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

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### Abstract

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.

### Keywords

change; *Macaca nemestrina*; personality; pigtailed macaque; repeatability; stability; temperament

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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

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(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 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 (Kone ná, 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 variables 'tenure at first test' and 'time elapsed since first test,' described below.

The monkeys were subjects in a wide variety of studies, including AIDS-related research, developmental biology, functional genomics, immunology, reproductive biology, neurophysiology and various primate disease models, among others (<http://www.wanprc.org>). Some monkeys were held in reserve for upcoming studies or assigned to timed breeding projects. Consequently, animals varied in the extent to which they experienced invasive procedures associated with biomedical research. The animal records available to us did not provide all specific project-related procedures performed on all subjects. We have no evidence to suggest that there is systematic variation between project-specific research experience and the variables examined in this study.

Animal rooms were maintained on a 12:12 h light:dark cycle, with an ambient temperature of 22.2–25.6 ° C. Subjects received commercial monkey biscuits twice daily and ad libitum water, as well as environmental enrichment such as a portable toy and foraging device, and fresh produce or foraging opportunities 7 days per week. The University of Washington Institutional Animal Care and Use Committee approved the observational techniques of this study, as well as all research protocols to which the animals were assigned. Our research methods complied with legal requirements of the U.S.A., the state of Washington and the Association for Assessment and Accreditation of Laboratory Animal Care International.

### Personality Testing

We used a rapid cage-front behavioural assessment to measure personality (RATR: rapid assessment of temperament and reactivity; Bentson 2003; Sussman et al., 2013). During a 4 min observation period, the observer (K.B.) recorded frequencies of 37 variables of interest using a PDA hand-held device. The observer stood directly in front of the subject's cage, but did not interact with the subject in any way. The observer was not known to the monkeys in any other context besides RATR testing. Four categories of mutually exclusive behaviours were measured by instantaneous (point) sampling every minute (posture/locomotion, facial/vocal expression, cage position, responsiveness to observer); some behaviours were measured by whether or not they occurred during each minute of the observation period (one-zero/yes-no sampling; see Supplementary Material).

Each monkey in our sample received two to four tests over the course of 3 years. Monkeys that entered the WaNPRC during the 3-year period ( $N = 140$ ) were tested beginning 8 weeks after arrival, and typically retested about 10–12 weeks later, and then annually. Monkeys that were already at the primate centre at the start of the 3-year period ( $N = 153$ ) were on an annual test schedule. Our use of growth curve modelling allowed us to combine data for individuals with different numbers of tests into a single, population-wide model (Rogosa et

al., 1982). Interval lengths between tests are reported in Table 1. These intervals reflect the mix of testing schedules for monkeys that arrived during the 3-year interval and those that were at WaNPRC for over 1 year before they were first tested.

### Personality Component Identification

Personality components were identified as described in Sussman et al. (2013). In the present study, we use the term ‘personality’ rather than ‘temperament’ because ‘personality’ is most often used in human studies of individual differences. Our analyses focused on 12 behavioural variables of interest from the original 37 measured as identified by analyses described in Sussman et al. (2013) (see Supplementary Material). These included whether the animal was in the front or back of the cage; whether it reached towards or approached the observer; whether it gave a lipsmack to the observer, showed quiet attention towards the observer, or ignored the observer; whether it performed a lunge or an open-mouth threat during instantaneous sampling or threatened the observer during a 1 min period; and whether it shrieked or fear grimaced. Using a principal components analysis (PCA), we identified four uncorrelated personality components, which we designated as ‘sociability towards humans’, ‘cautiousness’, ‘aggressiveness’ and ‘fearfulness’ (Sussman et al., 2013). Because of the methodology used here, all of these components reflect reactions to a human; consequently, they may not describe the full range of pigtailed macaque behaviour, but instead describe individual differences in a specific context.

In our first identification analysis (Sussman et al., 2013), we used only a single observation for each individual (the first test conducted when the subject had been at the facility for at least 1 year) and did not attempt to assess the repeatability of the measures. Given the goals of the present study, we wanted to make sure that the structure of the personality components was the same at each of the testing periods within pigtailed macaques before proceeding. To do this, we performed PCAs, using the 12 variables previously identified, and specifying four components, for each of the first three behavioural observations. We compared the structure of the orthogonally rotated component matrices for the first, second and third tests using Tucker’s congruence coefficient (Lorenzo-seva & ten Borge, 2006). The fourth test was not included in the component congruency analysis because of small sample size. We also compared all three tests to the structure of the full-sample PCA from our previously published study, which included a much larger number of subjects ( $N = 899$ ), and subjects from three species of macaque, including some monkeys that had been nursery-reared.

We found that all comparisons between observation periods were congruent, exceeding the minimum congruence level of 0.85 suggested by Lorenzo-seva and ten Borge (2006). In other words, this analysis showed that the same personality components existed for the first, second and third tests. To maintain maximum consistency with our past work, we chose to calculate individual component scores for each test using the same methods as in our 2013 publication. We used the regression method to calculate individual scores, specifying the same equation values as in our previous analysis. We used SPSS 18.0 (IBM, 2008) for these analyses.

### Repeatability Analyses

In addition to our model fitting, we calculated repeatabilities for each of our temperament components to compare to those published elsewhere in the literature. In the interest of maximizing comparability, we calculated repeatability using both intraclass correlation (ICC) (Bell et al., 2009) and Pearson’s correlations between tests (Freeman & Gosling, 2010). These analyses were conducted in R 2.15.2 using version 2.1 of the ICC package.



## Population-wide Model

To investigate population-wide patterns of change, we fitted linear mixed effect models to each component score with the random effect of subject ID and a set of predictors. Predictors included sex, age upon arriving at the current primate facility ('entry age'), tenure at the current primate centre at the time of the first personality test ('1st test tenure') and time elapsed between the first personality test and subsequent tests ('time elapsed'). All variables were measured in years. These predictors were chosen because they were not strongly correlated, but together encoded information on trends that occurred with age and with tenure at the facility. Entry age and 1st test tenure were correlated ( $r = -0.22$ ), while the other variables were uncorrelated ( $|r| < 0.10$ ). Although animals sometimes entered the current primate facility long before they received a personality test, entry age was highly correlated with the age at which they received this test ( $r = 0.81$ ). The summed effects of all three predictors are equivalent to an animal's age at its current test, while the sum of 1st test tenure and time elapsed gives the animal's tenure at its current test. Therefore, to examine the effect of age while controlling for tenure, we looked at the only predictor that contributed to age but not to tenure (entry age). We interpreted a significant effect of entry age as a personality change purely related to age and experience in a previous facility, while the effects of 1st test tenure and time elapsed reflected the summed effect of increasing age and increasing time spent at the current facility. A significant effect of 1st test tenure without a significant effect of entry age would suggest that experience, or time at the current facility, was the main predictor of a personality component. The effects of time elapsed were interpreted based on their parameter values and whether they more closely matched the size and direction of the parameters for the other components.

We examined only linear effects here and included the interactions of each predictor with sex. We also tested the interaction effect of entry age and 1st test tenure to ensure that there were no unexpected developmental effects for younger or older animals entering the primate centre. As no significant interaction effects were found, this term did not appear in any of our final models. All distinct subsets of effects were examined, under the usual constraint that no subset contained an interaction unless it also contained the main terms. This resulted in a total of 35 models. All models were fitted with R 2.15.2, using version 3.1-108 of the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2010).

The explanatory power of models was judged by the Akaike's Information Criterion with small-sample correction (AICc; Hurvich & Tsai, 1989). As  $P$  values can be inaccurate for nested data, this approach is preferable (Pinheiro & Bates, 2000). Because of the large number of models compared and the real possibility that there would be multiple models with near-minimal AICc values, we followed a model-averaging approach as described by Burnham and Anderson (2002). Each model is assigned an Akaike weight inversely proportional to the exponential of its AICc value, and predictions are averaged across all models using these weights. This approach avoids overly privileging the single 'best' model if it has very close competitors in AICc values and has repeatedly shown superior predictive performance to the best-model approach (Burnham & Anderson, 2004). Model averaging was performed in R 2.15.2 with version 1.27 of the AICcmodavg package.

For heuristic purposes, we assessed the goodness of fit of our model-averaged predictions using classical  $R^2$ . To assess the significance of each individual parameter, we again followed Burnham and Anderson (2002). We examined the subset of models containing that parameter but not containing any associated interactions. The value and confidence intervals for this parameter were then found by averaging across this subset, using renormalized Akaike weights. If a value differed significantly from zero, this would indicate that the parameter had a significant effect on the response in the most informative models that included it.

## RESULTS

### Repeatability

Measuring repeatability using ICC, we found that sociability and cautiousness had fairly high repeatability, while fearfulness was slightly less repeatable, and aggressiveness was not very repeatable (Table 2). We obtained similar values when using mean Pearson's correlations.

These repeatability findings were consistent with the results of our mixed effect model, although the model better explained the within-individual variation than did the repeatability analyses. We identify the best-fitting models for each personality component (identified by lowest Akaike weight) in Table 3, along with the significant predictors within that model. We briefly discuss trends in significant predictors below.

### Population-wide Model

The best-fitting models for population-wide trends explained much of the variance in sociability and cautiousness but not in aggressiveness or fearfulness. Specifically, the best-fit model for the population trends explained 31% of the variance in sociability and 18% of the variance in cautiousness, but only 5% of the variance in aggressiveness and 3% of the variance in fearfulness (Table 3). These  $R^2$  values increased dramatically when individual ID was added as a predictor variable. When ID was included, all models predicted more than 50% of the variance in the personality components.

There were mean-level differences in personality components within our samples based on sex. Males were significantly more sociable but less cautious than females.

There were also several directional relationships between our temporal measures (entry age, 1st test tenure and time elapsed) and personality. Entry age was a significant predictor of cautiousness and aggressiveness (Table 3). Animals entering at a younger age tended to be more cautious but also less aggressive (unstandardized coefficients of predictors are given in Table 4). For sociability, there was a significant, disordinal, interaction between entry age and sex. Females' predicted sociability did not vary with increasing entry age, while male sociability decreased with increasing age at entry.

Tenure at 1st test was a significant predictor of sociability and cautiousness. Animals that had been at the current facility for longer at the time of their first test were less cautious and more sociable. There was a significant, disordinal, interaction effect on sociability between 1st test tenure and sex. Predicted sociability increased with increasing 1st test tenure in females, whereas it decreased slightly in males.

Time elapsed between tests was a significant predictor of sociability and fearfulness, but not of cautiousness or aggressiveness. Sociability and fearfulness both increased with greater time elapsed between personality tests, and there were significant, ordinal interaction effects on both traits between time elapsed and sex; as time elapsed increased, predicted scores increased more strongly for females than for males. As a result, females tended to diverge from males on fearfulness, and converge towards them on sociability, as time elapsed increased.

## DISCUSSION

We used repeated assessments of individually housed adult pigtailed macaques to evaluate component repeatability and population-wide patterns of change in four personality

components. Personality components at each assessment were similar to those identified in a previous analysis of a larger data set including three macaque species (Sussman et al., 2013).

### Repeatability

Overall, we found significant component repeatability. Using ICC, the repeatability scores of three of our components (sociability, cautiousness and fearfulness) exceeded the mean repeatability of 0.37 reported in Bell et al.'s (2009) meta-analysis. Aggressiveness, with a repeatability of only 0.28, was our least repeatable component. Our test–retest correlation values also compared favourably with those reported in the primate literature, as reviewed by Freeman and Gosling (2010); sociability, cautiousness and fearfulness were within their reported range of 0.35–0.88, although all were smaller than their weighted average of 0.58. Aggressiveness was, again, the least repeatable component with a test–retest correlation of just 0.28. In contrast, aggressiveness tended to be among the most repeatable traits in other studies (Bell et al., 2009). The discrepancy with our results is likely due to limited variance in our measure of aggressiveness, which reduced ICC. Pigtailed macaques showed lower average scores on both aggressiveness and fearfulness, and less variance, than longtailed and rhesus macaques (Sussman et al., 2013), a result consistent with physiological comparisons of the species (Westergaard, Suomi, Higley, & Mehlman, 1999).

### Population-wide Patterns of Change

Our results suggest that, for the animals in this sample, both age and experience at the primate centre predicted personality. After controlling for the effects of tenure, the relationships observed between entry age and cautiousness and aggressiveness demonstrate that personality tends to follow some predictable changes over the life span of pigtailed macaques. Macaques entering at an older age were less cautious and more aggressive. These patterns occurred independently of experience at the primate facility, as entry age was largely uncorrelated with tenure at the facility, and there were no significant age-by-tenure interaction effects. These results are consistent with some age-related patterns of change observed in humans; the increase in aggressiveness might be analogous to the commonly cited increase in social dominance with age (Roberts et al., 2006), and the decrease in cautiousness parallels a decrease in neuroticism in humans as they grow older (McCrae et al., 2000). Some recent work (Gottlieb, Capitanio, & McCowan, 2013) indicates that behaviour in rhesus macaques varies with entry age, and, in that study, was measured as entry into indoor housing from outdoor housing.

Experience at the current primate facility was a significant predictor of both cautiousness and sociability, with animals being less cautious and more sociable with increasing tenure at 1st test and more sociable with greater time elapsed between tests. This pattern suggests that most decreases in cautiousness occur in a fairly brief period after arrival at the primate facility, while increases in sociability occur on a longer timescale. This pattern of change in cautiousness is consistent with previously identified habituation responses in macaques. Past studies have demonstrated that, in rhesus macaques, behaviours and physiological measures become more stable after about 3 months in a given housing situation (Capitanio et al., 2006). Urinary cortisol levels also continue to decline for more than 1 year after arrival at a new primate facility in adult longtailed macaques (Crockett, et al., 1993, 1994). The changes in sociability identified here appear to occur on a longer time frame than previously identified habituation changes. Recent work suggests that captivity alters behaviour differentially across species (Mason et al., 2013), and the relationships between tenure and personality described here might be unique to pigtailed macaques. Some studies suggest that pigtailed macaques are receptive to human interactions. For example, pigtailed macaques are more neophilic than some other macaque species (Montgomery, Bentson, & Crockett, 2005), are likely to direct social behaviours towards human observers (Oettinger, Crockett,



& Bellanca, 2007) and are more easily trained to perform some tasks than are long-tailed macaques (Crockett & Wilson, 1980). Comparative studies are needed to establish whether tenure at current facility is an important predictor of personality in other captive species. Based on the tenure finding, we encourage other investigators to include similar factors in their models of personality stability.

The patterns of change for fearfulness in our study were more difficult to interpret than those of the other personality components. Fearfulness increased with time elapsed between tests but not with other predictors. This unusual pattern might suggest that there are opposite directional effects of increasing age and increasing time spent in the facility (Table 4), which cancel out for monkeys within their first months or years at the primate facility, when physiological effects of habituation are occurring (Capitanio et al., 2006; Crockett et al., 1993, 1994). However, after this initial period, the effects of further habituation appear to decline, and fearfulness begins to increase again, perhaps due to sensitization for other reasons.

There were mean-level sex differences in sociability and cautiousness in our sample. In both cases, the differences were consistent with the sex differences we identified previously (Sussman et al., 2013). Males were more sociable towards humans and less cautious than females. In addition, we identified several sex interaction effects, which suggest that females exhibit more change in their sociability and fearfulness scores with respect to tenure but less change in sociability with respect to entry age than do males. This latter interaction result must be interpreted with caution, as the male and female distributions for entry age differed considerably, leading to a correlation of 0.47 between entry age and sex. More females entered the primate centre at older ages than did males, while most males entered as young adults. Despite these issues of sampling validity, these effects are consistent with the theory that males have more stable personalities than females. Some researchers have suggested that males should be more stable in traits such as aggressiveness, which are strongly linked to male-specific hormones (Andrew, 1972; Wingfield, 1994), while others have suggested that sexually selected traits would be more stable in males than in females (Garamszegi et al., 2006; Kokko, 1998). Such sex differences in personality change deserve further study.

Including individual ID in the model greatly increased the amount of variance explained to 51–70% (Table 3), but a large amount of variance remained unexplained by either ID or the time-related predictors, indicating that individuals differed in the direction and rate of change of their personality scores over testing. The variance explained by individual ID is related to individual differences in intercept, while the unexplained variance can be interpreted as variation due to differences in individual slopes. Several other studies have noted that the repeatability or changeability of personality scores differ from one individual to another. In some cases this variability is considered a distinct personality trait, ‘consistency’ (Bell et al., 2009; Dingemanse, Kazem, Reale, & Wright, 2010) or ‘intraindividual variability’ (Stamps, Briffa, & Biro, 2012). Similar individual differences in personality stability or consistency have been described in humans (reviewed in Roberts & Mroczek, 2008).

The relatively poorer model fit for aggressiveness and fearfulness and the lower unexplained variance for sociability and cautiousness may reflect slight differences in genetic contributions to personality between breeding facilities as well as differences in experiences before and after arrival at the research centre. For example, climate, size and composition of groups, animal density, substrate and diet likely varied among breeding sites. Similarly, assignment of monkeys to a wide variety of projects after arrival influenced such factors as the number and type of veterinary and research procedures, room size and number of moves within the facility that were experienced by each monkey. Since personality develops over

time with interplay between genes and environment, it is remarkable that in spite of these variations in conditions before and after arrival, there were identifiable population-wide changes in some personality variables.

The sample used in this study consisted of captive animals that were typically mother-reared in outdoor groups. These animals are representative of pigtailed macaques held in captivity in the United States and we feel confident that our large sample allows us to generalize to this population. While our research is consistent with the literature in demonstrating that personality changes with age and experience, the patterns of change described here may be specific to laboratory animals with backgrounds similar to those of our subjects. Some recent work suggests that time spent in outdoor housing may affect behaviour in macaques (Gottlieb, Capitanio, & McCowan, 2013). In our study, entry age was used as a proxy for time spent outdoors. Further studies examining effects of captivity on personality in pigtailed macaques housed in social groups or other settings would help distinguish the effects of captivity from the effects of individual caging described here. Note, however, that personality components studied here were all measures of animals' responses to a human observer, and as such, only capture a portion of the species' behavioural repertoire. Personality measured in different contexts might well show distinct patterns of change as well as revealing more components.

## Conclusions

Our analysis offers a significant contribution to the literature, as the first study to model population-wide changes in personality in a large sample of adult pigtailed macaques over a multiyear time frame. Our repeatability analysis demonstrates that our methods of measuring personality are about as reliable as other methods reported in the literature. Our modelling of population-wide change demonstrates that pigtailed macaques show population-wide changes in personality throughout adulthood, including a decrease in cautiousness and an increase in aggressiveness. These trends seemed to occur regardless of individuals' life experiences. At the same time, life experience (here, time in individual caging at the current biomedical primate research facility) was also an important predictor of personality, with animals becoming less cautious and more sociable with increased tenure. We recommend that other researchers include information about tenure in current facility into their stability analyses, as well as age, when it is known. Finally, like other studies before ours, we found that individuals differed significantly in their personality consistency. It is important for researchers to acknowledge this phenomenon when extrapolating from a single personality score to predict a subject's future behaviour. Overall, the model-fitting techniques used here represent a powerful tool for understanding change and consistency in personality. We think these techniques may be used to identify specific aspects of experience in breeding colonies and in biomedical research facilities that influence personality traits, and we recommend that other animal personality researchers adopt similar methods in their studies.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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### Highlights

- We examined personality stability in a large sample of captive adult macaques.
- We identified population and individual stability with linear effects mixed models.
- Age predicted changes in cautiousness and aggressiveness.
- Tenure at the current primate facility predicted changes in personality.
- Individuals differed in their personality consistency.

**Table 1**

Demographic information for adult pigtailed macaques in the present study

	Full sample			Males			Females			
	Mean	SD	Range	N	Mean	SD	N	Mean	SD	N
Entry age (years)	5.99	3.38	1.0–15.7	293	3.98	1.90	115	7.29	3.49	178
Age at first test (years)	7.85	3.58	4.0–17.2	293	6.58	2.79	115	8.68	3.79	178
Tenure at 1st test (years)	1.86	2.25	0.1–12.8	293	2.60	2.39	115	1.38	2.02	178
Time elapsed: 1st – 2nd test (days)	185.24	170.52	20–931	293	176.75	164.90	115	190.65	174.24	178
Time elapsed: 1st – 3rd test (days)	580.74	231.84	77–1007	150	493.89	171.72	53	628.20	247.01	97
Time elapsed: 1st – 4th test (days)	818.82	109.18	424–1000	40	851.81	90.97	21	782.37	118.23	19

**Table 2**

Repeatability for four temperament traits over 3 years (2–4 testing periods) in pigtailed macaques

	Sociability	Cautiousness	Aggressiveness	Fearfulness
Single measures ICC	0.54	0.53	0.28	0.42
95% CI for ICC	0.47–0.60	0.46–0.60	0.19–0.36	0.34–0.50
Within-test variance	0.40	0.40	0.30	0.25
Between-test variance	0.47	0.45	0.12	0.18
Mean correlation	0.48	0.45	0.28	0.42
95% CI for correlation	0.46–0.69	0.46–0.69	0.27–0.50	0.35–0.58

CI: confidence interval; ICC: intraclass correlation. Measures include ICC (Bell et al., 2009) and mean Pearson's correlation (Freeman & Gosling, 2010).  $N=293$ ; estimated  $k$  for individuals is 2.66.

**Table 3**

Fixed estimates of the best-fitting models of population-wide personality change in adult pigtailed macaques

Outcome	Akaike $w_i$	Significant predictors	$R^2$	$R^2$ with ID	RMSE	RMSE with ID	$f^2$
<b>Sociability = Sex + entry age + 1st test tenure + time elapsed + (sex × entry age) + (sex × 1st test tenure) + (sex × time elapsed)</b>							
	0.83	Sex ***	0.31	0.70	0.83	0.57	0.45
		1st test tenure ***					
		Time elapsed ***					
		Sex × entry age interaction ***					
		Sex × 1st test tenure interaction ***					
		Sex × time elapsed interaction *					
<b>Cautiousness = Sex + entry age + 1st test tenure + (sex × entry age)</b>							
	0.25	Sex ***	0.18	0.68	0.91	0.60	0.22
		Entry age ***					
		1st test tenure ***					
<b>Aggressiveness = Sex + entry age + time elapsed + (sex × time elapsed)</b>							
	0.17	Entry age ***	0.05	0.51	0.97	0.77	0.05
<b>Fearfulness = Sex + time elapsed + (sex × time elapsed)</b>							
	0.36	Time elapsed ***	0.03	0.65	0.98	0.64	0.04
		Sex × time elapsed interaction ***					

Equations show the best-fitting model, as determined by highest Akaike weight ( $w_i$ ). Significant predictors are those variables with coefficients that differed significantly from zero in the more informative models.  $R^2$  without subject ID describes the variance in personality explained by the model as shown, and  $R^2$  with ID describes the variance explained by the model with 'ID' included as a predictor. Root-mean-square error (RMSE) describes model residuals, and Cohen's  $f^2$  is a measure of effect size.

\*\*\*  $P < 0.01$

\*  $P < 0.05$

\*\*\*  $P < 0.001$ .

Table 4

Unstandardized coefficients for predictors in the best-fitting models of population-wide personality change in adult pigtailed macaques

Component	Predictor	Estimate	Unconditional SE
Sociability	Sex	-0.29	0.05
	Entry age	-0.07	0.02
	1st test tenure	0.06	0.02
	Time elapsed	0.19	0.03
	Sex × entry age	0.08	0.02
	Sex × 1st test tenure	0.09	0.02
	Sex × time elapsed	0.08	0.03
	Sex	0.27	0.06
Cautiousness	Entry age	-0.10	0.02
	1st test tenure	-0.15	0.02
	Sex × entry age	0.04	0.02
Aggressiveness	Sex	0.08	0.05
	Entry age	0.05	0.01
Fearfulness	Sex	0.08	0.05
	Time elapsed	0.12	0.04
	Sex × time elapsed	0.13	0.04

Entry age, 1st test tenure and time elapsed are measured in years and are mean centered. Sex is measured as 1 for females and as -1 for males.