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Tenure in current captive setting and age predict personality changes in adult pigtailed macaques

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Personality change in nonhuman primates is a topic that warrants more research attention. Many studies focus on intraindividual repeatability, but few note population-wide trends in personality change. In part, this results from the large sample size that is required to detect such trends. In the present study, we measured personality in a large sample ($N = 293$) of adult, mother-reared pigtailed macaques, *Macaca nemestrina*, over a period of 3 years. We looked at four personality components (sociability towards humans, cautiousness, aggressiveness and fearfulness) derived from behavioural observations at two to four time points per subject. We found these components to have repeatabilities similar to those reported elsewhere in the literature. We then analysed population-wide changes in personality components over time using a linear mixed effects model with three predictors: entry age at the current primate facility, tenure at the primate facility at the time of the first personality test and time elapsed since the first personality test. We found that adult personality changed with life experiences (here, tenure at the facility where tested) and age. Throughout adulthood, pigtailed macaques became less cautious and more aggressive. At the same time, subjects became less cautious and more sociable with increasing time in individual caging at the current primate research facility. We also found that individuals differed significantly in their personality consistency. Other researchers may benefit by applying similar methodology to that described here as they extrapolate about personality measures over time.

Animals across a broad spectrum of species show consistent individual differences in their behavioural patterns, which are referred to as temperament or personality traits. The existence and evolutionary importance of individual and species differences in behaviour were noted by Darwin (1872), but received relatively little research attention until recently. These traits are analogous to human personality traits in structure and measurement (Gosling, 2001), especially as observed in our nearest relatives, the nonhuman primates (Brosnan, Newton-Fisher, & van Vugt, 2009; Freeman & Gosling, 2010). However, theories of personality are better developed in humans than in nonhuman primates, especially in regard to how personalities change throughout an individual's lifetime. In the human literature, temperament is considered to be a genetically rooted set of behavioural tendencies, which eventually develop into personality as these biological predispositions interact with experiences and the environment (Rothbart, Ahadi, & Evans, 2000).

While some controversy surrounds the measurement and context generalizability of personality in humans (e.g. Lewis, 2001; Mischel, 1968), a large literature suggests that personality changes predictably throughout adulthood (Helson, Kwan, Jon, & Jones, 2002; McCrae et al., 2000; Roberts & DelVecchio, 2000; Roberts, Walton, & Viechtbauer, 2006; Terracciano, McCrae, Brant, & Costa, 2005). These studies suggest that more change occurs during adolescence and early adulthood, and traits become more stable later in life. The most commonly described changes are an increase in social dominance, conscientiousness and emotional stability (sometimes described as a decrease in neuroticism) and a decrease in social vitality (Helson et al., 2002; McCrae et al., 2000; Roberts et al., 2006). Some investigators consider these changes to follow 'intrinsic paths of development' (McCrae et al., 2000), but other evidence suggests that these changes are more strongly related to environmental factors, such as experiences that commonly occur in adulthood (Roberts et al., 2006). In the quickly growing pool of

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animal personality studies, only a few examine the influences of age and/or experience on population-level changes in personality in nonhuman primates.

The few studies examining population trends in personality change in nonhuman primates have found that, as in humans, personality trait scores change with age. These developmental changes in infant and juvenile macaque personality are well documented (e.g. Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Sussman & Ha, 2011), as are changes with age in adult chimpanzees (King, Weiss, & Sisco, 2008; Weiss, King, & Hopkins, 2007) and other great apes (Weiss, King, Inoue-Murayama, Matsuzawa, & Oswald, 2012). The latter studies suggest that personality change in chimpanzees follows a pattern similar to that observed in humans, becoming more stable with age. Other studies reported that personality can be predicted by age in several species, including vervet monkeys, *Chlorocebus pygerythrus* (McGuire, Raleigh, & Pollack, 1994), capuchins (*Cebus capucinus*: Manson & Perry, 2013) and callitrichids (Kendal, Coe, & Laland, 2005). For most primate species, though, such group trends in personality changes over the lifetime have not been investigated.

Although longitudinal, population-wide studies are fairly rare in the primate literature, studies reporting short-term intraindividual trait repeatability are more common. Measures of repeatability, such as correlation of trait scores at two time points or intraclass correlation (ICC), are important for establishing the reliability of proposed personality traits. Such analyses have used very different measurement intervals, ranging from 1–2 months (Higley et al., 1996; Uher, Asendorpf, & Call, 2008) to 1 year (Konečná, Weiss, Lhota, & Wallner, 2012; Maestripieri, 2000; Martau, Caine, & Candland, 1985), to several years (Capitanio, 1999; Koski, 2011; Stevenson-Hinde et al., 1980). Bell, Hankison, and Laskowski (2009) found measurements taken over short periods to be significantly more repeatable than measurements over longer periods. They found no difference in repeatability with age, but their analysis included a large variety of taxa, including insects, which might not be expected to adhere to the same lifetime patterns of change as humans or other primates. The average repeatability in the Bell et al. (2009) study was 0.37, while in an analysis of nonhuman primate studies, the average repeatability was 0.58 (Freeman & Gosling, 2010). Both of these values suggest less-than-perfect repeatability, which may be due measuring error, random variation or developmental changes. Repeatability measures do not distinguish between these sources of variance. Moreover, repeatability measures do not reflect differences in consistency between individuals (Bell et al., 2009). More complex analyses of population-wide patterns of change can identify which aspects of personality change reflect consistent developmental patterns (as seen in the human literature), as well as identify any interindividual differences in behavioural consistency.

Population-wide analyses are uncommon in the primate literature, because they require more data than repeatability analyses. To identify patterns of change most powerfully, researchers require large sample sizes (ideally, $N > 100$) and at least three measurement points (Maas & Hox, 2005; Rogosa, Brandt, & Zimowski, 1982). The most powerful data sets are longitudinal measurements, which, through hierarchical analyses, can provide information about both individual- and population-level changes over time (Rogosa et al., 1982). Using model-fitting techniques in place of traditional significance testing is an especially powerful way to analyse such nested data (Anderson, Burnham, & Thompson, 2000).

In this project, we used a large sample of captive mother-reared adult pigtailed macaques, *Macaca nemestrina*, to identify population-wide patterns of personality change using model-fitting techniques. In a previous analysis, we had identified four personality components (sociability towards humans, cautiousness, aggressiveness and fearfulness) in these subjects (Sussman, Ha, Bentson, & Crockett, 2013). Subjects were tested up to four times over a 3-year period. Our model identified population-wide patterns of change over the study period and the extent to which these changes were related to age, sex and experiences besides age, especially tenure in the current primate facility. We predicted that, as in humans, pigtailed macaques' personality would show population-wide trends of change with age. We believed that tenure might affect personality as animals habituated to individual caging and proximity of humans at the primate facility, as habituation is well documented in macaques (Capitanio, Kyes, & Fairbanks, 2006; Crockett, Bowers, Bowden, & Sackett, 1994; Crockett, Bowers, Sackett, & Bowden, 1993). Relative to longtailed macaques, *Macaca fascicularis*, or rhesus macaques, *Macaca mulatta*, pigtailed macaques that had resided at the National Primate Research Center, University of Washington, Seattle (WaNPRC) for at least 1 year scored high on sociability towards humans and low on cautiousness (Sussman et al., 2013). We were interested to learn whether sociability increased and cautiousness decreased as the animals habituated to the facility and whether there were any additional changes with increasing time there. Finally, we predicted that, as in previous studies, individuals would differ in their personality consistency, as demonstrated by a significant random effect of individual ID in our model.

METHODS

Subjects and Housing

Behavioural data were collected between 2003 and 2006 on monkeys housed at WaNPRC. The sample included 293 mother-reared pigtailed macaques that were at least 4 years old at time of first testing. Demographic information for this sample is given in Table 1. The subjects were a subset of those in Sussman et al. (2013). We restricted our analysis to the species with the largest sample size. We also excluded nursery-reared subjects to reduce the number of variables in our analysis, and because our prior research (Sussman et al., 2013) found nursery-reared subjects to differ somewhat from mother-reared macaques in levels of identified personality components.

When studying animals with complex social systems, like primates, it can be difficult to disentangle the effects of social rank and individual tendencies on a subject's behaviour. By using individually housed monkeys for our study subjects, we were able to focus on individual tendencies (although this raises some issues of interpretability, as described below). The subjects were housed indoors at the WaNPRC in single cages or in grooming-contact cages (Crockett, Bellanca, Bowers, & Bowden, 1997) constructed of stainless steel and of a size conforming to U.S. Animal Welfare Regulations. Monkeys had visual contact with conspecifics, and those in grooming-contact also had tactile contact through widely spaced bars. About 30% of subjects were in grooming contact.

Prior to arriving at our primate facility, subjects were housed in various domestic and international breeding facilities where they were typically housed outdoors in social groups. The majority were captive born in Bogor, Indonesia or in Louisiana, U.S.A., and were of captive born Sumatran genetic stock. Details of individual animals' early life experiences were generally unknown, but they were assumed to be mother-reared. Although they may have occasionally experienced indoor laboratory caged housing in the prior facilities, we considered that the move to the WaNPRC facility represented a significant change in the social and physical environmental conditions for these animals. To capture the effect of experience at the WaNPRC biomedical research facility, we used the