



## Comparative Personality Assessment of Three Captive Primate Species: *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*

K. R. Baker<sup>1,2</sup> · S. E. G. Lea<sup>2</sup> · V. A. Melfi<sup>1,3</sup>

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**Abstract** Comparative studies of primate personality offer informative insights into the evolutionary origins of personality structure in primate species. Primate personality research has, however, focused on a limited number of species. We investigated personality in three relatively understudied species: Sulawesi black crested macaques (*Macaca nigra*), Barbary macaques (*Macaca sylvanus*), and common squirrel monkeys (*Saimiri sciureus*). We sent a 38-item questionnaire to all European zoological institutions holding the study species and keepers were required to rate individuals on all items. Assessments achieved good levels of interrater reliability. Principal components analysis (PCA) revealed Sociability and Dominance personality dimensions in all study species, an Emotionality dimension in both *M. nigra* and *M. sylvanus*, a Cautiousness dimension in *S. sciureus*, and a Human–Animal Sociability dimension in *M. sylvanus*. Sociability and Dominance dimensions were shown to have good construct validity, as assessed through appropriate relationships with sex and age and correlations with behavioral measures. The Sociability, Dominance, Emotionality, and Cautiousness dimensions were comparable with analogous dimensions in other primate species but aggressive-type traits did not load onto the Dominance dimension in the two *Macaca* spp. We suggest that this may be attributed to their more tolerant social systems compared to those of other primate species. The Human–Animal Sociability dimension could not be compared with other primate studies as, to date, there has been limited

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✉ K. R. Baker  
Kathy.baker@newquayzoo.org.uk

<sup>1</sup> The Whitley Wildlife Conservation Trust, Newquay Zoo, Trenance Gardens, Cornwall TR7 2LZ, UK

<sup>2</sup> The University of Exeter UK, University of Exeter, Washington Singer Laboratories, Exeter EX4 4QG, UK

<sup>3</sup> Present address: Taronga Conservation Society Australia, Mosman, NSW 2088, Australia

investigation of human-directed personality dimensions in captive primates. Our findings suggest that the two *Macaca* species are more similar to each other, in terms of their personality structure, than either is to *S. sciureus*, which suggests phylogenetic similarity is an important predictor of personality. However, further comparative analysis of a wider range of primate species is needed to inform theories regarding the evolution of primate personality structure.

**Keywords** Cross-species · Macaque · Personality · Primates · Squirrel monkey · Zoo

## Introduction

The study of primate personality, “individual differences in behaviour which are or are thought to be stable across time and situations” (Freeman and Gosling 2010, p. 654), informs our understanding of the evolution of personality in humans (Weiss *et al.* 2011) and can be a valuable tool in captive management (Coleman 2012). However, much of the published literature has focused on a limited number of species; only 7 % of the known primate species have been studied, with the largest proportion of research dedicated to chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*) (Freeman and Gosling 2010). Species comparisons offer us opportunities to investigate ecological and/or phylogenetic origins of personality (Gosling 2001; Gosling and Graybeal 2007; Smith and Blumstein 2008). To achieve these comparisons we need to investigate fully the reliability and validity of personality assessments in a wider range of primate species; fewer than a third of primate personality studies report reliability and/or validity data (Freeman and Gosling 2010). Another issue when comparing species is that most studies of primate personality use similar rating instruments even though they originally may have been developed for very different species. Although this makes cross-species comparisons possible, some authors suggest that the rating instruments should be more species specific or at least include some species-specific traits (Gosling 2001; Uher 2008).

It is not usually practicable to make interspecific comparisons at the level of personality traits, partly because there are simply too many traits, but mainly because not all traits are expected to reach the required standard of reliability in all species (Gosling and Vazire 2002). Accordingly, it is usual to reduce the large list of personality traits to a smaller number of underlying personality dimensions using factor analysis. Interspecific comparisons are made by comparing personality structure, i.e., the personality dimensions described in each species. Anywhere from three (*Macaca mulatta*: Stevenson-Hinde and Zunz 1978) to six (*Pan troglodytes*: King *et al.* 2005; *M. mulatta*: Weiss *et al.* 2011) underlying personality dimensions have been suggested in studies of primate personality, and the resulting personality structure is necessarily influenced by the original rating instrument used by the researchers.

The validity of resulting dimensions is normally assessed through relationships between personality ratings and variables such as life-history parameters and/or behavior. For example, sex differences in personality are known to occur because of the different ecological niche each sex occupies (Gosling and John 1999). Males in many primate species must engage in activities such as male–male aggression to secure mating rights and, as such, score higher than females on Dominance type personality

dimensions (King *et al.* 2008). Although personality dimensions should generally be resistant to large changes over time, minor changes in dimensions across age groups are known to occur such as declines in Extraversion, particularly facets related to gregariousness, as animals age (King *et al.* 2008). Personality assessments are validated through correlations with behavior observed under natural conditions (Pederson *et al.* 2005) or during experimental conditions such as novel object tests. Novelty tests have been widely used to directly assess personality traits such as boldness in nonprimate animals (Carere *et al.* 2005; Dingemanse *et al.* 2002; Schuett and Dall 2009), and their use in assessing novelty-seeking and/or boldness in both wild and captive primates has also been well demonstrated (Carter *et al.* 2012; Massen *et al.* 2013).

The relevance of a comparative approach to primate personality has been demonstrated recently through the use of the hominid personality questionnaire with *Macaca mulatta* (Weiss *et al.* 2011). The authors established that personality traits can be reduced to six dimensions in this species: Confidence, Openness, Dominance, Friendliness, Activity, and Anxiety (Weiss *et al.* 2011), and, when compared to research that also used the hominid personality questionnaire with *Pan troglodytes* (King and Figueredo 1997) and orangutans (*Pongo* spp.: Weiss *et al.* 2006), they suggest that similarities and differences between the three species' extant personality structures can inform personality phylogeny. Specifically they suggest that 1) Anxiety and Confidence in *Macaca* spp. blend to form Neuroticism in *P. troglodytes* and *Pongo* spp. and that Sociability and Activity blend to form Extraversion; 2) Openness combines with Conscientiousness to establish Intellect in extant *Pongo* spp. (and their ancestral relatives); 3) Conscientiousness is formed from items that historically loaded onto Neuroticism and Dominance; and 4) Humans have lost a separate Dominance dimension as it has combined with Altruism to form human Agreeableness (Weiss *et al.* 2011).

The first objective of our study was to assess the personality of three previously understudied species, the Sulawesi crested black macaque (*Macaca nigra*), the Barbary macaque (*Macaca sylvanus*), and the common squirrel monkey (*Saimiri sciureus*), using the same set of trait adjectives. We chose *M. nigra* and *M. sylvanus* as study species as they both exhibit the typical features of macaque sociality: multimale multifemale groups, female biased sex ratio, male dispersal and female philopatry, stable female hierarchies, and male dominance ranks dependant on competitive abilities (Thierry 2007). However, both species exhibit a more tolerant social style than other macaque species for which personality data exist such as *M. mulatta* (Thierry 2007); they therefore offer an interesting social comparison with other macaque species. In addition, Thierry *et al.* (2000) hypothesize that ancestral macaque species would have resembled grade three species such as *M. sylvanus* so comparing them with other species in the *Macaca* genus is especially useful for investigating the influence of phylogeny on personality structure in the genus. We chose *S. sciureus* as a study species as they are a more distantly related species but their social structure is not unlike that of *Macaca* spp. in that they exist in large multimale multifemale groups; exhibit female philopatry and male dispersal; have a male dominant, linearly ranked social organization; and males are usually dominant over all females (Boinski *et al.* 2001).

We tested the interrater reliability of personality assessments, i.e., the ability of two or more raters to agree on the ratings given to a particular individual, and the construct validity of personality assessments, i.e., the ability of the rating procedure to measure a "postulated attribute" (Cronbach and Meehl 1955; Uher 2011b). Primate personality

studies that have been subjected to reliability testing have demonstrated that high interrater reliability estimates, comparable to human and other animal personality research, can be achieved (Freeman and Gosling 2010). Thus we predicted that good levels of interrater agreement would be demonstrated for our study species.

The validity of the derived personality measures for each species was tested in three ways.

- 1) Across the entire sample for each species, we compared personality measurements between the sexes and assessed relationships between personality measurements and age. Previous studies have demonstrated that personality will vary as a function of age and sex (King *et al.* 2008), so we predict that valid personality measurement will show such variation in our study species.
- 2) At selected zoos for each species, we conducted systematic detailed observations of the spontaneous behavior of individuals. We predicted that personality measurements should show relationships with appropriate behavioral measures.
- 3) Again at selected zoos, we carried out an experiment in which a novel object was placed in the monkeys' enclosures, and behavior toward it was observed. Given the pervasive evidence of individual differences in boldness/shyness, we predicted that personality measures in our study would correlate with behavior in novel test situations.

The second objective of our study was to compare the personality structure of the three species. We predicted that the personality structure in all our study species will resemble that of other primates, in that broad dimensions such as Sociability will emerge in all three species, but that we will find more similarities between *Macaca nigra* and *Macaca sylvanus*, than between either of the *Macaca* species and *Saimiri sciureus*, owing to their closer phylogenetic relatedness.

## Methods

### Personality Questionnaires

Questionnaires consisted of a list of personality traits, which we developed using an Eclectic approach (Uher 2008). We used the original list of traits from Stevenson-Hinde and Zunz (1978) as a starting point, as many other primate studies have used this original list for their studies (Capitanio 2011; Martin 2005). Based on consultation with other researchers and animal keepers we changed some of the trait labels to aid understanding (definitions were kept similar). It is also important to include traits that have relevance to the species' natural ecology and behavior (Uher and Assendorpf 2008), so we added traits to the list based on the behavioral repertoire of *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*, as determined from existing literature, and by discussing the traits with various primate experts and animal keepers. We also added traits that focused on human–animal interactions, as humans can be an important element of a captive animal's environment (Gosling 1998). Each trait adjective was accompanied with a two- to three-sentence behavioral definition. We included this to help the raters understand what was meant by the trait adjective in an attempt to

improve interrater reliability. We kept the trait adjectives the same across all species but adjusted some definitions according to species-specific behavior.

The final questionnaire contained 38 personality traits; 32 traits referred to the individual behavior toward conspecifics and the environment, and 6 traits referred to human–animal interactions. We asked raters to rate each individual on a 7-point scale (1 = the trait is not represented in the individual; 7 = the trait is highly represented in the individual). We included detailed instructions for the raters to ensure questionnaires were filled out as accurately as possible. We obtained support letters from the British and Irish Association of Zoos and Aquaria (BIAZA) Research Group, and the third author in her capacity as European *Macaca nigra* studbook keeper, which we sent with the questionnaires. We could not obtain support letters from the *Macaca sylvanus* and *Saimiri sciureus* studbook keepers as, at the time of development, those positions were vacant.

We sent the majority of personality questionnaires via hard copy and e-mail in November 2009 to European zoos holding *Macaca nigra*, *Macaca sylvanus*, and/or *Saimiri sciureus* as recorded by the International Species Information System (ISIS). For any zoos that were included in the behavioral study we sent questionnaires to the institutions 1 week before the behavioral observations were due to take place and the first author (K. Baker) collected them in person after the behavioral observations had taken place. For *M. nigra*, 11 of 18 institutions returned personality questionnaires (61 % response rate), and 64 individuals (23 males and 41 females; age range 1–21 yr) were rated using the questionnaire. For *M. sylvanus*, 6 of 28 institutions returned personality questionnaires (22 % response rate) and 62 individuals (29 males and 33 females; age range 2–21 yr) were rated. For *S. sciureus*, 7 of 52 institutions returned personality questionnaires (13.4 % response rate), and 69 individuals (34 males and 35 females; age range 2–19 yr) were rated using the questionnaire. All primates included in the study were captive bred and parent reared unless otherwise stated.

### Behavior Observations and Novel Object Tests

For *Macaca nigra* K. Baker conducted behavioral observations and novel object tests at three institutions (Paignton Zoo Environmental Park UK, Newquay Zoo Environmental Park UK, and Marwell Wildlife UK) on a total of 22 individuals (9 males and 13 females). For *Macaca sylvanus* K. Baker conducted behavioral observations at three institutions (Edinburgh Zoo UK, Folly Farm Zoo UK, and Apenheul Primate Park, Netherlands) on a total of 28 individuals (9 males and 19 females) and novel object tests at two institutions (Edinburgh Zoo and Folly Farm) on a total of 20 individuals (6 males, 14 females). For *Saimiri sciureus* K. Baker conducted behavioral observations at two institutions (Living Links Research Centre at Edinburgh Zoo UK, Shaldon Zoo UK), and a second trained observer conducted behavioral observations at one institution (Dudley Zoo UK) on a total of 19 individuals (9 males and 10 females) and novel object tests at two (Living Links research center and Shaldon Zoo) institutions on a total of 13 individuals (6 males and 7 females).

During 10-min focal follows, K. Baker recorded state behaviors using instantaneous sampling every 30 s and event behaviors using all-occurrence sampling (Martin and Bateson 2007). Species ethograms used for behavioral data collection are included in the electronic supplementary material (ESM). K. Baker carried out at least one focal

observation per individual, per day, for a minimum of 9 d, and these observations were counterbalanced across the hours of the day. For *Macaca nigra* K. Baker observed each individual for a mean of 1 h 48 min ( $\pm 6$  min); for *Macaca sylvanus* K. Baker observed each individual for a mean of 2 h 8 min ( $\pm 8$  min); for *Saimiri sciureus* K. Baker and the second trained observer observed each individual for a mean of 1 h 51 min ( $\pm 12$  m). Using the behavioral data we established the mean percentage of time spent performing each of the state behaviors, and the mean frequency (per minute) of all event behaviors, during the observation period for each individual.

We chose a traffic cone as the novel object because of its durability and ease of use; although the subjects may have seen traffic cones in the vicinity of their enclosures before the experiment they had never been placed inside an enclosure, e.g., as part of an enrichment program, so the situation could still be considered novel. K. Baker used the following standardized method for novel object tests. Animal keepers shut out all primates from one area of the enclosure while the traffic cone was placed in view of the observer (test area). A video camera was set up and K. Baker recorded the subjects' responses on release back into the test area; K. Baker recorded 1 h of the primates' behavior, post release, and coded it at a later date. The behavioral measures that we used to gauge the subjects' responses to the cone were latency to make contact (*latency to contact*) and frequency of contacts with the cone (*frequency of contacts*).

## Data Analysis

We performed the following data analysis separately for each species (unless otherwise stated). We conducted all statistical analyses using SPSS v. 18 (SPSS®, IBM®, Chicago, IL).

To determine the interrater reliability of each personality trait, we used questionnaire data for individuals that were rated by two or more observers to calculate intraclass correlation coefficients (ICC[3,  $k$ ] and ICC[3, 1]; Shrout and Fleiss 1979) for each personality trait. ICC[3,  $k$ ] represents the reliability of the mean of  $k$  raters, so is of interest if researchers want to use the mean of  $k$  raters in further analysis, while ICC[3, 1] represents the reliability of an individual rater so it would be of interest if using just one rater's data or if comparing results to previous studies (reliability estimates can be inflated if the number of raters is increased). We used ICC[3,  $k$ ] to assess the traits that should be retained for further analysis, as we used mean ratings of animal personality to construct the personality dimension scores. We included only traits reaching moderate reliability (ICC[3,  $k$ ]  $> 0.50$ ) in the principal components analysis (PCA). Although we could conduct the reliability analysis using only the data from a subset of subjects, owing to sampling constraints, i.e., number of individuals and/or raters at each zoo, if we found traits to be reliable they were assumed to be reliable across all zoos so that all the personality data could be entered into the PCA analysis.

As data collection at each zoo was performed by a single observer we did not conduct interobserver reliability testing on the behavioral observations themselves. Before the beginning of the study, however, two observers (the principal author, K. Baker, and another researcher familiar with primate behavior) carried out observations on example individuals of each species using the method employed in the study. We tested observations using Cohen's  $\kappa$  (Kaufman and Rosenthal 2009) so that we could ensure the reliability of species ethograms and data collection methods for future use.

Observations were found to show substantial interobserver agreement (*Macaca* spp.  $\kappa = 0.74$ ,  $P < 0.001$ ; *Saimiri sciureus*  $\kappa = 0.64$ )

We ran an exploratory PCA using the mean trait scores for each individual. We used the Kaiser criterion, interpretation of the scree plot, and parallel analysis to establish the number of components that should be retained (O'Connor 2000). We conducted the analysis using a Varimax rotation but also ran a PCA with Promax rotation to establish the degree of correlation between the resulting components and to establish whether allowing components to correlate altered the structure (Weiss *et al.* 2011). We labeled dimensions based on the individual traits that loaded onto them. We created personality dimension scores using subjects' original scores on all traits that had salient loadings ( $>0.40$ ) on a particular dimension and establishing a mean score for that dimension; for negatively loaded traits we calculated a reverse score by subtracting the original score from 8, i.e., to correspond to our original 1–7 scale for each trait. If a trait had salient loadings on more than one dimension we assigned it to the dimension with the higher loading. We conducted independent samples *t*-tests to test for any differences in the mean personality dimension scores between males and females. We also calculated Pearson's product-moment correlations to examine any relationship between age (years) and personality dimension scores.

We reduced state behaviors into broad behavioral categories: active, social positive, social negative, solitary, and environment interaction. Slightly different event behaviors were recorded depending on species: Event behaviors of *Macaca nigra* were scratching, lipsmacking, dominance events, and submissive events; event behaviors of *Macaca sylvanus* were scratching, open-mouth display, dominance events, and submissive events; and event behaviors of *Saimiri sciureus* were social positive, scent marking, and anxiety events. Full species ethograms are included in ESM Appendix 1. To correct for any interzoo differences we standardized data used for validity analysis, using *z*-scores, within each zoo (Uher 2011a). To evaluate the relationship between personality and behavior while taking into account the effect of age and sex on the behavioral measures, we analyzed the data using generalized linear models (GLMs). We ran separate models with each behavioral measure, and the response to novelty measures, entered as the response variable. Predictor variables included in each model were sex (male vs. female) as a factor, and age (years) and personality dimension scores as covariates. We included all main effects and first-order two-way interactions between personality scores and each of the contextual variables (age and sex) in the model. We fitted models using a backward elimination process to find the minimum adequate model for explaining the variance of the response variable. We retained only significant explanatory variables and two-way interactions and interpreted models with the lowest Akaike's information criterion (AIC) value. All significance tests were two-tailed. Depending on the distribution of the data we ran GLMs with normal distribution and identity link functions, inverse Gaussian distribution with identity link functions, or  $\gamma$  distribution with log link functions.

Several individuals of *Macaca* spp. did not touch the novel object during the novel object tests (*Macaca nigra*  $N = 8$ , *Macaca sylvanus*,  $N = 7$ ), so we ran two separate analyses: 1) a GLM with a binomial distribution and logit link function to assess the main effects and first-order two-way interactions of personality scores, age, and sex on the binary response variable touched/did not touch the novel object; and 2) using only data from individuals that had touched the novel object (*M. nigra*  $N = 14$ , *M. sylvanus*  $N = 13$ ), a GLM with a Tweedie distribution and log link function to assess the main

effects of personality scores, age, and sex on the *latency to contact* and *frequency of contacts* scores. We could only assess main effects in these models owing to the reduced sample size. For *Saimiri sciureus* none of the individuals subjected to the novel object test touched the object within the observation period. The two behavior measures that we recorded during the novel object tests were therefore latency to approach within 10 body lengths of the novel object (*latency to approach*) and frequency of occurrences of the subject being present within 10 body lengths of the novel object (*frequency of approaches*). We used a GLM with a Tweedie distribution and log link function to assess the main effects of personality scores, age, and sex on the *latency to approach* scores. We used a GLM with a normal distribution and identity link function to assess the main effects of personality scores, age, and sex on the *frequency of approaches* scores.

## Results

### Interobserver Reliability

For *Macaca nigra* the mean ICC[3, *k*] values for each trait ranged from  $-0.89$  (cautious) to  $0.92$  (dominant) with an overall mean of  $0.54$  (Table I). For *Macaca sylvanus* the mean ICC[3, *k*] values for each trait ranged from  $-0.66$  (relaxed) to  $0.92$  (playful) with an overall mean of  $0.52$  (Table I). For *Saimiri sciureus* the mean ICC[3, *k*] for each trait ranged from  $-0.58$  (persistent) to  $0.81$  (dominant) with an overall mean of  $0.39$  (Table I). The number of traits reaching the criterion of ICC[3, *k*]  $>0.50$ , and therefore used for further analysis were 24 for *M. nigra*, 25 for *M. sylvanus*, and 18 for *S. sciureus* (Table I).

### Principal Components Analysis

Component structure did not differ qualitatively between the Varimax and Promax rotations and we report results from the Varimax rotation for all further analysis. The first three eigenvalues for the *Macaca nigra* and *Saimiri sciureus* datasets and the first four eigenvalues for the *Macaca sylvanus* dataset were greater than expected by chance at the 95 % confidence level. To summarize, we labeled *M. nigra* dimensions as Dominance, Sociability, and Emotionality; *M. sylvanus* dimensions as Sociability, Dominance, Human–Animal Sociability, and Emotionality; and *S. sciureus* dimensions as Sociability, Dominance, and Cautiousness (Table II). We have included a full breakdown of trait loadings for each species in ESM Appendix 2. Cronbach  $\alpha$  values for the scales based on the traits loading on each dimension ranged from  $0.57$  to  $0.91$  (Table II).

### Sex/Age Relationships with Personality

Male *Macaca nigra* scored significantly higher than female *M. nigra* on both the Dominance (*t*-test:  $t = 2.49$ , d.f. = 61,  $P = 0.03$ , Cohen's  $d = 0.74$ ; Fig. 1a) and Sociability (*t*-test:  $t = 2.49$ , d.f. = 61,  $P = 0.03$ , Cohen's  $d = 0.56$ ; Fig. 1a) dimensions but there was no significant difference in Emotionality scores between the two sexes (*t*-test:  $t = 0.53$ , d.f. = 61,  $P = 0.60$ , Cohen's  $d = 0.15$ ; Fig. 1a). There were no significant



**Table 1** Mean reliability estimates (ICC[3, *k*] and ICC[3,1]) for each personality questionnaire item

Personality trait	<i>Macaca nigra</i>		<i>Macaca sylvanus</i>		<i>Saimiri sciureus</i>	
	ICC[3, <i>k</i> ]	ICC[3,1]	ICC[3, <i>k</i> ]	ICC[3,1]	ICC[3, <i>k</i> ]	ICC[3,1]
Active <sup>a</sup>	<b>0.82</b>	0.64	<b>0.78</b>	0.61	<b>0.57</b>	0.47
Affiliative <sup>a</sup>	<b>0.62</b>	0.52	<b>0.71</b>	0.52	<b>0.65</b>	0.47
Aggressive <sup>a</sup>	<b>0.83</b>	0.69	<b>0.68</b>	0.49	<b>0.76</b>	0.59
Alert	0.48	0.40	<b>0.63</b>	0.46	0.44	0.26
Allogroom	0.38	0.44	<b>0.59</b>	0.36	-0.02	0.08
Assertive <sup>a</sup>	<b>0.92</b>	0.76	<b>0.56</b>	0.42	<b>0.69</b>	0.56
Calm	-0.07	0.31	0.32	0.15	0.18	0.15
Cautious	-0.89	0.07	<b>0.52</b>	0.33	<b>0.69</b>	0.49
Curious	<b>0.69</b>	0.53	0.38	0.20	<b>0.80</b>	0.62
Dominant <sup>a</sup>	<b>0.92</b>	0.81	<b>0.87</b>	0.74	<b>0.81</b>	0.66
Eccentric	<b>0.72</b>	0.60	<b>0.62</b>	0.48	0.22	0.10
Effective <sup>a</sup>	<b>0.55</b>	0.41	<b>0.51</b>	0.30	<b>0.59</b>	0.43
Excitable	0.04	0.43	0.48	0.30	<b>0.63</b>	0.47
Fearful	<b>0.70</b>	0.61	0.42	0.29	<b>0.51</b>	0.37
Flexible <sup>a</sup>	<b>0.67</b>	0.63	<b>0.62</b>	0.39	<b>0.55</b>	0.43
Friendly	0.34	0.17	<b>0.68</b>	0.45	0.05	0.14
Imaginative	<b>0.56</b>	0.43	<b>0.63</b>	0.45	0.05	0.20
Inquisitive <sup>a</sup>	<b>0.87</b>	0.69	<b>0.78</b>	0.60	<b>0.76</b>	0.58
Intelligent	0.39	0.37	<b>0.62</b>	0.39	0.30	0.33
Irritable	<b>0.50</b>	0.43	<b>0.67</b>	0.44	0.10	0.16
Jealous <sup>a</sup>	<b>0.75</b>	0.53	<b>0.69</b>	0.54	<b>0.71</b>	0.52
Lazy	<b>0.84</b>	0.67	0.36	0.27	0.24	0.11
Obstinate	0.14	0.18	0.09	0.07	-0.04	0.06
Opportunistic	<b>0.85</b>	0.69	0.40	0.24	-0.03	0.31
Persistent	<b>0.68</b>	0.58	0.49	0.36	-0.58	0.31
Playful <sup>a</sup>	<b>0.89</b>	0.76	<b>0.92</b>	0.82	<b>0.68</b>	0.59
Scapegoating	-0.38	0.16	<b>0.51</b>	0.37	0.12	0.05
Relaxed	0.44	0.20	-0.66	0.08	-0.18	0.13
Shy	<b>0.82</b>	0.66	0.37	0.20	<b>0.65</b>	0.52
Solitary	<b>0.57</b>	0.63	<b>0.58</b>	0.46	0.30	0.27
Subordinate <sup>a</sup>	<b>0.87</b>	0.72	<b>0.73</b>	0.50	<b>0.73</b>	0.52
Tense	<b>0.75</b>	0.65	0.24	0.22	<b>0.50</b>	0.40
HA-Sociable <sup>a</sup>	<b>0.64</b>	0.53	<b>0.80</b>	0.50	<b>0.67</b>	0.54
HA-Cautious	0.48	0.41	<b>0.76</b>	0.52	0.44	0.36
HA-Cooperative	0.19	0.20	<b>0.66</b>	0.29	0.30	0.21
HA-Nervous	-0.02	0.36	<b>0.62</b>	0.20	0.43	0.29
HA-Aggressive	<b>0.56</b>	0.57	-0.01	0.26	0.28	0.18
HA-Oblivious	0.49	0.47	0.19	0.15	0.17	0.16

The reliability estimates were calculated using data from zoos where more than one rater assessed the primates: *Macaca nigra* (six zoos), *Macaca sylvanus* (three zoos), *Saimiri sciureus* (five zoos). Questionnaire data were collected from European zoos between November 2009 and February 2011. Bold values indicate that the ICC[3, *k*] > 0.50. HA indicates the trait refers to Human-Animal interactions

<sup>a</sup> Trait ratings achieved mean ICC[3,*k*] > 0.50 across all three species

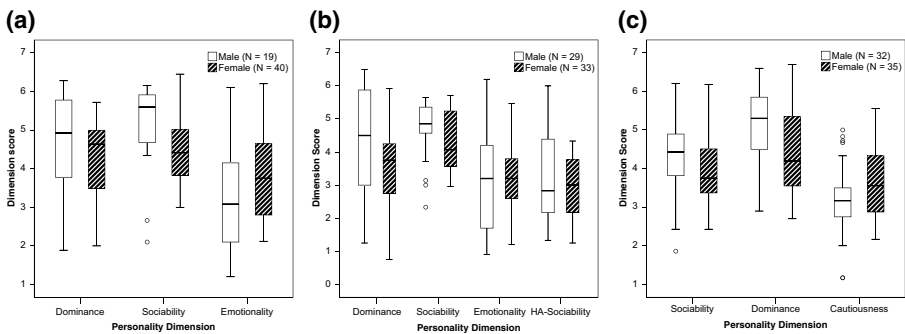
**Table II** Summary of principal components analysis (PCA) performed using reliable personality traits (those achieving ICC[3, *k*] >0.50) for *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*

Species	No. of traits	Personality dimension label	Eigenvalue	% variance explained by dimension	Cronbach's $\alpha$
<i>M. nigra</i> (N = 64)	24	Dominance	8.15	33.52	0.77
		Sociability	3.66	15.47	0.90
		Emotionality	3.16	12.90	0.80
<i>M. sylvanus</i> (N = 62)	25	Sociability	6.86	27.43	0.88
		Dominance	5.85	23.41	0.84
		Human–Animal Sociability	3.09	12.36	0.63
		Emotionality	2.08	8.33	0.87
<i>S. sciureus</i> (N = 69)	18	Sociability	6.64	36.87	0.83
		Dominance	3.30	18.32	0.91
		Cautiousness	1.93	10.69	0.57

Dimensions were retained based on parallel analysis. Questionnaire data were collected from European zoos between November 2009 and February 2011

differences between male and female mean scores for *Macaca sylvanus* on any of the personality dimensions (*t*-tests: Dominance,  $t = 1.87$ , d.f. = 60,  $P = 0.06$ , Cohen's  $d = 0.49$ ; Sociability,  $t = 1.94$ , d.f. = 60,  $P = 0.06$ , Cohen's  $d = 0.50$ ; HA [Human–Animal]–Sociability,  $t = 0.27$ , d.f. = 60,  $P = 0.78$ , Cohen's  $d = 0.07$ ; Emotionality,  $t = -0.45$ , d.f. = 60, Cohen's  $d = 0.12$ ; Fig. 1b). Male *Saimiri sciureus* scored significantly higher than females on both the Dominance (*t*-test:  $t = 2.28$ , d.f. = 65,  $P = 0.03$ , Cohen's  $d = 0.57$ ; Fig. 1c) and Sociability (*t*-test:  $t = 2.08$ , d.f. = 65,  $P = 0.04$ , Cohen's  $d = 0.52$ ; Fig. 1c) dimensions but there was no significant difference in Cautiousness scores between the two sexes (*t*-test:  $t = -1.93$ , d.f. = 65,  $P = 0.06$ , Cohen's  $d = 0.48$ ; Fig. 1c).

Age of *Macaca nigra* correlated significantly negatively with scores on the Sociability dimension (Pearson's correlation:  $r = -0.54$ ,  $P < 0.001$ ,  $N = 63$ ) but not with scores on the other personality dimensions (Pearson's correlations: Dominance



**Fig. 1** Personality scores for each species by sex class. (a) *Macaca nigra*. (b) *Macaca sylvanus*. (c) *Saimiri sciureus*. All data were collected from European zoos between November 2009 and February 2011. Shown is a boxplot of dimension scores representing the interval between the first and third quartile, with the median symbolized by the thick line inside. Whiskers indicate the values within 1.5 times the interquartile range (IQR). Outliers are represented by circles.

$r = 0.03$ ,  $P = 0.85$ ,  $N = 63$ ; Emotionality  $r = -0.24$ ,  $P = 0.85$ ,  $N = 63$ ). Age of *Macaca sylvanus* correlated negatively with Sociability (Pearson's correlation:  $r = -0.81$ ,  $P < 0.001$ ,  $N = 50$ ), and positively correlated with Emotionality scores (Pearson's correlation:  $r = 0.32$ ,  $P < 0.05$ ,  $N = 50$ ) but not with scores on the other personality dimensions (Pearson's correlations: Dominance,  $r = 0.16$ ,  $P = 0.27$ ,  $N = 50$ , HA–Sociability  $r = 0.13$ ,  $P = 0.36$ ,  $N = 50$ ). Age of *Siamiri sciureus* correlated negatively with Sociability (Pearson's correlation:  $r = -0.48$ ,  $P < 0.01$ ,  $N = 52$ ), and positively with Cautiousness (Pearson's correlation:  $r = 0.28$ ,  $P < 0.05$ ,  $N = 52$ ) but not with Dominance (Pearson's correlation:  $r = 0.22$ ,  $P = 0.12$ ,  $N = 52$ ).

### Validity Analysis

In all three species, personality measures on at least one personality dimension correlated with behavioral measures. We present each species' results separately in the text that follows. As age was a covariate, if any significant interactions between Age and Personality score were identified we explored these through comparing young (<5 yr) and old individuals for clarity of exposition.

**Macaca nigra** In *M. nigra* the Dominance dimension had the most significant relationships with observed behavior (Table III). It had significant positive relationships with time spent solitary, frequency of scratching, and frequency of dominant events (yawning and displacements) and significant negative relationships with time spent engaged in positive social behavior and time spent interacting with environmental stimuli. Where there were interactions between Dominance and sex the nature of the relationship, i.e., positive or negative, remained the same but it was more pronounced in one sex (Table III). There were interactions between Dominance and age, and in some cases the relationship was reversed in one age class; e.g., there was a positive relationship between Dominance scores and social positive behavior in young (<5 yr) individuals (Table III). There was a significant positive main effect of Emotionality on the rate of scratching that was affected by age; older individuals exhibited a negative relationship between Emotionality and scratching (Table III). Sociability exhibited significant interactions with sex on both social positive behavior and frequency of scratching. There was a negative relationship between Sociability and social positive behavior in females and a neutral relationship in males (Table III). There was a negative relationship between Sociability and scratching in males and a positive relationship in females (Table III). In the analysis of the novel object tests, there were no significant predictors in the GLM model using touched/did not touch the novel object as a binary response variable, or in the GLM model using *frequency of touches* as the response variable. There was a significant negative main effect of Dominance on *latency to touch*, indicating that individuals scoring higher on this dimension were quicker to touch the novel object (Table IV).

**Macaca sylvanus** In *M. sylvanus* the Dominance dimension had the most significant relationships with observed behavior (Table III). Dominance had significant positive relationships with time spent active and negative relationships with frequency of open-mouth display and frequency of submissive events. Where there were interactions between Dominance and sex/age the nature of the relationship remained the same,

**Table III** Summary of generalized linear model (GLM) statistics showing 1) significant main effects of personality dimension scores and 2) interactions between personality dimensions scores and sex/age on behavioral measures for *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*

Species	Behavior	Significant main effects and interactions	Wald $\chi^2$	d.f.	P value	Nature of relationship
<i>M. nigra</i>	Social Positive	Age	22.30	1	<0.001	Positive
		Dominance	13.31	1	<0.001	Negative
		Sex*Dominance	5.66	1	0.017	♂ = <b>Negative</b> , ♀ = negative
		Sex*Sociability	14.43	2	0.001	♂ = Neutral, ♀ = negative
		Age*Dominance	10.40	1	0.001	Old = negative, young = positive
	Solitary	Dominance	8.96	1	0.003	Positive
		Age*Dominance	8.46	1	0.004	<b>Old = positive</b> , young = positive
	Environmental Interaction	Sex	14.27	1	<0.001	Higher in males
		Dominance	12.00	1	0.001	Negative
		Sex*Dominance	10.74	1	0.001	♂ = <b>Negative</b> , ♀ = negative
	Scratch (E)	Age	4.70	1	0.030	Positive
		Dominance	9.07	1	0.003	Positive
		Emotionality	28.03	1	<0.001	Positive
		Sex*Sociability	33.67	2	<0.001	♂ = Negative, ♀ = positive
		Age*Dominance	7.42	1	0.006	Old = positive, young = negative
		Age*Emotionality	17.57	1	<0.001	Old = negative, young = positive
	Dominance (E)	Dominance	61.13	1	<0.001	Positive
Sex*Dominance		38.95	1	<0.001	♂ = Positive, ♀ = <b>positive</b>	
<i>M. sylvanus</i>	Active	Age	6.84	1	0.009	Negative
		Dominance	18.83	1	<0.001	Positive
		Emotionality	12.17	1	<0.001	Positive
		Sex*Sociability	40.01	2	<0.001	♂ = Positive, ♀ = <b>positive</b>
		Age*Dominance	23.95	1	<0.001	Old = Negative, young = positive
		Age*Emotionality	16.23	1	<0.001	Old = positive, young = negative
	Social negative	Sex*Dominance	21.35	1	<0.001	♂ = <b>Negative</b> , ♀ = negative
	Solitary	Sociability	85.34	1	<0.001	Negative
	Open-mouth (E)	Dominance	3.88	1	0.049	Negative
		Age*Dominance	6.25	1	0.012	<b>Old = negative</b> , young = negative
	Scratch (E)	Dominance	9.44	1	0.002	Negative
		Age*Dominance	6.25	1	0.012	<b>Old = negative</b> , young = negative
	Dominance (E)	Sex	8.10	1	0.004	Higher in males
		Age*Dominance	10.26	1	0.001	Old = positive, <b>young = positive</b>
	Submissive (E)	Dominance	15.15	1	<0.001	Negative
		Dominance	22.69	1	<0.001	Negative
	<i>S. sciureus</i>	Active	Cautiousness	36.80	1	<0.001
Sex*Dominance			20.43	1	<0.001	♂ = <b>Negative</b> , ♀ = negative
Age*Dominance			45.18	1	<0.001	Old = negative, young = positive
Age*Cautiousness			45.55	1	<0.001	Old = neutral, young = positive
Sociability			14.36	1	<0.001	Positive
Social		Sociability	14.36	1	<0.001	Positive
		Sex	7.36	1	0.007	Higher in females
Environmental Interaction		Sex	7.36	1	0.007	Higher in females
		Age	8.69	1	0.003	Negative

**Table III** (continued)

Species	Behavior	Significant main effects and interactions	Wald $\chi^2$	d.f.	P value	Nature of relationship
		Dominance	6.85	1	0.009	Negative
		Cautiousness	6.74	1	0.009	Positive
		Sex*Sociability	19.14	2	<0.001	<b>♂ = Positive</b> , ♀ = positive
		Sex*Dominance	8.07	1	0.005	<b>♂ = Negative</b> , ♀ = negative
		Age*Dominance	6.71	1	0.010	Old = negative, young = positive
		Age*Cautiousness	12.17	1	<0.001	Old = positive, young = negative
	Anxiety (E)	Sociability	6.65	1	0.010	Negative
		Age*Sociability	6.64	1	0.010	Old = negative, young = positive
		Age*Cautiousness	7.09	1	0.008	Old = positive, <b>young = positive</b>

(E) Indicates event behaviors. Relationships in bold indicate that the relationship is more pronounced for that particular age/sex class

but was more pronounced in one age/sex class, in all but one case, which was the interaction between Dominance and age on active behavior for which the relationship was negative in older (>5 yr) individuals (Table III). There was a significant positive main effect of Emotionality on activity that was affected by age; older individuals exhibited a negative relationship between Emotionality and activity (Table III). There was a significant negative main effect of Sociability on solitary behavior, indicating that individuals scoring higher on the Sociability dimension spent less time alone (Table III). There was a significant interaction between sex and Sociability on active behavior; for both sexes the relationship was positive, indicating that individuals scoring higher on Sociability are more active but this relationship was more pronounced in females (Table III). In the analysis of the novel object tests, there were no significant predictors in the GLM model using touched/did not touch the novel object as a binary response variable, or in the GLM using *frequency of touches* as the response variable. There was a significant negative main effect of HA Sociability 1 on *latency to touch*, indicating that individuals scoring higher on this dimension were quicker to touch the novel object (Table IV).

**Saimiri sciureus** For *S. sciureus* all three personality dimensions had two main relationships with observed behavior. Sociability had a significant positive relationship

**Table IV** Summary of generalized linear model (GLM) statistics showing significant main effects of personality dimension scores, age, and sex on behavioral measures recorded during novel object tests

Species	Response	Significant main effects	Wald $\chi^2$	d.f.	P	Nature of relationship
<i>Macaca nigra</i>	Latency to touch	Dominance	8.47	1	0.004	Negative
<i>Macaca sylvanus</i>	Latency to touch	Human–Animal Sociability	3.92	1	0.048	Negative
<i>Saimiri sciureus</i>	Latency to approach	Sociability	14.08	1	<0.001	Negative

with time spent performing social behavior and a significant negative relationship with frequency of anxiety-related behaviors. Dominance had a significant negative relationship with both active and environmental interaction behaviors. Cautiousness had positive relationships with both active and environmental interaction behaviors (Table III). Where interactions between sex and personality dimension scores occurred, the nature of the relationship remained the same but was more pronounced in one sex (Table III). There were significant interactions between age and personality dimension scores and in most cases we found opposite relationships depending on the age class; e.g., in older individuals there is a negative relationship between Dominance and activity but in younger individuals the reverse is true (Table III). There was a significant interaction between sex and Sociability on environmental interaction; in both sexes the relationship was positive but it was more pronounced in males (Table III).

There was a significant interaction between age and Cautiousness on anxiety behavior; for both age groups the relationship was positive, indicating that individuals scoring high on Cautiousness exhibited more anxiety behaviors but this is more pronounced in younger individuals (Table III). In the analysis of the novel object tests there were no significant predictors in the GLM model using *frequency of approaches* as the response variable. There was a significant negative main effect of Sociability on *latency to approach*, indicating that individuals scoring higher on this dimension were quicker to touch the novel object (Table IV).

## Discussion

### Reliability of Personality Assessments

We found that all three species' personality ratings had good overall mean reliabilities that were comparable with those found in other primate personality research (Freeman and Gosling 2010), but there is some evidence to suggest that raters may be more reliable at rating *Macaca* spp. compared to *Saimiri sciureus*. Although it is generally assumed that different species will exhibit different behavioral repertoires and will therefore be easier to judge on certain traits than others (Gosling 2001), there is little empirical evidence to demonstrate that this is the case in primates. It has been suggested that humans may have more difficulty in rating individuals that have limited behavioral repertoires or those that are more divergent from humans; e.g., humans may find it easier to rate a trait such as "fear" in primate species than in reptiles, although both would experience "fear" (Gosling 2001). Human observers may also find it difficult to rate species that rely heavily on communication that is difficult for us to recognize or interpret, such as vocalizations or scent; subtle social behaviors may be missed, leading to unreliable human observations (Meagher 2009). The three species in our study exhibit differences in their social behavior that could affect the accuracy of observers' ratings of their personalities. Macaque social behavior is exhibited through behaviors such as grooming, body postures, facial expressions, aggressive threats and physical aggression, and vocalizations (Thierry *et al.* 2000). In *Saimiri* species such behaviors are also exhibited, but their expression can be more discreet or cryptic because a large proportion of their social communication is achieved through vocalizations and scent

marking (Boinski and Mitchell 1997; Candland *et al.* 1980; Joseph and Wilson 1978; Laska and Hudson 1995). Despite the species differences in reliability of personality ratings, our findings support previous studies showing that it is possible to determine personality structures for difference species in a way that allows for meaningful cross-species comparisons by using a common list of traits across species coupled with rigorous reliability assessment (Weiss *et al.* 2011).

### Validity of Personality Assessments

In *Macaca nigra* and *Saimiri sciureus* males scored significantly higher on the Dominance dimension than females, which is unsurprising given that males show strict linear hierarchies enforced through both threat gestures and physical aggression (*M. nigra*: Riley 2010; *S. sciureus*: Boinski *et al.* 2001). Male *M. nigra* and *S. sciureus* also scored higher on Sociability than females, which probably reflects the playfulness component of Sociability because males at all ages generally spend more time playing than females, and females withdraw from play behavior much earlier than males as they begin to travel, forage, and rest more with adult females (Baldwin 1969; Biben 1998; Petit *et al.* 2008). All of our study species showed a negative relationship between scores on the Sociability personality dimension and age. This relationship again reflects the playfulness component of Sociability, one of the most important components of this dimension; it is well known that young primates in general play more than adults (Petit *et al.* 2008), and this has been demonstrated for other *Macaca* spp. (Caine and Mitchell 1979; Ciani *et al.* 2012) and *S. sciureus* (Baldwin 1969; Biben, 1998). Thus the two personality dimensions that were found in all three species, Sociability and Dominance, showed the kinds of variation with age and sex that would be expected of valid personality measures. The remaining dimensions (Emotionality as seen in the two macaque species, Confidence as seen in the squirrel monkeys, and Human–Animal Sociability as seen in *Macaca sylvanus*) did not.

In the *Macaca* spp. Dominance had the most significant main effects with observed behavior. The relationships we observed reflect the fact that Dominant individuals generally exhibit a greater diversity of behaviors related to maintaining a high rank; e.g., yawning in macaque species is generally accepted to be a threat or dominance enforcing gesture (Thierry *et al.* 2000) and displacements can be used as a way of determining dominance in primate species, as generally the more dominant individual will be able to displace all other individuals. Highly Dominant individuals may also exhibit behaviors that are related to the stress of maintaining a high rank such as scratching (Maestriperieri *et al.* 1992). For *Saimiri sciureus* all three personality dimensions had significant main relationships with two of the observed behaviors but, of the three, Sociability was the least affected by age/sex. This finding supports a series of studies on *Macaca mulatta* that identify Sociability as one of the most important dimensions of primate personality in terms of predicting behavior and health-related variables (Capitanio 2011). Specifically, Sociability may have an impact on the primates' physiology; low sociable *M. mulatta* exhibit differences in their lymph nodes that make them more susceptible to the progression of Simian immunodeficiency virus (SIV) than high Sociable individuals. Sociability was also associated with biobehavioral relationships and SIV; individuals rated as low Sociable were more likely to

respond in a nonappropriate way in unstable social situations and as such potentially suffered more stress and were more susceptible to progression of SIV (Capitanio 2011).

Relationships between personality dimensions and behavior did vary to some extent as a function of age and sex. These relationships should be used to interpret the validity of personality dimensions further. For example, we found a positive relationship between Dominance and scratching in *Macaca nigra*. This is to be expected, as scratching can be used as an indicator of stress (Maestriperi *et al.* 1992) and more dominant individuals may scratch more in response to the high stress levels of obtaining a high dominance rank. In females, however, the relationship is reversed; i.e., females scoring high on Dominance actually scratch less. Dominance is achieved through very different mechanisms in male and female macaques. Female *M. nigra* do exist within a social dominance hierarchy, but they tend to be related to one another as they are the philopatric sex and so exhibit high levels of tolerance to each other and females inherit their mother rank (Thierry 2007) whereas males have strict linear hierarchies enforced through both threat gestures and physical aggression (Riley 2010). Being a Dominant female therefore may not be as stressful as being a Dominant male.

We did not find good construct validity, in terms of predicting behavior, for some of the personality dimensions in our study, e.g., Human–Animal Sociability in *Macaca sylvanus*. This does not necessarily mean the dimensions are not valid but it does mean that we did not record appropriate behavioral measures to validate them. For example, Human–Animal Sociability refers to interactions with keepers, behaviors that happened rarely during the behavioral data collection phase. Perhaps a better validation technique for this dimension would be to collect behavioral data during a routine husbandry event such as a training session or a veterinary procedure. We identified all our behavioral measures used for validation purposes before obtaining any personality data but in an exploratory analysis this may not be the best course of action, as, if we do not know what dimensions may result from the exploratory analysis, we do not know what behavioral data to collect for validation purposes.

For each species there was a significant main effect of one of the personality dimensions on the behavioral measures recorded during the novel object tests. Each of these individual relationships seems logical; more dominant *Macaca nigra* approach novel stimuli first, *Macaca sylvanus* with a good Human–Animal relationship appear less afraid of items human caregivers have provided, and more sociable *Saimiri sciureus* explore new objects faster because of the playful component of Sociability. We found no consistency, in terms of which personality dimension best predicts behavior under novel object conditions, across species. This potentially indicates that the novel object test we conducted was not a good universal measure for validating personality; i.e., the presence of the object may stimulate different responses from each species. Recent critical analysis of the use of novel objects to test Boldness has suggested that, as Boldness has been defined in many different ways, such as the propensity to take risks or the individual's response to risky situations (excluding reactions to novel situations or stimuli), and tested in different ways, e.g., through predator simulations or novel environments/objects, it is at risk of becoming a jingle fallacy, i.e., two or more similarly labeled traits that correspond to different constructs (Carter *et al.* 2012). For example, when wild chacma baboons (*Papio ursinus*) are exposed to a threat (fake puff adder model) and a novel object (novel food item), behavior toward the threat does not correlate with behavior toward a novel food item.



Therefore *P. ursinus* response to “novelty” needs to be considered as two separate traits of anxiety and investigative boldness (Carter *et al.* 2012). Another concern of novel object tests is the fact that captive individuals are regularly exposed to many different environmental changes, e.g., changing enclosure furnishing or addition of enrichment items. Captive individuals might become habituated to, and therefore generalize their response to, “novelty” and thus novel object tests in a captive setting become a measure of exploration or investigative personality.

## Personality Structure

In making comparisons with previous research, the number and structure of dimensions that emerge through PCA are inevitably influenced by the instrument (trait list) used; i.e., we may have found different dimensions compared to those authors using, say, the hominid trait list, based purely on the items used to rate the primates; the more similar the instruments used in two studies, the more informative the comparison between them will be. Using the same rating instrument we identified five personality dimensions across the three study species. All three species showed Sociability and Dominance dimensions. The two macaque species showed an Emotionality dimension but *Saimiri sciureus* did not, instead showing a Cautiousness dimension that demonstrated little if any overlap with Emotionality in trait content. *Macaca sylvanus* alone showed a dimension of Human–Animal Sociability. Similar dimensions have been found in the personality structures of other primate species, though with varying frequency.

Along with Fearfulness, Sociability is the most commonly examined personality dimension, identified in 16 out of 17 factor analytical studies (Freeman and Gosling 2010). Although the traits contributing to the dimension may differ slightly between studies using different methods, in general Sociability dimensions are identified by individuals’ positive behavior toward other individuals. Our findings suggest traits related to individuals’ activity levels; playfulness and curiousness also load highly on the Sociability dimension. Similar results have also been found in other primate studies (Stevenson-Hinde *et al.* 1980), but recent research has found that in certain species traits relating to Sociability load highly onto an Extraversion personality factor, e.g., *Pan troglodytes* (King and Figueredo 1997), *Pongo pygmaeus* and *Pongo abelii* (Weiss *et al.* 2006). When comparing the personality of *P. troglodytes*, *P. pygmaeus*, *P. abelii*, and *Macaca mulatta*, using the hominid personality questionnaire, traits related to Extraversion in the three former species defined two separate dimensions in *M. mulatta*: Friendliness (Sociability) and Activity (Weiss *et al.* 2011). Further investigation using the hominid personality questionnaire would be needed to establish whether an “Activity type” dimension could be found in our study species. Indeed a recent study of personality of *Macaca sylvanus* using this rating instrument has suggested a Friendliness and an Activity/Excitability dimension exists (Konečná *et al.* 2012).

As with Sociability, evidence for a Dominance-related dimension has been found in many other primate species, e.g., Confidence in *Macaca mulatta* (Stevenson-Hinde *et al.* 1980; Weiss *et al.* 2011) and Dominance in *Pan troglodytes* (King and Figueredo 1997; Dutton 2008) and *Pongo pygmaeus* and *Pongo abelii* (Weiss *et al.* 2006). Our study suggests that the trait content of Dominance in *Macaca nigra* and *Macaca sylvanus* differs from analogous dimensions in other species but the Dominance

dimension of *Saimiri sciureus* is very similar to that of other species. In the two *Macaca* species we found high positive loadings of *aggressive* traits on the Emotionality dimension rather than Dominance. This result concurs with that of Konečná *et al.* (2012), who found that the trait *aggressive* loads negatively on the Friendliness dimension rather than positively on the Confidence dimension in *M. sylvanus*. These results suggest that in *M. nigra* and *M. sylvanus* aggressive personality traits are not intrinsically linked with dominance personality traits; i.e., dominant individuals are not necessarily aggressive ones. Interestingly, within the validity analysis, we found no significant relationships between Dominance scores and time spent engaged in negative social behaviors (which encompassed aggressive behavior), which provides support for the suggestion that Dominant individuals are not more “aggressive.” It is likely that this difference in personality dimension structure is linked to the fact that they are both considered to be more tolerant than other *Macaca* species (Thierry 2007). We conclude from our study that Dominance is an important personality dimension in primate species that exhibit any kind of dominance hierarchy whether despotic or egalitarian, but the content of the dimension is different in those species that have evolved more tolerant lifestyles. Recent evidence has suggested an Aggression personality dimension in wild *M. nigra* (Neumann *et al.* 2013). This study constructed dimensions through behavioral rather than questionnaire data and focused only on males; therefore direct comparisons with our study data are difficult; however, it poses an interesting future research agenda in terms of comparing the overall structure of personality dimensions between sexes of the same species, which, to our knowledge, has not been attempted within the published literature.

Across species, Emotionality is a less pervasive dimension of primate personality than either Sociability or Dominance (Freeman and Gosling 2010). Our findings were consistent with this observation; we found it in only two of our three study species. Similar dimensions in other species include Emotionality in *Pan troglodytes* (King and Figueredo 1997), Neuroticism in *Pongo* spp. (Weiss *et al.* 2006), Anxiety in *Macaca mulatta* (Weiss *et al.* 2011) and *Macaca nigra* (Neumann *et al.* 2013), Excitability in *M. mulatta* (Stevenson-Hinde *et al.* 1980) and *Macaca arctoides* (Mondragon-Ceballos and Santillán-Doherty 1994), and Reactivity in *Macaca nemestrina* (Sussman and Ha 2011). These dimensions have many similarities with the Neuroticism dimension of human personality: High scorers on the human Neuroticism dimension experience high levels of tension, depression, frustration, self-consciousness, and poor impulse control and coping abilities (McRae and John 1992). It has been suggested that Neuroticism in humans, *P. troglodytes*, and *Pongo* spp. is derived from ancestral variants, i.e., Confidence and Anxiety, as traits related to Neuroticism define these two separate dimensions in *M. mulatta* (Weiss *et al.* 2011). However, our study did not find evidence for two separate dimensions, but for a dimension that is analogous to the Neuroticism dimensions in humans and related dimensions in *P. troglodytes* and *Pongo* spp. This may be due to species differences between *M. nigra*, *Macaca sylvanus*, and *M. mulatta*, but it is more likely that it is due to the different rating instrument employed in our study.

Alone among our three study species, *Saimiri sciureus* showed a Cautiousness dimension. In many ways it resembles the dimension of Fearfulness that has been identified in other primate studies and generally involves individuals removing themselves from fearful/novel stimulus as quickly as possible (Freeman and Gosling 2010). In turn, Cautiousness is analogous to the bold/shy dimension of personality that is

perhaps one of the most well studied personality dimensions in nonprimate species (Gosling 2001). Our findings suggest the Cautiousness dimension in *S. sciureus* contains traits that are also associated with the negative pole of Confidence in other species, e.g., *fearful* in *Macaca mulatta* (Stevenson-Hinde *et al.* 1980; Weiss *et al.* 2011) and traits such as *tense* that are associated with the Neuroticism type dimensions discussed in the preceding text. Species differences between *S. sciureus* and *Macaca* species could be the reason for not finding a Cautiousness dimension in the other study species. *Macaca nigra* and *Macaca sylvanus* have few natural predators, whereas *Saimiri* species are subject to intense predation pressures (Mitchell *et al.* 1991), so there may be an evolutionary advantage to developing a Cautiousness personality dimension in *Saimiri* species. Predation pressure has also been suggested as an important variable in shaping personality within other *Macaca* spp. (Sussman *et al.* 2012).

Although evidence for a Human–Animal Sociability dimension was found only in *Macaca sylvanus*, in the other study species Human–Animal traits could not be reliably rated and thus were not included in the PCA; therefore it was not possible for an Human–Animal Sociability dimension to emerge. This reflects our caveat at the start of this discussion that data reduction techniques rely implicitly on the data that are entered at the start of any analysis. Although we know that in a captive environment animals come into close contact with humans and therefore develop human–animal relationships (HARs; Hosey 2013), very few authors have included traits that relate to the human–animal relationship in primate personality research within the zoo environment. However, recent studies on primates in a research setting have focused on these interactions. A study of *Macaca mulatta*, *Macaca fascicularis*, and *Macaca nemestrina* identified a personality dimension interpreted as Sociability toward humans. When comparing the three species the authors found that *M. nemestrina* scored significantly higher on this dimension, indicating that there may be distinct differences between species in their response to human caregivers (Sussman *et al.* 2012). The issue of human-related personality dimensions warrants further attention in the literature. Within our study we have demonstrated that at least one of the species — *M. sylvanus*— can be reliably rated on traits relating to human–animal relationships but we did not find similar results for the other species in our study. Potentially there is variation in management and husbandry variables between zoos that influences the type of human–animal interactions that occur, and thus whether human–animal traits can be reliably rated.

## Conclusions

At least three dimensions are needed to describe personality, as derived from keepers' trait ratings of proven reliability, in our study species. Future studies that include ratings of more traits may show that more dimensions are needed. Across the three species, five distinct personality dimensions were identified in total. The construct validity of two dimensions, Dominance and Sociability, was demonstrated as they showed variations with sex and age and relationships with observed behavior in unconstrained situations, and were able to predict behavior toward a novel object. The validity of the remaining dimensions remains to be demonstrated, but they are clearly needed to account for the variations in the ratings that zoo staff gave to the individual monkeys.

The personality structure we observed was more similar between *Macaca nigra* and *Macaca sylvanus* (members of the same genus) than between either *Macaca* spp. and *Saimiri sciureus*. The differences are not enormous, and it would be premature to conclude that personality structure reflects phylogeny rather than ecology on the basis of these three species. A first attempt at such a multispecies comparison (Baker 2012, Chapter 6) suggests that primate personality structure is more closely determined by ecology than by phylogeny. Further data on a range of primate species encompassing different social systems and ecologies are needed to inform conclusions regarding the relative importance of phylogeny or socioecology in shaping primate personality structure.

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