**The sums of their parts: Juvenile rhesus macaque personality, dominance, behavior, and health**

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**Highlights**

Tested if behavior, dominance, or personality were associated with rhesus health.

Dominance status that was neither high nor low were associated with injury.

In models with all variables, only low Confidence was associated with injury.

**Abstract**

Individual differences in personality, behavior, and dominance status are associated with primate health. However, the studies that find these effect typically focus on a single measure, and so it is difficult to know the degree to which these individual differences are independently associated with health. The goal of this study was to assess the unique associations between health and individual differences in personality, behavior, and dominance status in juvenile rhesus macaques (*Macaca mulatta*). We studied 41 socially-housed macaques at the Oregon National Primate Research Center and used veterinary records to determine the number of injuries and illnesses for each macaque. We measured personality using a 12-item scale, performed focal observations of behaviors, and calculated dominance status using Normalized David’s scores from directional supplant data. Eleven personality questionnaire items were reliable and were used to create scores representing four of the six personality dimensions identified in a previous study of rhesus macaques: Dominance, Confidence, Openness, and Anxiety. Following this, we fit one hurdle model for history of injury and a second for history of illness. Predictor variables included the personality dimensions, behavior, and dominance status; age was included as an offset variable. Initial models indicated that dominance status was associated with injuries, but later models indicated that this association was attributable to the variance that dominance status shared with Confidence. None of the predictor variables were associated with a history of illness. Future studies may want to assess the mechanisms that underlie these associations.

**Keywords:** health, personality, play, dominance, macaque, welfare

**Introduction**

Why is one animal healthier than another? This is a deceptively simple question, which has major implications for animal welfare. If non-invasively assessed individual characteristics can be used to identify patterns of stress and immune responses, or the likelihood that an individual animal will be injured, then these characteristics can aid in animal management and husbandry, and in biomedical research. Many studies have focused on the connection between a single characteristic, such as dominance, and health [Sapolsky, 2005]. However, individual characteristics, including not just dominance status, but also personality traits and behavior, are interrelated [Pederson et al., 2005; Konečná et al., 2008, 2012; Weinstein & Capitanio, 2008; Murray, 2011]. For example, adult Barbary macaques (*Macaca sylvanus*) rated as being higher in Confidence had higher rank [Konečná et al., 2012]. Therefore, studies that focus on single individual characteristics are unable to rule out the possibility that the associations that they identify are confounded by some other individual characteristic.

The goal of this study was to examine the association between health and individual differences in behavior, dominance status, and personality in juvenile and young-adult rhesus macaques (*Macaca mulatta*). Previous research has identified associations between individual characteristics and health in multiple primate species. For example, play and grooming, which are indicative of positive welfare [Wittig et al., 2008; Oliveira et al., 2009], may be less common among injured or ill individuals than among non-injured, healthy individuals [Broom & Johnson, 1993]. Dominance is related to health and stress [Sapolsky, 2004, 2005]. For example, Archie et al. [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 [reviewed in Cavigelli et al., 2013]. For example, highly sociable adult rhesus macaques have reduced viral loads [Capitanio et al., 1999] and more stable immune responses [Maninger et al., 2003].

Although it is not possible to identify the causal direction of these associations, results such as these inform our understanding of individual characteristics and health. Including multiple individual characteristics in models has the advantage of making animal studies more similar to studies of human personality and health [For example, 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 influencing common health problems, such as gastrointestinal diarrhea, in rhesus macaques [Prongay et al., 2013], and in other nonhuman primate species. By accounting for dominance status, personality, and behavior, therefore, we seek to identify whether relationships between these characteristics and health are independent or whether these associations are attributable to variance shared between these characteristics.

**Methods**

**Ethical Approval**

The study was approved by the University of Edinburgh’s Biological Services Unit, AWERB OS2-14, and the Oregon National Primate Research Center (ONPRC) Institutional Animal Care and Use Committee. 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 ONPRC is fully accredited by AAALAC, International.

**Subjects**

We studied 41 group-housed rhesus macaques (30 males) at the ONPRC (Beaverton, Oregon). The macaques ranged in age from 1.78 to 7.40 years (mean ± SD=4.59 ± 3.98 years) at the start of the study. The macaques lived in one of three identical indoor/outdoor corn crib shelters containing a rectangular indoor (6.69m2) enclosure and connected oval covered outdoor (25.46m2) enclosure. Each enclosure contained perches, fire hose swings, and toys, which were rotated on a regular basis. By the end of the study, two groups (N=15 each) lived in the enclosures for 154 days and a third group (N=11) lived in the enclosure for 119 days. All macaques were physically healthy at the beginning of the study. Prior to living in the corn cribs, the macaques lived in 1 acre open air corrals that housed 100 to 250 macaques at any given time. 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.

**Measures**

**Questionnaire development:** Staff working at the ONPRC and other research facilities have limited time to fill out lengthy questionnaires. Therefore, as part of a pilot study, we developed a 12-item version of the Hominoid Personality Questionnaire [Weiss et al., 2011]. In developing this questionnaire, we chose four dimensions: Confidence, Anxiety, Openness, and Dominance (henceforth “trait Dominance”). At the suggestion of the ONPRC, we changed the adjective label “Depressed” to “Socially withdrawn”.

We used existing ratings of rhesus macaque personality from Weiss et al.’s 2011 study to identify 12 items to represent Confidence, Anxiety, Openness, and trait Dominance. To do so we identified the combinations of items for each dimension that had the best combination of attenuation, reliability, and coverage [Smith et al., 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 scales that were suboptimal. Finally, 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 (figures and tables available in Supplementary Methods I).

**Personality ratings:** LMR and five animal care technicians who were responsible for animal husbandry, and who were familiar with the macaques, filled out shortened questionnaires. One to three raters were responsible for rating each macaque. The mean number of raters per macaque was 2.44. 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 the macaques’ behavior we took continuous focal observations [Altmann, 1974] on every individual within each group 15 min per day for 20 days. Groups were observed sequentially. On each observation day, all members of the focal group were observed for 15-minutes. Frequencies and durations of behaviors were recorded using The Observer (Version 10.5, Noldus Information Technology, The Netherlands) on a Psion Workabout Pro3. The focal macaque was observed for behaviors relating to dominance status, personality, and welfare. The ethogram (provided in 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). Observation order was randomized. If a macaque was consistently out-of-sight during an observation, then it was not observed for that day.

Each macaque was observed an average of 19.15 times for an average of 288.6 minutes of total observation. Because the macaques spent the majority of their time in the outdoor enclosure (LMR personal observation), observations were performed at the outdoor enclosure. Animals who entered the indoor portion of the enclosure were not visible and thus we subtracted the time each macaque spent out-of-sight (i.e., inside) from total time observed to calculate the total time each macaque was visible to the observer (mean ± SD = 264 ± 32.17 minutes per macaque). Behaviors were calculated as durations (percentage of time) or frequencies (behaviors/min), based on time visible. We did not find an effect of time of day on any behavior (Supplementary Figure I).

**Health evaluation:** At the ONPRC, every time a macaque is examined or treated by veterinary staff for an illness or injury the information is recorded in the macaque’s electronic records. These records include the date of the examination and a description of the injury or illness. We used these data to determine the number of injuries and illnesses for each macaque from birth to the end of the study (June, 2015). Because there were no concurrent cases of injury and illness, we treated each injury and illness as independent.

**Data Analysis**

**Interrater reliabilities**:For macaques rated by two or more raters we determined the degree to which ratings were reliable by calculating two intraclass correlation coefficients [Shrout & Fleiss, 1979]. The first intraclass correlation, *ICC*(3,1), indicates the reliability of individual ratings. The second, *ICC*(3,*k*), indicates the reliability of mean ratings. Reliable items were then used to create unit-weighted component scores [Gorsuch, 1983] based on the known rhesus macaque personality structure (see Table 1 in Weiss et al., 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 et al., 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. To determine whether to rotate the components using an orthogonal or oblique procedure, we performed a varimax (orthogonal) and promax (oblique) rotation. 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.

**Hurdle models**: Before fitting hurdle models, we checked for nonlinear relationships by examining plots of dominance status, personality, and behavioral components against the number of injuries and against the number of illnesses. Because macaques who were neither high nor low dominance status at the time of this study appeared to be more likely to have been injured (Supplementary Figure II), we included a linear and a quadratic term for dominance status in our models.

Hurdle models [Zeileis et al., 2008] were used to fit these data. For these models, injury and illness were treated as count variables. The predictors were dominance status, the personality components, and the behavioral components. For ease of interpretability, we converted the independent variables to z-scores (mean ± SD=0 ± 1). Finally, because older macaques may have accumulated more injuries and illnesses than younger macaques, age was included as an offset [Zeileis et al., 2008].

Hurdle models are a variant of Poisson regression [Kuhn et al., 1994] and appropriate for predicting rare, discrete events, and for data that include a large number of zeroes [Zeileis et al., 2008]. Hurdle models consist of two parts. The first part tests whether the predictor variables are associated with the class to which an individual belongs. In the case of hurdle models that predict injuries, for example, this part of the model would test whether the predictors are associated with an individual having one or more injuries as opposed to being injury free. The second part tests whether there are associations between the number of events. Taking the same example as before, this part of the model would test whether the predictors are associated with the number of injuries. The use of hurdle models was appropriate for our study because they allow for the inclusion of offset variables, which control for the influence a variable may have on the rates of the predicted variable.

We used likelihood ratio tests (LRT) to compare each injury and illness model against the null model using the lmtest package in R [Zeileis & Hothorn, 2002]. This enabled us to control for the increase in type I error rates associated with the running of multiple statistical tests [Forstmeier & Schielzeth, 2011].

**Results**

**Interrater Reliabilities**

The *ICC*(3,1) estimates for items ranged from -0.04 to 0.59 (mean ± SD=0.25 ± 0.21). The *ICC*(3,*k*) estimates for items ranged from -0.12 to 0.78 (mean ± SD=0.39 ± 0.29). The item *socially withdrawn* had negative reliability estimates and therefore was not included in further analyses (Table I).

**---Table I about here---**

**Data Reduction**

Parallel analysis and examination of the scree plot indicated that behaviors defined two components. Promax rotation revealed that the correlation between these components was -0.21 (Supplementary Table II), which is low, and indicates that these components were mostly orthogonal. We therefore interpreted the varimax-rotated components (Table II). A high score on the first component (Playful) indicated that a macaque received less aggression, yawned more, spent less time shaking/shivering/twitching, and spent more time playing socially, playing independently, and playing with toys. This component accounted for 19% of the variance. A high score on the second component (Social) indicated that a macaque received more grooming, spent more time stationary and within a meter from others, spent less time exploring their environment, and performed more locomotor stereotypies. This component accounted for 17% of the variance.

**---Table II about here---**

**Hurdle Models**

There were few injuries: of the 41 macaques, 14 experienced injuries in the past 3 to 7 years and 6 had experienced more than 1 injury during this time period. Injuries ranged from mild abrasions and lacerations to contusions with associated swelling of the affected region. Veterinary clinical care included administration of topical and systemic analgesics and antibiotics, cleaning and suturing wounds, and, in a few instances, partial digit amputation. Of the 41 macaques, 7 experienced some type of illness or health issue in the past 3 to 7 years. Diarrhea was the most common illness and three macaques experienced more than one bout. Other treatment included prophylactic dental care to manage gingivitis or the removal of a deciduous tooth.

The model of injury that only included Playful and Social (Table III) did not significantly differ from the null model (LRT, compared with null model, df=4, *x*2=7.34, P>0.05). The model of injury that only included dominance status (Table III) differed significantly from the null model (LRT, compared with null model, df=4, *x*2=18.40, P=0.001) and indicated that macaques that had been injured were those whose dominance status was neither high nor low. The model of injury that only included personality (Table III) did not significantly differ from the null model (LRT, compared with null model, df=8, *x*2=13.12, P>0.05). The full model that included all predictors (Table III) differed significantly from the null model (LRT, compared with null model, df=16, *x*2=32.25 P=0.009) and indicated that macaques with lower Confidence were more likely to have been injured . Spearman rank-order correlations of the variables included in the full model are available in Supplementary Table III.

The model of illness that only included Playful and Social (Table IV) did not differ significantly from the null model (LRT, compared with null model, df=4, *x*2=2.64, P>0.05). The model of illness that only included dominance status (Table IV) did not differ significantly from the null model (LRT, compared with null model, df=4, *x*2=0.28, P>0.05). The model of illness that only included personality (Table IV) did not differ significantly from the null model (LRT, compared with null model, df=8, *x*2=10.62, P>0.05). The inflated coefficients and standard errors in the count model for illness that only included personality variables suggested to us that there was too little variation in illness for this to be a reliable model. Given this, we did not run an illness model that included all of the variables.

**---Table III and Table IV about here---**

**Discussion**

Our models that tested one type of individual difference measure at a time indicated that macaques whose dominance status was neither high nor low were significantly more likely to have been injured. Our models that included the behavioral components, dominance status, and the personality variables indicated that dominance status was not significantly associated with likelihood of injury, and that low Confidence was associated with a greater likelihood of injury.

Our findings of an association between average dominance status and injuries is similar to findings by Archie et al. [2012] in male baboons. Our findings are also consistent with studies that find 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]. This leads to the question of why young, mid-ranking rhesus macaques are at greater risk. It may be that macaques with dominance status that is neither high nor low face aggression from those who are more dominant while also needing to defend their position from subordinates.

When personality, dominance status, and the behavioral components were included in the model, only lower Confidence was significantly associated with a greater likelihood of a history of injury. In this model the size of the effect of dominance status was reduced and no longer statistically significant, which suggests that the previously described association between dominance status and injuries is attributable to variation that dominance shares with Confidence. It is unclear by what means low Confidence results in a greater risk of injury. One possibility is that macaques with lower 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.

One way to handle personality data is to use data reduction techniques, such as principal components analysis. This has the advantage of creating scales or composites made up of many items, which are more reliable [Li et al., 1996]. However, when used this approach to analyze our behavioral data, neither the Playful or Social component were associated with injury or illness. As such, using data reduction or other means to group traits or behaviors may not always be the best approach as the importance of individual behaviors may be lost [Mõttus et al., 2016].

This study had several limitations. One set of limitations were related to the use of a shortened personality questionnaire. Confidence and trait Dominance were associated with similar behaviors, and so their discriminant validity was low. This may be because we selected the most reliable items for each domain but did not rule out items that loaded highly onto multiple domains. In our case, for example, the item *dominant* is associated with Confidence and trait Dominance [Weiss et al., 2011]. Also, because the Friendliness and Activity dimensions were not assessed by this questionnaire, we could not determine whether they were associated with injury. Although future studies may benefit by including discriminant validity as a criterion in selecting items for abbreviated questionnaires, we do not recommend their use for future research. Another limitation of this study was that our sample was made of up juveniles and young adults. As a consequence, there was little variation in the number of injuries and illnesses, and so the available statistical power was low. Finally, because we only observed each macaque for 20 days and did not know their dominance status in their previous group, we do not know whether their dominance status was stable over time. This, and the study design, did not enable us to establish the direction of causality.

It is also worth noting that, by visually inspecting the association between injury and dominance status and then including the quadratic term in hurdle models, we mixed exploratory and confirmatory methods. As such, our finding of a nonlinear relationship between dominance status and injury could have resulted from our capitalizingon chance. We hope that future researchers will conduct confirmatory tests to determine whether the association between rank and injuries describes a quadratic function.

We evaluated how multiple individual characteristics influence nonhuman primate injuries. This provided us with a multifaceted picture of how individuality affects health in young macaques. However, limitations in our study design rule out our ability to reach stronger conclusions, and so there is a need for future, longitudinal studies of adults to better understand these associations. Still, as is the case in studies of human characteristics, including personality, and health, the use of multiple measures is bound to enrich our understanding of these associations and to improve our ability to care for and improve the welfare of rhesus macaques and other primates.

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