	0.75 [0.27, 0.93]	0.18 [−0.39, 0.65]
Affiliation	0.06 [−0.56, 0.64]	0.53 [−0.01, 0.83]
Grooming	0.26 [−0.40, 0.74]	0.37 [−0.20, 0.75]
Physical aggression	0.35 [−0.72, 0.43]	−0.14 [−0.61, 0.45]
Nonphysical aggression	0.13 [−0.23, 0.81]	0.34 [−0.188, 0.76]
Agonistic approach	0.28 [−0.33, 0.77]	0.48 [−0.07, 0.81]
Submissiveness	−0.53 [−0.86, 0.10]	0.75 [0.36, 0.91]
Proximity	−0.16 [−0.77, 0.34]	0.82 [0.53, 0.94]
Resting	0.22 [−0.44, 0.72]	0.46 [−0.09, 0.80]
Friendly approach	−0.26 [−0.61, 0.58]	0.74 [0.37, 0.91]

The 95% confidence intervals are in parentheses. Significant results are in bold. Note that confidence intervals are generally wide due to low sample sizes.

**Figure A1.** The parallel analysis suggested the extraction of three factors.