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Rhesus macaque personality, dominance, behavior, and health

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Short title: Rhesus health

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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.

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 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 (6.69m²) 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. 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 m²) connected by a rectangular cage (7.25 m²). 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 Pro³ 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 $236.02 (\pm SD=66.42)$ 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 \pm SD = 224.09 \pm 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 $\geq |0.4|$ 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 zeroinflated 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.

---Table I about here---

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.

---Table II about here---

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.

----Tables III and IV and Figures 1 and 2 about here---

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.

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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.

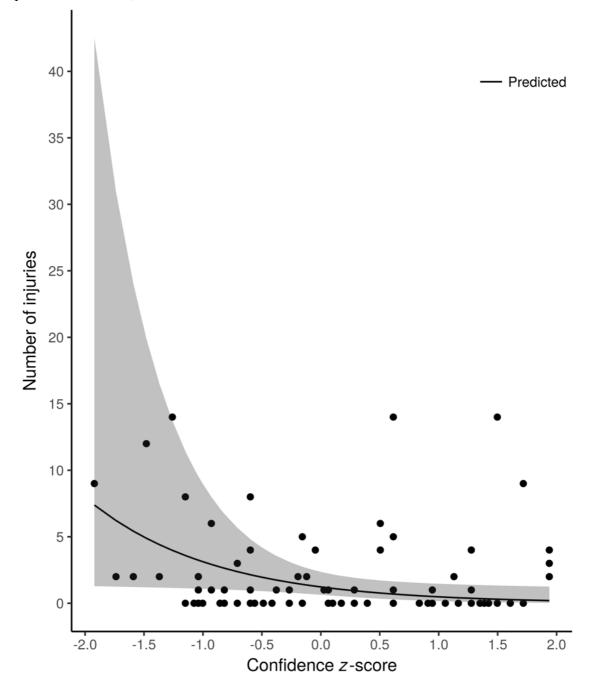
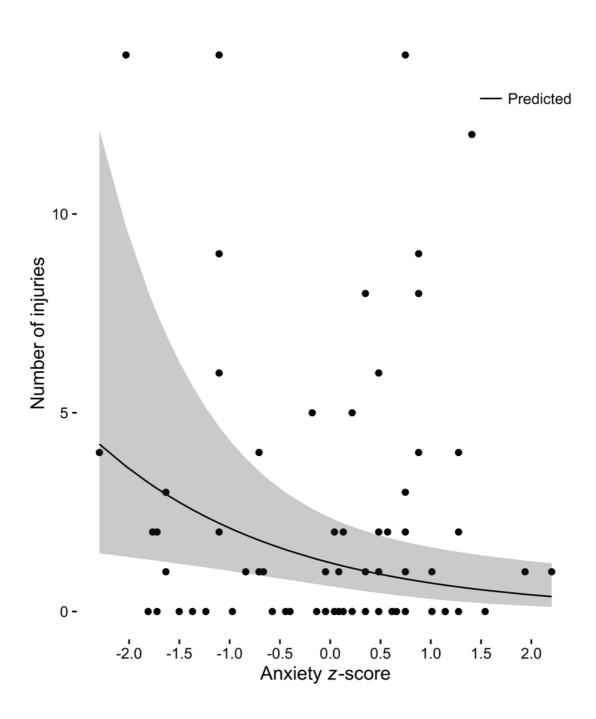


Figure 2. Scatterplot and predicted function describing the association between Anxiety and number of injuries obtained in a generalized linear mixed effects model with a negative binomial error distribution without zero inflation. To generate the predicted function, the offset and fixed effects were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



Interrater reliability of personality items							
Item	<i>ICC</i> (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					

Table I Interrater reliability of personality items

Mean \pm SD	0.39 ± 0.23	0.54 ± 0.26
N=84, <i>k</i> =2.23		

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			

Table II

Principal component analysis with varimax rotation of behaviors

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

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

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

Table IV

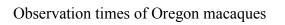
Negative binomial models of injury predicted by behavioral components, David's Score, and
personality

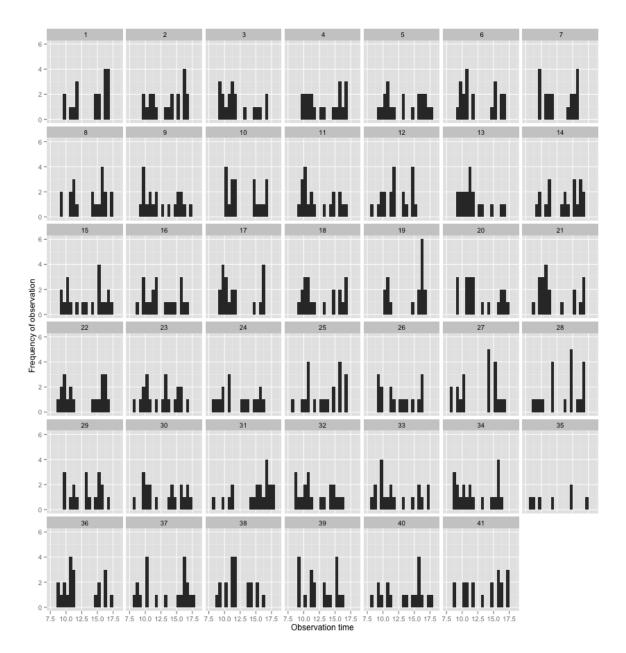
Injury model					
Fixed effects	b	SE	Z	Р	VIF
Intercept	-1.60	0.36	-4.50	< 0.001	
Male	-0.10	0.16	-0.59	0.55	1.12
Social	0.05	0.15	0.32	0.75	1.44
Displacement	-0.05	0.16	-0.30	0.77	1.28
Playful	-0.26	0.17	-1.55	0.12	1.28
David's Score	0.04	0.24	0.18	0.86	1.26
Confidence	-0.89	0.44	-2.02	0.044	1.13
Dominance	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			
Negative binomial dispe	ersion paramet	er = 4.18 (SE	= 2.36)		
Illness model					
		6F	-		

Fixed effects	b	SE	Ζ	Р	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						
Facility intercept	0.89	0.94						
Negative binomial dispers	Negative binomial dispersion parameter = 1.17 (SE = 0.57)							

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

Supplementary Figure 1





Supplementary Table I

Behavioral ethogram	
Durational behaviors	
*Give/receive grooming	Focal macaque manipulates a conspecific's hair or has their hair manipulated by a conspecific using their hands and/or mouth.
Self-groom	The focal macaque moves their fingers and/or mouth through and/or strokes and/or licks at their own hair and/or body without pulling out the hair.
Social play	Focal macaque engages or is engaged by a conspecific in an interaction that has an apparent low tension. May include wrestling, sham biting, hugging, jumping on/over, fleeing, hiding, non-aggressive chasing, and grabbing. One macaque may give a conspecific directed relaxed face with an open mouth that doesn't display canine teeth (known as "play face"). Differs from aggressive fighting by its low tension and lack of barking, ear flattening, threat display, and piloerection. May involved socially playing on or with objects.
Independent play	Solitary, non-repetitive climbing, leaping, swinging, running, chewing, and that does not appear to achieve any obvious goal such as acquiring food or confronting a conspecific.
Environment explore	Biting, licking, inspecting, and/or manipulating of bars, floor, and permanent enclosure features (includes objects not usually removed such as fire hoses). Does not include active movement, if active then this is independent play.
Toy play	Chewing, biting, inspecting, and/or manipulating of non-permanent enclosure features (things that may regularly be added and removed). If there is locomotion with the toy in hand this is coded as toy play rather than independent play. If the animal is touching the device without doing anything else this is not coded as play.
Locomotor stereotypy	 Animal paces, rocks, bounces, backflips, swings, head tosses, or twirls in a stereotypic way. Individual definitions are as follows: <i>Pace</i>: Repetitive, seemingly non-functional, locomotion within enclosure. Requires that the animal does not alter the locomotion path and that the movement be repeated at least twice. <i>Rock</i>: Repetitive, seemingly non-functional shift of the upper body either side to side or back and forth. <i>Bounce</i>: Subject moves up and down using their feet.; is repetitive and seemingly non-functional. <i>Backflip</i>: Subject jumps into the air and rotates body backwards end over end in a repetitive, seemingly non-functional way. The hands may make contact with the ground during the movement. <i>Swing</i>: Subject hangs from enclosure and shifts lateral body back and forth in a repetitive, seemingly non-functional way.

	<i>Head toss:</i> Repetitive, apparently non-functional quick up and down head movement.
Stationary alone	<i>Twirl</i> : Repetitive, apparently non-functional moving of the head in a circular motion. Focal macaque is not engaged in social interactions and is over a meter from any conspecific in any direction (includes above and below).
Stationary in proximity	Focal macaque is within a meter of a conspecific with any body part. The macaque may be in physical contact (huddling) as long as they are not interacting in any other way (grooming, aggression) or self-grooming.
Out of sight	The animal leaves the outdoor observation area for less than 30 seconds in the first three minutes of observation or for any amount of time after the first three minutes
Frequency behaviors	
* ¹ Be supplanted/supplant conspecific	Focal macaque is touched by a conspecific and the focal macaque moves and conspecific may or may not take the focal macaque's spot or focal macaques moves in response to a conspecific's touch. These behaviors are performed by focal macaque upon another in 'supplant conspecific'.
*Give/receive aggression	Focal macaque bites, slaps, pushes, pulls, grabs, or scratches a conspecific. The focal macaque may also head bob, scream, cage shake, cringe, crook their tail, ear flick, brow flash, stare, open-mouth stare, rapid glance, attempt to bite, lunge at, or aggressively chase a conspecific. Any of these may be directed at focal macaque in 'receive aggression'.
Yawn	Focal macaque opens its mouth very wide and inhales air, usually baring teeth; does not appear to be directed at conspecific or researcher.
Shake/shiver/twitch	Focal macaque's head or entire body shakes and/or spasms.
Scratch	Focal macaque moves its hand or foot rapidly drawing its fingers/fingernails, toes/toenails, or the back of the hand across the hair or skin, when the hand or food stops moving the event is done.

* Data collected on which actors are involved. ¹Used to calculate hierarchical rank Normalized David's Scores. *Note:* Ethogram included floating limb, self-suck/clasp, self-bite/injure, salute/eye-poke, copraphagy, teeth grinding, and

regurgitation but these were extremely rare and not seen at all in one facility.

	Con	Opn	Dom	Anx	\mathbf{SW}	DS	Social	Displacement
Openness	0.59							
Dominance	0.92	0.57						
Anxiety	-0.61	-0.26	-0.47					
Socially withdrawn	-0.57	-0.54	-0.49	0.4				
Normalized David's Score	0.76	0.5	0.8	-0.49	-0.49			
Social	0.03	-0.24	0.09	-0.05	0.24	0.03		
Displacement	-0.12	-0.15	-0.13	-0.11	-0.11	-0.19	-0.05	
Playful	0.35	0.5	0.33	-0.11	-0.27	0.11	-0.42	-0.08

Supplementary Table II Spearman rank correlation of David's score personality dimensions, and behavioral components

N=85. DS=David's score; Con=Confidence; Opn=Openness; Dom=Dominance; Anx=Anxiety; SW=Socially withdrawn.

· _ ·	Social	Displacement	*Playful	h^2
Receive grooming	0.84	0.04	0.18	0.65
Environment explore	-0.67	-0.18	0.15	0.52
Receive aggression	-0.61	-0.07	-0.53	0.47
Alone	0.59	-0.07	-0.25	0.52
Yawn	0.17	0.75	0.01	0.57
Scratch	-0.31	0.67	-0.14	0.55
Stationary in proximity	0.06	0.64	-0.27	0.42
Locomotor stereotypy	-0.11	-0.49	-0.35	0.41
Giving grooming	0.32	-0.44	-0.34	0.56
Social play	-0.15	-0.29	0.79	0.72
Independent play	-0.08	-0.24	0.78	0.65
Shiver/shiver/twitch	-0.15	-0.17	-0.67	0.47
Regurgitation and reingestion	0.30	-0.15	-0.11	0.16
Toy play	-0.25	0.32	0.18	0.26
Self-grooming	0.14	0.30	-0.38	0.23
Give aggression	0.03	0.30	-0.14	0.10

Supplementary Table III

Principal component analysis with proxmax rotation of behaviors

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=15%.

 h^2 =communalities. Prior to reflection, Social correlated with Displacement at -.10 and Playful at 0.29; Displacement and Playful correlated at -0.17.

Supplementary Methods I

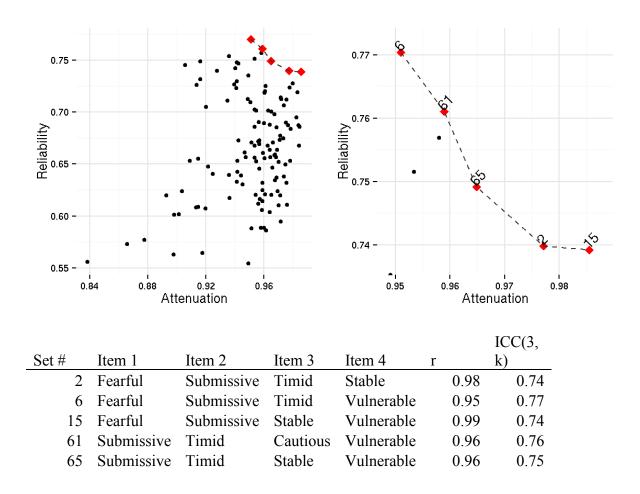
Shortening questionnaires with multi-objective optimization

We used three criteria to select items for a shortened version of the questionnaire: attenuation, reliability, and coverage. To derive an index of attenuation we first calculated item scores for each macaque. As each macaque was rated by multiple observers we first averaged scores across raters. Then, using the item scores, we calculated unit-weighted component scores (Gorsuch, 1983) using the reduced set of items. Finally, we calculated the correlation between component scores on the reduced and the full item sets. We thus calculated component scores for each domain using the reduced items for each rater on each monkey and calculated a measure of the interrater reliabilities of mean ratings, ICC(3,k) (Shrout & Fleiss, 1979).

Because it was possible that none of the reduced scales would be optimal on both attenuation and reliability, we sought to discard reduced scales that were suboptimal on both to find scales for which choosing any other possible reduced scale would lower either attenuation or reliability. We found the set of best reduced scales on these criteria for each domain using a Skyline algorithm (Borzsony et al., 2001) that we coded in R (R Development Core Team, 2014). In this technique the set of "best" options is known as the Pareto frontier (Marler & Arora, 2004), which separates the optimal sets from all the candidate sets that are worse on the input criteria. Below we plot the reliability and attenuation of each candidate scale and highlight the scales identified by the Skyline algorithm as optimal, and then use content analysis to select 2 or more items to use in the final reduced scale.

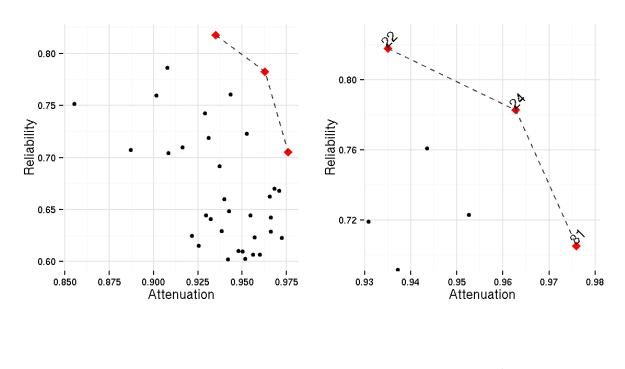
In the plots, each point represents a different combination of four items from each scale. Reliability = ICC(3, k) of interrater agreement from unit-weighted component scores on the reduced scale, Attenuation = correlation between individuals' scores on the reduced and full

scales. Red dots connected by dashed lines show the Pareto optimal item sets (the sets that dominate every other set on one of the criteria). The left panel shows all item sets and right panel shows a zoomed in view of the Pareto frontier, with arbitrary enumerative labels.



Confidence

Because there was little different in attenuation or reliability among the optimal sets, we selected items based on the largest coverage of meanings: fearful, submissive, cautious, and timid. We also elected to add the item depressed because although it loads most highly on the dimension Friendliness it also has salient cross-loadings on Confidence and because we thought it was likely to tap facets of Confidence related to welfare. This was confirmed by allowing depressed to be included as an item when running the Skyline algorithm: it appeared in four out of the five item sets on the Pareto frontier. Because of a clerical error the item timed was dropped from the final shortened questionnaire.

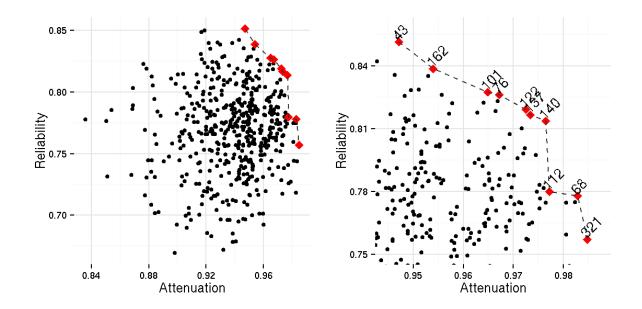


Openness

							ICC(3,
Set #	Item 1	Item 2	Item 3	Item 4	r		k)
22	Thoughtless	Innovative	Inventive	Imitative		0.94	0.82
24	Thoughtless	Innovative	Curious	Imitative		0.96	0.78
31	Innovative	Inventive	Curious	Imitative		0.98	0.71

For the Openness scale we chose the items Innovative and Curious.

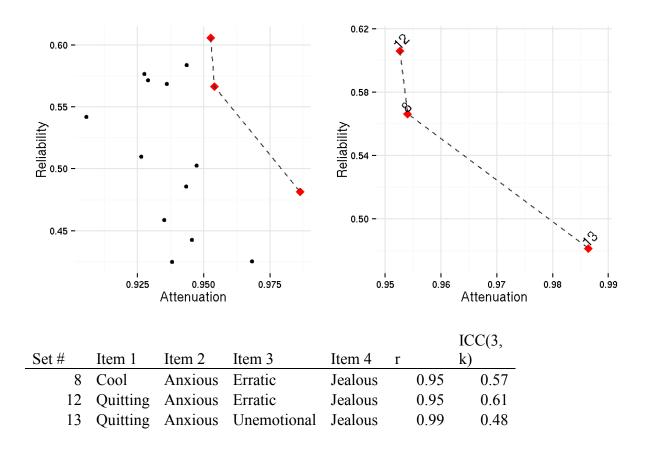
Dominance



							ICC(3,
Set #	Item 1	Item 2	Item 3	Item 4	r		k)
43	Bullying	Stingy	Dominant	Independent		0.95	0.85
68	Bullying	Aggressive	Excitable	Gentle		0.98	0.78
76	Bullying	Aggressive	Gentle	Dominant		0.97	0.83
101	Bullying	Irritable	Reckless	Dominant		0.96	0.83
112	Bullying	Manipulative	Defiant	Gentle		0.98	0.78
122	Bullying	Manipulative	Reckless	Dominant		0.97	0.82
137	Bullying	Defiant	Reckless	Dominant		0.97	0.82
140	Bullying	Defiant	Gentle	Dominant		0.98	0.81
162	Bullying	Gentle	Dominant	Independent		0.95	0.84
321	Aggressive	Manipulative	Excitable	Gentle		0.98	0.76

For Dominance we selected the items bullying and dominant as these two items covered the salient aspects of this domain.

Anxiety



While none of the options for a reduced scale showed high reliability, we selected from among the items making up the sets those with the broadest meaning: cool, quitting, anxious, and erratic.