Title
Rhesus macaque personality, dominance, behavior, and health

Journal
American Journal of Primatology, 80(2)

ISSN
0275-2565

Authors
Robinson, Lauren M
Coleman, Kristine
Capitanio, John P
et al.

Publication Date
2018-02-01

DOI
10.1002/ajp.22739

Peer reviewed

Published in final edited form as:
Am J Primatol. 2018 February ; 80(2): . doi:10.1002/ajp.22739.

Rhesus macaque personality, dominance, behavior, and health

Lauren M. Robinson[1,2,3,*], **Kristine Coleman**[4], **John P Capitanio**[5], **Daniel H. Gottlieb**[4], **Ian G. Handel**[6], **Mark J. Adams**[7], **Matthew C. Leach**[8], **Natalie K. Waran**[3,6,9], and **Alexander Weiss**[1,2]

[1]Department of Psychology, School of Philosophy, Psychology and Language Sciences, The University of Edinburgh, Department of Psychology, 7 George Square, Edinburgh, UK, EH8 9JZ [2]Scottish Primate Research Group, UK [3]Jeanne Marchig International Centre for Animal Welfare Education, Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush Veterinary Centre, Roslin, UK, EH25 9RG [4]Oregon National Primate Research Center, 505 NW 185th Ave, Beaverton, OR, 97006 [5]California National Primate Research Center, Department of Psychology, One Shields Avenue, University of California, Davis, CA, 98616 [6]The Roslin Institute and The Royal (Dick) School of Veterinary Studies, University of Edinburgh, Roslin, UK, EH25 9RG [7]Department of Psychiatry, University of Edinburgh, Royal Edinburgh Hospital, Edinburgh, UK, EH10 5HF [8]School of Agriculture, Food & Rural Development, Agriculture Building, Newcastle University, Newcastle upon Tyne, UK, NE1 7RU [9]Faculty of Education, Humanities and Health Science, Eastern Institute of Technology, Hawke's Bay, New Zealand

Abstract

Previous studies of nonhuman primates have found relationships between health and individual differences in personality, behavior, and social status. However, despite knowing these factors are intercorrelated, many studies focus only on a single measure, e.g., rank. Consequently, it is difficult to determine the degree to which these individual differences are independently associated with health. The present study sought to untangle the associations between health and these individual differences in rhesus macaques (*Macaca mulatta*). We studied 85 socially-housed macaques at the Oregon and California National Primate Research Centers, and used veterinary records to determine the number of injuries and illnesses for each macaque. We measured personality using 12 items from a well-established primate personality questionnaire, performed focal observations of behaviors, and calculated dominance status from directional supplant data. All twelve personality questionnaire items were reliable and were used to represent five of the six personality dimensions identified in rhesus macaques---Dominance, Confidence, Openness, Anxiety, and Friendliness (also known as Sociability). Following this, we fit generalized linear mixed effects models to understand how these factors were associated with an animal's history of injury and history of illness. In the models, age was an offset, facility was a random effect, and the five personality dimensions, behavior, sex, and dominance status were fixed effects. Number of injuries and illnesses were each best represented by a negative binomial distribution. For the injury models, including the effects did improve model fit. This model revealed that more confident and more anxious macaques experienced fewer injuries. For the illness models, including the fixed

*Corresponding author: Lauren M. Robinson. Department of Psychology, The University of Edinburgh, 7 George Square, Edinburgh EH8 9JZ, United Kingdom. drlmrobinson@gmail.com.

effects did not significantly improve model fit over a model without the fixed effects. Future studies may seek to assess mechanisms underlying these associations.

Keywords

health; personality; individual differences; macaque; welfare

Introduction

Why is one animal healthier than another? This is a deceptively simple question, which has implications for animal welfare. Many studies have focused on the connection between a single characteristic, such as dominance status (Sapolsky, 2005), and health. However, individual characteristics, including, not just social status, but personality traits and behavior, are interrelated (Konečná et al., 2008; Konečná, Weiss, Lhota, & Wallner, 2012; Murray, 2011; Pederson, King, & Landau, 2005; Weinstein & Capitanio, 2008). For example, adult Barbary macaques (*Macaca sylvanus*) rated as higher in Confidence had higher rank (Konečná et al., 2012). Therefore, studies that focus on single individual characteristics cannot exclude the possibility that the associations that they identify are confounded by some other individual characteristic.

In this study, we examined associations between injuries and illnesses and individual differences in behavior, dominance status, and personality in rhesus macaques (*Macaca mulatta*). Previous studies identified associations between individual characteristics and health in multiple primate species. For example, play and grooming, which may be indicative of positive welfare (Oliveira, Rossi, Silva, Lau, & Barreto, 2009; Wittig et al., 2008), may be less common among injured or ill individuals than among healthy animals (Broom & Johnson, 1993). Although, the relationship between primate play and welfare may not be as straightforward as previously thought (see Yamanashi, Nogami, Teramoto, Morimura, & Hirata, in press). Dominance status is also related to health and stress (Sapolsky, 2004, 2005). For example, Archie, Altmann, and Alberts (2012) found that higher ranking adult male baboons (*Papio cynocephalus*) had reduced rates of illness and wounds that healed more quickly than lower ranking individuals. Finally, personality is linked to illness (reiewed in Cavigelli, Michael, & Ragan, 2013). For example, more sociable adult rhesus macaques have reduced viral loads (Capitanio, Mendoza, & Baroncelli, 1999) and more stable immune responses (Maninger, Capitanio, Mendoza, & Mason, 2003).

Although it is not possible to identify the causal direction of these associations, these results inform our understanding of individual characteristics and health. Including multiple individual characteristics in models enables us to identify whether relationships between these characteristics and health are independent or whether they are attributable to variance shared between these characteristics. Moreover, this approach brings studies of individual characteristics and health outcomes in nonhuman primates in line with studies of human personality and health (e.g., Jonassaint et al., 2010). A better understanding of the links between individual characteristics and health is important as it enables us to better understand what factors influence common health problems, such as diarrhea (Prongay, Park, & Murphy, 2013), in nonhuman primate species.

Methods

Ethical Approval

This study was non-invasive and complied with the United States Animal Welfare Act (2013) and the “Principles for the Ethical Treatment of Non-Human Primates” (American Society of Primatologists, 2001). The study was approved by the University of Edinburgh’s Biological Services Unit, AWERB OS2-14 and A3433-01, and the Oregon National Primate Research Center (ONPRC) Institutional Animal Care and Use Committee. As the study was observational, it did not require review by the California National Primate Research Center’s (CNPRC) Institutional Animal Care and Use Committee. However, approval to conduct the study was sought and granted at both institutions. Both ONPRC and CNPRC are fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC), International.

Subjects

We studied 41 group-housed rhesus macaques (30 males) at the ONPRC (Beaverton, Oregon) and 44 group-housed rhesus macaques (12 males) at the CNPRC (Davis, California). All macaques were physically healthy at the beginning of the study. The macaques ranged in age from 0.84 to 20.94 years (mean±SD=5.88±4.15 years) at the start of the study. The ONPRC macaques lived in one of three identical indoor/outdoor corn crib shelters (Ns=15, 15, 11) that contained a rectangular indoor (6.69m^2) enclosure and connected oval covered outdoor (25.46m^2) enclosure. Each enclosure contained perches, fire hose swings, and toys, which were rotated on a regular basis. Macaques were fed twice daily with monkey chow (Purina 5000 high-protein lab diet) and fruit, vegetables, seeds, or oats; water was always available. During the study, three macaques were removed from their groups for research or for veterinary purposes.

The CNPRC macaques also lived in three identical crib cages (Ns=15, 16, 13). These crib cages were made up of two cylindrical cages (roughly 12.57 m^2) connected by a rectangular cage (7.25 m^2). The entire crib cage was covered with a metal ceiling and the ground is covered with gravel substrate. Each crib cage included plastic balls and plastic barrels hanging from the enclosure ceiling to provide enrichment. Macaques were fed twice daily with monkey chow and given one additional feeding (sunflower seeds, apples, etc.) during the day; water was always available. During the study, six macaques were removed for veterinary purposes.

Measures

Personality—We measured personality using two versions of the Hominoid Personality Questionnaire or HPQ (Weiss, 2017; Weiss et al., 2009; Weiss, Adams, Widdig, & Gerald, 2011). One author (LMR) and one staff member at CNPRC completed the full 54-item HPQ. However, to respect their other time commitments and in light of the time needed to train five ONRPC staff members, we developed a brief version of the questionnaire for them to complete.

To develop a brief version of the HPQ, we chose four dimensions: Confidence, Anxiety, Openness, and Dominance. At the suggestion of the ONPRC, we also changed the HPQ adjective label “Depressed” to “Socially withdrawn”. We used ratings of rhesus macaque personality from Weiss et al.’s 2011 study to identify 12 items to represent these dimensions. To do so, we identified the $\binom{n}{4}$ combinations of items for each dimension that had the best combination of attenuation, reliability, and coverage (Smith, McCarthy, & Anderson, 2000) compared to the full scale. Attenuation was calculated as the correlation between the full and brief dimensions. Reliability was assessed by the interrater agreement of the dimensions on the brief version of the questionnaire. We used multi-objective optimization (see Supplementary Methods I for full description) to discard suboptimal scales. To choose among the numerically optimal brief scales, we used content analysis to ensure that the items making up these scales captured the full description of the dimension. We used trait adjectives and their descriptor sentences to select two to four items that did not overlap too much in meaning and that appeared more frequently in the optimal reduced scales (see Figures and Tables in Supplementary Methods I).

The brief HPQ had a scale for Confidence identified by the items fearful, submissive, and cautious (note: items were reverse scored), a scale for Anxiety identified by the items quitting, anxious, erratic, and cool, a scale for Openness identified by the items innovative and curious, and a scale for Dominance identified by the items bullying and dominant. In addition, because it has an inverse loading on the Friendliness dimension, we used the inverse of the item ‘depressed’ (or ‘socially withdrawn’) to represent this dimension. Although the macaques at CNPRC were assessed using the full HPQ, to ensure that the personality scales from both facilities matched, we only used the items common to both facilities to create the personality scores.

At ONPRC, LMR and five animal care technicians responsible for animal husbandry, and who were familiar with the macaques, filled out the shortened questionnaires. One to three raters were responsible for rating each macaque. At the CNPRC, LMR and one research technician, who was familiar with the macaques, completed the full questionnaire. The mean number of raters per macaque across both facilities was 2.23. The technicians were the primary caregivers, had worked with the macaques they rated for at least a month, and were blind to the purpose of the study. LMR performed personality ratings at the end of each observation period, before reviewing the technicians’ ratings, the behavioral data, and the medical histories.

Focal observations—To measure behaviors, we took continuous focal observations at both facilities (Altmann, 1974) on every individual within each group, for 15 min per day. Macaques at ONPRC were observed for 20 days and macaques at CNRPC were observed for 15 days. In both facilities, groups were observed sequentially, observation order was randomized, and, if a macaque was consistently out-of-sight during an observation, it was not observed for that day. Frequencies and durations of behaviors were recorded using The

Observer (Version 10.5, Noldus Information Technology, The Netherlands) on a Psion Workabout Pro[3] at the ONCRC and Noldus Pocket Observer 3.2 on an Android tablet at the CNPRC. The focal macaque was observed for behaviors relating to dominance status, personality, and welfare. The ethogram (Supplementary Table I) included behaviors indicative of positive (e.g., grooming and play) and negative welfare (e.g., stereotypy, self-injury, scratching), and dominance (e.g., supplanting).

Each macaque was observed for an average of 236.02 (±SD=66.42) minutes. Because the macaques at ONPRC spent most of their time in the outdoor enclosure (LMR personal observation), observations there were performed at the outdoor enclosure. At CNPRC, the macaques were only housed outdoors and could be freely followed between the sections of their enclosure. Animals who entered the indoor portion of the enclosure at ONPRC were not visible and thus we subtracted the time each macaque spent out-of-sight (i.e., time inside) from total time observed to calculate the total time each macaque was visible to the observer. Being out-of-sight was less frequent for macaques at CNPRC and only occurred when a macaque was in the domed roof. Subtracting time out-of-sight resulted in a mean ±SD = 224.09±57.22 minutes of observation per macaque. Behaviors were calculated as the percentage of time (for durational behavioral behaviors) or number of behaviors per minute (for frequency behaviors), based on the time that they were visible. We did not find time of day effects for observation time at ONRPC (Supplementary Figure 1). The macaques at CNPRC were always viewable (other than short periods in the domed roof area), therefore we did not check for effect of time of day with these macaques as they were all observed in their scheduled order.

Health evaluation—At ONPRC and CPNRC, every time a macaque is examined or treated by veterinary staff for an illness or injury, the information is recorded in electronic records. These records include the date of the examination and a description of the presenting injury or illness. We used these data to determine the number of injuries and illnesses for each macaque from their birth to the end of the study (June 2015 at ONRPC and April 2016 at CNPRC). Because there were no cases in which a macaque presented an injury and an illness at the same time, we treated injury and illness as separate dependent variables.

Data Analysis

Interrater reliabilities—For macaques rated by two or more raters, we determined the degree to which ratings on the 12 items rated at both ONPRC and CNPRC were reliable by calculating two intraclass correlation coefficients (Shrout & Fleiss, 1979): $ICC(3,1)$ indicates the reliability of individual ratings and $ICC(3,k)$, indicates the reliability of mean ratings. Reliable items were used to create unit-weighted component scores (Gorsuch, 1983) based on the known rhesus macaque personality structure (Table 1 in Weiss, Adams, Widdig, & Gerald, 2011).

Normalized David's Scores—To measure dominance status we created a directional supplant matrix for each group. We then used this matrix to compute Normalized David's Scores (De Vries, Stevens, & Vervaecke, 2006).

Behavior data reduction—We used the principal function from the psych package (Revelle, 2011) in R, version 3.1.1 (R Development Core Team, 2014), to group behaviors by means of a principal components analysis. To determine the number of components to extract, we conducted a parallel analysis using the paran function (Dinno & Dinno, 2010), and inspected the scree plot. We examined an orthogonal (varimax) and oblique (promax) rotation of the components to determine whether to retain the uncorrelated or correlated components, respectively. Finally, based on these results, we created unit-weighted component scores for each macaque. This entailed assigning a weight of +1 to behaviors with loadings ≥ 0.4, a weight of −1 to behaviors with loadings ≤ 0.4, and a weight of 0 to all other behaviors. If a behavior had a loading ≥ |0.4| on multiple components, we assigned the weight to the component with the highest loading.

Generalized linear mixed effects models—We fit one set of models in which number of illnesses was the response variable (illness models) and one set of models in which number of injuries was the response variable (injury models). Given that these were count data and there appeared to be a preponderance of zeros, we first tested which of four distributions for modeling count and/or zero-inflated data best described the response variables. To do so we fit four illness and four injury models, each specifying a different model for the distribution of errors. Each model included a random intercept for facility and, because older macaques may have accumulated more injuries and illnesses than younger macaques, age as an offset. We compared the models' balance of model fit and parsimony by means of Akaike's Information Criterion. The four distributions of errors included a Poisson distribution and a zero-inflated Poisson regression (Kuhn, Davidson, & Durkin, 1994; Zeileis, Kleiber, & Jackman, 2008), and also a negative binomial distribution and a zero-inflated negative binomial distribution (Greene, 1994). These and all other generalized linear mixed effects models were fit using the glmmadmb function from the glmmADMB package in R (Fournier et al., 2012; Skaug, Bolker, Magnussen, & Nielsen, 2016). Model comparisons were performed using the AICtab function in R (Mazerolle, 2015).

After determining which distribution had the lowest AIC, we used the lmtest package in R (Zeileis & Hothorn, 2002) to conduct likelihood ratio tests (LRT) that tested whether adding the fixed effects of sex, dominance status, the personality scores, and the behavioral components improved model fit. This controlled for the increased type I error rates associated with multiple statistical tests of significance (Forstmeier & Schielzeth, 2011). For ease of interpretability, sex was coded −1 for females and 1 for males and the remaining fixed effects were scaled so that they were z-scores (mean±SD=0±1). To check for multicollinearity, we examined the variable inflation factors (VIF), which we calculated using the vif function in the car package in R (Fox et al., 2016). Spearman rank-order correlations of the variables included in the models are available in Supplementary Table II.

Results

Interrater Reliabilities

The interrater reliabilities of the items are presented in Table I. None of the items had *ICC*s equal to or below zero.

Data Reduction

Parallel analysis and examination of the scree plot indicated that the behaviors defined three components. Promax rotation revealed that the highest correlation between these components was 0.29 (Supplementary Table III), which is low. We therefore interpreted the varimax-rotated components (Table II). A high score on the first component (Social) indicated that a macaque received and gave more grooming, spent more time alone while stationary, and spent less time exploring their environment. This component accounted for 16% of the variance. A high score on the second component (Displacement) indicated that a macaque yawned and scratched more, spent more time near other macaques, and performed fewer locomotor stereotypies. This component accounted for 15% of the variance. We multiplied the loadings of the third component by −1 to improve the interpretability of the results. A high score on this component (Playful) indicated that a macaque spent more time socially and independently playing, received less aggression, and spent less time alone and shaking/shivering/twitching. This component accounted for 14% of the variance.

Generalized Linear Mixed Effects Models

Of the 85 macaques, 45 experienced injuries from birth to the end of the study and 30 experienced more than 1 injury during this time. Injuries ranged from mild abrasions and lacerations to contusions with swelling of the affected region. Veterinary care included administration of topical and systemic analgesics and antibiotics, cleaning and suturing wounds, and, in a few instances, partial digit amputation. Of the 85 macaques, 32 experienced some type of illness or health issue from birth to the end of the study and 21 experienced illness more than once during this time. Diarrhea was the most common illness.

The data on injuries and illnesses were best and most parsimoniously described by negative binomial distributions without zero inflation (Table III). For injury, adding the fixed effects (i.e., behavioral components, dominance status, sex, and personality components) significantly improved model fit (LRT df=9, χ^2=20.03, P<0.02), but for illness, adding the fixed effects did not significantly improve model fit (LRT df=9, χ^2=12.82, P>0.05). Two personality dimensions were associated with injuries (Table IV): macaques rated as higher in Confidence (Figure 1) and Anxiety (Figure 2) were injured less often.

Discussion

We found that being higher in the personality dimensions of Confidence and Anxiety was associated with having fewer injuries. Associations between injuries and the other personality dimensions and the other measures of variation were not significant. None of the measures of variation were associated with number of illnesses.

It is unclear why low Confidence results in a greater risk of injury. One possibility is that macaques who are lower in Confidence, i.e., those who are more *fearful*, *submissive*, and *cautious*, are less likely to retaliate against aggression, and so may be more likely to be injured in altercations. Confidence has been found to be connected to physiological responses in rhesus macaques. Specifically, lower Confidence was found to be associated with lower cortisol in the morning (Capitanio, Mendoza, & Bentson, 2004). This suggests that Confidence is an important personality component to measure when studying rhesus macaque health. Concerning Anxiety, it may be that more Anxious macaques have fewer injuries because at the first sign of trouble they remove themselves from the situation and/or more effectively signal their acquiescence. In other words, they may be more vigilant and more willing to escape than to stand their ground and risk injury. These results therefore suggest that there are two avenues by which rhesus macaques can avoid injury. Future research might benefit from using a different sampling technique, such as event, rather than focal sampling, to better understand how personality Confidence and Anxiety affect behavioural responses during aggressive encounters.

In this study, even after we accounted for dominance status, behavior, and sex, we found that personality had predictive power for understanding individual variations in injury. Capitanio and Weinstein (2008) also found personality to have predictive power even when controlling for dominance and sex, though in relation to affiliative relationships. They demonstrated that even when controlling for kinship, rank, and sex, it was variations in personality that predicted affiliative preferences in rhesus macaques. Given these results and our own we suggest that personality is a key factor to measure when studying individual variation in nonhuman primate health and welfare.

This study had several limitations. For one, because we used a brief personality questionnaire, the reliability of individual dimensions was lower than what would have been the case with the full-length questionnaire. Moreover, the brief questionnaire did not include a measure of the Activity dimension and so we could not determine whether this dimension was associated with injuries or illnesses. Our use of only one item to measure Friendliness may explain why we found no association between this dimension and either number of injuries or illnesses despite the established correlations between sociability and health (reviewed by Capitanio, 2011) and overall welfare and subjective well-being (e.g., Robinson et al., 2016, 2017; Schaefer & Steklis, 2014) in nonhuman primates. Another limitation of this study was that we only observed each macaque for 15 (CNPRC) and 20 (ONRPC) days and did not know their dominance status in their previous group. As such, we cannot be sure whether their dominance status was stable over time. Other studies have found that dominance certainty, i.e., how consistently dominance interactions go in a unilateral direction, is more strongly associated with health outcomes than dominance status (McCowan et al., 2016). Dominance certainty, therefore, may be worth including in future studies of this sort. A final limitation is that our retrospective study design did not enable us to rule out reverse causality.

In addition to these limitations, it is worth noting that, although using data reduction techniques, such as principal components analysis, has its advantages, such as generating composites that are more reliable than single items (Li, Rosenthal, & Rubin, 1996), it may not always be the best approach to examining associations between personality traits and assorted outcomes. This is because the importance of individual items or behaviors may be lost when they are included in a composite score (Mõttus, Kandler, Bleidorn, Riemann, & McCrae, 2016). Thus, although this was not a limitation of our study per se, larger studies may seek to identify whether specific behaviors are associated with the incidence or prevalence of illnesses or injuries.

We tested whether individual characteristics were associated with illnesses or injuries in nonhuman primates. This provided a multifaceted picture of how individuality affects health in macaques. Future, longitudinal studies will be needed to better understand these associations. Still, as is the case in studies of human characteristics, such as personality, and health, these studies will only enrich our understanding of these associations and improve our ability to care for and improve the welfare of others.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We would like to thank Drew Altschul for providing R support. Special thanks to the ONPRC and CNRPC staff for filling out the personality questionnaires and the ONPRC Behavioral Services Unit and CNPRC Neuroscience and Behavior Unit for their feedback and support on this project. Support is acknowledged from NIH P51OD011092 and P51OD011107.

References

Altmann J. Observational study of behavior: Sampling methods. Behaviour. 1974

American Society of Primatologists. Principles for the Ethical Treatment of Non-Human Primates. 2001

Animal Welfare Act and Animal Welfare Regulations. US: 2013.

Archie EA, Altmann J, Alberts SC. Social status predicts wound healing in wild baboons. Proceedings of the National Academy of Sciences. 2012; 109(23):9017–9022. https://doi.org/10.1073/pnas.1206391109.

Broom, DM., Johnson, KG. Stress and animal welfare. London: Chapman and Hall; 1993.

Capitanio, JP. Nonhuman primate personality and immunity: Mechanisms of health and disease. In: Weiss, A.King, J., Murray, L., editors. Personality and temperament in nonhuman primates. New York: Springer Science & Business Media; 2011. p. 233-255.

Capitanio JP, Mendoza S, Baroncelli S. The relationship of personality dimensions in adult male rhesus macaques to progression of simian immunodeficiency virus disease. Brain, Behavior, and Immunity. 1999; 13:138–154. https://doi.org/10.1006/brbi.1998.0540.

Capitanio JP, Mendoza SP, Bentson KL. Personality characteristics and basal cortisol concentrations in adult male rhesus macaques (*Macaca mulatta*). Psychoneuroendocrinology. 2004; 29:1300–1308. https://doi.org/10.1016/j.psyneuen.2004.04.001. [PubMed: 15288709]

Cavigelli, S., Michael, K., Ragan, C. Behavioral, physiological, and health biases in laboratory rodents: A basis for understanding mechanistic links between human personality and health. In: Carere, C., Maestripieri, D., editors. Animal Personalities. Behavior, physiology, and evolution. London: The University of Chicago Press; 2013. p. 442-498.

De Vries H, Stevens JMG, Vervaecke H. Measuring and testing the steepness of dominance hierarchies. Animal Behaviour. 2006; 71:585–592. https://doi.org/10.1016/j.anbehav.2005.05.015.

Dinno, A., Dinno, M. R package "paran". 2010.

Forstmeier W, Schielzeth H. Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. Behavioral Ecology and Sociobiology. 2011; 65(1):47–55. https://doi.org/10.1007/s00265-010-1038-5. [PubMed: 21297852]

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, … Sibert J. AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software. 2012; 27(2):233–249. https://doi.org/10.1080/10556788.2011.597854.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-bovy, G., Ellison, S., … Venables, W. Package "car". 2016. Retrieved from https://cran.r-project.org/web/packages/car/car.pdf

Gorsuch, RL. Factor Analysis. 2. Hillsdale, NJ: Erlbaum; 1983.

Greene WH. Accounting for excess zeros and sample selection in Poisson and Negative Binomial regression models. NYU Working Paper No. EC-94-10. 1994; 9:265–265. https://doi.org/10.1007/BF00857937.

Jonassaint CR, Boyle SH, Kuhn CM, Siegler IC, Copeland WE, Williams R. Personality and inflammation: The protective effect of openness to experience. Ethnicity and Disease. 2010; 20(1):11–14. [PubMed: 20178176]

Konečná M, Lhota S, Weiss A, Urbánek T, Adamová T, Pluhácek J. Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. Journal of Comparative Psychology. 2008; 122:379–389. https://doi.org/10.1037/a0012625. [PubMed: 19014262]

Konečná M, Weiss A, Lhota S, Wallner B. Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. Journal of Research in Personality. 2012; 46(5):581–590. https://doi.org/10.1016/j.jrp.2012.06.004.

Kuhn L, Davidson LL, Durkin MS. Use of Poisson regression and time series analysis for detecting changes over time in rates of child injury following a prevention program. American Journal of Epidemiology. 1994; 140(10):943–955. [PubMed: 7977282]

Li H, Rosenthal R, Rubin DB. Reliability of measurement in psychology: From Spearman-Brown to maximal reliability. Psychological Methods. 1996; 1(1):98–107. https://doi.org/10.1037/1082-989X.1.1.98.

Maninger N, Capitanio JP, Mendoza SP, Mason WA. Personality influences tetanus-specific antibody response in adult male rhesus macaques after removal from natal group and housing relocation. American Journal of Primatology. 2003; 61(2):73–83. https://doi.org/10.1002/ajp.10111. [PubMed: 14582129]

Mazerolle MJ. Package "AICcmodavg". R Environment (c). 2015:1–141.

McCowan B, Beisner BA, Bliss-Moreau E, Vandeleest JJ, Jin J, Hannibal D, Hsieh F. Connections matter: Social networks and lifespan health in primate translational models. Frontiers in Psychology. 2016; 7(433):1–11. [PubMed: 26858668]

Mõttus R, Kandler C, Bleidorn W, Riemann R, McCrae RR. Personality traits below facets: The consensual validity, longitudinal stability, heritability, and utility of personality nuances. Journal of Personality and Social Psychology. 2016 Aug.112(3):474. https://doi.org/10.1037/pspp0000100. [PubMed: 27124378]

Murray, L. Predicting primate behavior from personality ratings. In: Weiss, A.Murray, L., King, JE., editors. Personality and temperament in nonhuman primates. New Y: Springer Science & Business Media; 2011. p. 129-167.https://doi.org/10.1007/978-1-4614-0176-6_6

Oliveira AFS, Rossi AO, Silva LFR, Lau MC, Barreto RE. Play behaviour in nonhuman animals and the animal welfare issue. Journal of Ethology. 2009; 28(1):1–5. https://doi.org/10.1007/s10164-009-0167-7.

Pederson AK, King JE, Landau VI. Chimpanzee (*Pan troglodytes*) personality predicts behavior. Journal of Research in Personality. 2005; 39:534–549. https://doi.org/10.1016/j.jrp.2004.07.002.

Prongay K, Park B, Murphy SJ. Risk factor analysis may provide clues to diarrhea prevention in outdoor-housed rhesus macaques (*Macaca mulatta*). American Journal of Primatology. 2013; 75(8):872–882. https://doi.org/10.1002/ajp.22150. [PubMed: 23568382]

R Development Core Team. R: A Language and Environment for Statistical Computing. R Development Core Team; 2014. Retrieved from http://www.mendeley.com/research/r-language-environment-statistical-computing-96/%5Cnpapers2://publication/uuid/A1207DAB-22D3-4A04-82FB-D4DD5AD57C28

Revelle MW. Package ‘ psych. 2011 Oct.:1–250.

Robinson LM, Altschul DM, Wallace EK, Ubeda Y, Llorente M, Machanda Z, … Weiss A. Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. Applied Animal Behaviour Science. 2017 Jun.191:90–97. https://doi.org/10.1016/j.applanim.2017.02.008.

Robinson LM, Waran NK, Leach MC, Morton FB, Paukner A, Lonsdorf E, … Weiss A. Happiness is positive welfare in brown capuchins (*Sapajus apella*). Applied Animal Behaviour Science. 2016; 181:145–151. https://doi.org/10.1016/j.applanim.2016.05.029.

Sapolsky RM. Social status and health in humans and other animals. Annual Review of Anthropology. 2004; 33:393–418. https://doi.org/10.1146/annurev.anthro.33.070203.144000.

Sapolsky RM. The influence of social hierarchy on primate health. Science (New York, NY). 2005; 308(5722):648–652. https://doi.org/10.1126/science.1106477.

Schaefer SA, Steklis HD. Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. American Journal of Primatology. 2014; 76(9):879–889. https://doi.org/10.1002/ajp.22275. [PubMed: 24677279]

Shrout PE, Fleiss JL. Intraclass correlations: Uses in assessing rater reliability. Psychological Bulletin. 1979; 86(2):420–428. https://doi.org/10.1037/0033-2909.86.2.420. [PubMed: 18839484]

Skaug HJ, Bolker D, Magnussen A, Nielsen A. Generalized Linear Mixed Models using “AD Model Builder”. R Package Version 0.8.3.3. 2016

Smith GT, McCarthy DM, Anderson K. On the sins of short-form development. Psychological Assessment. 2000; 12:102–111. https://doi.org/10.1037/1040-3590.12.1.102. [PubMed: 10752369]

Weinstein TAR, Capitanio JP. Individual differences in infant temperament predict social relationships of yearling rhesus monkeys (*Macaca mulatta*). Animal Behaviour. 2008; 76:455–465. https://doi.org/10.1016/j.anbehav.2008.01.024. [PubMed: 23483039]

Weiss, A. Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire. In: Vonk, J.Weiss, A., Kuczaj, S., editors. Personality in nonhuman animals. Springer; 2017. https://doi.org/10.1007/978-3-319-59300-5

Weiss A, Adams MJ, Widdig A, Gerald MS. Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. Journal of Comparative Psychology. 2011; 125(1):72–83. https://doi.org/10.1037/a0021187. [PubMed: 21341912]

Weiss A, Inoue-Murayama M, Hong KW, Inoue E, Udono T, Ochiai T, … King JE. Assessing chimpanzee personality and subjective well-being in japan. American Journal of Primatology. 2009; 71:283–292. https://doi.org/10.1002/ajp.20649. [PubMed: 19199350]

Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. Focused grooming networks and stress alleviation in wild female baboons. Hormones and Behavior. 2008; 54(1):170–177. https://doi.org/10.1016/j.yhbeh.2008.02.009. [PubMed: 18396288]

Yamanashi, Y., Nogami, E., Teramoto, M., Morimura, N., Hirata, S. Adult-adult social play in captive chimpanzees: Is it indicative of positive animal welfare?. Applied Animal Behaviour Science. (In press)https://doi.org/https://doi.org/10.1016/j.applanim.2017.10.006

Zeileis A, Hothorn T. Diagnostic checking in regression relationships. R News. 2002; 2(3):7–10.

Zeileis A, Kleiber C, Jackman S. Regression models for count data in R. Journal Of Statistical Software. 2008; 27:1076–84. https://doi.org/10.1093/jpepsy/jsn055.

Highlights

Tested whether behavior, dominance, or personality was associated with rhesus health.

None of the variables were related to number of illnesses.

High Confidence and high Anxiety were associated with fewer injuries.

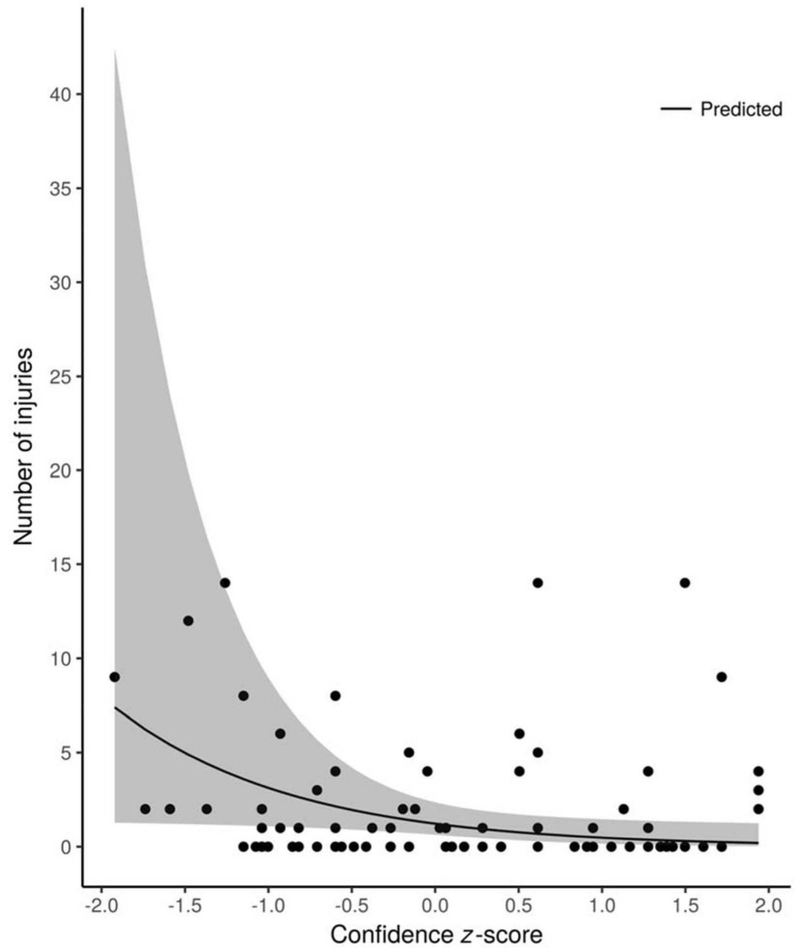

Figure 1.

Scatterplot and predicted function describing the association between Confidence and number of injuries obtained in a generalized linear mixed effects model with a negative binomial error distribution without zero inflation. To generate the predicted function, the offset and fixed effects were held constant.

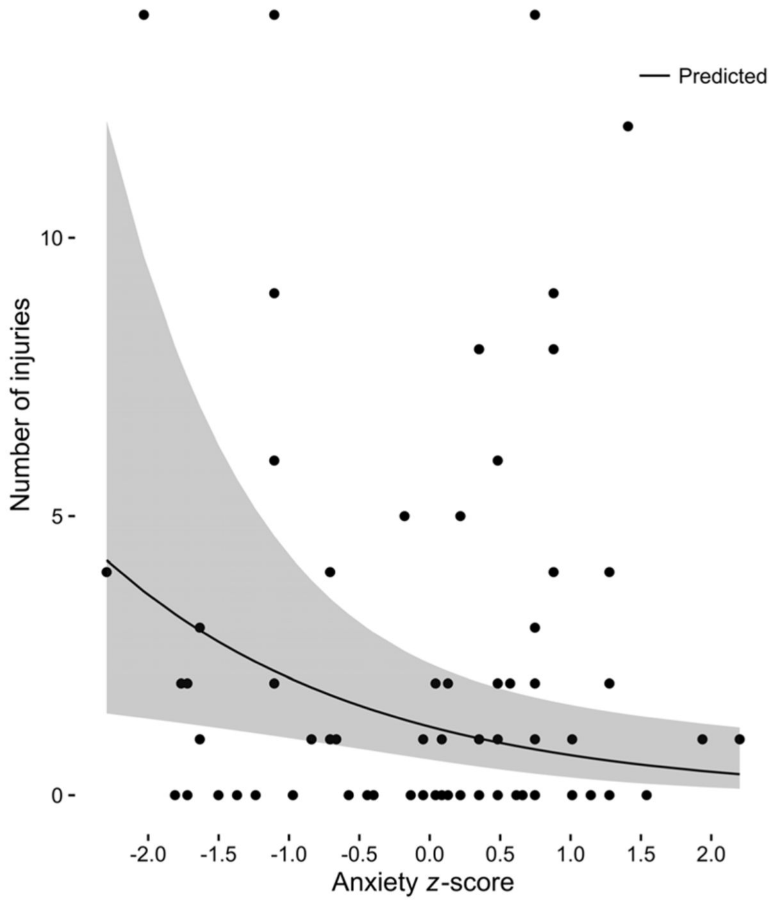

Figure 2.
Scatterplot and predicted function describing the association between Anxiety and number of injuries obtained in a generalized linear mixed effects model with a negative binomial error distribution without zero inflation. To generate the predicted function, the offset and fixed effects were held constant.

Table I

Interrater reliability of personality items

Item	*ICC*(3,1)	*ICC*(3,*k*)
Dominant	0.70	0.84
Submissive	0.68	0.82
Bullying	0.64	0.80
Cautious	0.55	0.73
Fearful	0.52	0.71
Anxious	0.45	0.64
Socially withdrawn	0.27	0.45
Curious	0.26	0.44
Innovative	0.25	0.43
Erratic	0.17	0.32
Quitting	0.11	0.21
Cool	0.03	0.07
Mean ± SD	0.39 ± 0.23	0.54 ± 0.26

N=84, *k*=2.23

Table II

Principal component analysis with varimax rotation of behaviors

	Social	Displacement	* Playful	h^2
Receive grooming	**0.79**	0.06	0.14	0.65
Environment explore	**−0.68**	−0.22	0.14	0.52
Stationary alone	**0.66**	−0.03	−0.29	0.52
Give grooming	**0.46**	−0.39	−0.43	0.56
Yawn	0.06	**0.74**	0.16	0.57
Scratch	−0.37	**0.64**	0.01	0.55
Stationary in proximity	0.04	**0.63**	−0.14	0.42
Locomotor stereotypy	0.04	**−0.46**	−0.43	0.41
Social play	−0.31	−0.33	**0.72**	0.72
Independent play	−0.24	−0.28	**0.71**	0.64
Shake/shiver/twitch	0.04	−0.13	**−0.67**	0.47
Receive aggression	−0.47	−0.06	**−0.49**	0.47
Toy play	−0.34	0.29	0.25	0.26
Self-grooming	0.19	0.32	−0.31	0.23
Give aggression	0.02	0.30	−0.07	0.10
Regurgitate and reingest	0.35	−0.12	−0.15	0.16

N=85.

* Values reflected to make component easier to interpret. Proportion of variance accounted by Social=16%. Proportion of variance accounted for by Displacement=15%. Proportion of variance accounted by Playful=14%. h^2=communalities.

Table III

Comparisons to see which distribution of error terms provides best fit of number of injuries and number of illnesses

Model	dAIC	df
Injury		
Negative binomial	0.00	3
Negative binomial with zero-inflation	2.00	4
Poisson	22.70	2
Zero-inflated	23.80	3
Illness		
Negative binomial	0.00	3
Negative binomial with zero-inflation	1.90	4
Poisson	12.80	3
Zero-inflated	35.50	2

Table IV

Negative binomial models of injury predicted by behavioral components, David's Score, and personality

Injury model					
Fixed effects	***b***	***SE***	***Z***	***P***	***VIF***
Intercept	−1.60	0.36	−4.50	<0.001	
Male	−0.10	0.16	−0.59	0.55	1.12
Social	0.05	0.15	0.32	0.75	1.44
Displacement	−0.05	0.16	−0.30	0.77	1.28
Playful	−0.26	0.17	−1.55	0.12	1.28
David's Score	0.04	0.24	0.18	0.86	1.26
Confidence	−0.89	0.44	−2.02	**0.044**	1.13
Dominance	0.40	0.40	1.00	0.32	1.20
Openness	0.03	0.15	0.19	0.85	1.44
Anxiety	−0.55	0.20	−2.69	**0.007**	1.26
Socially withdrawn	0.13	0.17	0.77	0.44	1.26
Random effects	*var*	*SD*			
Facility intercept	0.21	0.46			

Illness model					
Fixed effects	***b***	***SE***	***Z***	***P***	***VIF***
Intercept	−2.16	0.70	−3.10	<0.001	
Male	0.23	0.23	1.01	0.31	1.17
Social	−0.49	0.23	−2.10	**0.036**	1.22
Displacement	0.04	0.21	0.21	0.83	1.11
Playful	−0.14	0.20	−0.69	0.49	1.20
David's Score	−0.27	0.34	−0.78	0.43	1.13
Confidence	0.93	0.65	1.43	0.15	1.10
Dominance	−0.69	0.60	−1.15	0.25	1.16
Openness	0.12	0.24	0.50	0.62	1.14
Anxiety	0.06	0.30	0.22	0.83	1.13
Socially withdrawn	0.10	0.30	0.35	0.73	1.13
Random effects	*var*	*SD*			

Illness model

Fixed effects	***b***	***SE***	***Z***	***P***	***VIF***
Facility intercept	0.89	0.94			

Negative binomial dispersion parameter = 4.18 (*SE* = 2.36)

Negative binomial dispersion parameter = 1.17 (*SE* = 0.57)

N = 85. VIF=variance inflation component. Boldface values were significant at P<0.05.