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## Behaviors that predict personality components in adult free-ranging Tibetan macaques *Macaca thibetana*

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**Abstract** To further the potential for applied personality studies, we present a methodology for assessing personality in nonhuman animals without *a priori* assumptions, using behavioral measures to discriminate personality survey results. Our study group consisted of 12 free-ranging, provisioned, adult Tibetan macaques *Macaca thibetana* at the Valley of the Wild Monkeys, China. We asked familiar Chinese park guards and scientists to rate each of the 12 macaques using 27-item personality surveys. We also recorded behavioral observations (> 100 hrs) from August–September, 2012. The personality surveys showed reliability in 22 of the items that were then utilized in a principal component analysis that revealed five components: Insecurity, Reactivity, Boldness, Sociability, and Leadership. Prior personality research on *Macaca* show comparable components. In order to determine which behaviors would best predict those five personality components, we conducted discriminant analyses using behavioral measures as predictors. We found that behavioral measures of *avoidance*, *lunging*, *fear-grinning*, *self-directed behaviors*, *touching*, *proximity* and *chasing* could significantly predict personality component scores in certain situations. Finally, we analyzed the effects of situation (provisioning and tourists) and found situation influenced proximity and rates of avoidance and self-directed behaviors. Wider implementation of this methodology may permit long-term analysis of personality using behavioral proxies for established personality traits, in particular on research investigating the effects of tourism and provisioning on personality [*Current Zoology* 60 (3): 362–372, 2014].

**Keywords** Tourism, Provisioning, Temperament, Surveys, Personality, Primate

Personality in nonhuman primates (hereafter: ‘primates’) is receiving attention from a variety of disciplines (Gosling, 2008; Freeman and Gosling, 2010) and has been defined by various researchers as inter-individual differences during adulthood that can be attributed to individual responses that remain temporally stable and influence behavioral and cognitive actions (Capitanio, 1999; Gosling, 2008; Koski, 2011; Uher, 2008). In some contexts, research on behavioral syndromes (e.g. Sih and Bell, 2008) and temperament (e.g. Réale et al., 2007) might be considered analogous to personality research, but, as indicated by Carter et al. (2013), Rothbart et al. (2000), Uher (2011) and Groothuis and Carere (2005), there are reasons to doubt whether temperament and behavioral syndromes are functionally equivalent to personality.

Importantly, primate personalities can be reliably

rated (Stevenson-Hinde and Zunz, 1978; Buirski et al., 1978; Martau et al., 1985; Gold and Maple, 1994; Uher and Asendorpf, 2008), measured with behavioral observations (Rouff et al., 2005; Konečná et al., 2008), observed through responses to test situations (Stevenson-Hinde et al., 1980a; Uher et al., 2008) and show intra-individual stability across time (Suomi et al., 1996; Capitanio, 1999; Uher et al., 2008). Together, these studies indicate that personality can be measured with reliability or reproducibility (e.g. Martin and Bateson, 2007) and show multi-method validity through convergent results following different methods of personality assessment (Martin and Bateson, 2007).

Applications beyond the simple measurement of nonhuman animal personality include clarification of research findings in group-based studies and assessment of changing environments on individual animals. For

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example, Stevenson-Hinde and Zunz (1978) quantified personality as a potentially confounding variable for group-based research. Gold and Maple (1994) reported that personality could inform decisions about translocations, introductions, and reproduction, and Carere and Locurto (2011) felt that personality factors should be considered when designing studies of cognition and methods of enrichment. Personality has been shown to influence an individual's immune responses (Maninger et al., 2003; Mehta and Gosling, 2008), captive digestive condition (Jin et al., 2013), group structure (McCowan et al., 2011), and relationships among individuals (Massen and Koski, 2014).

Situational changes may affect the expression of personality (Funder, 2001; Uher, 2011), but consistent behavioral responses have been observed over time, indicative of individual personalities (Suomi et al., 1996; Capitanio, 1999; Uher et al., 2008; Freeman and Gosling, 2010). However, environmental variability may affect the development and evolution of personality characteristics in a group (Archard and Braithwaite, 2010) particularly among captive-bred or provisioned groups (McDougall et al., 2006). For example, if bold individuals gain a nutritional advantage by obtaining and consuming more provisioned resources, then shy individuals may be selected against if the majority of a population's resources are provisioned (see McDougall et al., 2006 for other examples).

Primate personality research can require significant investments in time and resources, especially if such research depends upon behavioral measures (Freeman and Gosling, 2010). Surveys of personality characteristics by caregivers provide an alternative to behavioral measures but rely on familiarity between the raters and the primate subjects (Martau et al., 1985; Highfill et al., 2009) and may be cumbersome to interpret over time due to possible changes in inter-rater error, perceptions of animals by the raters, or changes in the monkeys themselves. Behavioral measures show comparability with survey-based quantifications (multi-method validity [Konečná et al., 2008; Uher and Asendorpf, 2008]), but few studies identify behaviors to use in such analyses with no *a priori* assumptions as to which behaviors best match specific personality traits (though see Uher, 2011; Uher, 2103; Freeman et al., 2013). Identification of key proxy behaviors for measuring specific personality characteristics would allow personality assessment to be conducted in on-going primate studies in which behavioral measures are already collected (for examples: Kappeler and Watts, 2012). Archival behavioral data

available at long-term captive and free-ranging sites might also be explored for possible changes in the development and evolution of specific personality characteristics. Given the possibility that behavioral data may provide useful information on primate and non-primate personalities, the current study sought to identify possible proxy behaviors for personality traits by collecting behavioral and survey data in the same population.

The goal of the current research was to identify behavioral measures that could predict survey responses on standard personality scales. In particular, discriminant analyses were used to evaluate which behavioral measures were the best predictors in classifying personality types established from survey ratings. Behavioral measures could then be used to explore possible anthropogenic effects on personality characteristics in nonhuman populations (Archard and Braithwaite, 2010; McDougall et al., 2006), using behavioral proxies. Since *Macaca* is one of the most studied genus in primate personality research and the current research was particularly interested in environmental effects on personality characteristics, the data to investigate the association between behavior and survey rates were collected from a group of free-living, provisioned Tibetan macaques *M. thibetana* habituated to humans (Berman and Li, 2002).

## 1 Material and Methods

### 1.1 Research site and subjects

The Yulingkeng A1 (YA1) group of Tibetan macaques *M. thibetana* in the Valley of the Wild Monkeys, Mt. Huangshan, China, is a provisioned, free-living population subject to tourism since 1992 (Berman and Li, 2002). Viewing platforms bordering an open area were constructed in 1994 (Berman et al., 2007). Guards monitored the monkeys and provisioned them with corn 3–4 times daily (Berman et al., 2004). Feeding times varied across days and frequency depended upon the guards and the presence/absence of tourists (AP pers. obs.). Tourists arrived in mean group sizes of 25 ( $SD = 19.2$ ), ranging in size from 6 to 113 individuals (Usui, 2013). Research during (Usui 2013), and prior to (Ruesto et al., 2010), the study period showed non-significant effects of tourist numbers on monkeys' self-directed and aggressive behaviors. Suomi et al. (1996) showed that primate personalities stabilize by adulthood; therefore, 12 adult monkeys present in YA1 (Table 1) were selected for study.

Data collection took place from 0800–1700 h across two summer months. All procedures were approved by

**Table 1** YA1 study subjects in 2012 (Xi Wang, personal communication, 2012)

Monkey	Sex	Mother	Birth Date	Infants (<1 year)	Infant Birth
Bai Tou	♂	(Immigrated)	Unknown		
Gao Shan	♂	(Unknown)	Est. 1984		
Tou Gui	♂	Tou Tai	26 February 2003		
Zi Long	♂	(Immigrated)	Est. 2006		
Hua Hong	♀	Hua (D.)	14 April 2003		
Hua Hui	♀	Hua (D.)	5 March 2005		
Tou Hong	♀	Tou Gou (D.)	16 March 2003	Tou Xialong ♂	01 June 2012
Tou Rui	♀	Tou Tai	19 May 2004	Tou Huaxue ♂	19 April 2012
Tou Tai	♀	Tou (D.)	2 April 1991	Tou Rongyu ♂	30 January 2012
Ye Hong	♀	Ye Mai	15 March 2003		
Ye Mai	♀	Ye (D.)	14 April 1990	Ye Chunlan ♀	15 September 2012
Ye Zhen	♀	Ye (D.)	16 January 1992	Ye Rongxue ♀	2 March 2012

(D.) denotes monkeys who died before this study

the Institutional Animal Care and Use Committee and the Institutional Review Board. The research did not violate Chinese laws protecting primates.

### 1.2 Personality surveys

A macaque rating system from Stevenson-Hinde and Zunz (1978) and Stevenson-Hinde et al. (1980b) was translated into Chinese by a native speaker and was used to obtain a personality profile for each adult monkey. Each survey included 27 items comprised of an adjective with an associated definition: *active, aggressive, apprehensive, confident, curious, eccentric, effective, equable, excitable, fearful, gentle, insecure, irritable, motherly, opportunistic, permissive, playful, popular, protective, sensitive, slow, sociable, solitary, strong, subordinate, tense, and understanding* (p. 481, Stevenson-Hinde and Zunz, 1978; p. 82 Stevenson-Hinde et al., 1980b; used with permission from Stevenson-Hinde, pers. comm., 2012). Raters were asked to rank each monkey relative to the other YA1 monkeys on each item using a scale from 1 (the adjective was the opposite of the monkey's personality) to 7 (the adjective strongly characterized that monkey). Raters were familiar (11 months–10 years) with the YA1 monkeys and consisted of Chinese scientists who had conducted research at the park ( $n = 4$ ) and Chinese park guards ( $n = 2$ ). Raters completed an informed consent form, identified each adult monkey, and then completed a survey for each of the 12 monkeys, without discussion with other raters.

### 1.3 Behavioral coding

Multiple measures of behavior were collected to ensure that a wide range of behaviors could be assessed for their ability to discriminate between personality

types. Two observers used focal sampling (Martin and Bateson, 2007) to observe a randomly selected adult monkey for 5 minutes from the viewing platform in one of four possible situations: No Corn & No Tourist; Corn; Tourist; and Corn & Tourist. Corn situations were those in which guard-provisioned corn was actively being foraged by  $\geq 3$  adult monkeys. Tourist situations had tourists present on the viewing platform for  $\geq 2.5$  min. Corn & Tourist situations simultaneously fulfilled both of the previous criteria whereas No Corn & No Tourist situations fulfilled neither criteria.

Observers recorded the frequencies of the following behaviors (Berman et al., 2004): *self-directed behaviors* (*self-groom* and *self-scratch*), *approach*, *lipsmack*, *teeth-chatter*, *embrace*, *touch*, *present*, *social mount*, *penis display*, *penis suck*, *genital inspection*, *bridge*, *hold bottom*, *fear grin*, *avoid*, *displace*, *flee*, *scream*, *threat*, *lunge*, *chase*, *slap*, *grab* and *bite* (p. 1288–1289, Berman et al., 2004). Proximity was recorded using three categories: 1) contact; 2) within 1m, but without contact; and 3) >1m from any monkey. In addition, whether the focal subject was grooming or being groomed every 30 seconds during the 5-min sample was recorded. If the focal subject was sleeping or not visible for > 1.5 min of the sample, then the observer selected the next focal subject from a randomized list generated each day. Recording continued if the location of the individual was known and the subject was only temporarily and partially obscured, with the observer noting that the focal subject was not fully visible. Data collection resulted in over 100 hrs of focal sampling with a mean of 25.42 focals per monkey in each of the four situations ( $SD = 9.07$ ).

#### 1.4 Inter-rater reliability

The six raters who completed the personality surveys had to be 100% reliable in identifying each adult monkey to be included in the analysis. Raters viewed several full-color photographs (10.16 × 15.24 cm) of each monkey taken from several perspectives. If a rater was not reliable in identifying a particular monkey, the data from that survey was discarded from subsequent analyses, resulting in 11 of the 72 completed surveys being discarded. The reliability of the remaining 61 surveys was assessed for each item using two-way mixed model intraclass correlations (ICC) (Shrout and Fleiss, 1979; McGraw and Wong, 1996). Two reliability analyses were conducted, one with missing values left blank, and a second in which missing values were replaced with whichever extreme score (1 or 7) resulted in lower reliability, producing a lower, more conservative, reliability score. ICC reliability criteria was set using Cicchetti's (1994) requirements for Cronbach's alpha in which 0.40–0.59 is defined as fair, 0.60–0.74 as good and > 0.74 as excellent correspondence between raters. ICC (3, k) reliabilities had an original reliability mean of 0.80 ( $SD = 0.23$ , Range: 0.02–0.97) and a conservatively estimated mean of 0.66 ( $SD = 0.21$ , Range: -0.03–0.83). Five items (*opportunistic*, *playful*, *sensitivity*, *understanding* and *eccentric*), showing both low original and conservatively estimated reliabilities ( $\leq 0.59$ ), were dropped from subsequent analysis.

#### 1.5 Behavioral reliability

Behavioral observers' reliability was assessed for monkey identification, ethogram behaviors, and proximity by having both observers engage in a simultaneous focal follow of the same monkey subject. Simultaneous follows of randomly sequenced monkeys were repeated until 90% concordance was achieved, after which data collection commenced. Concordance and kappa coefficients were calculated prior to and during the study (Martin and Bateson, 2007), resulting in concordance levels  $\geq 90\%$  for monkey identification and 95.2–96.3% (kappa = 0.905–0.926) and 90–100% (kappa = 0.798–1.000) for behavioral and proximity reliability.

#### 1.6 Data analysis

*Principal components analysis and regularized exploratory factor analysis:* Principal components analysis (PCA) with varimax rotation was conducted on the survey items to simplify the data into underlying components. Each rater was processed as a distinct rating in order to enhance the low sample-to-item ratio (Osborne and Costello, 2004) although this contradicted assumptions of independence. Cross-checks against the re-

search literature suggest that the resultant PCA is consistent with previous data (see section 3.1). A regularized exploratory factor analysis (REFA) with varimax rotation, Kaiser criterion for component selection, and an anti-image assumption for smaller sample sizes (Jung and Lee, 2011) was used as a confirmatory analysis (Jung and Lee, 2011; Konečná et al., 2012) to correct for the low sample-to-item ratio. Lastly, component scores from the PCA were calculated for each monkey.

*Preparation of behavioral data:* Instantaneous behaviors were converted to rates per monkey per min. Grooming given and received were converted to rates per monkey per focal. Finally, proximity was converted to an average score per monkey per focal, with low scores representing increased proximity to other individuals. Situations (No Corn & No Tourist; Corn; Tourist; Corn & Tourist) were not combined into averages across conditions; rather, per-monkey averages of each variable were calculated for each situation.

*Discriminant analysis:* Five separate discriminant analyses (DAs) were used to determine which behavioral, proximity, or grooming variables ( $n = 27$ ) in each situation (No Corn & No Tourist; Corn; Tourist; Corn & Tourist) would best predict negative or positive scores on each of the five components identified in the PCA. Monkeys were split into dichotomous groups for each PCA component. Each analysis resulted in a discriminant function score (comprised of a weighted value from one or two behaviors) that can be used to predict whether a monkey would be rated negatively or positively for each principal component. Significance for all discriminant analyses was set at a  $P$ -value of  $< 0.05$ .

*Spearman's correlations:* Discriminant analyses only discriminate between group-memberships and cannot be used to assess the value of the specific behaviors for each individual. Therefore, Spearman's correlations were performed for each set of PCA component scores and DA function scores (calculated using behavioral variables' function coefficients) to determine if the DA functions accurately represented each of the monkeys' personalities. Significance for the Spearman's correlations was set at a two-tailed  $P$ -value of  $< 0.05$ .

*General linear models of repeated measures:* General linear models of repeated measures (GLM-RMs) were performed to determine if any of the behavioral variables isolated in the discriminant analyses differed across the four situations (No Corn & No Tourist; Corn; Tourist; Corn & Tourist). The average rate per-monkey per-minute for each of the seven behaviors from the discriminant analyses was included in the analysis. A

Holm-Bonferroni method of correction was selected due to its strength and minimalism as a corrective tool to reduce the likelihood of producing a type I error due to multiple comparisons (Holm, 1979; Ludbrook, 1998).

*Computer programs:* IBM SPSS Statistics 21.0 was used to perform all analyses except for the REFA, which was performed using MATLAB 2012a.

## 2 Results

### 2.1 PCA and REFA results

The 22 reliable items from the personality surveys were simplified into five components that represented the underlying structure using a PCA with varimax rotation (loadings presented in Table 2). Visual inspection of the scree plot suggested two to five components but the five component model fulfilled 70% variance and eigenvalue criterion, with a mean variable communality of 0.74 and 30% of variables with residuals greater than 0.05. The first component (eigenvalue = 8.63), labeled

**Table 2** Principal component analysis (with varimax rotation) component loadings

Items	Components and Loadings				
	1	2	3	4	5
Insecure	<b>0.89</b>	-0.04	0.00	-0.03	-0.01
Fearful	<b>0.85</b>	-0.02	-0.25	-0.01	-0.10
Subordinate	<b>0.81</b>	-0.34	-0.14	0.02	0.08
Tense	<b>0.72</b>	-0.23	-0.10	-0.17	-0.23
Apprehensive	<b>0.63</b>	0.25	-0.16	-0.01	-0.43
Permissive	<b>0.61</b>	-0.52	-0.06	0.09	0.29
Aggressive	-0.28	<b>0.73</b>	0.50	-0.05	0.00
Excitable	-0.30	<b>0.70</b>	0.37	0.12	0.18
Effective	-0.23	<b>0.57</b>	0.28	0.04	0.39
Irritable	-0.25	<b>0.54</b>	0.34	0.02	0.27
Strong	-0.44	<b>0.50</b>	0.48	0.15	0.13
Slow	-0.15	<b>-0.53</b>	-0.33	-0.40	-0.13
Gentle	0.31	<b>-0.76</b>	-0.14	0.07	0.15
Equable	-0.21	<b>-0.79</b>	0.03	0.06	-0.07
Curious	-0.04	0.08	<b>0.89</b>	0.25	0.21
Active	-0.12	0.28	<b>0.89</b>	0.06	0.04
Confident	-0.45	0.34	<b>0.66</b>	0.15	0.22
Sociable	-0.07	-0.19	0.14	<b>0.83</b>	0.02
Motherly	0.21	-0.52	-0.08	<b>0.53</b>	0.12
Solitary	0.19	-0.29	-0.21	<b>-0.81</b>	-0.08
Popular	-0.01	0.03	0.20	0.10	<b>0.84</b>
Protective	-0.53	0.34	0.07	0.07	<b>0.59</b>

*Note:* For simplicity, only the heaviest loadings are shown for each item.

Insecurity, was comprised of positively loaded items *apprehensive, fearful, insecure, permissive, subordinate* and *tense*. The second component (eigenvalue = 2.68), labeled Reactivity, was comprised of positively loaded items *aggressive, excitable, effective, irritable* and *strong*, and negatively loaded items *equable, gentle* and *slow*. The third component (eigenvalue = 2.63), labeled Boldness, was comprised of positively loaded items *active, confident* and *curious*. The fourth component (eigenvalue = 1.28), labeled Sociability, was comprised of positively loaded items *sociable* and *motherly* and the negatively loaded item *solitary*. The fifth component (eigenvalue = 1.06), labeled Leadership, was comprised of positively loaded items *popular* and *protective*.

An oblique rotation resulted in a similar five-component solution; however, there was a reordering of components (suggesting a different assignment of variability for each component), and the item *strong* was in the Boldness component. The REFA resulted in a similarly structured five-component solution, though with slightly different component loadings. In addition, the item *motherly* was in the Reactivity component. There was a high level of agreement between the three methods of analysis and, therefore, the varimax five-component model with *strong* in the Reactivity component and *motherly* in the Sociability component (Table 2) was selected due to the comparable use of PCA with varimax rotation in the literature.

For each monkey, component scores from the PCA were extracted and averaged (Table 3). Monkeys who scored high on the positive scale of a component exemplified a stronger expression of the positively loaded items in that component relative to the other monkeys in this group. Conversely, monkeys who scored more negatively exemplified a strong expression of the negatively loaded items in that component relative to the other monkeys in this group. For components that had no negatively loaded items (Insecurity, Boldness, and Leadership), a more negative score suggests an expression of the opposites of the positive items.

### 2.2 Discriminant analyses results

Five stepwise discriminant analyses using the variables of behaviors, proximity, sex, and rank were conducted to determine which variables best predicted membership in the five distinct personality components. For the Insecurity component, a stepwise discriminant analysis revealed one significant function,  $\Lambda = 0.433$ ,  $\chi^2_{1, n=12} = 7.945$ ,  $P = 0.005$ . Only one variable was a significant predictor for the function with the behavioral measure of *avoidance*, in the no corn & no tourist situa-

tion, significantly predicting Insecurity group membership. Table 3 presents discriminant scores for this and all subsequent DAs. Table 4 shows group variability explained by the function, group classification results, and standardized function and correlation coefficients.

For the Reactivity component, a separate stepwise discriminant analysis revealed one significant function,  $\Lambda = 0.228$ ,  $\chi^2_{2, n=12} = 13.288$ ,  $P = 0.001$ . Two variables were entered into the function as they explained >75% of the variability: *lunging* in the corn & tourist situation and *fear-grinning* in the corn situation. Behavioral measures of *lunging*, around tourists with provisioning, and *fear-grinning*, in provisioned situations, significantly predicted Reactivity group membership.

For the Boldness component, a separate stepwise discriminant analysis revealed one significant function,  $\Lambda = 0.091$ ,  $\chi^2_{2, n=12} = 21.606$ ,  $P < 0.001$ . Two variables were entered into the function as they explained >75% of the variability: *self-scratching/self-grooming* in the tourist situation and *touching* (an instantaneous, non-grooming, hand-to-body contact directed towards another monkey [p. 1288, Berman et al., 2004]) in the corn situation. The behavioral measures of *self-directed behaviors*, around tourists, and *touching*, during provisioned situations, significantly predicted Boldness group membership.

For the Sociability component, a separate stepwise discriminant analysis revealed one significant function,

$\Lambda = 0.198$ ,  $\chi^2_{2, n=12} = 14.571$ ,  $P = 0.001$ . Two variables were entered into the function as they explained >75% of the variability: *proximity* in the no corn & no tourist situation and *proximity* in the tourist situation. The behavioral measure of *proximity*, in non-provisioned situations, significantly predicted Sociability group membership.

For the Leadership component, a stepwise discriminant analysis revealed one significant function,  $\Lambda = 0.655$ ,  $\chi^2_{1, n=12} = 4.024$ ,  $P = 0.045$ . Only one variable was a significant predictor for the function: *chase* in the no corn & no tourist situation. The behavioral measure of *chasing*, in the no corn & no tourist situation, significantly predicted Leadership group membership.

**2.3 Correlations**

Spearman's correlations were performed for each set of PCA component and DA function scores to determine if there was a more direct rank-based relationship between the behavioral measures and the component scores (Table 3). The components of Insecurity, Reactivity, Boldness and Sociability showed significant ( $P < 0.05$ ) Spearman's correlations with  $r > 0.50$ .

**2.4 General linear models of repeated measures**

GLM-RMs were performed to determine the effect of the four situations (No Corn & No Tourist; Corn; Tourists; Corn & Tourist) on the behavior variables isolated from the discriminant analyses (i.e., *avoidance*, *chasing*, *fear-grinning*, *lunging*, *proximity*, *self-directed*

**Table 3 Component and function scores with Spearman's correlations**

Monkey	Sex	PCA Component Scores					Discriminant Function Scores				
		1	2	3	4	5	1	2	3	4	5
Bai Tou	♂	1.71	0.49	-0.91	-0.83	-0.09	0.68	3.75	-1.94	2.28	2.05
Gao Shan	♂	-0.77	-0.30	-1.00	-1.18	-0.12	-1.36	-0.27	-3.41	2.08	-0.78
Tou Gui	♂	-0.91	1.32	0.88	-0.53	1.33	-0.62	1.22	1.50	0.16	-0.78
Zi Long	♂	-0.15	1.50	0.52	-0.06	-1.10	-1.99	2.24	1.90	3.05	6.59
Hua Hong	♀	0.69	-1.25	0.47	-0.09	0.24	1.72	-2.31	2.22	1.04	-0.78
Hua Hui	♀	0.53	0.34	0.58	0.81	-0.29	1.35	0.81	4.36	-2.94	-0.78
Tou Hong	♀	0.19	0.68	-0.99	1.49	-0.18	-0.54	0.50	-3.48	-1.87	1.59
Tou Rui	♀	0.10	-0.18	-0.86	0.51	-1.06	2.97	-1.91	-3.64	-1.18	1.05
Tou Tai	♀	-0.16	-0.90	-0.46	0.69	0.97	-0.31	-1.37	-2.38	-2.22	-0.78
Ye Hong	♀	-0.35	-0.89	1.44	0.76	0.20	-0.23	-2.31	4.28	-2.66	-0.78
Ye Mai	♀	-0.75	-1.01	-1.11	-0.36	0.51	-1.54	-1.94	-2.49	2.25	-0.78
Ye Zhen	♀	-0.32	0.07	0.09	-0.11	-0.72	-0.12	1.55	3.08	0.02	-0.78
Spearman's Correlations Between Components Scores and Discriminant Scores											
		1	2	3	4	5					
		0.63*	0.83**	0.78**	-0.75**	-0.49					

Notes: Tou Hong, Tou Rui, Tou Tai, Ye Mai and Ye Zhen have < 1 y infant. Hua Hong and Hua Hui have 1-2 y juvenile. \*  $P < 0.05$  (2-tailed) \*\*  $P < 0.01$  (2-tailed).

behaviors and touching). Of the seven GLM-RM analyses, only *chasing* violated Mauchly's test of sphericity ( $P < 0.05$ ); Huynh-Feldt correction was used to alter  $df$  for *chasing*. Significant effects of situation were found on *avoidance*, GLM-RM:  $F_{3,33} = 8.450$ ,  $P < 0.0071$ , partial  $\eta^2 = 0.434$ ; *proximity*, GLM-RM:  $F_{3,33} = 53.867$ ,  $P < 0.0083$ , partial  $\eta^2 = 0.830$ ; and *self-directed behaviors*, GLM-RM:  $F_{3,33} = 33.711$ ,  $P < 0.01$ , partial  $\eta^2 = 0.754$  (Table 5). Holm-Bonferroni step-down correction resulted in non-significance for *fear-grinning*, *chasing*, *lunging*, and *touching*. For behaviors that differed significantly across situations, Bonferroni post-hoc analyses revealed: 1) lower rates of *avoidance* in the No Corn & No Tourist situation relative to the Tourist and Corn & Tourist situations ( $ps < 0.05$ ); 2) lower distances between monkeys (*proximity*) during the No Corn & No Tourist situation relative to the other three situations ( $P$ -values  $< 0.05$ ); 3) lower distances (*proximity*) in the Tourist situation relative to Corn and Corn & Tourist situations ( $P$ -values  $< 0.001$ ); and 4) lower rates of *self-directed behaviors* in the Corn and Corn & Tourist situations relative to No Corn & No Tourist and Tourist situations ( $P$ -values  $\leq 0.001$ ).

### 3 Discussion

#### 3.1 Components

The personality components identified in this study show strong comparability with other, similar studies within the genus *Macaca*. For example, five macaque studies showed personality characteristics similar to Insecurity, while nine showed comparability with Boldness, Reactivity and Sociability components (Bolig et al., 1992; Capitanio, 1999; Konečná et al., 2012; Maninger et al., 2003; McCowan et al., 2011; Neumann et al., 2013; Rouff et al., 2005; Stevenson-Hinde and Zunz, 1978; Stevenson-Hinde et al., 1980b; Sussman and Ha, 2011). Furthermore, the traits identified in this study have parallels with human personality measures that focus on the Five Factor Model's dimensions of Neuroticism, Extroversion, and Openness (e.g., McCrae and Costa, 1987; McCrae and Costa, 2008; Funder, 2001). These traits are also similar to the Five Factor Model with dominance found in chimpanzees (e.g., King and Figueredo, 1997; Weiss et al., 2000). The presence of a Leadership component in the current study may be due to raters' difficulties in assessing the items *protec-*

**Table 4** Results of the discriminant analyses

Function	Predictor Variables	$P$	Variability Explained	Classification	Standardized Function Coefficient	Functional Correlation Coefficient
1	<i>Avoidance</i> N	0.005	56.7%	91.7%	1.000	1.000
2	<i>Lunging</i> C&T	0.001	77.1%	100.0%	1.301	0.519
	<i>Fear Grinning</i> C				1.158	0.281
3	<i>Self-directed Behaviors</i> T	0.001	91.0%	100.0%	1.265	0.569
	<i>Touching</i> C				1.078	0.261
4	<i>Proximity</i> N	0.001	80.1%	100.0%	1.787	0.625
	<i>Proximity</i> T				-1.400	0.084
5	<i>Chase</i> N	0.045	34.6%	75.0%	1.000	1.000

Notes: Functions predict relative numerical components. Situation abbreviations are N = No Corn & No Tourist; C = Corn; T = Tourists; C&T = Corn & Tourist. All classification results were supported with identical cross-validations.

**Table 5** Results of the general linear models of repeated measures

Behavior	$df$	Error	$F$	$P$	$\eta^2$	Power	$\alpha$
<i>Avoidance</i> *	3	33	8.450	<0.0001	0.434	0.987	0.0071
<i>Proximity</i> *	3	33	53.867	<0.0001	0.830	1.000	0.0083
<i>Self-directed Behaviors</i> *	3	33	33.711	<0.0001	0.754	1.000	0.01
<i>Fear Grinning</i>	3	33	4.190	0.013	0.276	0.810	0.0125
<i>Chasing</i>	2	19	5.569	0.016	0.336	0.747	0.0167
<i>Lunging</i>	3	33	3.033	0.043	0.216	0.659	0.025
<i>Touching</i>	3	33	0.593	0.624	0.051	0.159	0.05

Notes: *Chasing* failed to pass Mauchly's test of sphericity and used the Huynh-Feldt correction. \* Indicates significance ( $P < \alpha$ ) using the Holm-Bonferroni correction.



*tive* and *popular*, which rely on interpreting other monkeys' behaviors relative to the focal monkey. Alternatively, the 22 reliable items in this study may inadequately represent a fifth component, such as Agreeableness (King and Landau, 2003). Future research could further examine these possibilities.

### 3.2 Behavioral predictors and situational effects

Discriminant analyses revealed seven behavioral predictors that differentiated personality characteristics in YA1 adults. Importantly, the distinct situations in which each behavior was observed were retained as key elements of the behavioral predictors as it was anticipated that changes in the social environment might provoke certain reactions in some individuals more than others (Funder, 2001; Uher, 2011). The findings of the current study support that conclusion with three of the seven behavioral predictors (*avoidance*, *proximity*, and *self-directed behavior*) significantly affected by the situation. These behaviors may be in response to humans (tourists, guards and/or researchers) and/or to other monkeys. The following sub-sections discuss the role of situation on each behavior and how each of the discriminated behaviors may be representative of personality traits isolated using the surveys.

*Avoidance*: The discriminant predictor of *avoidance* in the No Corn & No Tourist situation as a measure of Insecurity is likely a fear or submissive response to another individual (Berman et al., 2004), depending on the behavioral context and proximate individual's demeanor. Comparisons across situations showed decreased rates of *avoidance* behaviors during the No Corn & No Tourist situation relative to the Tourist and Corn & Tourist situations. This may be due to: decreased monkey-monkey agonistic *avoidance*, decreased monkey *avoidance* of park guards, decreased monkey *avoidance* of researchers, and/or absence of *avoidance* attributable to tourists. The YA1 monkeys often approach park guards and tourists during provisioning times, apparently to increase access to food, this may have resulted in a subsequent increase in the observed rates of *avoidance*.

*Lunging*: The discriminant predictor of *lunging* in the Corn & Tourist situation as a measure of Reactivity represents a volatile response to stimuli that other methods may overlook. A total of 32 lunges were observed throughout the study period. Monkeys that scored positively on Reactivity account for 26 of the total lunges. Half of the total lunges occurred in the Corn & Tourist situation. Relative to other situations, the Corn & Tourist situation stimulates a higher frequency of reactive responses (see also Berman et al., 2007), perhaps in part

due to tourists' tendencies to bring calorie-dense foods to the viewing platforms.

*Fear-grinning*: *Fear-grinning* in the Corn situation also was a discriminant predictor of Reactivity. Macaques typically maintain social distances to prevent agonism during provisioning (Wada and Ogawa, 2009), and after provisioning, the YA1 monkeys focused on eating dispersed corn (AP pers. obs.). However, due to heightened aggression observed in the study population during provisioning (Berman et al., 2007), it is possible *fear-grins* were in response to monkey agonism, researchers, and/or guards.

*Self-directed behaviors*: The discriminant predictor of *self-directed behaviors* (SDBs) in the Tourist situation as a measure for Boldness is logical given previous research showing a positive correlation of monkeys' SDBs and their proximity to tourists (Matheson et al., 2007). SDBs are behavioral manifestations of stress in many primate species (Honeess and Marin, 2006; Maestriperi, 2003). It is possible that Bold monkeys are more likely to expose themselves to frustrating or stressful situations resulting in an increase in SDBs for those monkeys, and that shy individuals are more likely to maintain their distance from tourists resulting in a decrease in SDBs for them. If so, this is a concern because socially stressful events and variations in personality affect immune responses (Mehta and Gosling, 2008; Maninger et al., 2003). The comparisons across situations showed mixed results for this relationship: increased rates of SDBs were found in the Tourist situation, but also in the No Corn & No Tourist situation relative to the two corn situations. It is possible that the increase in SDBs is an effect only seen after active foraging. Future research should examine this relationship in more detail: does Boldness predict proximity to humans, how do monkeys cope with an increase in stress, are Bold monkeys more stressed, and/or do they exhibit depressed immune-responses?

*Touching*: *Touching* during Corn situations was also a discriminant predictor for Boldness. *Touching* is an affiliative behavior (Berman et al., 2004) and may be a method of reassurance. Frequencies of *touching* were low overall in the dataset. Given that *proximity* and co-feeding are indicators of tolerance (Berman et al., 2004; Wada and Ogawa, 2009), it is possible that *touching* indicates a level of Boldness sufficient to test tolerance. However, further research is needed as other confounds, such as kinship, may also affect tolerance (Berman et al., 2004).

*Proximity*: The discriminant predictor of *proximity*

indicates that monkeys who maintain closer proximities to other monkeys in the No Corn & No Tourist and Tourist situations score highly in Sociability. Proximity correlates with Sociability (Capitani, 1999) and is a proxy for sociability in primate personality research (Konečná et al., 2008; Rouff et al., 2005; Suomi et al., 1996). Our findings support, and are supported by, such prior uses of proximity as a key behavior for measuring sociability. Comparisons across situations show a significant increase in *proximity* in the two provisioned situations. Previous research on macaques support an increase in *proximity* during provisioning, possibly due to how provisioned food is dispersed, which can contribute to increased agonism (Hill, 1999). The history of increased aggression with provisioning documented at this site (e.g., Berman, 2007) may be due to heightened *proximity*. Situational comparisons also show a significant increase in *proximity* during the Tourist situation relative to the No Corn & No Tourist situation. This may be due to: 1) a preference for increased social reassurance during Tourist situations, and/or 2) tourists occupying the platforms, which may cause monkeys to cluster around the tourists to access foods tourists brought (AP pers. obs.).

*Chase*: The discriminant predictor of *chase* in the No Corn & No Tourist situation showed moderate discrimination for Leadership. If Leadership represents an aspect of Agreeableness, then individuals that *chase* are disagreeable. However, given the reduced discrimination of Leadership and the infrequency of *chase* in this situation, it is difficult to draw conclusions for this component.

### 3.3 Component and function comparability

Discriminant scores and component scores were compared to determine if behavioral variables accurately predicted personality. These correlations allow for future analyses of behavioral data-sets *within this population* as proxies for personality components. Significant Spearman's correlations were found for four components: Insecurity, Reactivity, Boldness and Sociability. Given that the raters were reliable for each item input into the PCA and that personality surveys are valid measures of primate personalities (Uher et al., 2008; Weiss et al., 2012), these significant correlations confirm that the behaviors used to generate these functions are accurate representations of each monkey's personality relative to others. Therefore, these behavioral functions could serve to rank individuals on their expression of the relative personality traits. Behavioral functions could also be calculated from past and future data, al-

lowing exploratory perspectives on an individual's personality over time and the personality differences within this group.

### 3.4 Limitations of the study

Confirmatory analyses were conducted to account for issues related to smaller sample sizes. However, given that the current study is not attempting to generalize these data to another population, the negative influences of small sample sizes are minimized. Larger sample sizes or examining multiple groups and populations, both in the field and in captivity, will permit greater generalizations and the use of surveys with more items (see King and Figueredo, 1997; Konečná et al., 2008; Konečná et al., 2012). However, developing more techniques for measuring personality (such as the present study's discrimination of observable behaviors) will allow for more expansive studies. Furthermore, it is possible that raters are using some or all of the behaviors to form their perceptions of these monkeys' personalities. More refined studies may extrapolate whether these behaviors are proxies for human perceptions of monkey personalities (which are not necessarily manifestations of anthropomorphic biases [Weiss et al., 2012]), are limited by their statistical relationship to the lexical encodings of the surveys (Uher et al., 2013; Uher, 2013), or are direct behavioral expressions of personality. Limitations may also occur due to the conversion of nominal and ordinal data to interval data, a flaw intrinsic to survey ratings and to the method of scoring proximity and grooming measures. Our treatment of the ratings as independent in our PCA may be a point of criticism. However, the results are consistent with other studies on macaque personalities using the same, or similar, surveys. Future studies should take into account other behaviors and behavioral states, including those that are non-social. Future studies may also examine how monkey-monkey and monkey-human behavioral responses differ across situations, and in what way. Finally, any research that expands on these findings should consider that this study took place during mating and tourist seasons.

### 3.5 Concluding remarks

Applications of personality research are increasing. McCowan et al. (2011) demonstrated that personality traits were influential in determining social group structure. Seyfarth et al. (2012) examined baboon personalities and found that personality types affected how individuals recognized and interacted with others. Tracking the personalities of provisioned and tourist-frequented populations of primates is crucial in meas-

uring how provisioning and tourism affect individuals and how wildlife managers might mitigate negative effects. The methodology presented here permits exploratory analyses of personality through the proxy of predictive behavioral functions. Therefore, examination of personality at this site (or other sites, after using this method) can use behavioral data collected for purposes other than personality research. This may be a valuable methodology for developing future applications of personality research, especially at long term research sites where ethological data are habitually collected on the same individual primates or non-primates.

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## References

- Archard G, Braithwaite V, 2010. The importance of wild populations in studies of animal temperament. *Journal of Zoology* 281: 149–160.
- Berman CM, Li JH, 2002. Impact of translocation, provisioning and range restriction on a group of *Macaca thibetana*. *International Journal of Primatology* 23: 383–397.
- Berman CM, Ionica CS, Li JH, 2004. Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology* 25: 1283–1312.
- Berman CM, Li JH, Ogawa H, Ionica C, Yin H, 2007. Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *International Journal of Primatology* 28: 1123–1141.
- Bolig R, Price CS, O'Neill PL, Suomi SJ, 1992. Subjective assessment of reactivity level and personality traits of rhesus monkeys. *International Journal of Primatology* 13: 287–306.
- Buirski P, Plutchik R, Kellerman H, 1978. Sex differences, dominance, and personality in the chimpanzee. *Animal Behaviour* 26: 123–129.
- Capitanio JP, 1999. Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology* 47: 299–320.
- Carere C, Locurto C, 2011. Interaction between animal personality and animal cognition. *Current Zoology* 57: 491–498.
- Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R, 2013. Animal personality: What are behavioural ecologists measuring? *Biological Reviews* 88: 465–475. doi: 10.1111/bvr.12007
- Cicchetti DV, 1994. Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments in psychology. *Psychological Assessment* 6: 284–290.
- Freeman HD, Gosling SD, 2010. Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology* 72: 653–671.
- Freeman HD, Brosnan SF, Hopper LM, Lambeth SP, Schapiro SJ et al., 2013. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology* 75: 1042–1053.
- Funder DC, 2001. Personality. *Annual Review of Psychology* 52: 197–221.
- Gold KC, Maple TL, 1994. Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology* 13: 509–522.
- Gosling SD, 2008. Personality in non-human animals. *Social and Personality Psychology Compass* 2: 985–1001.
- Groothuis TGG, Carere C, 2005. Avian personalities: Characterization and epigenesis. *Neuroscience and Biobehavioral Reviews* 29: 137–150.
- Highfill L, Hanbury D, Kristiansen R, Kuczaj S, Watson S, 2009. Rating vs. coding in animal personality research. *Zoo Biology* 29: 509–516.
- Hill DA, 1999. Effects of provisioning on the social behaviour of Japanese and rhesus macaques: Implications for socioecology. *Primates* 40: 187–198.
- Holm S, 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70.
- Honess PE, Marin CM, 2006. Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews* 30: 390–412.
- Jin J, Su Y, Tao Y, Guo S, Yu Z, 2013. Personality as a predictor of general health in captive golden snub-nosed monkeys *Rhinopithecus roxellana*. *American Journal of Primatology* 75: 524–533.
- Jung S, Lee S, 2011. Exploratory factor analysis for small samples. *Behavioral Research* 43: 701–709.
- Kappeler PM, Watts DP, 2012. *Long-term Field Studies of Primates*. New York: Springer.
- King JE, Figueredo AJ, 1997. The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality* 31: 257–271.
- King JE, Landau VI, 2003. Can chimpanzee *Pan troglodytes* happiness be estimated by human raters? *Journal of Research in Personality* 37: 1–15.
- Konečná M, Lhota S, Weiss A, Urbánek T, Adamovská T et al., 2008. Personality in free-ranging Hanuman langur *Semnopithecus entellus* males: Subjective ratings and recorded behavior. *Journal of Comparative Psychology* 122: 379–389.
- Konečná M, Weiss A, Lhota S, Wallner B, 2012. Personality in barbary macaques *Macaca sylvanus*: Temporal stability and social rank. *Journal of Research in Personality* 46: 581–590.
- Koski SE, 2011. How to measure animal personality and why does it matter? Integrating the psychological and biological approaches to animal personality. In: Inoue-Murayama M, Kawamura S, Weiss A ed. *From Genes to Animal Behavior*. Osaka, Japan: Springer, 115–136.
- Ludbrook J, 1998. Multiple comparison procedures updated.

- Clinical and Experimental Pharmacology and Physiology 25: 1032–1037.
- Maestripietri D, 2003. Primate Psychology. Cambridge: Harvard University Press.
- Maninger N, Capitanio JP, Mendoza SP, Mason WA, 2003. Personality influences tetanus-specific antibody response in adult male rhesus macaques after removal from natal group and housing relocation. *American Journal of Primatology* 61: 73–83.
- Martau PA, Caine NG, Candland DK, 1985. Reliability of the emotions profile index, primate form, with *Papio hamadryas*, *Macaca fuscata*, and two *Saimiri* species. *Primates* 26: 501–505.
- Martin P, Bateson P, 2007. Measuring Behaviour. Cambridge: Cambridge University Press.
- Massen JJ, Koski SE, 2014. Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior* 35: 1–8.
- Matheson MD, Hartel J, Whitaker C, Sheeran LK, Li JH et al. 2007. Self-directed behavior correlates with tourist density in free-living Tibetan macaques *Macaca thibetana* at the Valley of the Wild Monkeys, Mt. Huangshan, China. *American Journal of Primatology* 69(S1): 41–42.
- McCowan B, Beisner BA, Capitanio JP, Jackson ME, Cameron AN et al., 2011. Network stability is a balancing act of personality, power, and conflict dynamics in rhesus macaque societies. *PLoS ONE* 6 e22350.
- McCrae RR, Costa Jr. PT, 1987. Validation of the five-factor model of personality across instruments and observers. *Journal of Personality and Social Psychology* 52: 81–90.
- McCrae RR, Costa Jr. PT, 2008. A five-factor theory of personality. In: John OP, Robins RW, Pervin LA ed. *Handbook of Personality: Theory and Research*. 3<sup>rd</sup> edn. New York: The Guilford Press, 139–153.
- McDougall PT, Reale D, Sol D, Reader M, 2006. Wildlife conservation and animal temperament: Causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation* 9: 39–48.
- McGraw KO, Wong SP, 1996. Forming inferences about some intraclass correlation coefficients. *Psychological Methods* 1: 30–46.
- Mehta PH, Gosling SD, 2008. Bridging human and animal research: A comparative approach to studies of personality and health. *Brain, Behavior, and Immunity* 22: 651–661.
- Neumann C, Agil M, Widdig A, Engelhardt A, 2013. Personality of wild male crested macaques *Macaca nigra*. *PLoS ONE* 8: e69383.
- Osborne JW, Costello AB, 2004. Sample size and subject to item ratio in principal components analysis. *Practical Assessment, Research & Evaluation* 9. Retrieved December 13, 2012, from <http://PAREonline.net/getvn.asp?v=9&n=11>.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82: 291–318.
- Rothbart MK, Ahadi SA, Evans DE, 2000. Temperament and personality: Origins and outcomes. *Journal of personality and social psychology* 78: 122–135. doi:10.1037/0022-3514.78.1.122
- Rouff JH, Sussman RW, Strube MJ, 2005. Personality traits in captive lion-tailed macaques *Macaca silenus*. *American Journal of Primatology* 67: 177–198.
- Ruesto LA, Sheeran LK, Matheson MD, Li JH, Wagner RS, 2010. Tourist behavior and decibel levels correlate with threat frequency in Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China. *Primate Conservation* 25: 99–104.
- Seyfarth RM, Silk JB, Cheney DL, 2012. Variation in personality and fitness in wild female baboons. *Proceedings of the National Academy of Sciences* 109: 16980–16985.
- Shrout PE, Fleiss JL, 1979. Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin* 86: 420–428.
- Sih A, Bell AM, 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior* 38: 227–281.
- Stevenson-Hinde J, Stillwell-Barnes R, Zunz M, 1980a. Individual differences in young rhesus monkeys: Consistency and change. *Primates* 21: 498–509.
- Stevenson-Hinde J, Stillwell-Barnes R, Zunz M, 1980b. Subjective assessment of rhesus monkeys over four successive years. *Primates* 21: 66–82.
- Stevenson-Hinde J, Zunz M, 1978. Subjective assessment of individual rhesus monkeys. *Primates* 19: 473–482.
- Suomi SJ, Novak MA, Well A, 1996. Aging in rhesus monkeys: Different windows on behavioral continuity and change. *Developmental Psychology* 32: 1116–1128.
- Sussman A, Ha J, 2011. Developmental and cross-situational stability in infant pigtailed macaque temperament. *Developmental Psychology* 47: 781–791.
- Uher J, 2008. Comparative personality research: Methodological approaches. *European Journal of Personality* 22: 427–455.
- Uher J, 2011. Individual behavioral phenotypes: An integrative meta-theoretical framework. Why “behavioral syndromes” are not analogs of “personality.” *Developmental Psychobiology* 53: 521–548.
- Uher J, 2013. Personality psychology: Lexical approaches, assessment methods, and trait concepts reveal only half of the story: Why it is time for a paradigm shift. *Integrative Psychological and Behavioral Science* 47: 1–55.
- Uher J, Asendorpf JB, 2008. Personality assessment in the great apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality* 42: 821–838.
- Uher J, Asendorpf JB, Call J, 2008. Personality in the behaviour of great apes: Temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour* 75: 99–112.
- Uher J, Werner CS, Gosselt K, 2013. From observations of individual behavior to social representations of personality: Development pathways, attribution biases, and limitations of questionnaire methods. *Journal of Research in Personality* 47: 647–667.
- Usui R, 2013. Behaviors of park rangers and their effects on Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China. MSc thesis, Ellensburg, WA: Central Washington University.
- Wada K, Ogawa H, 2009. Identifying inter-individual social distances in Japanese monkeys. *Mammalia* 73: 81–84.
- Weiss A, Inoue-Murayama M, King JE, Adams MJ, Matsuzawa T, 2012. All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour* 83: 1355–1365.
- Weiss A, King JE, Figueredo AJ, 2000. The heritability of personality factors in chimpanzees *Pan troglodytes*. *Behavior Genetics* 30: 213–221.