**Personality and rhesus macaque (*Macaca mulatta*) health, welfare, and happiness.**

**Running title:** Rhesus personality and welfare

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**Abstract**

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**Personality and rhesus macaque health, welfare, and happiness.**

When we accept that animals differ in their personalities, we can begin to consider how this may relate to their health, welfare, and happiness. Connections between personality, well-being, and health have been long-studied in humans (Costa and McCrae 1980; Deary et al. 2010; Diener et al. 2003; Friedman 2008). By studying the same factors in nonhuman animals and understanding how personality, health, and welfare relate, we can determine ways to use this information to individualise animal care and welfare.

This study aimed to investigate the association between rhesus macaque (*Macaca mulatta*) personality and welfare, measured using two of these assessment methods: questionnaires and veterinary records. Several studies indicate that questionnaires are a reliable and valid method for assessing animal welfare. Studies that use qualitative behavioural assessment, for example, have found that observers agree on ratings of animal affective states, and that these ratings are associated with behaviour (Wemelsfelder et al. 2001) and physiological response (Stockman et al. 2011; Wickham et al. 2015) across multiple species (Minero et al. 2009; Napolitano et al. 2012). Studies using questionnaires designed to assess subjective well-being, a construct taken from the human happiness literature (Sandvik et al. 1993), have also found that ratings on these scales are consistent (King and Landau 2003). Moreover, subjective well-being measured in this way has been associated with longevity in orangutans (Weiss, Adams, and King 2011).

In previous studies, we examined the associations between subjective well-being and ratings of welfare in brown capuchins (*Sapajus apella*) (Robinson et al. 2016) and in chimpanzees (*Pan troglodytes*) (Robinson et al., in press). Both studies found that observers agreed on their ratings of welfare and subjective well-being. Furthermore, observer ratings was associated with frequency of stereotypic behaviour in brown capuchin monkeys (2016), and multiple behavioural indicators of welfare in chimpanzees (in press), such as coprophagy and urophagy. Welfare and subjective well-being ratings were also associated with personality in both species (Robinson et al., 2016, in press). This matches multiple studies that have shown the connections between subjective well-being and personality in primates (Schaefer and Steklis 2014; Weiss et al. 2006). For example, rhesus macaque higher in Confidence and Friendliness and lower in Neuroticism are rated higher in subjective well-being (Weiss, Adams, Widdig, et al. 2011). However, this research did not include ratings of welfare. By looking at the relationship between personality and welfare, we can identify the personality traits that may predispose animals to thrive in captivity.

We wanted to test the use of welfare ratings in a different nonhuman primate species to determine the generalizability of the results of our studies on brown capuchin monkey and chimpanzee welfare. We chose to study rhesus macaques (*Macaca mulatta*) because large numbers are kept in captivity (Carlsson et al. 2004) and live in suboptimal environments (DiVincenti and Wyatt 2011), which may compromise their welfare (Baker et al. 2014; Pomerantz et al. 2013; Rommeck et al. 2009). This suggests that rhesus macaques may benefit from a practical assessment method that will enable xxx to identify those in need of additional care.

The second reason we chose to study rhesus macaques is that it enables us to follow up a previous study we performed at the Oregon National Primate Research Center, where we looked at personality in relation health, measured with veterinary records. In that study we found that rhesus macaques with lower Confidence were more likely to have injured at some point in their life (Robinson et al., in review). One limitation of our Oregon study was that we did not collect data on all six rhesus macaque personality dimensions (Confidence, Openness, Dominance, Friendliness, Activity, Anxiety) (Weiss, Adams, Widdig, et al. 2011). Given the importance of social traits in particular (Capitanio 2011), collecting data on all personality dimensions would make it possible to better understand the association between personality and health in rhesus macaques.

Across humans and nonhuman animals personality has been found to relate to health outcomes (Cavigelli 2005; van Heck 1997) and disease progression (Capitanio 2008; Friedman 2008). For example, Jin, Su, Tao, Guo, & Yu (2013) found that golden snub-nosed monkeys with less aggressive personalities had more illness and that their illnesses lasted longer. These area of research is important for animal welfare because if we can identify the personality traits that are associated with reduced health outcomes, then we can use this information to more carefully monitor and care for individuals with those traits. However, much of the work on personality and health in animals does not include multiple measures of individual variation. For species where factors like dominance status may be influence health, such as nonhuman primates (Sapolsky 2005), this means we cannot rule out the potential that these factors are influencing results. Therefore, when studying personality and health it is important to include more than one measure of individual variation.

The present study had three main goals. Our first goal was to test if observers agreed on ratings of welfare and subjective well-being and if these ratings were related to behaviour. Our second goal was to test whether personality was associated with welfare and subjective well-being. Our third goal was to test whether there was an association between personality, dominance status, behaviour, and the prevalence of injury or illness.

**2. Methods**

**2.1 Ethical Note**

This study was non-invasive and complied with the US Animal Welfare Act (2013) and the ARRIVE guidelines (Kilkenny et al. 2013).

**2.2 Subjects**

The study took place at the California National Primate Research Center (CNPRC) in Davis, California. Subjects were 44 (13 males) group-housed rhesus macaques. The macaques ranged in age from 0.92 to 20.97 years (mean ± SD = 8.06 ± 4.88 years).

The macaques lived in three identical crib cages (n1 = 15; n2 = 16; n3 = 13). These crib cages are made up of two cylindrical cages (roughly 4m in diameter) connected by a rectangular cage (2.9 x 2.5m). The entire crib cage is 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. During the study, six macaques were removed for veterinary purposes.

**2.3 Instruments, observations, and veterinary records**

We used three questionnaires: The welfare questionnaire (Robinson et al., 2016), the subjective well-being questionnaire (King and Landau 2003), and the Hominoid Personality Questionnaire (Weiss et al. 2009). We also performed behavioural observations and used existing veterinary records.

**2.3.1 Welfare questionnaire.**

The welfare questionnaire was based on five factors that McMillan identified as contributing to animal quality of life (McMillan 2005). These factors include social relationships, physical health, stress and coping, mental stimulation, and control of both the physical and social environment. The questionnaire is made up of two parts. The first part asks raters about their background and to define the indicators they use to decide if an animal has positive and negative welfare. The second part is made up of 12 questions.

The animal welfare questionnaire was designed to be used across social species (Robinson et al. 2016). To improve our understanding of nonhuman primate welfare, we added four items relating to factors that commonly affect captive primates’ welfare and are under investigation by other researchers. These problems include hair loss (Honess et al. 2005; Kroeker et al. 2013), obesity (Bauer et al. 2011), dominance status (Beisner and Isbell 2011), and interactions with humans (Davey 2007; Stoinski et al. 2012). The newly added questions were:

This individual’s rank within the hierarchy is \_\_\_\_\_\_\_\_\_\_ to the individual’s welfare.

This individual’s weight has a(n) \_\_\_\_\_\_\_\_ influence on the individual’s welfare.

How often does this individual display abnormal overgrooming of themselves?

This individual finds the presence and/or interactions with humans ...

Responses to each of the 16 items were made on a five-point scale indicating very bad to very good welfare. The wording of the scale points was consistent with the wording of the items. For example, potential responses regarding the benefits of rank ranged from ‘1. extremely harmful’ to ‘2. extremely beneficial’. The questionnaire is available in Appendix #.

**2.3.2 Subjective well-being questionnaire.**

Happiness was assessed using the subjective well-being questionnaire (King and Landau 2003). This questionnaire consists of four questions that ask raters to estimate how happy the animal is, how much pleasure they derive from social relationships, how successful they are at achieving their goals, and how happy the rater thinks they would be if they were that animal for a week. Raters choose an answer on a seven point Likert scale that ranges from “Displays either total absence or negligible amounts of the trait or state” to “Displays extremely large amounts of the trait”.

**2.3.3 Personality questionnaire.**

We assessed personality using the Hominoid Personality Questionnaire (HPQ), which consists of 54 items. Each item is made up of an adjective and up to three descriptive sentences (Weiss, Adams, Widdig, et al. 2011). For example, the item ‘friendly’ is written: “**FRIENDLY:** Subject often seeks out contact with other monkeys for amiable, genial activities. Subject infrequently initiates hostile behaviours towards other monkeys.”

Each item on the HPQ is accompanied by a seven-point Likert scale that ranges from “Displays either total absence or negligible amounts of the trait” to “Displays extremely large amounts of the trait”.

**2.3.4 Focal Observations**

The first author (LMR) spent three days learning to identify individuals within one group. This group was then observed for 15 days with each macaque being observed once a day for a 15-minute focal animal observation. Observation order was randomized on the first day and then the order progressed so that the first macaque observed on Day 1 was the last macaque observed on Day 2, and so forth. LMR repeated this process until all three groups had been observed. Focal observations took place in January to March of 2016. Each macaque was observed for an average of 186.85 minutes (± SD 48.87).

Focal observations were performed using Noldus Pocket Observer 3.2 on an Android tablet. The macaques were observed for behaviours that were performed for enough time to record duration (durational behaviours), such as independent play and locomotor stereotypy, and behaviours that occur in short bursts that can be record for frequency (frequency behaviours), such as scratch and give aggression. We used a previously designed ethogram, which can be found in Supplementary Table 1.

**2.3.5 Veterinary records**

The CNPRC keeps electronic veterinary records with details of each animal’s veterinary examinations and descriptions of any injuries or illnesses. We used these records to determine for each macaque the number of injuries and illnesses from birth to the end of the study period.

**2.4 Data collection.**

Two researchers acquainted with the macaques (hence referred to as ‘acquainted researchers’) completed the welfare and subjective well-being questionnaires based on their most recent experience with the macaques. Two researchers were unacquainted with studied macaques (hence referred to as ‘unacquainted researchers’) prior to the study and before rating the macaques, they were instructed to observe a least one of the studied macaque groups for a minimum of 30 minutes a day for five days. At the end of the observation period the acquainted and unacquainted researchers completed the welfare and subjective well-being questionnaires. Across all four researchers time known ranged from 7 days to 6.5 years (mean ± SD = 2.81 ± 2.59 years). One of the acquainted researchers, in addition to LMR, completed the personality questionnaires based on their previous experience with the macaques. LMR rated all the macaques on personality before she reviewed the researchers’ ratings, the behavioural data, and the veterinary records.

Welfare, subjective well-being, and personality data were collected between February and June of 2016. We collected 97 welfare ratings of the 44 rhesus macaques using the welfare questionnaire (mean = 2.20 ratings per macaque; two macaques were rated only once) and 77 ratings using the subjective well-being questionnaire (mean = 1.61 ratings per macaque; 17 macaques were rated only once). We collected 88 ratings of the 44 macaques using the HPQ (mean = 2 ratings per macaque).

**2.5 Data analysis**

Statistical analyses were performed using R, version 3.1.1 (R Development Core Team 2014). In the mixed-effect, linear, and Poisson models including continuous variables (six personality domains, age, behaviour, and dominance status) and a binary variable (sex) we centred and divided the continuous variables by 2xSD to make them comparable to the binary variable (Gelman 2008).

**2.5.1 Missing data.**

There were 7 missing data points out of 1552 possible welfare responses, no missing data points out of 308 possible subjective well-being responses, and no missing data points out of 2376 possible personality responses. In all cases missing values were replaced with the mean value for that item (Downey and King 1998).

**2.5.2 Intraclass correlations.**

To assess the interrater reliabilities of the items, we used two intraclass correlations (*ICC*s). *ICC*(3,1) estimates the reliability of single ratings and *ICC*(3,*k*) assesses the reliability of mean ratings based on *k* raters (Shrout and Fleiss 1979). We used *ICC*s on the ratings for the rhesus macaques rated more than once on the welfare (N = 42), the subjective well-being (N = 27), and the personality questionnaire (N = 44). Items found to be unreliable as this stage were removed from further analysis.

**2.5.3 Principal component analysis.**

We took averages of the welfare and subjective well-being item scores across raters to obtain a single score per macaque. We then conducted a parallel analysis (Dinno and Dinno 2010; Horn 1965) and examined the scree plot to determine the number of components to extract using principal component analysis (PCA).

**2.5.4 Component scores.**

We calculated unit-weighted scores based on the component loadings (Gorsuch 1983). Loadings greater than or equal to .4 were assigned a weight of +1, loadings less than or equal to -.4 were assigned a weight of -1, and all other loadings were assigned a weight of 0. If an item had a loading greater than or equal to |.4| on multiple components, we assigned the item to the component onto which it had the highest loading.

To calculate personality component scores, we aggregated the reliable HPQ items across raters. We then generated component scores for the six rhesus macaque personality dimensions based on the 2011 published structure (Table 1 in Weiss et al., 2011).

**2.5.5 Normalised David’s scores.**

To calculate dominance status, we created a directional matrix for each group using supplant data. We then calculated Normalized David’s scores (De Vries et al. 2006) for each macaque.

**2.5.6 Mixed effects models.**

Using the nlme package in R (Pinheiro et al. 2012) we fit [number] linear mixed-effect models. The dependent variables in these models were sum frequency of observed behaviour. To reduce the number of models, we summed behaviours together. For example, stereotypies (pacing, back-flipping, rocking, head toss/twirl) were summed together as the dependent variable of one model. The summed behaviours are included in the results of these models. The fixed effects in the model included age, sex, the component score based on the results of the PCA of the welfare and subjective well-being items. We also included the sum of time out of out-of-sight during observations to adjust each model for the fact that some animals were less often visible to the observer. Animal ID was included as a random effect. We corrected for multiple testing using a Bonferroni correction.

**2.5.7 Linear models.**

We fit a linear model using the lm function in R. The dependent variable was the component score based on the results of the PCA. The six personality dimensions were included in the model as independent variables, as were sex and age. The dependent variable was converted into a z-score (mean ± SD = 0 ± 1). We calculated the marginal *r*2, a measure of explained variance, with the MuMIn package (Barton 2015).

**2.5.8 Poisson models.**

To model the number of injuries and illnesses we used Poisson models, which are appropriate for predicting count variables (Zeileis et al. 2008). Poisson regression also allows for the inclusion of offset variables, which adjust for the influence a factor may have on prevalence of the predicted variable.

We included a linear and a quadratic term for dominance status as we previously found a quadratic association between dominance status and injury (Robinson et al., under review). We included *give grooming* and *receive grooming* in the Poisson models because previous studies found associations between grooming, stress, and general health (e.g. Akinyi et al., 2013; Balasubramaniam, Beisner, Vandeleest, Atwill, & McCowan, 2016; Shutt, MacLarnon, Heistermann, & Semple, 2007).

Sex was included in each model as a control variable; age was included as an offset because older animals are likely to have accumulated more injuries and illnesses over the years (Zeileis et al. 2008). Using these variables, we ran four Poisson models for each dependent variable predicted by the following independent variables: 1) behaviour; 2) dominance status; 3) the six personality domains; 4) behaviour, dominance status, and the six personality domains.

**3. Results**

**3.1 Interrater Reliabilities of Items**

For the 16 welfare items, *ICC*(3,1) estimates ranged from 0.04 to 0.61 (Table 1). The mean of these interrater reliabilities was 0.25. The *ICC*(3,*k*) estimates for these items ranged from 0.09 to 0.78. The mean of these interrater reliabilities was 0.40. For the four subjective well-being items, *ICC*(3,1) ranged from -0.03 to 0.54 with a mean of 0.25. The comparable *ICC*(3,*k*) estimates ranged from -0.06 to 0.70 with a mean of 0.35 (Table 1).

For the HPQ items, *ICC*(3,1) estimates ranged from -0.18 to 0.89 with a mean of 0.44. The *ICC*(3,*k*) estimates ranged from -0.46 to 0.94 with a mean of 0.54 (Supplementary Table 2). One subjective well-being item, *time animal is happy*, and four personality items, *stable, solitary, affectionate,* and *protective*, had interrater reliabilities below zero and were excluded from further analyses.

Table 1

*Interrater reliability of welfare and SWB items*

|  |  |  |
| --- | --- | --- |
| Item | *ICC*(3,1) | *ICC*(3,*k*) |
| \*Benefit of rank | 0.61 | 0.78 |
| Social control | 0.53 | 0.72 |
| SWB Goal achievement | 0.54 | 0.70 |
| Positive/negative experience | 0.33 | 0.53 |
| Stress frequency | 0.32 | 0.51 |
| Negative welfare | 0.31 | 0.50 |
| Stress coping | 0.27 | 0.46 |
| Psychological stimulation | 0.23 | 0.40 |
| SWB Social satisfaction | 0.23 | 0.38 |
| SWB Happiness as animal | 0.23 | 0.38 |
| Positive welfare | 0.22 | 0.38 |
| \*Overgrooming | 0.21 | 0.38 |
| Effect of experience | 0.20 | 0.36 |
| Physical health | 0.18 | 0.33 |
| Number of relationships | 0.15 | 0.29 |
| Environmental control | 0.15 | 0.28 |
| Quality of relationships | 0.12 | 0.24 |
| \*Interactions with humans | 0.08 | 0.17 |
| \*Effect of weight | 0.04 | 0.09 |
| SWB Time animal is happy | -0.03 | -0.06 |
| Average | 0.25 | 0.39 |

Note. SWB = subjective well-being. Welfare ratings based on 42 rhesus macaques; SWB ratings based on 27 rhesus macaques. Welfare k = 2.26 raters per animal; SWB k = 2.0. \* indicates item is one of four newly designed questions.

**3.2 PCA of Welfare and SWB Items**

Parallel analysis and scree plot of the 16 welfare items and the 3 reliable subjective well-being items comprised a single component (Table 2). The three reliable subjective well-being items and all but one welfare item (*effect of weight*) had salient loadings on this component. We named this component welfareSWB.

Table 2

12 welfare items, 4 new items, and subjective well-being items

|  |  |  |
| --- | --- | --- |
| Item | Loading | *h*2 |
| SWB Social Satisfaction | 0.90 | 0.80 |
| Number of relationship | 0.89 | 0.80 |
| Positive/negative experiences | 0.88 | 0.78 |
| Social control | 0.88 | 0.77 |
| SWB Happiness as animal | 0.88 | 0.77 |
| Positive welfare | 0.87 | 0.76 |
| Stress frequency | -0.85 | 0.73 |
| SWB Goal achievement | 0.85 | 0.72 |
| Negative welfare | -0.84 | 0.70 |
| Environmental control | 0.81 | 0.65 |
| Quality of relationships | 0.78 | 0.60 |
| \*Benefit of rank | 0.76 | 0.58 |
| Stress coping | 0.76 | 0.57 |
| Effect of experience | 0.72 | 0.51 |
| \*Overgrooming | -0.64 | 0.41 |
| Psychological stimulation | 0.57 | 0.32 |
| Physical health | 0.50 | 0.25 |
| \*Interactions with humans | 0.44 | 0.20 |
| \*Effect of weight | 0.21 | 0.04 |

Note. N=44. SWB = subjective well-being. Proportion of variance = 58%. h2 = commonalities. \*Newly designed question.

**3.3 Mixed effects model**

Macaques that performed fewer stereotypic behaviours were rated as being higher on welfareSWB (last model in Table 3). Macaques that performed fewer displacement behaviours (i.e. yawning, scratching, and shake/twitching) were rated as being higher on welfareSWB (Table 4). However, this association was not significant after correcting for multiple tests.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table 3 |  |  |  |  |  |
| Mixed effects models of durational behaviour predicted by welfareSWB, time out of sight, age, and sex with macaque as a random effect. | | | |  |  |
|  |  |
|  |  |
| Model | *b* | CI | p |  |  |
| **Receive grooming** | | | |  |  |
| Intercept | 122.73 | [102.83,201.21] | <0.001 |  |  |
| WelfareSWB | 42.93 | [8.62,77.26] | 0.17 |  |  |
| Male | -44.31 | [-82.16,-6.46] | 0.26 |  |  |
| Age | 52.14 | [16.88,87.44] | **0.048** |  |  |
| Out of sight | -22.30 | [-51.95,9.25] | 1.00 |  |  |
| **Give grooming** | | | |  |  |
| Intercept | 70.43 | [57.06,83.83] | <0.001 |  |  |
| WelfareSWB | 0.95 | [-22.13,24.03] | 1.00 |  |  |
| Male | -35.97 | [-61.44,-10.51] | 0.070 |  |  |
| Age | 18.12 | [-5.61,41.84] | 1.00 |  |  |
| Out of sight | -9.01 | [-29.65,12.00] | 1.00 |  |  |
| **Self-grooming** | | | |  |  |
| Intercept | 23.24 | [16.68,29.79] | <0.001 |  |  |
| WelfareSWB | -10.93 | [-22.24,0.38] | 1.00 |  |  |
| Male | -4.60 | [-17.06,7.86] | 1.00 |  |  |
| Age | -10.77 | [-22.37,0.84] | 1.00 |  |  |
| Out of sight | 11.39 | [2.70,19.79] | 1.00 |  |  |
| **Playing independently, with toys, and socially and exploring the environment** | | | | | |
| Intercept | 54.40 | [40.08,68.72] | <0.001 |  |  |
| WelfareSWB | 2.63 | [-22.05,27.32] | 1.00 |  |  |
| Male | -8.41 | [-35.57,18.75] | 1.00 |  |  |
| Age | -70.72 | [-96.00,-45.45] | **<0.001** |  |  |
| Out of sight | 29.94 | [16.01,43.84] | **<0.001** |  |  |
| **In proximity of conspecifics** | | |  |  |  |
| Intercept | 193.10 | [164.13,222.03] | <0.001 |  |  |
| WelfareSWB | 9.48 | [-40.41,59.35] | 1.00 |  |  |
| Male | 41.66 | [-13.25,96.60] | 1.00 |  |  |
| Age | 55.41 | [4.27,106.52] | 0.39 |  |  |
| Out of sight | -26.27 | [-59.46,7.16] | 1.00 |  |  |
| **Out of proximity of conspecifics** | | |  |  |  |
| Intercept | 137.47 | [117.48,157.45] | <0.001 |  |  |
| WelfareSWB | 11.87 | [-22.59,46.33] | 1.00 |  |  |
| Male | 19.22 | [-18.73,57.18] | 1.00 |  |  |
| Age | 86.73 | [51.40,122.07] | **<0.001** |  |  |
| Out of sight | -4.68 | [-28.90,18.70] | 1.00 |  |  |
| **Pacing, backflipping, rocking, and head toss/twirl** | | | | | |
| Intercept | 11.21 | [3.82,18.60] | <0.001 |  |  |
| WelfareSWB | -19.02 | [-31.76,-6.27] | **0.043** |  |  |
| Male | -4.28 | [-18.30,9.74] | 1.00 |  |  |
| Age | 6.84 | [-6.20,19.87] | 1.00 |  |  |
| Out of sight | -0.84 | [-7.33,5.69] | 1.00 |  |  |
| *Note.* N = 44. P-values after correction for multiple tests. Boldface values were significant at p<0.05. | | | | | |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table 4 |  |  |  |  |
| Mixed effect models of count behaviour predicted by welfareSWB, time out of sight, age, and sex with macaque as a random effect. | | | |  |
|  |
|  |
| Model | *b* | CI | p |  |
| **Receive aggression** | | | |  |
| Intercept | 1.43 | [-1.57,4.43] | 1.00 |  |
| WelfareSWB | 2.75 | [-2.42,7.93] | 1.00 |  |
| Male | 3.97 | [-1.72,9.67] | 1.00 |  |
| Age | 0.95 | [-4.36,6.25] | 1.00 |  |
| Out of sight | -0.19 | [-3.79,3.35] | 1.00 |  |
| **Floating limb, self-suck/clasp, and self-bite/injure** | | | | |
| Intercept | 0.10 | [0.01,0.19] | 0.36 |  |
| WelfareSWB | -0.07 | [-0.23,0.12] | 1.00 |  |
| Male | -0.06 | [-0.23,0.08] | 1.00 |  |
| Age | 0.01 | [-0.15,0.17] | 1.00 |  |
| Out of sight | -0.01 | [-0.06,0.05] | 1.00 |  |
| **Yawning, scratching, and shaking/twitching** | | | | |
| Intercept | 3.31 | [2.85,3.77] | <0.001 |  |
| WelfareSWB | -1.11 | [-1.90,-0.32] | 0.076 |  |
| Male | 0.49 | [-0.38,1.37] | 1.00 |  |
| Age | -0.83 | [-1.64,-0.01] | 0.52 |  |
| Out of sight | 0.18 | [-0.39,0.72] | 1.00 |  |
| *Note.* N = 44. P-values presented after correction.  Boldface values were significant at p<0.05. | | | | |
|  |  |  |  |  |

**3.4 Linear model of welfare, subjective well-being, and personality**

In the model of welfareSWB predicted by personality it was found that macaques that were younger and higher in Confidence were rated as having higher welfareSWB (Table 5). This model accounted for 80% of the variance.

|  |  |  |  |
| --- | --- | --- | --- |
| Table 5 |  |  |  |
| Rhesus macaque welfareSWB predicted by personality components | | | |
| Predictor | *b* | CI | p |
| Intercept | 0.02 | [-0.16,0.19] | 0.83 |
| Age | -0.64 | [-1.16,-0.18] | **0.013** |
| Male | -0.07 | [-0.43,0.31] | 0.73 |
| Confidence | 1.99 | [0.96,3.26] | **0.001** |
| Openness | 0.12 | [-0.76,0.99] | 0.79 |
| Dominance | -0.35 | [-1.3580.74] | 0.55 |
| Friendliness | 0.05 | [-0.54,0.48] | 0.86 |
| Activity | 0.31 | [-0.50,1.10] | 0.44 |
| Anxiety | 0.00 | [-0.72,0.70] | 1.00 |
| *Note.* N = 44. | |  |  |

**3.5 Poisson model of injury, illness, and personality, dominance, and behaviour**

Of the 44 studied macaques, 26 experienced an illness at some point in their life; 19 had experienced more than one illness. There was an average of 1.91 ± SD = 2.26 illnesses per macaque. As is typical with rhesus macaques, diarrhea was the most commonly reported illness (Prongay et al. 2013). Veterinary clinical care included administration of fluids and bismuth subsalicylate. Of the 44 macaques, 32 experienced an injury at some point in their life and 24 experienced more than one injury. Overall, there was an average of 3.54 ± SD = 4.12 injuries per macaque. The most injuries were those inflicted by other macaques, such as bites and abrasions. Veterinary clinical care of injuries and illnesses included suturing of wounds and administration of analgesics and antibiotics.

The three models of injury that only included dominance status, behaviour, or personality indicated that rhesus macaques with a higher prevalence of injury tended to be female and lower in dominance status (Table 6). The full model that included all predictors indicated that macaques with a higher prevalence of injury were female (Table 6).

The three models of illness that only included dominance status, behaviour, and personality indicated that rhesus macaques with a higher prevalence of illness were male, received less grooming, and higher in Confidence and Friendliness, and lower in Dominance (Table 7). The full model that included all predictors indicated that macaques with more illnesses were groomed less often and were higher in Confidence and Friendliness (Last model in Table 7).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table 6 |  |  |  |  |  |
| *Poisson models of injury* | |  |  |  |  |
| Model | *b* | SE | Z | P |  |
| **Injury predicted by David's Score** | | | | |  |
| Intercept | -0.66 | 0.11 | -6.07 | <0.001 |  |
| Male | -0.70 | 0.25 | -2.83 | **0.005** |  |
| David's Score | -0.40 | 0.18 | -2.26 | **0.024** |  |
| David's Score^2 | -0.19 | 0.35 | -0.54 | 0.59 |  |
|  |  |  |  |  |  |
| **Injury predicted by grooming** | | |  |  |  |
| Intercept | -0.72 | 0.09 | -7.63 | <0.001 |  |
| Male | -0.68 | 0.26 | -2.67 | **0.008** |  |
| Give groom | 0.09 | 0.16 | 0.58 | 0.57 |  |
| Receive groom | 0.10 | 0.15 | 0.62 | 0.53 |  |
|  |  |  |  |  |  |
| **Injury predicted by personality** | | | | |  |
| Intercept | -0.73 | 0.11 | -6.65 | <0.001 |  |
| Male | -0.91 | 0.30 | -3.08 | **0.002** |  |
| Confidence | 0.57 | 0.75 | 0.76 | 0.44 |  |
| Openness | -0.08 | 0.53 | -0.16 | 0.87 |  |
| Dominance | -1.14 | 0.72 | -1.58 | 0.11 |  |
| Friendliness | 0.05 | 0.32 | 0.16 | 0.87 |  |
| Activity | 0.65 | 0.45 | 1.44 | 0.15 |  |
| Anxiety | -0.52 | 0.44 | -1.18 | 0.24 |  |
|  |  |  |  |  |  |
| **Injury predicted by David's Score, grooming, and personality** | | | | | |
| Intercept | -0.68 | 0.15 | -4.42 | <0.001 |  |
| Male | -0.84 | 0.32 | -2.63 | **0.008** |  |
| David's Score | -0.33 | 0.50 | -0.67 | 0.50 |  |
| David's Score^2 | -0.20 | 0.47 | -0.44 | 0.66 |  |
| Give groom | -0.01 | 0.23 | -0.03 | 0.98 |  |
| Receive groom | 0.31 | 0.21 | 1.44 | 0.15 |  |
| Confidence | 0.56 | 0.81 | 0.69 | 0.49 |  |
| Openness | 0.19 | 0.56 | 0.34 | 0.73 |  |
| Dominance | -1.04 | 0.82 | -1.27 | 0.21 |  |
| Friendliness | -0.11 | 0.36 | -0.30 | 0.76 |  |
| Activity | 0.74 | 0.48 | 1.53 | 0.13 |  |
| Anxiety | -0.61 | 0.46 | -1.33 | 0.18 |  |
| N = 44. Boldface values were significant at p<0.05. | | | | |  |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table 7 |  |  |  |  |
| *Poisson models of illness* | |  |  |  |
| Model | *B* | SE | Z | P |
| **Illness predicted by David's Score** | | | | |
| Intercept | -1.70 | 0.16 | -10.46 | <0.001 |
| Male | 0.99 | 0.22 | 4.39 | **<0.001** |
| David's Score | -0.31 | 0.22 | -1.40 | 0.16 |
| David's Score^2 | -0.21 | 0.38 | -0.55 | 0.58 |
|  |  |  |  |  |
| **Illness predicted by grooming** | | |  |  |
| Intercept | -1.68 | 0.15 | -11.14 | <0.001 |
| Male | 0.62 | 0.26 | 2.36 | **0.018** |
| Give groom | -0.54 | 0.30 | -1.84 | 0.07 |
| Receive groom | -1.10 | 0.27 | -4.03 | **<0.001** |
|  |  |  |  |  |
| **Illness predicted by personality** | | | | |
| Intercept | -1.68 | 0.16 | -10.24 | <0.001 |
| Male | 0.38 | 0.31 | 1.24 | 0.22 |
| Confidence | 2.48 | 0.89 | 2.79 | **0.005** |
| Openness | -0.47 | 0.76 | -0.62 | 0.54 |
| Dominance | -3.49 | 0.88 | -3.95 | **<0.001** |
| Friendliness | 1.33 | 0.44 | 3.01 | **0.003** |
| Activity | 1.04 | 0.61 | 1.70 | 0.089 |
| Anxiety | 0.85 | 0.64 | 1.32 | 0.18 |
|  |  |  |  |  |
| **Illness predicted by David's Score, grooming, and personality** | | | | |
| Intercept | -1.66 | 0.22 | -7.71 | <0.001 |
| Male | -0.02 | 0.38 | -0.04 | 0.97 |
| David's Score | -1.01 | 0.52 | -1.95 | 0.052 |
| David's Score^2 | -0.02 | 0.60 | -0.04 | 0.97 |
| Give groom | -0.53 | 0.36 | -1.50 | 0.13 |
| Receive groom | -1.21 | 0.37 | -3.28 | **0.001** |
| Confidence | 2.41 | 0.95 | 2.54 | **0.011** |
| Openness | -0.70 | 0.85 | -0.82 | 0.41 |
| Dominance | -1.86 | 0.96 | -1.93 | 0.054 |
| Friendliness | 1.44 | 0.46 | 3.13 | **0.002** |
| Activity | -0.15 | 0.78 | -0.19 | 0.85 |
| Anxiety | 1.33 | 0.72 | 1.85 | 0.064 |
| N = 44. Boldface values were significant at p<0.05. | | | | |

**4. Discussion**

Staff ratings of welfare and happiness in rhesus macaques were reliable and described a single component. This component (welfareSWB) was associated with motor stereotypies and displacement behaviour, which suggests that the ratings were based on observed behaviors. Younger, more confident macaques were rated as higher in welfare and happiness. In addition, having more illnesses was associated with macaques being rated as higher in confidence and friendliness, and receiving less grooming.

We studied welfare and happiness in three nonhuman primate species (rhesus macaques, brown capuchins, and chimpanzees; Robinson et al., 2016, in press) and across all three we found observers agree on their ratings of primate welfare and subjective well-being and that these two measures comprised a single component, welfareSWB. Observers showed less agreement than in our studies of brown capuchins (Robinson et al. 2016) and chimpanzees (Robinson et al., in press). Despite half the raters having as little as 2.5 hours of experience with the macaques, we found observer agreement on all but one item. This matches others studies that have shown that unacquainted observers may have lower reliability but still accurate raters of animal personality (Petelle and Blumstein 2014) and emotion (Martau et al. 1985). The agreement between observers suggests that the welfare questionnaire may be a viable tool for large research facilities where staff may not be as familiar with individual animals as are keepers in zoos, sanctuaries, and small facilities.

Macaques rated as having higher welfare and subjective well-being performed fewer stereotypies and displacement behaviours. This finding suggests that ratings were based on observed behaviours. The limited association between behaviour and ratings contrasts with our work with chimpanzees where we found multiple behaviours (e.g., reingestion and regurgitation of ??, proximity) to be associated with observer ratings (Robinson et al., in press). Other work on animal welfare ratings have shown ratings to related to behaviour and physiological response (Stockman et al. 2011; Wemelsfelder et al. 2001; Wickham et al. 2015) reinforcing the utility and validity of welfare ratings. The reason we found limited associations between ratings and behaviours may be that our observers, under time-constraints, focused on the most easily interpreted behavioural cues of welfare, such as stereotypy. Alternatively, the limited association between ratings and observed behaviour may be due to the welfare questions not being specific enough to pick up on more than a couple obvious behaviours. Though our results with chimpanzees suggest this not to be the case (Robinson et al., in press). Going forward, we need to perform studies aimed at understanding which factors are associated with increased accuracy and reliability of observer ratings, such as time spent with the animals, animal welfare education, and experience with the observed species.

When we included all six personality dimensions in a linear model, we found that higher welfareSWB was associated with higher Confidence. This was similar to the results of our study on brown capuchins where animals that were younger with higher Assertiveness had higher welfareSWB. Previous work on subjective well-being in rhesus macaques (Weiss, Adams, Widdig, et al. 2011) found higher Confidence and Friendliness and lower Neuroticism were associated with subjective well-being. The differences between our results and theirs may be due to two possible explanations. First, including questions on more traditional aspects of welfare, such as physical health and stress, changes the association. Alternatively, it may be that we lacked the statistical power to find these associations as the previous study included 125 rhesus macaques whereas ours included 44. Testing the welfare questionnaire with a larger sample of rhesus macaques would allow us to tease these two possibilities part.

We found individual differences in ??? were associated with health in multiple ways. First, females tended to be injured. This contrasted with our previous research (Robinson et al., in review) where we found that rhesus macaques with lower Confidence were more likely to have been injured. However, we did not account for Activity in that study and used shortened personality questionnaire. We also used a different variation of the Poisson model, the Hurdle model, due to a low number of injuries and illnesses, likely because our sample was primarily made up of juvenile macaques. Here, we used Poisson models and did not find any association between personality and injury. Many of these differences in results may be attributable to the age of sample in this study and that it was primarily made up of adult females whereas our other sample was mostly made up of juvenile/sub-adult males.

Regarding illness, macaques with higher prevalence of illness were groomed less often and were rated as higher in Confidence and Friendliness. Grooming has many benefits in regards to social bonding and maintenance in rhesus macaques (Balasubramaniam et al. 2016; McCowan et al. 2011). Our results suggest that it is a one-way street in regards to illness, it is better to receive grooming than to give it. Friendlier macaques may have a higher prevalence of illness due to increased exposure to more pathogens through more contact with conspecifics. The relationship between higher Confidence and prevalence of illness was different to the finding with welfareSWB, where macaques with higher Confidence were rated as happier and with better welfare. The difference in direction of effect on health compared to over welfare speaks to physical health being only one part of an animal’s welfare (Dawkins 1990). It may also reflect that illness differently was measured over from birth to present whereas the welfare ratings represent one time point. An animal’s welfare is seen to be a transient state that changes over time and the environment (Honess and Wolfensohn 2010; Matheson et al. 2008; Richter et al. 2012; Silva and Furr 2013) therefore we need to measure it consistently to fully understand it. Were we able to measure welfare, including aspects other than physical health, consistently over the lifetime of the animals then we may find different personality domains influence welfare over time.

Given the attention that primate welfare has received, it is important to find ways to measure and identify the factors that influence welfare. In 2016 the US National Institutes of Health workshop the CNPRC’s director, John Morrison, pointed out that we need to “converge on the animal” by collecting as much data from one animal as possible to answer multiple research questions. By doing so, with research methods such as those presented here, we may be able to reduce the number of animals used in research. Additionally, through the inclusion of measures that are associated with health variation, such as personality, into animal studies, we may be able to control for the influence of individual variation on the results. Promoting research that increases our understanding and ability to improve animal welfare, along with improving the quality of science we produce, is a priority we support for future research.

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