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Personality in Captive Killer Whales (*Orcinus orca*): A Rating Approach Based on the Five-Factor Model

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The comparative study of animal personality has received great interest in recent years. Some studies have analyzed personalities in cetaceans (exclusively in dolphins), but none have analyzed the factorial structure of personality of any species in this order. Our objective was to evaluate a sample of captive killer whales ($n = 24$) adapting one of the most widely used models of personality in humans and nonhuman animals: the five-factor model. A total of 38 personality descriptive adjectives were rated by 55 raters (mainly trainers and curators). Principal components analysis and regularized exploratory factor analysis revealed four statistically significant factors with acceptable standards of interrater reliability and validity, accounting for 49.85% of the variance. The first factor indicated an Extraversion factor, the second one revealed a combined factor of Conscientiousness and Agreeableness, the third one yielded in a Dominance factor, and the fourth one reflected a Careful factor very close to a combination of Conscientiousness and Agreeableness factor. The results were compared with the results obtained for humans and chimpanzees in prior studies. The similarities could be explained as a result of convergent adaptive traits despite a deep evolutionary divergence, adaptation to physically dissimilar environments, and very different neuroanatomical organization.

Keywords: killer whale, orca, personality, temperament, five factor model

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Studies investigating personality in nonhuman animals have been carried out over a wide range of species (see Gosling, 2001 and Carere & Maestripieri, 2013, for review). The species studied range from invertebrates, such as mollusks and arthropods, to vertebrates, such as amphibians, reptiles, birds and fish, but the majority of studies examined personality in mammals. Regarding cetaceans, personality studies have been carried out exclusively in dolphins. Those studies have documented individual differences that remain consistent over time (Highfill & Kuczaj, 2007) and across contexts (Highfill & Kuczaj, 2010; Kuczaj, Highfill, & Byerly, 2012). Moreover, it has been documented how individual differences can predict neophilia (Skrzypczak, 2016) for the Atlantic spotted dolphin (*Stenella frontalis*) and how these differences play a role in various social contexts including play behavior (Kuczaj & Eskelinen, 2014), social rank (Frick, 2016; Highfill & Kuczaj, 2010), learning (Kuczaj, Yeater, & Highfill, 2012), and bonds (Birgersson, 2011; Moreno, 2017) for bottlenose dolphins (*Tursiops truncatus*). However, none of these studies have analyzed the factor structure of personality for the species by using data reduction. The current study examines the personality structure of a previously unstudied cetacean, the killer whale (*Orcinus orca*).

The study of animal personality has been approached from very different perspectives, including to analyzing the structures of

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personality for different species (Gosling, 2001), comparing the personality profiles among species (Gosling & John, 1999; Morton et al., 2013; Uher & Asendorpf, 2008), validating the methodologies used (Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Highfill, Hanbury, Kristiansen, Kuczaj, & Watson, 2010; Pederson, King, & Landau, 2005; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012), comparing with humans (Budaev, 2000; Herrmann, Hare, Cissewski, & Tomasello, 2011; Nettle, 2006), or analyzing from an evolutionary perspective (Wolf, van Doorn, Leimar, & Weissing, 2013; Wolf & Weissing, 2012), among others. Moreover, some research has been focused on finding practical applications in the field of conservation (Bremner-Harrison, Prodohl, & Elwood, 2004; Carlstead, Mellen, & Kleiman, 1999; Martin & Réale, 2008; Powell et al., 2008; Wielebnowski, 1999; Wielebnowski, Fletchall, Carlstead, Busso, & Brown, 2002), management (Barlow, Caldwell, & Lee, 2006; Stoinski, Lukas, Kuhar, & Maple, 2004; Watters & Powell, 2012; Wielebnowski et al., 2002), health and well-being (Capitanio, 2011; Gartner & Weiss, 2013a; Jin, Su, Tao, Guo, & Yu, 2013; King & Landau, 2003; Maninger, Capitanio, Mendoza, & Mason, 2003; Mehta & Gosling, 2008; Weiss, Adams, & King, 2011), or welfare (Gartner & Weiss, 2013b; Martin, 2005; Murray, 1998; Weiss et al., 2009; Wielebnowski, 1999), among others.

There are two primary methods for evaluating personality in nonhuman animals: behavioral coding and trait rating (Gosling, 2001; Highfill et al., 2010; Vazire & Gosling, 2004). In the behavioral coding method, the researcher measures the frequency or duration of specific activities that occur during a period of time or exposes subjects to some novel environmental factor or a problem to solve, and records individual responses to the test conditions (Capitanio, 2017). In the trait rating method, raters such as keepers, researchers, or volunteers who are familiar with the animals are responsible for evaluating the personality of the individuals, usually using Likert's scale adjectives lists (Vazire & Gosling, 2004). This method has a number of advantages over coding because it is shown as an effective, quick, and easy method (see Freeman, Gosling, & Schapiro, 2011 for a review).

Personality-rating instruments have relied on two main methods: top-down and bottom-up (Freeman & Gosling, 2010). These lists of adjectives are created by a "bottom-up" approach, specific for the species of the study, or by the "top-down" approach, adapting instruments originally designed to be used in another species, usually humans (Freeman et al., 2013; Uher, 2008). Top-down models have been applied in nonhuman animals using different approaches, for example, the Subjective Well-Being Scale has been used to measure happiness (King & Landau, 2003), whereas the Emotions Profile Index (Buirski, Kellerman, Plutchik, Weininger, & Buirski, 1973), the Eysenck model (Úbeda & Llorente, 2015), or the five-factor model (FFM; King & Figueredo, 1997) have been used to measure personality. In fact, one of the most widely used instruments to measure personality in nonhuman animals with a top-down perspective has been the five-factor model (Goldberg, 1990). This model has been used in chimpanzees (*Pan troglodytes*; King & Figueredo, 1997), horses (*Equus* sp.; Kristiansen & Kuczaj, 2013), dogs (*Canis familaris)*, cats (*Felis catus*), rabbits (*Oryctolagus* sp.*)*, hedgehogs (*Atelerix* sp.), and ferrets (*Mustela putorius furo*; Gosling & Bonnenburg, 1998), among others.

The FFM is a hierarchical model with five bipolar factors (Goldberg, 1990; McCrae & Costa, 1999): Neuroticism, Extraversion, Agreeableness, Conscientiousness, and Openness to Experience. One review summarized the evidence for cross-species commonalities in personality factors (Gosling & John, 1999) of 12 different species. It concluded that the dimensions of Extraversion, Neuroticism, and Agreeableness showed considerable generality across all the species included in the review, whereas other factors showed less cross-species generality. Although the five factors of the model are proposed as temperament dimensions, the first three are considered to be associated with emotional reactivity and individual physiological processes.

The main objective of this study was to evaluate the factor structure of personality in a group of captive killer whales following the "top-down" method (Freeman et al., 2013) by using the FFM. The intent is to analyze the factorial personality profile of a cetacean by data reduction and compare these results with humans and chimpanzees.

Materials and Method

Sample and Study Site

This research was reviewed and approved by Loro Parque's and Sea World's Institutional Animal Care and Use Committee and was performed in accordance with the Animal Welfare Act for the care of Marine Mammals. We studied 24 killer whales (13 females and 11 males) hosted at Loro Parque (Tenerife, Spain), SeaWorld Orlando (Florida), and SeaWorld San Diego (California). Six of the killer whales were caught in the wild, whereas the remaining 18 were born in captivity and ranged in age from 3.16 to 29.42 years ($M = 15.89 \pm SD = 8.58$ years).

The whales are housed in interconnected pools with a mean total volume of 22.845 m^3 ($SD = 571.77$ m^3). Water quality management programs are based on treatment of marine water, whereas canopies provide direct shade. Training sessions including public presentations occur three to eight times daily and vary in time, duration, and focus. The total diet is distributed across six to eight feedings daily. The diet comprises herring, sardines, capelin, sprat, mackerel, squid, and salmon fed in quantities from 22.7 kg to 68 kg per animal. Animal groupings and pool access are variable throughout the day.

Raters

Questionnaires were completed by 17 raters from Loro Parque (13 trainers, three show audio-visual staff, and one behavioral researcher), 20 raters from SeaWorld Orlando (17 trainers and three curators), and 21 raters from SeaWorld San Diego (16 trainers, four curators, and one veterinarian). All raters had a high level of contact with the animals. Trainers and curators were in contact with the animals for a mean of over 94 months ($SD = 18.04$) and audio-visual staff a mean of 52 months ($SD = 2.42$). The veterinarian has over 9 years of continuous contact with the subjects, whereas the researcher developed an intensive behavioral research during 5 months. All of the raters evaluated all the subjects in their facility. Raters were instructed to base their judgments on general impressions of the killer whales, not on

frequency estimates of past behaviors. Raters were asked to avoid discussing their answers with others completing the surveys.

Questionnaire

The questionnaire was the same used by Úbeda and Llorente (2015) with chimpanzees, which was based on Goldberg's study (1990) in humans. The total number of adjectives used in the FFM questionnaire in our study was 38, with a Likert rating scale of 1 to 7 (see in the online supplemental materials). We used the synonym–antonym evaluation, whereby the antonyms were based on the adjectives used in the King and Figueredo (1997) study.

Interrater Reliability of Adjectives

The observer agreement of the 58 raters was assessed for each adjective using two intraclass correlation coefficients (ICC; Shrout & Fleiss, 1979). To compute ICCs, the mean squares for killer whales and Rater × Killer whales were obtained using a general linear model with Type III sums of squares (SAS Institute, 1999). The first ICC (3, 1) indicates the reliability of the scores for a single evaluator. The second ICC (3, k) indicates the reliability for the mean scores of the evaluators, in our case, based on an average of 19 raters per killer whale ($SD = 0.99$). Internal agreement of each component was measured using Cronbach's α, which assesses the correlation of two tests that measure the same variables.

Data Reduction: Principal Components Analysis and Regularized Exploratory Factor Analysis

To determine the personality trait domains, we first transformed our data into *z* scores using a principal components analysis (PCA) to identify the dimensions underlying the mean ratings. To determine the number of factor components to extract (only the factors that exceeded the 95th percentile of the values derived from random matrices were extracted), we examined the scree plot and used parallel analysis (Horn, 1965; O'Connor, 2000). After determining the number of components, we subjected those components to an orthogonal (varimax) and oblique (promax) rotation. For the purpose of interpreting and scoring factors, we defined absolute loadings ≥0.40 as salient. The component scores were unit-weighted, and thus the *z* scores of items with salient primary loadings were assigned weights of +1 or −1, depending on the direction of the loading. Items with nonsalient loadings were assigned weights of 0. Unit-weighted scores are more generalizable across studies and are highly correlated with differentially weighted scores (Gorsuch, 1984). Moreover, due to the small sample, we used regularized exploratory factor analysis (REFA), a technique specifically designed to derive factors when the sample size is very small (Jung & Lee, 2011; Jung & Takane, 2008). For this analysis, we used quartimax rotation and specified unweighted least squares for factor extraction. As REFA loadings are shrunk toward zero (Jung & Lee, 2011), they are more conservative than loadings obtained via PCA. We, therefore, defined loadings ≥0.30 as salient.

Cross-Species Comparisons

We compared the killer whale factor structure of personality with the structure of personality obtained for chimpanzees using the same questionnaire (Ubeda and Llorente, 2015). To do so we created unit-weighted factor scores and examined the correlations between them.

Results

Interrater Reliability of Adjectives

The ICCs for the single (3, 1) and average (3, k) ratings were strong, indicating that raters tended to agree in their judgments about the personality traits of the killer whales. The mean ICC (3, 1) was .37 ($SD = .15$; range = .06–.73). The mean ICC (3, k) was .96 ($SD = .03$; range = .81–.99). The overall reliability of the 38 adjectives was 0.96, and Cronbach's α levels ranged from 0.73 to 0.99. The interrater reliabilities of all 38 items are presented in Table 1.

Data Reduction: PCA and REFA

An examination of the scree plot for the mean ratings of the 24 killer whales suggested four principal components, and the parallel

Table 1
Interrater Reliabilities of Adjectives

Adjective	ICC (3,1)	ICC (3,k)
Playful	.61	.99
Inquisitive	.48	.98
Cheerful	.44	.98
Sociable	.49	.98
Affectionate	.34	.97
Active	.64	.99
Imitative	.32	.97
Friendly	.33	.97
Gregarious	.60	.99
Inventive	.42	.98
Patient	.42	.98
Constant	.47	.98
Peaceable	.43	.98
Predictable	.33	.97
Not defiant	.31	.96
Gentle	.33	.97
Stable	.37	.97
Trustful	.19	.94
Not bullying	.21	.94
Calm	.28	.96
Stubborn	.25	.95
Impulsive	.37	.97
Generous	.12	.90
Unemotional	.19	.94
Bold	.50	.98
Brave	.36	.97
Dominant	.73	.99
Protective	.47	.98
Intelligent	.33	.97
Laborious	.59	.99
Helpful	.24	.95
Prudent	.24	.95
Sensitive	.14	.91
Sympathetic	.26	.96
Organized	.34	.97
Responsible	.33	.97
Independent	.32	.97
Not decisive	.06	.81

Note. ICC = intraclass correlation coefficient.

analysis (Horn, 1965; O'Connor, 2000) indicated that the eigenvalues of the first four components exceeded the 95th percentile of eigenvalues expected by chance. Therefore, a PCA with varimax rotation was used to extract four components. The analysis indicated appropriate sampling adequacy (Kaiser–Meyer–Olkin measure = .86), accounting for the 49.9% of the total variance.

We extracted four factors from the mean ratings of the 24 killer whales using REFA and subjected these factors to a quartimax rotation. From the 38 adjectives analyzed, two of them (Decisive and Dependent) did not have salient loadings in any factor from both PCA and REFA. The dimensions extracted by REFA and those extracted by PCA were comparable (Table 2). Correlations obtained between the same labeled factors for PCA and REFA show statistical concordance, whereas correlations obtained between some of the other factors show statistical similarities that could be due to the sample size (Table 3). None of the extractions led to differences in how the dimensions were interpreted. From the four components extracted, the promax rotation revealed that the absolute interfactor correlations ranged from .03 to .37, with a mean of .14 (Table 4).

The first factor was described by the adjectives Playful, Social, Active, Cheerful or Gregarious, among others. These adjectives in humans and chimpanzees load on the factor Extraversion (Table 5). Therefore, we labeled this factor Extraversion. The second factor was characterized by the adjectives Patient, Predictable, Gentle, Generous, or Peaceable, among others, where some of them are related with the Conscientiousness and Neuroticism factors in humans, but most of them are related with the Agreeableness factor in humans. Likewise, most of those adjectives loaded on a factor termed Conscien-agreeableness in chimpanzees (Table 5), which correlates with the same labeled factor obtained for killer whales (Table 6). Therefore, we decided to label this factor as Conscien-agreeableness. The third factor was defined by the traits Bold, Brave, Dominant, Protective, Intelligent and La-

Table 2
Factor Loadings Obtained According to the Five-Factor Model for Captive Killer Whale Personalities

	Principal component analysis				Regularized exploratory factor analysis			
Adjectives	Ext	Cons-agr	Dom	Care	Ext	Cons-agr	Dom	Care
Playful	**.83**	−.03	.16	−.06	**.84**	−.05	.03	−.05
Inquisitive	**.75**	−.07	.19	.06	**.75**	−.04	.10	.07
Cheerful	**.68**	.19	.35	−.06	**.71**	.15	.22	−.17
Sociable	**.68**	.11	**.42**	−.02	**.72**	.10	**.30**	−.13
Affectionate	**.64**	.15	.07	.31	**.62**	.25	.04	.19
Active	**.64**	−.07	**.41**	−.12	**.67**	−.11	.28	−.12
Imitative	**.63**	−.01	−.06	.07	**.56**	.02	−.09	.08
Friendly	**.63**	**.40**	.04	.03	**.59**	**.38**	−.05	−.09
Gregarious	**.60**	−.03	**.50**	.02	**.66**	−.02	**.40**	−.08
Inventive	**.54**	−.13	.26	.23	**.55**	−.04	.22	.18
Patient	.19	**.72**	−.02	.14	.17	**.70**	−.05	−.08
Constant	−.20	**.69**	.20	.28	−.16	**.73**	.23	−.04
Peaceable	.24	**.69**	−.31	.17	.19	**.70**	−.33	.01
Predictable	−.19	**.67**	.11	.18	−.17	**.66**	.12	−.09
Not defiant	.07	**.65**	−.10	.22	.05	**.66**	−.09	.03
Gentle	.19	**.59**	−.11	.29	.17	**.63**	−.10	.10
Stable	.13	**.53**	**.51**	.02	.20	**.49**	**.42**	−.25
Trustful	.23	**.52**	.36	−.13	.26	**.41**	.24	−.27
Not bullying	−.04	**.50**	−.34	−.03	−.10	**.42**	**−.32**	−.06
Calm	−.28	**.43**	−.12	.09	−.26	**.39**	−.08	−.01
Stubborn	−.26	**−.42**	.04	−.20	−.22	**−.43**	.03	−.07
Impulsive	.34	**−.42**	.39	−.07	**.37**	**−.40**	**.32**	.01
Generous	.13	**.42**	.03	.33	.12	**.47**	.06	.14
Unemotional	−.23	**.42**	.02	−.07	−.20	**.32**	.00	−.12
Bold	.22	−.22	**.74**	−.05	**.32**	−.23	**.67**	−.12
Brave	.16	.01	**.74**	−.03	.26	−.02	**.64**	−.14
Dominant	.00	−.22	**.72**	.09	.12	−.17	**.67**	−.01
Protective	.03	−.06	**.52**	.28	.12	.04	**.48**	.10
Intelligent	.15	.18	**.51**	.23	.23	.23	**.46**	.05
Laborious	**.41**	−.01	**.45**	.27	**.46**	.08	**.41**	.16
Helpful	.23	.27	.26	**.65**	.27	**.47**	**.33**	**.42**
Prudent	−.17	.20	.19	**.65**	−.11	**.39**	**.30**	**.39**
Sensitive	.33	.07	−.23	**.62**	.29	.28	−.13	**.50**
Sympathetic	.31	.38	−.14	**.62**	.29	**.56**	−.07	**.46**
Organized	−.15	.30	**.41**	**.55**	−.07	**.45**	**.48**	.28
Responsible	−.32	**.47**	.20	**.48**	−.27	**.59**	.29	.20
Independent	−.35	.24	.20	−.13	−.28	.15	.15	−.13
Not decisive	−.16	−.04	−.30	.03	−.19	−.02	−.22	.05

Note. Ext = Extraversion; Cons-agr = Conscien-agreeableness; Dom = Dominance; Car = Careful. Boldface indicates salient loadings.

Table 3
Correlations Between Principal Component Analysis and Regularized Exploratory Factor Analysis Results for Captive Killer Whales

Factor	Principal component analysis			
	Extraversion	Conscien-agree	Dominance	Careful
Regularized exploratory factor analysis				
Extraversion	**.99**	−.21	**.72**	.19
Conscien-agree	−.15	**.99**	−.01	**.82**
Dominance	**.55**	−.02	**.99**	.39
Careful	−.01	.37	−.14	**.67**

Note. Conscien-agree = Conscien-agreeableness.

borious (only present in the PCA). We named this factor Dominance according to the same labeled factor found for chimpanzees, with which it also correlates (Table 6). Finally, on the fourth factor, two of the adjectives that loaded on this factor in PCA changed their distribution in REFA. This factor was characterized by adjectives related with the Agreeableness (Helpful, Sympathetic, or Sensitive) and Conscientiousness (Organized, Prudent, and Responsible) factors for humans (Goldberg, 1990). We could have labeled this factor as Conscien-agreeableness; instead, we decided to maintain this name for the second factor and to label this factor Careful.

Cross-Species Comparisons

Correlations of factor scores obtained for killer whales and chimpanzees, using the FFM as a framework, revealed that the factors of Extraversion, Conscien-agreeableness, and Dominance are highly positively correlated for both species (+0.80 to + 0.94). The factor Careful in killer whales was positively correlated (+0.75) with the factor Conscien-agreeableness in chimpanzees (Table 6).

Discussion

This study provided two main results. First, captive killer whales present a clear personality structure, characterized by four factors with acceptable standards of interrater reliability and validity. Second, the results found are similar to those found in humans and chimpanzees.

Gosling (2001) found that the mean interrater reliability of animal personality studies is around 0.52. The overall reliability of the 38 adjectives of the current study was high (0.96), indicating that raters tended to agree in their judgments about the personality traits of the killer whales (Table 1).

The validity for the data obtained in this study is expressed from the convergent and discriminant validity of the factors (Campbell & Fiske, 1959). By using the magnitudes of the adjectives loadings onto the factors to which they are assigned, convergent validity can be estimated. From the 38 adjectives evaluated, in the PCA, 29 loaded with values superior to .50, whereas seven adjectives ranged between .50 and .40, and two of them did not have salient loading on any of the factors, even though the ICC values were moderately high. In any case, there was a good evidence of convergent validity as indicated by the overall pattern of factor loadings. The low intercorrelation values of the oblique factors demonstrate factorial independence and discriminate validity. In our case, the mean absolute value is .14 (Table 4). This value falls into the range of mean factor intercorrelations reported for chimpanzees (.13; King & Figueredo, 1997), rhesus macaques (.14; Weiss, Adams, & Johnson, 2011), white-faced capuchins (.15; Manson & Perry, 2013), orangutans (.18; Weiss, King, & Perkins, 2006), or Barbary macaques (.19; Konečná, Weiss, Lhota, & Wallner, 2012), among others. However, one of our values was moderately high (0.37), but we should take into account that human studies (Borkenau & Ostendorf, 1990; Costa, McCrae, & Dye, 1991; Graziano & Ward, 1992) typically show at least two or three moderately high interfactor correlations (viz., approaching .50).

Regarding the labeling of the factors, those obtained for killer whales are similar to those found in humans and chimpanzees, although with some distinctive features. Both Extraversion and Conscien-agreeableness factors are related with the equivalent factors for humans and are positively correlated with the same factors for chimpanzees. Dominance factor correlates positively with the same factor for chimpanzees. We decided to use the label "Dominance" for this factor because many authors have emphasized the importance of this factor in primates and other orders (Freeman & Gosling, 2010; Gosling, 2008; Gosling & John, 1999). Finally, we could label the fourth factor as Conscien-agreeableness because we found adjectives related with the Conscientiousness and Agreeableness factors for humans (Goldberg, 1990), and this factor correlates with chimpanzee Conscien-agreeableness factor. However, we decided to maintain this name for the second factor because it has more loading and to label the fourth factor Careful (despite the fact that this label has not been found previously in other nonhuman animals).

Table 4
Factor Intercorrelation Matrix for the Factor Obtained for Captive Killer Whales

Factor	Ext	Cons-agr	Dom	Care
Ext	—			
Cons-agree	.06			
Dom	.21	.05		
Care	.10	.37	.03	—

Note. Ext = Extraversion; Con-agr = Conscien-agreeableness; Dom = Dominance; Car = Careful.

Table 5
Personality Structure Obtained in This Study (According to Regularized Exploratory Factor Analysis) for Killer Whales Using the Five-Factor Model (Compared With Humans [Goldberg, 1990] and Chimpanzees [Úbeda & Llorente, 2015])

Adjectives	Killer whales This study	Humans Goldberg, 1990	Chimpanzees Úbeda & Llorente, 2015
Playful	Extraversion	Extraversion	Extraversion
Inquisitive	Extraversion	Openness	Extraversion
Cheerful	Extraversion	Extraversion	Extraversion
Sociable	Extraversion	Extraversion	Extraversion
Affectionate	Extraversion	Agreeableness	Extraversion
Active	Extraversion	Extraversion	Extraversion
Imitative	Extraversion	Openness	—
Friendly	Extraversion	Agreeableness	Extraversion
Gregarious	Extraversion	Extraversion	Extraversion
Inventive	Extraversion	Openness	Conscien-open
Patient	Conscien-agree	Agreeableness	Conscien-agree
Constant	Conscien-agree	Conscientiousness	Conscien-open
Peaceable	Conscien-agree	Agreeableness	Conscien-agree
Predictable	Conscien-agree	Conscientiousness	Conscien-agree
Not defiant	Conscien-agree	Agreeableness	Conscien-agree
Gentle	Conscien-agree	Agreeableness	Extraversion
Stable	Conscien-agree	Neuroticism	Conscien-agree
Trustful	Conscien-agree	Neuroticism	Extraversion
Not bullying	Conscien-agree	Agreeableness	Conscien-agree
Calm	Conscien-agree	Neuroticism	Conscien-agree
Stubborn	Conscien-agree	Conscientiousness	Conscien-open
Impulsive	Conscien-agree	Extraversion	Conscien-agree
Generous	Conscien-agree	Agreeableness	Conscien-agree
Unemotional	Conscien-agree	Neuroticism	Dominance
Bold	Dominance	Extraversion	Extraversion
Brave	Dominance	Neuroticism	Dominance
Dominant	Dominance	Neuroticism	Dominance
Protective	Dominance	Conscientiousness	—
Intelligent	Dominance	Openness	Conscien-open
Laborious	Extraversion	Openness	Conscien-open
Helpful	Conscien-agree	Agreeableness	Extraversion
Prudent	Careful	Conscientiousness	Conscien-agree
Sensitive	Careful	Agreeableness	Extraversion
Sympathetic	Conscien-agree	Agreeableness	Extraversion
Organized	Dominance	Conscientiousness	Conscien-open
Responsible	Conscien-agree	Conscientiousness	Conscien-agree
Independent	—	Neuroticism	Conscien-open
Not decisive	—	Conscientiousness	Extraversion

Note. Ext = Conscien-agree = Conscien-agreeableness; Conscien-open = Conscien-openness.

To better define the personality factors, it would be interesting to compare the results obtained for killer whales in the current study with other cetaceans (e.g., dolphins). However, despite the fact that some studies have analyzed personality in cetaceans (exclusively in bottlenose dolphins) by using the rating method (Birgersson, 2011; Highfill & Kuczaj, 2007, 2010; Kuczaj et al., 2012), as yet, none of them have analyzed the factorial structure of this order by applying a data reduction. Instead, we compared our results for killer whales with those for primates, for which there are relevant data. Despite their deep evolutionary divergence, adaptation to physically dissimilar environments, and very different neuroanatomical organization, some primates and cetaceans show convergence in complex cognitive abilities (Marino, 2002, 2011), self-awareness (Marino, 2011), and very similar encephalization quotient (Marino, 1998) (EQ; chimpanzee EQ = 2,3; killer whales EQ = 2,6; Jerison, 1973; which is a measure of observed brain size relative to expected brain size, derived from a regression of brain weight on body weight for a sample of species). Like chimpanzees, killer whales have a fission–fusion social structure (at least for some types of killer whales; Beck, Kuningas,

Table 6
Correlations Between Captive Killer Whale (This Study) and Sanctuary Chimpanzee Personality Structures (Úbeda & Llorente, 2015)

Chimpanzee structure	Killer whale structure			
	Extraversion	Conscien-agree	Dominance	Careful
Extraversion	**.80**	.34	.23	.32
Conscien-agree	−.02	**.91**	−.04	**.75**
Dominance	.16	−.06	**.94**	−.19
Conscien-openness	−.68	.23	.44	.03

Note. Conscien-agree = Conscien-agreeableness. Boldface indicates correlations among factors.

Esteban, & Foote, 2012; Ivkovich, Filatova, Burdin, Sato, & Hoyt, 2010), present cooperative behavior (Pitman & Durban, 2012; Similä & Ugarte, 1993), and possess cultural traditions (Rendell & Whitehead, 2001). Cultural learning of behaviors may proceed through motor imitation or perhaps even through direct teaching (pedagogy), (Galef, 1992; Tomasello, 1994) as may be the case for killer whale calves instructed in the beach capture of pinnipeds by their mothers (Guinet & Bouvier, 1995; Rendell & Whitehead, 2001). Action imitation (Abramson, Hernández-Lloreda, Call, & Colmenares, 2013), hunting imitation (Baird, 2000; Similä & Ugarte, 1993), and vocal imitation (Bain, 1986; Deecke, Ford, & Spong, 2000; Foote et al., 2006; Ford, 1991; Janik & Slater, 1997; Yurk, Barrett-Lennard, Ford, & Matkin, 2002) also occurs, such as the development of new motor schema, hunting techniques not seen in any other killer whale populations, or dialects among killer whale family groups.

Given the small sample size of our study, we must be cautious in our conclusions. However, the similarity of personality structure across primate species and killer whales suggests evolutionary convergence (Marino, 2002, 2011). Perhaps this type of personality structure, and the distinct individual differences in behavior that this structure implies, are associated with complex sociality (including long-term dyadic relationships) and the cognitive abilities that go along with complex sociality. Alternatively (and not mutually exclusively), this type of personality structure may support behavioral variability across varying ecological contexts. However, it should be taken into account that some differences may be found because disparities have been described even within the same species (e.g., between Western and non-Western cultures for humans; Church & Katigbak, 1989; Narayanan, Menon, & Levine, 1995; Yang & Bond, 1990). It should also be kept in mind that adjectives can have different connotations in different species. For example, the adjective "inquisitive" in humans has connotations of acquisition of experience, and therefore it is often related to the Openness factor (Goldberg, 1990), whereas "affectionate," which can have connotations of warmth with a conspecific, is identified as a Agreeableness component in humans. However, both adjectives are related with the Extraversion factor in killer whales and chimpanzees, reflecting differences in social style. Accordingly, the degree of convergence in personality structure across species cannot be measured simply or directly from the agreement in factor labels and the magnitude of loadings of specific adjectives on certain factors. In future research, it will be interesting to adapt this methodology to other cetaceans to obtain the factor structure to compare from an evolutionary perspective.

References

Abramson, J. Z., Hernández-Lloreda, M. V., Call, J., Colmenares, F. (2013). Experimental evidence of action imitation in killer whales (*Orcinus orca*). *Animal Cognition, 16,* 11–22. http://dx.doi.org/10.1007/s10071-012-0546-2

Bain, D. (1986). Acoustic behavior of Orcinus: Sequences, periodicity, behavioral correlates and an automated technique for call classification. In B. C. Kirkevold & J. S. Lockard (Eds.), *Behavioral biology of killer whales* (pp. 335–371). New York, NY: Alan R. Liss.

Baird, R. W. (2000). The killer whale: Foraging specializations and group hunting. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 127–153). Chicago, IL: University of Chicago Press.

Barlow, C. J. C., Caldwell, C. A., & Lee, P. C. (2006). Individual differences and reactions to visitors in zoo-housed Diana monkeys. In S. Dow & F. Clark (Eds.), *Proceedings of the Eighth Annual Symposium on Zoo Research* (pp. 131–142). London, United Kingdom: British and Irish Association of Zoos and Aquariums.

Beck, S., Kuningas, S., Esteban, R., & Foote, A. D. (2012). The influence of ecology on sociality in the killer whale (*Orcinus orca*). *Behavioral Ecology, 23,* 246–253. http://dx.doi.org/10.1093/beheco/arr151

Birgersson, S. (2011). *Personality assessment and interactions in eight captive bottlenose dolphins* (*Tursiops truncates*; Master's thesis). Retrieved from http://urn.kb.se/resolve?urn=urn:nbn:se:liu:diva-70136

Borkenau, P., & Ostendorf, F. (1990). Comparing exploratory and confirmatory factor analysis: A study on the 5-factor model of personality. *Personality and Individual Differences, 11,* 515–524. http://dx.doi.org/10.1016/0191-8869(90)90065-Y

Bremner-Harrison, S., Prodohl, P. A., & Elwood, R. W. (2004). Behavioural trait assessment as a release criterion: Boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation, 7,* 313–320. http://dx.doi.org/10.1017/S1367943004001490

Budaev, S. V. (2000). *The dimensions of personality in humans and other animals: A comparative and evolutionary perspective.* Retrieved from http://cogprints.org/5474/2/budaev-2000-personality-manuscript-3.0b.pdf

Buirski, P., Kellerman, H., Plutchik, R., Weininger, R., & Buirski, N. (1973). A field study of emotions, dominance, and social behavior in a group of baboons (*Papio anubis*). *Primates, 14,* 67–78. http://dx.doi.org/10.1007/bf01730516

Campbell, D. T., & Fiske, D. W. (1959). Convergent and discriminant validation by the multitrait-multimethod matrix. *Psychological Bulletin, 56,* 81–105. http://dx.doi.org/10.1037/h0046016

Capitanio, J. P. (2011). Individual differences in emotionality: Social temperament and health. *American Journal of Primatology, 73,* 507–515. http://dx.doi.org/10.1002/ajp.20870

Capitanio, J. P. (2017). Variation in biobehavioral organization. In S. J. Schapiro (Eds.), *Handbook of primate behavioral management* (pp. 55–73). Boca Raton, FL: CRC Press.

Carere, C., & Maestripieri, D. (2013). *Animal personalities: Behavior, physiology, and evolution.* Chicago, IL: University of Chicago Press. http://dx.doi.org/10.7208/chicago/9780226922065.001.0001

Carlstead, K., Mellen, J., & Kleiman, D. G. (1999). Black rhinoceros (*Diceros bicornis*) in U.S. zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology, 18,* 17–34. http://dx.doi.org/10.1002/(SICI)1098-2361(1999)18:1<17::AID-ZOO4>3.0.CO;2-K

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2012). Evaluating animal personalities: Do observer assessment and experimental test measure the same thing? *Behavioral Ecology and Sociobiology, 66,* 153–160. http://dx.doi.org/10.1007/s00265-011-1263-6

Church, T. A., & Katigbak, M. S. (1989). Internal, external, and self-report structure of personality in a non-Western culture. An investigation of cross-language and cross-cultural generalizability. *Journal of Personality and Social Psychology, 57,* 857–872. http://dx.doi.org/10.1037/0022-3514.57.5.857

Costa, P. T., Jr., McCrae, R. R., & Dye, D. A. (1991). Facet scales for agreeableness and conscientiousness: A revision of the NEO personality inventory. *Personality and Individual Differences, 12,* 887–898. http://dx.doi.org/10.1016/0191-8869(91)90177-D

Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural trans-

mission. *Animal Behaviour, 60,* 629–638. http://dx.doi.org/10.1006/anbe.2000.1454

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O., & Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. *Biology Letters, 2,* 509–512. http://dx.doi.org/10.1098/rsbl.2006.0525

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology, 69,* 1454–1483. http://dx.doi.org/10.1139/z91-206

Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (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. http://dx.doi.org/10.1002/ajp.22168

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology, 72,* 653–671. http://dx.doi.org/10.1002/ajp.20833

Freeman, H. D., Gosling, S. D., & Schapiro, S. J. (2011). Comparison of methods for assessing personality in nonhuman primates. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 17–40). New York, NY: Springer. http://dx.doi.org/10.1007/978-1-4614-0176-6_2

Frick, E. E. (2016). *Establishing a link between personality and social rank in a group of bottlenose dolphins* (*Tursiops truncates*; Master's thesis, Paper 186). Retrieved from http://aquila.usm.edu/masters_theses/186

Galef, B. G. (1992). The question of animal culture. *Human Nature, 3,* 157–178. http://dx.doi.org/10.1007/BF02692251

Gartner, M. C., & Weiss, A. (2013a). Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management. *Applied Animal Behaviour Science, 147,* 261–267. http://dx.doi.org/10.1016/j.applanim.2012.11.002

Gartner, M. C., & Weiss, A. (2013b). Personality in felids: A review. *Journal of Applied Animal Behavioral Sciences, 144,* 1–13.

Goldberg, L. R. (1990). An alternative "description of personality": The big-five factor structure. *Journal of Personality and Social Psychology, 59,* 1216–1229. http://dx.doi.org/10.1037/0022-3514.59.6.1216

Gorsuch, R. L. (1984). *Factor analysis* (2nd ed., p. 425). Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin, 127,* 45–86. http://dx.doi.org/10.1037/0033-2909.127.1.45

Gosling, S. D. (2008). Personality in non-human animals. *Social and Personality Psychology Compass, 2,* 985–1001. http://dx.doi.org/10.1111/j.1751-9004.2008.00087.x

Gosling, S. D., & Bonnenburg, A. V. (1998). An integrative approach to personality research in anthrozoology: Ratings of six species of pets and their owners. *Anthrozoös, 11,* 148–156. http://dx.doi.org/10.2752/089279398787000661

Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science, 8,* 69–75. http://dx.doi.org/10.1111/1467-8721.00017

Graziano, W. G., & Ward, D. (1992). Probing the big five in adolescence: Personality and adjustment during a developmental transition. *Journal of Personality, 60,* 425–439. http://dx.doi.org/10.1111/j.1467-6494.1992.tb00979.x

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology, 73,* 27–33. http://dx.doi.org/10.1139/z95-004

Herrmann, E., Hare, B., Cissewski, J., & Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Developmental Science, 14,* 1393–1405. http://dx.doi.org/10.1111/j.1467-7687.2011.01082.x

Highfill, L., Hanbury, D., Kristiansen, R., Kuczaj, S., & Watson, S. (2010). Rating vs. coding in animal personality research. *Zoo Biology, 29,* 509–516.

Highfill, L. E., & Kuczaj, S. A. (2010). How studies of wild and captive dolphins contribute to our understanding of individual differences and personality. *International Journal of Comparative Psychology, 23,* 269–277.

Highfill, L. E., & Kuczaj, S. A., II. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic Mammals, 33,* 380–389. http://dx.doi.org/10.1578/AM.33.3.2007.380

Horn, J. L. (1965). A rationale and test for the number of factors in factor analysis. *Psychometrika, 30,* 179–185. http://dx.doi.org/10.1007/BF02289447

Ivkovich, T. V., Filatova, O. A., Burdin, A. M., Sato, H., & Hoyt, E. (2010). The social organization of resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed through association patterns and acoustic similarity. *Mammalian Biology, 75,* 198–210. http://dx.doi.org/10.1016/j.mambio.2009.03.006

Janik, V. M., & Slater, P. J. B. (1997). Vocal learning in mammals. *Advances in the Study of Behavior, 26,* 59–99. http://dx.doi.org/10.1016/S0065-3454(08)60377-0

Jerison, H. J. (1973). *Evolution of the brain and intelligence* (p. 482). New York, NY: Academic Press.

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. http://dx.doi.org/10.1002/ajp.22127

Jung, S., & Lee, S. (2011). Exploratory factor analysis for small samples. *Behavior Research Methods, 43,* 701–709.

Jung, S., & Takane, Y. (2008). Regularized common factor analysis. In K. Shigemasu, A. Okada, T. Imaizumi, & T. Hoshino (Eds.), *New trends in psychometrics* (pp. 141–149). Tokyo, Japan: Universal Academy Press.

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31,* 257–271. http://dx.doi.org/10.1006/jrpe.1997.2179

King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality, 37,* 1–15. http://dx.doi.org/10.1016/S0092-6566(02)00527-5

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. http://dx.doi.org/10.1016/j.jrp.2012.06.004

Kristiansen, R. E., & Kuczaj, S. A. (2013). The use of a five factor model in equine personality research. *International Journal of Comparative Psychology, 26,* 267–280.

Kuczaj, S. A., & Eskelinen, H. C. (2014). Why do dolphins play? *Animal Behavior and Cognition, 1,* 113–127. http://dx.doi.org/10.12966/abc.05.03.2014

Kuczaj, S. A., Highfill, L., & Byerly, H. (2012). The importance of considering context in the assessment of personality characteristics: Evidence from ratings of dolphin personality. *International Journal of Comparative Psychology, 25,* 309–329.

Kuczaj, S. A., Yeater, D., & Highfill, L. (2012). How selective is social learning in dolphins? *International Journal of Comparative Psychology, 25,* 221–236.

Maninger, N., Capitanio, J. P., Mendoza, S. P., & Mason, W. A. (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. http://dx.doi.org/10.1002/ajp.10111

Manson, J. H., & Perry, S. (2013). Personality structure, sex differences, and temporal change and stability in wild white-faced capuchins (*Cebus capucinus*). *Journal of Comparative Psychology, 127,* 299–311. http://dx.doi.org/10.1037/a0031316

Marino, L. (1998). A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior and Evolution, 51,* 230–238. http://dx.doi.org/10.1159/000006540

Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution, 59,* 21–32. http://dx.doi.org/10.1159/000063731

Marino, L. (2011). Cetaceans and primates: Convergence in intelligence and self-awareness. *Journal of Cosmology, 14,* 1063–1079.

Martin, J. E. (2005). The influence of rearing on personality ratings of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science, 90,* 167–181. http://dx.doi.org/10.1016/j.applanim.2004.08.019

Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. *Animal Behaviour, 75,* 309–318. http://dx.doi.org/10.1016/j.anbehav.2007.05.026

McCrae, R. R., & Costa, P. T. (1999). A five-factor theory of personality. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality theory and research* (pp. 139–153). New York, NY: Guilford Press.

Mehta, P. H., & Gosling, S. D. (2008). Bridging human and animal research: A comparative approach to studies of personality and health. *Brain, Behavior, and Immunity, 22,* 651–661. http://dx.doi.org/10.1016/j.bbi.2008.01.008

Moreno, K. R. (2017). *Does personality similarity in bottlenose dolphin pairs influence dyadic bond characteristics?* (Unpublished master's Thesis). University of Southern Mississippi.

Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., . . . Weiss, A. (2013). Personality structure in brown capuchin monkeys (*Sapajus apella):* Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology, 127,* 282–298. http://dx.doi.org/10.1037/a0031723

Murray, L. E. (1998). The effects of group structure and rearing strategy on personality in Chimpanzees (*Pan troglodytes*) at Chester, London ZSL and Twycross Zoos. *International Zoo Yearbook, 36,* 97–108. http://dx.doi.org/10.1111/j.1748-1090.1998.tb02890.x

Narayanan, K., Menon, S., & Levine, E. L. (1995). Personality structure: A culture-specific examination of the five-factor model. *Journal of Personality Assessment, 64,* 51–62.

Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist, 61,* 622–631. http://dx.doi.org/10.1037/0003-066X.61.6.622

O'Connor, B. P. (2000). SPSS and SAS programs for determining the number of components using parallel analysis and velicer's MAP test. *Behavior Research Methods, Instruments, and Computers, 32,* 396–402. http://dx.doi.org/10.3758/BF03200807

Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality, 39,* 534–549. http://dx.doi.org/10.1016/j.jrp.2004.07.002

Pitman, R. L., & Durban, J. W. (2012). Cooperative hunting behaviour, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antartic Peninsula waters. *Marine Mammal Science, 28,* 16–36. http://dx.doi.org/10.1111/j.1748-7692.2010.00453.x

Powell, D., Lin, H., Carlstead, K., Kleiman, D. G., Zhang, H.-M., Zhang, G.-Q., . . . Snyder, R. (2008). Relationships between temperament, husbandry, management, and socio-sexual behavior in captive male and female giant pandas, Ailuropoda melanoleuca. *Dong Wu Xue Bao, 54,* 169–175.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences, 24,* 309–324. http://dx.doi.org/10.1017/S0140525X0100396X

SAS Institute. (1999). *SAS/STAT user's guide, Version 8*. Cary, NC: SAS Institute.

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin, 86,* 420–428. http://dx.doi.org/10.1037/0033-2909.86.2.420

Similä, T., & Ugarte, F. (1993). Surface and underwater observation of cooperatively feeding killer whales in Northern Norway. *Canadian Journal of Zoology, 71,* 1494–1499. http://dx.doi.org/10.1139/z93-210

Skrzypczak, N. (2016). Personality traits in the Atlantic spotted dolphin (*Stenella frontalis*): Syndromes and predictors of neophilia. (Unpublished master's thesis). Florida Atlantic University, Boca Raton, FL.

Stoinski, T. S., Lukas, K. E., Kuhar, C. W., & Maple, T. L. (2004). Factors influencing the formation and maintenance of all-male gorilla groups in captivity. *Zoo Biology, 23,* 189–203. http://dx.doi.org/10.1002/zoo.20005

Tomasello, M. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 301–317). Cambridge, MA: Harvard University Press.

Úbeda, Y., & Llorente, M. (2015). Personality in sanctuary-housed chimpanzees: A comparative approach of psychobiological and pentafactorial human models. *Evolutionary Psychology, 13,* 182–196. http://dx.doi.org/10.1177/147470491501300111

Uher, J. (2008). Comparative personality research: Methodological approaches. *European Journal of Personality, 22,* 427–455. http://dx.doi.org/10.1002/per.680

Uher, J., & Asendorpf, J. B. (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. http://dx.doi.org/10.1016/j.jrp.2007.10.004

Vazire, S., & Gosling, S. D. (2004). Personality and temperament: A comparative perspective. In M. Bekoff (Ed.), *Encyclopedia of animal behavior* (pp. 818–822). Westport, CT: Greenwood Publishing Group.

Watters, J. V., & Powell, D. M. (2012). Measuring animal personality for use in population management in zoos: Suggested methods and rationale. *Zoo Biology, 31,* 1–12. http://dx.doi.org/10.1002/zoo.20379

Weiss, A., Adams, M. J., & Johnson, W. (2011). The big none: No evidence for a general factor of personality in chimpanzees, orangutans, or rhesus macaques. *Journal of Research in Personality, 45,* 393–397. http://dx.doi.org/10.1016/j.jrp.2011.04.006

Weiss, A., Adams, M. J., & King, J. E. (2011). Happy orang-utans live longer lives. *Biological Letters, 7,* 872–874. http://dx.doi.org/10.1098/rsbl.2011.0543

Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Udono, T., Ochiai, T., . . . King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology, 71,* 283–292. http://dx.doi.org/10.1002/ajp.20649

Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012). All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour, 83,* 1355–1365. http://dx.doi.org/10.1016/j.anbehav.2012.02.024

Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology, 90,* 501–511. http://dx.doi.org/10.1037/0022-3514.90.3.501

Wielebnowski, N. C. (1999). Behavioural differences as predictors of breeding status in captive cheetahs. *Zoo Biology, 18,* 335–349. http://dx.doi.org/10.1002/(SICI)1098-2361(1999)18:4<335::AID-ZOO8>3.0.CO;2-X

Wielebnowski, N. C., Fletchall, N., Carlstead, K., Busso, J. M., & Brown, J. L. (2002). Noninvasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population. *Zoo Biology, 21,* 77–98. http://dx.doi.org/10.1002/zoo.10005

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2013). The

evolution of animal personalities. In C. Carere & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 252–275). Chicago, IL: Chicago University Press. http://dx.doi.org/10.7208/chicago/9780226922065.003.0010

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution, 27,* 452–461. http://dx.doi.org/10.1016/j.tree.2012.05.001

Yang, K. S., & Bond, M. H. (1990). Exploring implicit personality theories with indigenous or imported constructs: The Chinese case. *Journal of Personality and Social Psychology, 58,* 1087–1095. http://dx.doi.org/10.1037/0022-3514.58.6.1087

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour, 63,* 1103–1119. http://dx.doi.org/10.1006/anbe.2002.3012

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