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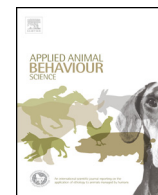


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Happiness is positive welfare in brown capuchins (*Sapajus apella*)

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ABSTRACT

Questionnaires that allow people who are familiar with individual animals to rate the welfare of these animals are an underutilised tool. We designed a 12-item welfare questionnaire and tested its reliability and associations with subjective well-being (SWB), locomotor stereotypy, and personality traits. The welfare questionnaire included questions relating to physical health, stress and coping, satisfaction with social relationships, psychological stimulation, and the display of positive and negative welfare indicators. We collected ratings of 66 brown capuchins (*Sapajus apella*) living in three facilities. Each capuchin was rated on the welfare questionnaire by an average of 2.8 raters. The interrater reliability of the welfare questionnaire items ranged from ICC(3,k) 0.51 to 0.86. A principal components analysis indicated that the 12 welfare items loaded onto one component. We repeated this process with the welfare and four items used to measure subjective well-being and found all the items were defined by a single component (welfareSWB). We then conducted three sets of analyses, one predicting the welfare component, one predicting the SWB component, and predicting the welfareSWB component. The independent variables were frequency of locomotor stereotypy, personality, age, and sex; facility was included as a random effect. In models including stereotypy, age, and sex we found frequency of stereotypy to be significantly associated with all three predicted components ($ps < 0.01$). After controlling for stereotypy ($b = -0.25$, $p = 0.17$), age ($b = -0.54$, $p = 0.01$), and sex ($b = -0.32$, $p = 0.07$), the personality traits of Sociability ($b = 1.02$, $p < 0.001$), Assertiveness, ($b = 0.63$, $p < 0.001$), and Attentiveness ($b = 0.54$, $p = 0.01$) were associated with higher scores on the joint welfareSWB component; Neuroticism was negatively associated with welfare SWB ($b = -0.60$, $p = 0.01$). Our results suggest that welfare questionnaires is a useful, reliable, and valid tool for primate welfare assessment.

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1. Happiness is positive welfare in brown capuchins (*Sapajus apella*)

People working within animal facilities are an often underutilised source of knowledge for improving animal welfare. These people use their experience to collect and interpret new information and, when shared, their observations can be used to track

animal welfare. However, in spite of these capabilities there are few studies using questionnaires to assess animal welfare.

The goal of our study was to test the utility of questionnaires as a tool for assessing nonhuman primate welfare. This is an increasingly important area of research given the growing interest in assuring the welfare of animals kept in research facilities. This is also important because in order to improve animal welfare we need to be able to accurately assess it. We chose to study brown capuchin monkeys (*Sapajus apella*) due to the large numbers in captivity (IUCN, 2014) and the fact that there has been extensive research on their behaviour and cognition (Fragaszy et al., 2004). In particular, the personality structure of brown capuchins has been studied

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(Morton et al., 2013), which presented the opportunity to study the association between ratings of welfare, subjective well-being, and personality.

Animal welfare is often assessed using physiological responses and behavioural observations (Broom and Johnson, 1993; Broom, 1988). These methods have drawbacks (Rushen, 1991). For example, blood draws may be stressful, which makes measures of glucocorticoids difficult to interpret (Laule et al., 2003). Behavioural observations, although they do not disrupt the animal, are time-consuming and need to be conducted multiple times to gain an accurate assessment of an individual's welfare state (Vazire et al., 2007). Alternatively, staff can fill out questionnaires, based on their daily observations of animals' behaviours and environmental responses, for a large number of animals in a time-efficient manner. As with other methods of welfare assessment, ratings are not perfect as raters may have individual biases. However, concerns about questionnaire reliability and validity can be assessed by testing the agreement between raters and whether responses are related to observed welfare states. If we can devise reliable and valid questionnaires for rating primate welfare, then facilities housing primates would have one more tool for monitoring and improving welfare.

One benefit of questionnaires is that they can cover several indicators and welfare states in a relatively short period of time. This is important because in order to effectively assess welfare it is crucial to assess multiple indices. For example, chronic stress is associated with reduced immune response (Broom, 2006; Cohen et al., 1992) and increased incidence of self-injury (Davenport et al., 2008; Lutz et al., 2003). There is also increased focus on accounting for the experience of positive emotions (or happiness) in welfare assessment (Boissy et al., 2007). A primate welfare questionnaire that covers a diverse set of welfare indicators, including those relating to both positive and negative welfare, could be used to further investigate how different aspects of welfare are interconnected.

One questionnaire designed to assess happiness in nonhuman primates is King and Landau's subjective well-being questionnaire (SWB) (2003), which was based on studies of human happiness (Sandvik et al., 1993). This questionnaire was initially used to assess chimpanzees (King and Landau, 2003) and has since been used with other nonhuman primate species (Weiss et al., 2011a,b, 2006) and felids (Gartner and Weiss, 2013) and other nonhuman primates (Weiss et al., 2011a,b, 2006). These studies have shown that the interrater and retest reliabilities of animal SWB are similar to those of humans (Diener, 2009). Also, as in humans (Diener and Chan, 2011; Diener et al., 2003), happier animals (those with higher SWB) tend to live longer (Weiss et al., 2011a) and share certain personality traits, such as higher Extraversion (King and Landau, 2003; Weiss et al., 2009, 2006).

In humans happiness and welfare are directly associated with one another (Diener, 2009) suggesting that they are measuring similar constructs. Both animal welfare and SWB involve the animal's ability to cope with their environment and the balance of positive and negative experiences (Broom, 2007; King and Landau, 2003). Does this mean SWB is equivalent to animal welfare? By assessing welfare and SWB in brown capuchins, we can determine the degree to which these constructs are related in this species.

Accounting for variation in personality has been suggested as another way of understanding and improving captive animal welfare (Tetley and O'Hara, 2012). Studying personality and welfare together may help researchers better understand why animals in a shared environment may have different welfare states. Until now the five brown capuchin personality traits (Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness) have not been studied in connection with welfare and SWB.

As such, in this study we assessed the reliability and validity of a 12-item welfare questionnaire in brown capuchins. We then

examined the convergence of ratings of welfare and happiness. Finally, we tested the association of ratings of welfare and SWB with locomotor stereotypy and personality traits.

2. Methods

2.1. Ethical approval

This project was approved by the participating facilities in July 2014. This study was non-invasive and complied with the US Animal Welfare Act (USDA, 2008).

2.2. Subjects

Subjects were 66 brown capuchins (31 males) housed at the National Institutes of Health, Georgia State University, and Franklin & Marshall College. Ages ranged from 0.55 years to 45.56 years (mean \pm SD = 12.47 years \pm 9.03 years). Across the facilities all the capuchins were socially housed in groups or pairs.

2.3. Instruments

2.3.1. Welfare questionnaire

We designed the welfare questionnaire with practicality in mind, and so it was relatively brief and applicable to multiple primate species. The questionnaire is comprised of three sections. The first section asks raters, who were caretakers or other individuals with extensive experience working with the animals that they rated, to answer questions about their experience working with animals. In addition, to prime raters for the welfare questions, this section of the questionnaire asks which physical and behavioural indicators raters use to determine whether an animal has positive or negative welfare. The second section consisted of 12 questions based on the five major contributors to animal quality of life proposed by McMillan (2005), including social relationships, mental stimulation, health, stress, and control of the social and physical environment. Some of the definitions and wording were influenced by Broom (2007, 1991), Broom and Johnson (1993), and by Green and Mellor (2011). Each of the items could be rated on a five point Likert scale ranging from very bad to very good, altered to fit the question wording and to capture negative and positive welfare states (Boissy et al., 2007; Yeates and Main, 2008). Each question also included a section for comments. The welfare questionnaire is available in Supplementary materials.

2.3.2. Subjective well-being ratings

We collected subjective well-being ratings for the capuchins using King and Landau's four-item questionnaire¹ (2003). This questionnaire asks raters to estimate how often each animal is happy, how satisfying each animal finds their social experiences, how successful the animal is at achieving its goals, and to imagine how happy they would be if they were that animal for a week. Raters used a seven point Likert scale to rate how well each adjective describes the individual animals 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 ratings

We collected personality ratings using the Hominoid Personality Questionnaire,² a 54-item questionnaire where each item consists of an adjective and one to three descriptive sentences (Weiss et al.,

¹ The SWB questionnaire can be found at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_wellbeing.pdf.

² The HPQ can be found at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf.

2011b). For example, the item *fearful* is “**FEARFUL**: Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away, or other signs of anxiety or distress.” The HPQ uses a seven point Likert scale from “Displays either total absence or negligible amounts of the trait” to “Displays extremely large amounts of the trait”.

2.3.4. Stereotypic behaviour

We collected data on the frequency of locomotor stereotypy to test the welfare and SWB questionnaires' relation to an observable welfare state. We asked staff to “Rate how often each animal performs any of the following behaviours by placing an X in the appropriate column”. This was followed by operational definitions taken from [Vandeleest et al. \(2011\)](#) for the following stereotypes: pace, flip, twirl, swing, bounce, head twist, and rock. Staff then rated each capuchins' stereotypic behaviour on a five point frequency scale from “never” to “constantly”.

2.4. Data collection

We collected welfare questionnaires and subjective well-being ratings from 7 May 2014 to 28 August 2014. Ten raters performed 185 ratings of the 66 capuchins using the welfare questionnaire (mean = 2.80 ratings per capuchin); nine raters performed 181 ratings using the SWB questionnaire (mean = 2.70 ratings per capuchin). Raters knew each capuchin for an average of 3.88 years (range: 0.50–16 years, $SD \pm 3.81$ years). There were 19 missing data points out of 2220 possible welfare responses and no missing data points out of 724 possible SWB responses. At the same time we collected 64 personality ratings of 18 animals. We used 140 personality ratings of 48 of these capuchins previously collected in 2010 and reported in [Morton et al. \(2013\)](#). Each of the 66 capuchins was rated on average 3.25 times; three animals were only rated once. Overall there were 230 missing data points out of 11016 possible personality responses. Lastly, in December, 2015 we collected 172 ratings of stereotypy frequency from seven raters (mean = 2.61 raters per animal); there were no missing data points. All seven raters had contributed to the 2014 data collection. Because we wanted to test the welfare and SWB questionnaires' validity by connecting them to an observable welfare state, we collected stereotypy ratings after we collected data from the questionnaires. Raters for all the questionnaires were researchers, care staff and/or students familiar with individual animals. For all the questionnaires any item with a missing value was replaced with that items' mean score ([Downey and King, 1998](#)).

2.5. Analysis

Statistical analyses were performed using R, version 3.1.1 ([R Development Core Team, 2014](#)).

2.5.1. Intraclass correlations

We used intraclass correlations (ICCs) to assess the interrater reliability of welfare and SWB ratings of the 48 animals that were assessed by multiple raters; the same animals were in both analyses. We also performed ICCs to assess the reliability of the personality items for the 63 capuchins that were assessed by multiple raters. $ICC(3,1)$ estimates the reliability of single ratings and $ICC(3,k)$ assesses the reliability across mean ratings based on k raters ([Shrout and Fleiss, 1979](#)).

2.5.2. Principal components analyses

We averaged the welfare item scores across raters leaving a single score per animal and then conducted separate principal component analyses (PCA) for the welfare items and the SWB items. We determined the number of components to extract by examining

Table 1
Interrater reliability of welfare and SWB items.

Item	ICC(3,1)	ICC(3,k)
Social control	0.63	0.86
Number of relationships	0.63	0.86
Physical health	0.56	0.82
Positive/negative experience	0.53	0.80
Quality of relationships	0.49	0.77
Positive welfare	0.46	0.75
Stress frequency	0.46	0.75
Negative welfare	0.45	0.74
Environmental control	0.37	0.67
Effect of experience	0.31	0.61
Psychological stimulation	0.26	0.55
Stress coping	0.23	0.51
Welfare average	0.45	0.72
SWB Goal achievement	0.74	0.91
SWB Happiness as animal	0.64	0.86
SWB Time animal is happy	0.63	0.85
SWB Social satisfaction	0.51	0.78
SWB Average	0.63	0.85

Note. Based on 48 brown capuchins. Welfare items $k=3.48$. SWB items $k=3.33$.

the scree plot and performing a parallel analysis ([Dinno and Dinno, 2010](#); [Horn, 1965](#)). We then computed unit-weighted component scores ([Gorsuch, 1983](#)) by assigning a weight of +1 to loadings that were greater than or equal to 0.4 and a weight of -1 to loadings that were less than or equal to -0.4. All other loadings were assigned weights of 0. In the event that an item had a loading greater than or equal to $|.4|$ on more than one component, we assigned the item to the component on which it had the highest loading. We then performed a joint-PCA with the 12 welfare items and the four SWB items.

To calculate personality component scores we aggregated HPQ item scores across raters and generated component scores for the personality dimensions based on the 2013 published structure ([Table 6 in Morton et al., 2013](#)). This structure includes five brown capuchin personality dimensions: Assertiveness is made up of items such as *bullying*, *aggressive*, and *dominant*; Openness is made up of items such as *inventive*, *innovative*, and *playful*; Neuroticism is made up of items such as (not) *stable*, (not) *predictable*, and *excitable*; Sociability which includes *affectionate*, *friendly*, and (not) *solitary*; Attentiveness is made up of items such as (not) *disorganised*, (not) *unperceptive*, and (not) *thoughtless*.

2.5.3. Pearson correlations

To examine the associations between personality, welfare, and SWB we used Pearson correlations. After standardising the variables we correlated the personality dimensions and the welfare and SWB items and components. We interpreted the results adjusted for multiple tests using a Holm-Bonferroni correction.

2.5.4. Generalizable linear mixed models

We fit linear mixed-effects models using the nlme package ([Pinheiro et al., 2012](#)). In all models we included age and sex as fixed effects and facility as a random effect. Our dependent variables were the component scores based on the results of the PCAs of the welfare and SWB items. Each of these models included three combinations of fixed effects: 1) locomotor stereotypy frequency; 2) the five capuchin personality dimensions; 3) the five personality dimensions and locomotor stereotypy frequency. Locomotor stereotypy frequency was included in models as the aggregation of stereotypy scores across raters. Housing was not included in our models as only three capuchins were reported to ever be pair-housed, the rest were group housed. The dependent variables were converted into z-scores (mean \pm SD = 0 ± 1). The continuous predictor variables (stereotypy, age, and personality dimension) were

Table 2
 PCA of brown capuchin welfare items.

Item	Loading	h^2
Positive/negative experience	0.93	0.87
Number of relationships	0.93	0.86
Stress frequency	−0.90	0.81
Negative welfare	−0.84	0.71
Positive welfare	0.84	0.70
Quality of relationships	0.83	0.69
Social control	0.82	0.67
Environmental control	0.80	0.65
Stress coping	0.72	0.52
Psychological stimulation	0.61	0.38
Effect of experience	0.60	0.36
Physical health	0.50	0.25

Note. N = 66. Proportion of variance = 62%. h^2 = commonalities.

centred and divided by $2 \times SD$ to make the effect size comparable with the binary variable (sex) (Gelman, 2008). We then calculated conditional R^2 , which gives the variation explained by the fixed and random effects in the model, using the MuMIn package (Barton, 2015).

3. Results

3.1. Items interrater reliabilities

For the welfare items the ICC(3,1) ranged from 0.23 to 0.63 with a mean of 0.45 and the ICC(3,k) ranged from 0.51 to 0.86 with a mean of 0.72 (Table 1). For the SWB items the ICC(3,1) ranged from 0.51 to 0.74 with a mean of 0.63 and the ICC(3,k) ranged from 0.78 to 0.91 with a mean of 0.85 (Table 1). For the HPQ items the ICC(3,1) ranged from 0.12 to 0.74 with a mean of 0.39 and the ICC(3,k) ranged from 0.30 to 0.90 with a mean of 0.64 (S1). For ratings of stereotypic behaviour the ICC(3,1) was 0.64 and ICC(3,k) was 0.82 ($k = 2.61$).

3.2. PCA of welfare items and SWB items

A parallel analysis and scree plot of the welfare items showed a single component (Table 2). When we included both the welfare and SWB items in a joint-PCA we again found a single component. All 16 items had salient loadings on this component (Table 3); we named this component welfareSWB.

Table 4
 Pearson correlation coefficients of brown capuchin personality components and welfare and SWB components.

Component	Welfare	95% CI	SWB	95% CI	WelfareSWB	95% CI
Assertiveness	0.37	[0.14, 0.56]	0.49	[0.28, 0.65]	0.41	[0.18, 0.59]
Openness	0.25	[0.01, 0.46]	0.27	[−0.03, 0.48]	0.26	[0.02, 0.47]
Neuroticism	−0.28	[−0.49, −0.05]	−0.24	[−0.46, 0.00]	−0.28	[−0.49, −0.04]
Sociability	0.72	[0.58, 0.82]	0.69	[0.54, 0.80]	0.72	[0.58, 0.82]
Attentiveness	−0.19	[−0.41, 0.05]	−0.22	[−0.44, 0.02]	−0.21	[−0.43, 0.04]

Note. N = 66. Boldface values were significant at $p < 0.01$. Adjusted for multiple tests.

Table 5
 Models of brown capuchin welfare component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	b	CI	p	b	CI	p	b	CI	p
Intercept	0.18	[−0.22, 0.58]	0.042	0.17	[0.07, 0.42]	0.008	0.16	[−0.06, 0.39]	0.003
Stereotypy	−0.77	[−1.21, −0.33]	<0.001	–	–	–	−0.26	[−0.63, 0.10]	0.16
Age	−0.55	[−1.00, −0.10]	0.018	−0.58	[−1.00, −0.15]	0.009	−0.57	[−0.99, −0.15]	0.009
Male	−0.36	[−0.80, 0.08]	0.11	−0.38	[−0.72, −0.04]	0.031	−0.35	[−0.69, −0.01]	0.045
Sociability	–	–	–	1.21	[0.76, 1.65]	<0.001	1.03	[0.54, 1.53]	<0.001
Assertiveness	–	–	–	0.56	[0.20, 0.92]	0.003	0.56	[0.20, 0.92]	0.003
Openness	–	–	–	−0.28	[−0.76, 0.20]	0.23	−0.16	[−0.67, 0.35]	0.53
Neuroticism	–	–	–	−0.55	[−1.03, −0.07]	0.025	−0.63	[−1.11, −0.14]	0.012
Attentiveness	–	–	–	0.58	[0.16, 1.01]	0.008	0.58	[0.16, 1.00]	0.007

Note. N = 66. Boldface values were significant at $p < 0.05$. Variance explained: left panel: $R^2 = 0.31$, middle panel: $R^2 = 0.62$, right panel: $R^2 = 0.62$.

Table 3
 PCA of brown capuchin welfare and subjective well-being items.

Item	Loading	h^2
SWB Happiness as animal	0.93	0.87
Number of relationships	0.93	0.87
SWB Time animal is happy	0.92	0.85
Positive/negative experience	0.92	0.85
Stress frequency	−0.90	0.80
SWB Social satisfaction	0.88	0.78
SWB Goal achievement	0.85	0.73
Social control	0.84	0.71
Quality of relationships	0.83	0.70
Positive welfare	0.83	0.69
Negative welfare	−0.82	0.68
Environmental control	0.76	0.58
Stress coping	0.74	0.54
Effect of experience	0.59	0.35
Psychological stimulation	0.57	0.33
Physical health	0.49	0.24

Note. N = 66. Proportion of variance explained = 66%. h^2 = commonalities.

3.3. Pearson correlations of welfare, SWB, and personality

The welfare component and SWB component were highly correlated ($r = 0.91$, $p < 0.001$, 95% CI 0.86–0.95). Higher Sociability correlated with the higher welfare, higher SWB, and higher welfareSWB scores (Table 4); capuchins rated as more sociable were rated as having better welfare and higher happiness. Assertiveness correlated with the SWB component but not the welfare or welfareSWB components. The full correlation matrix including all items and components is available in Supplementary Table 2.

3.4. Mixed-effects models

3.4.1. Welfare

In the model that included stereotypy but not personality we found that capuchins that performed locomotor stereotypies more frequently were rated as being significantly lower in welfare (Table 5, left panel). In both the model with the five personality dimensions and in the model that included stereotypy frequency, capuchins lower in Neuroticism and higher in Sociability, Assertiveness, and Attentiveness were rated as having significantly better welfare (Table 5, middle and right panels).

Table 6

Models of brown capuchin SWB component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	<i>b</i>	CI	<i>p</i>	<i>b</i>	CI	<i>p</i>	<i>b</i>	CI	<i>p</i>
Intercept	0.09	[-0.23,0.40]	0.091	0.10	[-0.18,0.39]	0.10	0.10	[-0.17,0.36]	0.099
Stereotypy	-0.68	[-1.14,0.21]	0.005	-	-	-	-0.19	[-0.58,0.19]	0.32
Age	-0.48	[-0.94,-0.01]	0.046	-0.40	[-0.85,0.05]	0.079	-0.40	[-0.84,0.05]	0.078
Male	-0.18	[-0.65,0.29]	0.44	-0.24	[-0.59,0.11]	0.18	-0.22	[-0.58,0.14]	0.22
Sociability	-	-	-	1.13	[0.66,1.59]	<0.001	0.99	[0.47,1.51]	<0.001
Assertiveness	-	-	-	0.79	[0.42,1.16]	<0.001	0.79	[0.41,1.16]	<0.001
Openness	-	-	-	-0.23	[-0.72,0.26]	0.35	-0.14	[-0.67,0.39]	0.59
Neuroticism	-	-	-	-0.40	[-0.90,0.10]	0.11	-0.45	[-0.96,0.05]	0.079
Attentiveness	-	-	-	0.44	[-0.01,0.88]	0.056	0.42	[-0.03,0.86]	0.066

Note. N = 66. Boldface values were significant at $p < 0.05$. Variance explained: left panel: $R^2 = 0.19$, middle panel: $R^2 = 0.60$, right panel: $R^2 = 0.60$.

3.4.2. SWB

In the model that included stereotypy but not personality we found that capuchins that performed more stereotypy were rated as having significantly lower SWB (Table 6, left panel). In both the model with the five personality dimensions and the model including the personality dimensions and stereotypy, capuchins with higher Sociability and Assertiveness were rated as having significantly higher SWB (Table 6, middle and right panels). None of the other personality traits were significantly associated with SWB.

3.4.3. WelfareSWB

In the model that included stereotypy we found that capuchins who displayed stereotypic behaviour more frequently were rated as being significantly lower in welfareSWB (Table 7, left panel). In the model that included the five personality traits we found that capuchins higher in Sociability, Assertiveness, and Attentiveness and lower in Neuroticism had significantly higher welfareSWB (Table 7, middle panel). Finally, in the model with the five personality dimensions and stereotypy we again found higher Sociability, Assertiveness, and Attentiveness dimensions and lower Neuroticism were significantly related to higher ratings of welfare and SWB (Table 7, right panel).

3.4.4. Sensitivity test

We conducted sensitivity tests of the models by removing the 18 capuchins that had been concurrently rated on the welfare, SWB, and HPQ questionnaires. We found some effects were no longer significant. However, the effect sizes were largely similar suggesting that this was due to loss of statistical power. See Supplementary Tables 3–5 for full models.

4. Discussion

We found there was good evidence for staff agreement of ratings of welfare. The welfare items formed a single component. The welfare ratings were correlated with ratings of SWB and formed a single component with SWB items. These results suggest that ratings of SWB and welfare ratings are indistinguishable in brown capuchins. Welfare and SWB ratings were associated with the exhibition of

stereotypic behaviour. Finally, four of the five brown capuchin personality dimensions were associated with their welfare, even after adjusting for the presence of locomotor stereotypies. In all models the effect of Sociability and Assertiveness was larger than age, sex, and stereotypy.

These findings suggest that facilities housing animals can make use of the knowledge and experience of their staff to collect additional data on animal welfare. The reliability of ratings were relatively high and on par with reliabilities with those in studies of human personality (Gosling, 2001) and subjective well-being (Diener, 2009). As suggested by other authors, our results demonstrate that staff members are reliable, credible, and valuable sources of welfare data (Meagher, 2009; Whitham and Wielebnowski, 2009). Additionally, the welfare questionnaire was reported to take as little as three minutes showing the utility of questionnaires as a quick addition to traditional assessment methods. In the future we can expand on this research by examining the validity of welfare ratings in other nonhuman primate species.

The welfare items formed a single component suggesting that the aspects of welfare that our questionnaire covered (stress coping, physical health, control, etc.) are connected. Lower welfare and SWB ratings were associated with the higher frequency of stereotypic behaviour. As stereotypy is an abnormal behaviour specific to captivity (Mason, 1991) this suggests that the SWB and welfare questionnaires are measuring an observed welfare state. An alternative explanation may be that raters are familiar with the literature surrounding stereotypy and see it as a negative welfare indicator. Raters who had noted stereotypies were presumably more likely to rate that animal lower in welfare and SWB thus biasing ratings downward. This may be problematic as the literature is mixed regarding the validity of stereotypy as a negative welfare indicator (Mason and Latham, 2004; Mason, 1991). The fact that our stereotypy results validated our welfare and SWB measures still indicates the utility of the measure, but highlights the need for additional metrics that may be less obvious to observers, such as stress hormone levels, to provide further validation.

Sociability had the largest effect on welfareSWB, which fits what we know about the importance of primate sociality. Socially deprived primates are prone to self-injury and are at greater risk

Table 7

Models of brown capuchin welfareSWB component predicted by stereotypy and personality, controlling for age and sex with facility as a random effect.

Predictor	<i>B</i>	CI	<i>p</i>	<i>b</i>	CI	<i>p</i>	<i>b</i>	CI	<i>p</i>
Intercept	0.15	[-0.22,0.53]	0.047	0.15	[-0.10,0.40]	0.015	0.15	[-0.08,0.38]	0.014
Stereotypy	-0.76	[-1.20,-0.31]	0.001	-	-	-	-0.25	[-0.62,0.11]	0.17
Age	-0.54	[-1.00,-0.09]	0.020	-0.54	[-0.97,-0.12]	0.013	-0.54	[-0.96,-0.12]	0.013
Male	-0.31	[-0.76,0.14]	0.17	-0.34	[-0.68,-0.00]	0.048	-0.32	[-0.65,0.02]	0.070
Sociability	-	-	-	1.19	[0.75,1.63]	<0.001	1.02	[0.53,1.51]	<0.001
Assertiveness	-	-	-	0.63	[0.28,0.99]	<0.001	0.63	[0.28,0.98]	<0.001
Openness	-	-	-	-0.24	[-0.73,0.22]	0.28	-0.14	[-0.64,0.36]	0.57
Neuroticism	-	-	-	-0.53	[-1.01,-0.06]	0.029	-0.60	[-1.08,-0.13]	0.014
Attentiveness	-	-	-	0.55	[0.12,0.97]	0.013	0.54	[0.12,0.95]	0.013

Note. N = 66. Boldface values were significant at $p < 0.05$. Variance explained: left panel: $R^2 = 0.28$, middle panel: $R^2 = 0.63$, right panel: $R^2 = 0.63$.

of displaying stereotypies (Gottlieb et al., 2013; Lutz et al., 2003). Conversely, primates who create high quality social relationships benefit in terms of their psychological and physical health. For example, they have lower stress levels (Shutt et al., 2007; Terry, 1970) and reduced parasite loads (Akinyi et al., 2013; Crofoot et al., 2011).

We found Assertiveness to have the second largest effect on welfareSWB. The link between Assertiveness and welfare rating may be connected to rank, as a previous study of 38 of these subjects found that Assertiveness and alpha status were associated (Lefevre et al., 2014). Within some primate species high rank confers advantages that may lead to better welfare, including primary access to food (Boccia et al., 1988; Janson, 1985; Wittig and Boesch, 2003) and grooming (Coelho et al., 1983; Leinfelder et al., 2001; Parr et al., 1997), and reduced stress levels (Abbott et al., 2003; Sapolsky, 2004). Thus, it may be the link between Assertiveness and alpha status that creates the positive association with welfare and subjective well-being.

Personality differences have potential real world applications. For example, Capitanio et al. (2015) found that female rhesus macaques with more similar personalities were more likely to be successfully pair-housed. In addition, personality traits are associated with self-injurious behaviour in chimpanzees (Herrelko et al., 2012) and illness duration in golden snub-nosed monkeys (Jin et al., 2013). Our study adds to this literature by demonstrating that certain personality traits are associated with welfare ratings, which can be used to more carefully monitor capuchins with these traits.

There were limitations to our study. We collected data on locomotor stereotypy using questionnaires but we could not assess the effect of type of stereotypy. Furthermore, we did not examine other types of stereotypical behaviour. This may be important as different types of stereotypy (pacing, rocking, oral) may be related to different aspects of welfare. The stereotypy data was also collected a year after the welfare ratings, which may mean that some of the reported stereotypic behaviour may have developed during that time. However, the strong association between welfare and SWB suggest this may not be the case. Additionally, we included stereotypy to check the validity of the welfare questionnaire, but lacked an equivalent positive welfare indicator such as grooming.

The reliability and validity means that this welfare questionnaire, in addition to traditional assessment methods, may be a viable and practical tool. These findings also show that to account for welfare we need to expand our definition to include positive states of subjective well-being or happiness. Finally, this study reaffirms the strong links, identified in other species, including humans, between personality and welfare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.applanim.2016.05.029>.

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