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Journal

Journal of Comparative Psychology, 127(3)

ISSN

0735-7036

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Publication Date

2013-08-01

DOI

10.1037/a0031316

Supplemental Material

https://escholarship.org/uc/item/1zk3537k#supplemental

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Personality Structure, Sex Differences, and Temporal Change and Stability in Wild White-faced Capuchins, *Cebus capucinus*

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In press, *Journal of Comparative Psychology*

Abstract

Research on nonhuman primate personality dimensions has focused on a small number of taxa, and little of this work has been done on wild populations. We used ratings to assess personality structure in wild white-faced capuchins over a 9-year period, using a capuchin-specific rating instrument based partly on existing instruments. Adequate levels of inter-rater reliability were found for 24 of 26 items. A longitudinal analysis found that 15 of these items showed significant rank-order stability from adolescence through early adulthood. Principal component analysis revealed five components. Four of these components were recognizable "Big Five" dimensions: Extraversion (E), Openness (O), Neuroticism (N) and Agreeableness (A). A dimension incorporating aspects of high O and high Conscientiousness (C) was labeled Eccentricity. Every dimension except for N showed significant rank-order stability from adolescence through early adulthood. Males were more Extraverted, Open, Neurotic and Eccentric than females, whereas females were more Agreeable than males. A cross-sectional analysis revealed that Openness and Agreeableness declined, whereas Eccentricity increased, during adulthood. The item content of capuchin Extraversion and Openness, and the existence of a distinctive Eccentricity dimension, are consistent with known characteristics of capuchin social and ecological adaptations, specifically the central roles of alliances, behavioral innovation and social learning.

Keywords: Personality, five factor model, trait rating, *Cebus capucinus*

Running headline: Capuchin personality structure

A growing body of research has documented that in many species of nonhuman animal, individuals vary in stable, cross-situational behavioral dispositions, i.e. personality dimensions (Gosling & John, 1999; Sih, Bell, Chadwick Johnson, & Ziemba, 2004; Wilson, 1998). For comparative psychologists, this variation poses the same general theoretical puzzles that are posed by human personality variation (Nettle, 2006): (1) Why do cross-situationally consistent dispositions persist, given that they impede adaptively flexible behavioral responses to variable circumstances (Sih et al., 2004)? (2) What evolutionary forces maintain the genetic variation associated with personality variation, given that natural selection generally eliminates all but the most fit allele at any locus (Fisher, 1930; see Keller et al. 2005, Adams et al. 2012 for recent discussions)? Several theoretical concepts have been fruitfully brought to bear on these questions, including frequency-dependent selection (e.g. Wilson, Clark, Coleman, & Dearstyne, 1994), temporally and spatially variable selection (e.g. Dingemanse, Both, & Drent, 2004), facultative calibration (Lukaszewski & Roney, 2011; Tooby & Cosmides, 1990), and trade-offs linked to alternative life history strategies (e.g. Wolf, Doorn, van Leimar, & Weissing, 2007).

As a foundation for such hypothesis-driven work, researchers need basic descriptive accounts of personality variation in a wide range of animal taxa. For psychologists interested primarily in the evolution of human personality, data on nonhuman primates are particularly relevant. According to a recent review (Freeman & Gosling, 2010), only 7% of all primate species have been the subjects of personality studies, and over 60% of published work concerns chimpanzees and rhesus macaques. Furthermore, only 9% of the published studies of nonhuman primate personality were conducted on wild populations. In this paper, we present the first data on personality variation in a wild New World primate and the longest continuous observational study of personality variation for any wild primate population. The genus *Cebus* (capuchins) has received little attention from personality researchers. Byrne and Suomi's (2002) study of tufted capuchins, *C. apella,* measured variation in individual trait items, but did not analyze personality structure. Morton et al. (under review) have described *C. apella* personality structure; one of our goals is to compare our findings in *C. capucinus* with their findings (see Discussion).

New World monkeys last shared a common ancestor with humans approximately 40 million years ago (Goodman et al., 1998). Because of its evolutionary convergence with chimpanzees with respect to encephalization (Stephan, Barbon, & Frahm, 1988), social complexity (Fragaszy, Visalberghi, & Fedigan, 2004; Perry & Manson, 2008), long/slow life history (Fragaszy et al., 2004) and reliance on social learning (Perry, 2011), *Cebus* is of particular interest to researchers of human behavioral evolution. Personality data from wild *Cebus* may also aid in reconstructing the phylogeny of personality dimensions (see Weiss, Adams, Widdig, & Gerald, 2011; Morton et al., under review).

In this research, we used trait ratings, one of the principal three methods (along with behavioral coding, and standardized situations presented to captive animals) used to measure nonhuman animal personality variation (Freeman, Gosling, & Schapiro, 2011; Freeman & Gosling, 2010). Observers' ratings have been

found to correlate with ethologically measured behavior patterns, thus manifesting construct validity, in several studies of primates. Most of these involved captive subjects (Capitanio, 1999; Pederson, King, & Landau, 2005; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Uher & Asendorpf, 2008; Vazire, Gosling, Dickey, & Schapiro, 2007), although a few (e.g. King, Weiss, & Farmer, 2005; Konečná et al., 2008) have used data from wild or at least semi-naturalistic settings. Ratings of the personality dimension *sociability* have also been found to predict immune function in rhesus macaques (Capitanio, 2011). In general, findings regarding interrater reliability, construct validity, and discriminant validity are widely held to justify fully the use of the trait rating method to measure nonhuman primate personality (Freeman et al., 2011; King & Weiss, 2011).

In developing rating scales, i.e. sets of items on which observers are asked to rate animals, researchers may follow one of two strategies, or a blend of the two. Drawing a parallel with cross-cultural research, Gosling & John (1998; cited in Weiss, King, & Perkins, 2006) distinguish between *etic* and *emic* sources of items (see also Uher 2008a, 2008b). Emic instruments are based on variable behavioral tendencies known, from previous research, to characterize a particular species. Etic instruments are imported from other species, including humans, and thus may be based on conceptual frameworks such as the five-factor model or FFM (Costa & McCrae, 1995; Digman, 1990).

Each of the FFM's dimensions, Extraversion (E), Neuroticism (N), Agreeableness (A), Conscientiousness (C) and Openness to Experience (O), is made up of 6 more specific facets (Costa & McCrae, 1992, 1995). For example, the facets of Extraversion are Warmth, Gregariousness, Assertiveness, Activity, Excitement Seeking, and Positive Emotions. In nonhuman primates, similar factors have been found in captive chimpanzees along with a sixth dimension, Dominance (King & Figueredo, 1997). Among captive orangutans assessed with a very similar instrument, Weiss et al. (2006) found evidence for E, N, A and Dominance, as well as a species-specific dimension, labeled Intellect, which included traits that in humans load positively on O and C and negatively on N. Slightly modified instruments have been used to measure personality dimensions in free-ranging rhesus macaques (Weiss, Adams, Widdig et al., 2011) and wild hanuman langurs (Konečná et al., 2008). Rhesus macaques showed a dimension corresponding to O, as well as dimensions labeled Confidence, Dominance, Friendliness, Activity and Anxiety (Weiss, Adams, Widdig, et al., 2011). Among the langurs, only three dimensions, Agreeableness, Confidence and Extraversion, emerged (Konečná et al., 2008).

Over a decade ago, Gosling and John (1999) encouraged researchers to seek evidence for the five factors in nonhuman species and to develop and test adaptationist hypotheses accounting for their presence or absence in comparative analyses (e.g. an Agreeableness dimension might not be found in solitary species). Weiss et al. (2006) suggested that at the finer-grained level of facets or individual traits, the five factors, though recognizable, may differ among species. Researchers who have sought FFM or FFM-like dimensions in nonhuman primates have drawn adaptive inferences. For example, langurs may lack an Openness dimension because they rarely engage in extractive foraging (Konečná et al., 2008). Researchers have also drawn phylogenetic inferences, e.g. that some macaque, great ape and human

personality dimensions are homologous (King & Figueredo, 1997; Weiss, Adams, Widdig et al., 2011; Weiss et al., 2006).

In humans, personality varies by age and by sex. As people transition from adolescence through to early and mid-adulthood, they become less Extraverted and Neurotic, and more Agreeable and Conscientious (Roberts, Walton, & Viechtbauer, 2006; Srivastava, John, Gosling, & Potter, 2003; Terracciano, McCrae, Brant, & Costa, 2005), with Openness increasing and later decreasing (but see Soto, John, Gosling, & Potter, 2011). These patterns are found cross-culturally (McCrae et al., 1999), although recent work in small-scale societies (Gurven, von Rueden, Massenkoff, & Kaplan, in press) challenges the view that the FFM applies to all human groups. Significant sex differences in most of the 30 FFM facets were found in 26 human societies (Costa, Terracciano, & McCrae, 2001). Among the major FFM dimensions, men in this multinational analysis were more Extraverted, and less Agreeable and Neurotic, than women, and slightly less Open and Conscientious.

Studies of age and sex differences in nonhuman primate personality dimensions show considerable cross-species variation. In captive rhesus macaques, Stevenson-Hinde et al. (1980) found a complex pattern of age- and sex-related differences in three personality dimensions: Confidence, Excitability and Sociability. Both sexes experienced a decline in Confidence in late adolescence. Adult females' Confidence scores remained low whereas adult males had higher Confidence scores than juveniles and adolescents of either sex. Females scored higher than males on Excitability as juveniles but not as adults. McGuire et al. (1994) identified three personality factors in captive vervets: Social competence, Opportunism and a Playful/Curious dimension. Juveniles scored higher than adults in Playful/Curious, whereas subadults scored higher than juveniles and adults, and females scored higher than males. Neither of the other two factors showed sex differences. In captive chimpanzees studied by King et al. (2008), age-related changes (but not sex differences) in the five factors roughly paralleled those found in humans. Extraversion declined with age through adulthood, and the sexes did not differ; Agreeableness increased significantly and Conscientiousness increased marginally with age, and females scored higher than males on both dimensions; Openness declined with age and showed no sex differences; and Neuroticism showed no age-related changes, and was higher in males than females.

In this paper, we use trait ratings made by experienced observers over a 9-year period to address the following questions for wild white-faced capuchins, *Cebus capucinus*: (1) What magnitude of interrater reliability is attainable for trait items? (2) How much rank-order stability do trait items manifest through early adulthood? (3) What components emerge when the items are subject to principal component analysis (PCA), and how well do these components conform to the FFM? (4) How are these components intercorrelated? (5) How much rank-order stability do these components manifest? (6) How do component scores vary by sex and by age during adulthood? Additionally, although this is not primarily a validation study, we present preliminary data examining the relationship between one rating item, *sociability*, and a behavioral measure, proportion of time observed alone during scan samples. Finally, we examine the relationship between proportion of time spent alone and each of the dimensions revealed by the PCA.

Methods

Study Population

Study subjects (*N* = 240) were white-faced capuchin monkeys (*Cebus capucinus*) aged 1-38 years, residing in Lomas Barbudal Biological Reserve, Costa Rica, and on nearby public and privately owned land (10°29-32'N, 85°21-24'W). The first study group was habituated to human observers in 1990, and two other groups were habituated in 1996 and 2002, respectively. Group fissions and migrations generated additional study groups; a total of 9 were under observation by 2011. All data presented in this paper were collected on fully habituated individuals. Females of this population give birth for the first time at a mean age of 6.2 years (Perry, Godoy, & Lammers, 2012). The youngest age at which a Lomas Barbudal male sired an offspring was 7.3 years (Perry et al., 2012), and males of this species do not reach adult size until age 10 (Fedigan, Avila, & Rose, 1996). Social groups that include females range in size from 5 to 40 individuals, and contain 1 to 13 adult males and 2 to 11 adult females (Perry, 2012). At any point in time, a minority of adult males resides in all-male groups of up to eight individuals (Perry, 2012). Males transfer from their natal group, usually in groups of two to three individuals, during adolescence or early adulthood, and most males make multiple transfers in later life as well (Jack & Fedigan 2004a,b; Perry et al., 2012; Perry, 2012). Females remain in their natal groups throughout their lives, although large groups occasionally fission. Ages of individuals born before habituation were estimated by comparing their physical and behavioral characteristics to those of individuals of known ages. See Perry and Manson (2008) for additional details about this study population and the long-term project of which the current research forms a part.

Rating Procedure

Observers (*N* = 51) were volunteer interns, field site managers, graduate students, postdoctoral scholars, and the Principal Investigator (SP). Observers spent 16-17 days per month collecting behavioral data from dawn to dusk. Observers completed trait questionnaires after completing a minimum of 12 continuous months working at the study site (most observers completed their questionnaire just before or just after finishing their internship). Except for SP and two other observers, each observer conducted observations on only a subset (e.g. two out of three) of the social groups that comprised the study population during his or her time at the study site. Each observer (hereafter, rater) rated each monkey that he or she had observed (on all questionnaire items) only once, regardless of how long the rater remained at the field site. Rating questionnaires were completed between Sep. 2002 and Oct. 2011. During this period, the study population expanded steadily. Thus, the number of monkeys rated per rater ranged from 52 to 142 (M = 82.5, *SD* = 23.0). Raters were instructed to refrain from discussing their ratings with other project personnel. They were asked to rate every monkey known to them on each questionnaire item before proceeding to the next questionnaire

item, i.e. to rate every monkey on *active* vs. *sluggish*, then rate every monkey on *aggressive* vs. *pacific*, etc. Raters were also asked to distribute their scores for each questionnaire item (except for one item, *eccentric* vs. *normal*) such that approximately 10%, 20%, 40%, 20% and 10% of monkeys received scores (on a 5-point scale) of 1, 2, 3, 4 and 5 respectively (following Stevenson-Hinde & Zunz, 1978). *Eccentric* was exempted from this normalization requirement because, in view of its semantic content, we lacked *a priori* confidence that this trait is naturally normally distributed. A positively skewed distribution seemed at least as likely as a normal distribution. Some raters declined to rate monkeys on particular trait adjectives (see "Missing Data," below).

Measurement instrument

Table 1 shows the 26 items that comprised the questionnaire. Each item was presented as two antonymous adjectives or descriptive phrases. *Reactive* was further defined as "easily outraged or alarmed." *Solicitous* was further defined as "responding to a distressed individual in a nurturing way." *Persistent/stubborn* was further defined as "won't give up on a project easily." *Understanding/compromising* was further defined as "good intuition about how to make a relationship work." *Reciprocating* was further defined as "refers to tendency to respond to a social initiation with like behavior."

Our instrument was partly based on several instruments used in personality research on other primate species. Like Stevenson-Hinde and Zunz's (1978) Madingley rhesus macaque questionnaire, it includes the items *active*, *aggressive*, *equable*, *fearful*, *opportunistic* and *sociable*. It shares with Capitanio's (1999) rhesus questionnaire the items *active*, *aggressive*, *fearful/confident* (used as a single antonymous item in our instrument), *curious*, *eccentric*, *equable*, *irritable*, *opportunistic*, *permissive*, *playful*, *popular*, *sociable*, *tense* and *understanding*. Our item *solicitous* resembles Capitanio's items *motherly* and *protective*, and our item *domineering* resembles (the opposite of) Capitanio's item *subordinate*. Like McGuire et al's (1994) vervet questionnaire, our instrument includes the item *assertive* (McGuire et al's instrument also includes *vigilant*, which appears in our instrument, but they defined it in a specific fashion that is not applicable to our study population). *Impulsive* and *persistent* are found in King & Figueredo's (1997) chimpanzee personality instrument, and their item *inventive* resembles our item *creative*. We included the items *creative* and *neophobic* because of the high frequencies of behavioral innovation, and the central role of social learning, in the acquisition of capuchin social interaction patterns (Perry et al., 2003), extractive foraging techniques, and food choices (reviewed by Perry, 2011). We included the items *meddlesome, attentive to conspecifics, understanding, reciprocating* and *socially intelligent* because of the central importance of coalition formation, triadic awareness, service exchange, and alliance partner choice in this species (Gros-Louis, Perry, & Manson, 2003; Jack & Fedigan, 2004a, 2004b; Manson, Navarrete, Silk, & Perry, 2004; Meunier, Molina-Vila, & Perry, 2012; Perry, Barrett, & Manson, 2004). Thus, our approach to instrument construction involved a blend of etic and emic approaches. We chose a set of items well-suited to determine whether four of the

FFM dimensions (Extraversion, Neuroticism, Agreeableness and Openness) characterize white-faced capuchins, but only 2 to 3 of the 26 items (*alert* and *persistent*, and possibly *reciprocating*) were likely candidates to load on a Conscientiousness factor.

Missing data

Eight of the 51 raters did not complete the questionnaire for every monkey that they were qualified to rate. The items *permissive* or *neophobic* were not rated at all by two raters, and the items *assertive*, *creative*, *opportunistic*, *attentive to conspecifics*, *persistent* and *socially intelligent* were not rated at all by one rater. One rater failed to rate 34 of 76 monkeys for *opportunistic*, and 29 of 76 monkeys for *reciprocating*. Besides these omissions, there were 16 other empty cells, i.e. individual monkeys not rated for particular items by raters who were qualified to rate them. Thus, 791 of 109,343 (0.72%) possible ratings were missing. For these missing values, we substituted the mean value for that item.

Behavioral observations

As one of several behavioral data collection protocols, observers used scan sampling to record monkeys' activities and the identities of their neighbors at four spatial proximity categories that ranged out to a distance of 10 monkey body lengths (roughly 400 cm) from the scanned individual. This paper draws on scan data collected on a subset of subjects, specifically all females in the five most intensively studied groups that (1) were alive during some portion of the period 2002-2006 and (2) gave birth at least once in 2007 or earlier (or, in one case, was an elderly female who had never given birth) (N = 38).

Statistical analysis

We carried out analyses using Stata 12.1. Only those monkeys who were rated by at least three raters were included in any of the analyses. Because the data had a crossed structure (each rater rated a subset of the subjects, and each subject was rated by a subset of the raters, and these sets overlapped to varying degrees), we assessed interrater reliability for each questionnaire item by calculating intraclass correlations (ICC[3,1] and ICC[3,k]) (Shrout & Fleiss, 1979). ICC is a widely used technique for assessing whether multiple judges agree above chance levels in ratings of nonhuman animal personality items (Freeman & Gosling, 2010). ICC(3,1) yields the inter-rater reliability of individual ratings, whereas ICC(3,k) yields the inter-rater reliability of mean ratings (here, each animal's mean rating across raters).

For each rater/monkey pair, we regarded the monkey's age at rating as its age three months before the rater completed the questionnaire. This adjustment takes into account that raters were instructed to consider all their experience observing each monkey over the preceding 12 months, yet were probably better able to remember more recent events than more remote events. To longitudinally

examine temporal stability of item ratings within individuals, we identified all monkeys (N = 21) who were rated by at least three raters during each of three age ranges: age 72-96 months, age 97-120 months, and 121-144 months. These age brackets correspond to late adolescence and early adulthood. Longitudinal examination of stability at older ages was not possible because of insufficient sample sizes. We calculated the mean rating for each questionnaire item for each individual in each of the three age brackets, and then calculated the Pearson product-moment correlations, among these 21 individuals, between each pair of age brackets. In other words, for these 21 individuals, we calculated, for each questionnaire item, three correlation coefficients: ages 6-8 years correlated with ages 8-10 years; ages 8-10 years with ages 10-12 years; and ages 6-8 years with ages 10-12 years. Significantly positive correlations indicate that monkeys' relative scores at these different ages are similar, i.e. they show rank-order stability.

For each monkey among those that were rated by at least three raters (N = 240), we calculated mean ratings for each item. We used principal component analysis (PCA: Gorsuch, 1983) to extract components from the items, and we generated a scree plot and used Horn's parallel analysis (Horn, 1965), implemented via Stata's paran command (Dinno, 2009), to determine the number of components to retain. Two rotations were applied to the components that we retained: a varimax procedure to obtain orthogonal components, and a promax procedure to obtain oblique components. The promax procedure enabled us to assess the correlations among the components. We considered an item to load on a component when (1) it had an absolute loading >0.40 and (2) it had the highest absolute loading on that component compared to all other components, except when two items' absolute loadings on the same component were within 0.10 of each other, in which case we regarded both items as loading on that component. Based on the varimax rotation, we calculated unit-weighted individual scores for each component. Also, for each retained component, we calculated internal consistencies (Cronbach's alpha) and inter-rater reliabilities (intraclass correlations using raters' unit-weighted component scores). Finally, we used the same sample of young adult monkeys described above (N = 21), and the same correlational analysis procedure, to examine longitudinal rank-order stability in unit-weighted component scores from ages 6 to 12 years.

For cross-sectional tests of the relationships between age and sex (independent variables) and component scores (dependent variable), we scored each monkey's age as its mean age at rating, across all raters that rated it. Because the age distribution was highly skewed toward younger ages (see below), we Box-Cox transformed these mean ages (Box & Cox, 1964) before using multivariate linear regression. Analysis was restricted to monkeys six years and older.

We used the scan sample data to calculate, for each female in the subsample (see above), the percentage of time spent alone, i.e. with no neighbors within 10 monkey body lengths. Females with infants <120 days old were scored as "alone" when their only neighbor was their infant. To adjust for year-to-year fluctuation in sampling intensity, and to create a behavioral score using a process parallel to the process that generated the rating score, we calculated, for each female, (1) the proportion of scan samples at which she was observed alone in each calendar year

from 2002-2006, (2) the mean value of these proportions across calendar years and (3) her mean score for each questionnaire item throughout the same time period. We then calculated the Pearson product-moment correlations, among these 38 females, between proportion of time alone and her mean rating for each questionnaire item. We expected that *sociability* would be strongly negatively correlated with time spent alone, and that *sociability* would show the highest absolute value of *r*, among all questionnaire items, with time spent alone. Finally, we calculated the correlations between time spent alone and all components retained from the PCA.

Results

Description of data set

Among the 240 monkeys that were rated by at least three raters, the mean number of raters (± *SD*) was 17.4 ± 12.4 (median: 12; range: 3-42). The mean (± *SD*) of mean ages at which monkeys were rated was 8.0 ± 7.7 years (median: 4.8 years; range: 1.0-36.6 years). The mean (± *SD*) age range of individual monkey ratings (i.e. the oldest age minus the youngest age at which a monkey was rated) was 4.5 ± 3.0 years (median: 3.4 years; range: 0.2-9.2 years).

As would be expected, because we instructed raters to distribute their ratings normally, the mean of mean ratings (± *SD*) was very close to 3.0, specifically 3.001 ± 0.122. The lowest mean value, 2.507, was for *eccentric*, which was the one item that we exempted from the normalization requirement. All other mean item ratings ranged from 2.903-3.186. The mean *SD* (± *SD*) of ratings was 0.581±0.091. From the scan samples of females, the mean (± *SD*) proportion of time spent alone was 0.42 ± 0.08 (median: 0.41; range: 0.27-0.62).

Interrater reliability of items

Table 1 shows ICC(3,1) and ICC(3,k) for the 26 items. Two items (*permissive* and *understanding*) were excluded from further analysis, partly because of their low reliabilities (no other items yielded ICC[3,k] below 0.70) and partly because these two items, and no others, appeared to perplex a substantial number of field assistants as they completed their questionnaires. The differences between ICC(3,1) and ICC(3,k) coefficients for each item were larger than in studies using comparable methods (e.g. Konečná et al., 2008; Weiss et al., 2011). This pattern is attributable to the larger number of raters in the present study compared to similar studies. ICC(3,1), which assesses the agreement among individual ratings, is reduced by large individual deviations from mean ratings, which are more likely in large sets of raters. Because all of our analyses used each animal's mean rating for each item, ICC(3,k), which assesses the reliability of mean ratings, is more relevant than ICC(3,1).

Temporal stability in individual item scores

Table 2 shows the correlations across the three age ranges (6-8, 8-10 and 10-12 years) of each of the 24 reliable item ratings. In this longitudinal analysis, only one item, *reactive*, failed to show significant consistency between any age ranges, but 9 items failed to show significant consistency between ages 6-8 and ages 10-12. The mean *r*, across items, between ages 6-8 and 10-12 was 0.41.

Principal component analysis

Examination of the scree plot (Fig. S1) and parallel analysis indicated that five components should be retained. Low unique variances of the items (M = 0.18) confirmed that PCA was appropriate. The loadings of individual items on the five varimax-rotated components are shown in Table 3.

Loadings on the first component included *socially intelligent, domineering,* (not) *fearful, popular, assertive, meddlesome, aggressive, sociable, persistent* and *attentive to others*. We infer that monkeys scoring high in this dimension frequently seek opportunities for social interaction, and are frequently sought out by others for social interaction. They are confident, at least in social situations, and they use aggression judiciously both to advance and maintain their own social status, and to assist valuable social partners. This dimension appears to encompass at least two of the facets of human Extraversion: Gregariousness and Assertiveness. It may also encompass the Excitement Seeking facet, since coalitional aggression (indicated by *meddlesome*) appears to be the most exciting of the frequent events in *C. capucinus* life (Perry & Manson, 2008). Only one item, *persistent*, seems more consistent with a different FFM factor, Conscientiousness. In view of the overall pattern of item loadings, we named this component Extraversion$_{CC}$, with the subscript (following Weiss et al., 2006) indicating that white-faced capuchin Extraversion is not exactly concordant with human, chimpanzee or orangutan E.

Loadings on the second component included *curious*, *playful, active*, (not) *neophobic*, *active, creative, impulsive*, *sociable* and *opportunistic*. We infer that monkeys scoring high on this dimension are willing to try new behaviors. They are actively engaged with both the physical world and with conspecifics. This dimension appears to correspond most closely to human Openness, although some facets of human Extraversion (Activity, Excitement Seeking, Positive Emotions) also appear associated with it. On the other hand, three facets of human O (Actions, Fantasy and Feelings) have been found to be associated with sensation seeking (Aluja, García, & García, 2003). We name this factor Openness$_{CC}$.

Loadings on the third component included *reactive*, (not) *tolerant* (i.e. *irritable*), (not) *relaxed* (i.e. *tense/anxious*), *alert*, *aggressive* and *impulsive*. We infer that monkeys scoring high on this dimension are hypervigilant and have poor internal control in the face of stressors. It is noteworthy that *meddlesome* and *assertive* also had fairly high loadings on this component, although they were not regarded as salient according to our pre-set criteria because of their much higher loadings on other components. Three facets of human Neuroticism – Anxiety, Angry

Hostility, and Impulsivity -- seem to be strongly related to this dimension. We call this dimension Neuroticism$_{CC}$.

Loadings on the fourth component included *solicitous*, *reciprocating* and *attentive to others*. We infer that monkeys scoring high on this dimension seek out friendly social interactions including grooming, other forms of affiliative physical contact, and carrying of infants and young juveniles. They can also be relied on to respond affiliatively to friendly behavior from others. As we defined *reciprocating*, it could also mean responding aggressively to aggression, but the total pattern of this component's loadings suggests that high-scoring individuals do not engage in frequent aggression. Monkeys high on this component may not be particularly valuable partners for coalitional aggression (*meddlesome* does not load on it), nor are they preferentially sought as social partners (neither *sociable* nor *popular* loads on it). Three facets of human Agreeableness – Trust, Altruism and Tender-Mindedness – seem to be strongly related to this dimension, and we therefore name it Agreeableness$_{CC}$.

Loadings on the fifth component included *eccentric* and *persistent*. *Creative* also loads modestly on this component, though it is not salient because of the much higher loading of *creative* on Openness$_{CC}$. This component appears to tap some aspects of human Openness, but unlike Openness$_{CC}$, it is not related to any of the items pertaining to the Extraversion facets Gregariousness or Activity. Two facets of human Conscientiousness, Achievement Striving and Self-Discipline, also seem to characterize this component. We speculate that monkeys scoring high on this dimension exhibit behavioral variants that are less commonly used by the majority of group members. We name this component after its predominant item, Eccentricity$_{CC}$.

The varimax and promax rotations of the first five components yielded qualitatively very similar results. Two loadings, both on Neuroticism$_{CC}$, differed between the two solutions. In contrast to the results shown in Table 3, in the promax solution *aggressive*'s loading on Neuroticism$_{CC}$ was 0.48 (i.e. not a salient loading according to our pre-set criteria, because *aggressive*'s loading on Extraversion$_{CC}$ was >0.10 greater than 0.48). Also, *impulsive*'s loading on Openness$_{CC}$ was 0.70, which was >0.10 than *impulsive*'s loading on Neuroticism$_{CC}$, meaning that *impulsive* no longer had a salient loading on Neuroticism$_{CC}$. Furthermore, for all five components, the correlation between the varimax item loadings and the promax item loadings was >0.97. We therefore used the varimax solution for all analyses except when assessing the intercorrelations among component scores. Internal consistencies of the varimax components (Cronbach's alpha) ranged from 0.51 to 0.94, while component inter-rater reliabilities (ICC[3,k]) ranged from 0.79 to 0.93 (Table 4).

Correlations among components

Table 5 shows the correlations among the promax-rotated components. The mean absolute value of the correlations was 0.157. This value falls into the range of mean component intercorrelations reported for chimpanzees (0.135: King &

Figueredo, 1997), rhesus macaques (0.14: Weiss, Adams, Widdig, et al., 2011) and orangutans (0.18: Weiss et al., 2006).

Rank-order stability of component scores

Table 6 shows the correlations across three age ranges (6-8, 8-10 and 10-12 years) of unit-weighted scores for each of the five components. In this longitudinal analysis, four of the components showed significant rank-order stability across all age ranges. Among the five components, the mean *r* between ages 6-8 and 10-12 was 0.49. Neuroticism$_{CC}$ did not show significant rank-order stability between ages 6-8 and ages 10-12.

Sex differences in personality dimensions

Table 7 incorporates data from monkeys of all ages. It shows mean values and standard errors of the two sexes for each of the five varimax-rotated unit-weighted component scores, as well as effect sizes (Cohen's *d*) and significance levels. Males were more Extraverted, Open, Eccentric, and Neurotic than females, whereas females were more Agreeable than males.

Age differences in personality dimensions

Table 8 and Figure 1 show the results of cross-sectional analyses of age effects (and sex effects) on personality dimensions in monkeys aged 6 years and older. Figure 1 shows actual (untransformed) ages for ease of interpretation. After controlling for age, and restricting the analysis to adults, all of the sex comparison results described in Section 3.6 remained qualitatively unchanged. Three of the five dimensions showed significant age effects after controlling for sex. Monkeys became less Open and Agreeable, and more Eccentric, as they aged. In another set of analyses, we used age, sex and the age × sex interaction as independent variables. All main effects remained qualitatively the same as in the analyses already described. Only one interaction effect, for Openness, was statistically significant ($p < .001$; Figure 1B): both sexes became less Open with age during adulthood, but males' scores declined more steeply than females' scores.

Ratings, dimensions and time spent alone

Among the 38 females that contributed data to this analysis, the correlation between mean *sociable* rating and proportion of time spent alone was -0.846 ($p < .0001$). None of the other 25 items was as strongly correlated with proportion of time spent alone. Among conceptually similar items, *attentive to conspecifics* was correlated at $r = -0.768$ ($p < .0001$), *popular* at $r = -0.674$ ($p < .0001$), and *solicitous* at $r = -0.255$ ($p = .12$). All five personality components were significantly correlated with proportion of time spent alone: Extraversion ($r = -0.741$, $p < .001$); Openness ($r = -0.706$, $p < .001$); Neuroticism ($r = -0.463$, $p = .004$); Agreeableness ($r = -0.742$, $p < .001$); and Eccentricity ($r = 0.392$, $p < .015$).

Discussion

We presented a descriptive account of personality structure in wild white-faced capuchin monkeys, *Cebus capucinus*, using a more extensive data set than any yet published on personality variation in a wild primate population. We created a *Cebus*-specific rating instrument by modifying existing instruments (e.g. Capitanio, 1999; King & Figueredo, 1997) to include items that are relevant to known features of capuchin behavior, particularly innovation, social learning and social complexity (e.g. frequent aggressive coalitions) (Perry & Manson, 2008). Of the 26 items comprising the instrument, 24 yielded adequate inter-rater reliability, consistent with findings in other primate species (Freeman et al., 2011; Freeman & Gosling, 2010) that high levels of reliability are attainable among trained observers with extensive experience. We validated one item, *sociability*, by finding a very strong negative correlation (stronger than for any other rating item) between it and the behavioral variable *proportion of time spent alone*.

Four of the dimensions revealed by PCA ($Extraversion_{CC}$, $Openness_{CC}$, $Neuroticism_{CC}$, and $Agreeableness_{CC}$) are similar to personality dimensions found in humans and chimpanzees (Costa & McCrae, 1995; King & Figueredo, 1997). Our failure to find a Conscientiousness dimension should not be taken as evidence that no such dimension exists in white-faced capuchins; as described above, the rating instrument was not well-suited to capture such a dimension. The five dimensions revealed by our analysis resemble the five dimensions (Assertiveness, Openness, Neuroticism, Sociability, and Attentiveness) reported for captive *Cebus apella* by Morton et al. (under review), but we tentatively infer that three of these dimensions differ sufficiently to merit different labels. As a caveat to the following remarks, Morton et al. used a different instrument (the Hominoid Personality Questionnaire [HPQ: Weiss et al., 2009]) from ours. Future studies using the same instrument(s) with both species are required to confirm the degree of similarity between their personality structures. $Extraversion_{CC}$ differs from *C. apella* Assertiveness, and from chimpanzee, orangutan and rhesus macaque Dominance (King & Figueredo, 1997; Weiss et al., 2006; Weiss, Adams, Widdig, et al., 2011), in including two items, *sociable* and *popular*, that indicate that individuals high on this dimension are attractive as social interaction partners in addition to being formidable competitors. The item content of $Extraversion_{CC}$ is consistent with the large role of alliance formation and maintenance, relative to the role of physical formidability, in white-faced capuchin status competition (Perry & Manson, 2008). For example, alpha males sometimes maintain their rank for up to 17 years, i.e. until their fighting prowess has declined substantially from its peak in early adulthood (Muniz et al., 2010). In contrast, coalitionary aggression is less common and is accompanied by a less elaborate signal repertoire in wild *C. apella* than in wild *C. capucinus* (Perry, 2012).

$Openness_{CC}$ closely resembles *C. apella* Openness (Morton et al., under review), except that the former includes *sociable*. $Neuroticism_{CC}$ closely resembles

C. apella Neuroticism. Agreeableness$_{CC}$ differs somewhat from *C. apella* Sociability. The former includes *solicitous*, whereas neither *gentle*, *sympathetic* nor *helpful* loads on the latter. On the other hand, *C. apella* Sociable includes *sociable*, whereas Agreeableness$_{CC}$ does not. Thus, whereas *C. apella* Sociable appears to capture both frequency and (to some extent) friendliness of social interaction, individuals high on Agreeableness$_{CC}$ do not necessarily spend a lot of time in social activity, but when they do interact with conspecifics, they probably provide a high level of services such as grooming and carrying. Eccentric$_{CC}$, like orangutan Intellect (Weiss et al., 2006) comprises a blend of facets from the FFM dimensions Openness and Conscientiousness, with no relationship to items related to sociability or general activity level. Unlike *Cebus apella* Attentive (Morton et al, under review), Eccentricity$_{CC}$ includes *persistent*, whereas *C. apella* Attentive does not include the HPQ item, (not) *conventional*, that most closely resembles our item *eccentric*. Interestingly, although Openness$_{CC}$ and Eccentricity$_{CC}$ overlap conceptually (both resembling FFM Openness), the correlation between them is slightly negative (Table 5), and they change in opposite directions during adulthood. Compared to other primates, capuchins frequently innovate, and learn socially, in the domains of both communicative social conventions (Perry et al., 2003) and food processing techniques (reviewed by Perry, 2011). Although *creative* loaded strongly positively on Openness$_{CC}$ and weakly positively on Eccentricity$_{CC}$, we speculate that high-Openness$_{CC}$ monkeys tend to acquire new behavioral variants socially, via direct interaction with conspecifics, whereas high-Eccentricity$_{CC}$ monkeys tend to acquire new variants more often by independent invention and persistent trial and error learning. Variation in Openness$_{CC}$ and Eccentricity$_{CC}$ might be maintained by balancing selection favoring a mix of innovation and social learning (e.g. Rendell et al., 2010).

In a subset of individuals followed from late adolescence through early adulthood, we found modest levels of rank-order temporal stability in individual rating items, and generally strong levels of stability in four of the five components. Fifteen of the 24 items showed significant correlations between age 6-8 years and ages 10-12 years. However, constraints imposed by our methods may have produced underestimates of the true strength of temporal stability of these items. The mandatory normalization instruction forced raters to compare each monkey to a reference group, and individual raters varied considerably with respect to the composition of this reference group. First, monkey group compositions changed over time because of births, deaths, male immigrations and emigrations, and group fissions. Second, each observer worked with a subset of the monkey groups, and these subsets overlapped to differing degrees with the subsets of other observers working at the study site at the same time.

Among the five personality dimensions identified by the PCA, the mean correlation between scores at age 6-8 and scores at age 10-12 was 0.49. This is roughly the same as the strength of rank-order stability shown for human FFM scores in the corresponding life history stages (ages 18-30) (meta-analysis: Roberts & DelVecchio, 2000). Studies of rank-order personality stability in nonhuman primates have mostly covered periods of 1.5 years or less (e.g. Uher, Asendorpf & Call, 2008; Weiss et al., 2011) and are therefore not directly comparable to our

analyses. An exception is Stevenson-Hinde et al's (1980) four-year longitudinal study of rhesus macaque personality. They found that multiparous females and fully adult males showed significant rank-order stability in dimensions labeled Confident, Excitable and Sociable. In our data set, $Neuroticism_{CC}$ was the least temporally stable dimension. We speculate that monkeys' scores on $Neuroticism_{CC}$, unlike their scores on other components, are strongly influenced by transient social conditions, at least through early adulthood. For example, males that transfer between social groups in late adolescence might become less Neurotic if they attain alpha rank, but more Neurotic if they become subordinates. Adult females with unweaned infants might become more Neurotic in response to the presence of potentially infanticidal males following male group membership or rank changes (Perry, 2012). The adaptive adjustment of personality configurations to other phenotypic traits, particularly those affecting social bargaining power, is predicted by the facultative calibration model (Lukaszewski & Roney, 2011; Tooby & Cosmides, 1990). Future research on our study population will test predictions from this model.

The observed sex differences in capuchin personality dimensions are interpretable in terms of both general primate behavioral sex differences, and the different life courses of the two sexes in capuchins specifically. Almost all males migrate before breeding, usually with one or two co-migrants (Jack & Fedigan, 2004a; Perry 2012), and the formation and maintenance of alliances with other males and with females can strongly influence reproductive success, and indeed survival (Gros-Louis et al., 2003; Perry, 2012; Perry & Manson, 2008). Thus, males probably benefit more than females from seeking out social opportunities and from taking the risks involved in forming new relationships and trying out new forms of social behavior (higher $Extraversion_{CC}$ and $Openness_{CC}$). Depending on the spatial scale of habitat heterogeneity, migrating males might also benefit more than females from being willing to try out new foraging behaviors (higher $Openness_{CC}$ and $Eccentricity_{CC}$). In general, male primates innovate more than females (Reader & Laland, 2001). Higher male than female $Neuroticism_{CC}$ is interpretable in terms of males' greater need for vigilance in response to the threat of escalated aggression (Gros-Louis et al., 2003). Females, on the other hand, might be more effective mothers and allomothers (Manson, 1999; Perry, 1996) by being higher in $Agreeableness_{CA}$.

Throughout adulthood, capuchins become less Open as they age. Viewing $Openness_{CC}$ as, roughly speaking, a mix of facets characterizing human Openness and Extraversion, this result is consistent with findings from captive chimpanzees (King et al., 2008), which show age-related declines in both dimensions in adults. The costs, particularly the risks, of forging new social relationships may be offset by greater benefits at younger ages than at older ages, particularly for males in species characterized by male transfer. Consistent with this hypothesis, we found that male $Openness_{CC}$ declined more steeply than female $Openness_{CC}$, whereas in chimpanzees (a female transfer species: Pusey, 1979), neither Extraversion nor Openness showed an age × sex interaction effect (King et al., 2008). Adult white-faced capuchins become less Agreeable with age, whereas both humans and chimpanzees become more Agreeable (King et al., 2008).

Future research on this population will make use of available genetic data and long-term behavioral data to address several questions regarding the causes and consequences of personality variation in *C. capucinus*. For example, what are the relative effects of heritable variation, early life experience (e.g. the stress caused by take-overs by infanticidal males), and later facultative calibration (see Tooby & Cosmides, 1990) on personality variation? How are personality dimensions, assessed during the juvenile phase, predictive of fitness-relevant outcomes later in life (see, e.g. Capitanio, 1999; Fairbanks et al., 2004)? These questions are still largely unanswered for wild primates.

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We thank the Lomas Barbudal Monkey project participants of 2002-2011 for completing the questionnaires. The following people were field site managers during this time period: H. Gilkenson, W. Lammers, C. Dillis, M. Corrales and S. Sanford. The following people contributed data to the project: B. Barrett, L. Beaudrot, M. Bergstrom, R. Berl, A. Bjorkman, L. Blankenship, J. Broesch, J. Butler, F. Campos, C. Carlson, M. Corrales, C. Dillis, N. Donati, R. Dower, K. Feilen, M. Fuentes A., C. Gault, H. Gilkenson, I. Godoy, I. Gottlieb, L. Hack, S. Herbert, S. Hyde, M. Kay, D. Kerhoas-Essens, W. Lammers, E. Johnson, L. Johnson, E. Kennedy, S. Kessler, S. Lee, S. Leinwand, T. Lord, M. Milstein, C. Mitchell, Y. Namba, A. Neyer, C. O'Connell, J.C. Ordoñez J., B. Pav, N. Parker, S. Perry, K. Potter, K. Ratliff, H. Ruffler, S. Sanford, M. Saul, I. Schamberg, C. Schmitt, A. Walker-Bolton, E. Wikberg, and E. Williams. This project is based on work supported by the funding provided to SP by the Max Planck Institute for Evolutionary Anthropology, the National Science Foundation (grants No. SBR-0613226 and BCS-0848360), the L.S.B. Leakey Foundation, and the National Geographic Society. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation or other funding agencies. We thank the Costa Rican park service (MINAET and SINAC), Hacienda Pelon de la Bajura, Hacienda Brin D'Amor, and the residents of San Ramon de Bagaces for permission to work on their land. This research was performed in compliance with the laws of Costa Rica, and the protocol was approved by the UCLA animal care committee (ARC #1996-122 and 2005-084 plus various renewals). We thank Phil Ender for statistical advice, and Aaron Lukaszewski for discussions. Lynn Fairbanks, Aaron Lukaszewski, Alexander Weiss and two anonymous reviewers commented on the manuscript.

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970 Table 1. Interrater reliability of trait items.

	Interrater reliability	
Trait	ICC(3,k)	ICC(3,1)
Active vs. *sluggish*	0.91	0.16
Aggressive vs. *pacific*	0.89	0.14
Meddlesome in ongoing interactions vs. *non-interfering*	0.87	0.12
Assertive/instigator vs. *non-assertive*	0.87	0.12
Reactive vs. *unperturbable/equable*	0.75	0.06
Impulsive vs. *self-controlled*	0.79	0.07
**Permissive* vs. *restrictive*	0.60	0.03
Popular vs. *unpopular*	0.89	0.13
Attentive to conspecifics vs. *more focused on own actions*	0.77	0.06
Fearful vs. *confident*	0.83	0.09
Relaxed vs. *tense/anxious*	0.72	0.05
Alert/vigilant vs. *inattentive*	0.78	0.06
Curious vs. *uninterested*	0.90	0.15
Neophobic vs. *neophilic*	0.81	0.08
Eccentric vs. *normal*	0.83	0.09
Tolerant vs. *irritable*	0.73	0.05
Solicitous vs. *uncaring*	0.78	0.06
Opportunistic vs. *narrow-minded/conservative*	0.72	0.05
Playful vs. *serious*	0.94	0.22
Creative vs. *unimaginative*	0.83	0.09
Sociable vs. *solitary*	0.90	0.15
Domineering vs. *submissive/passive*	0.90	0.16
Persistent/stubborn vs. *easily discouraged*	0.75	0.05
**Understanding/compromising* vs. *uncompromising*	0.65	0.04
Reciprocating vs. *nonreciprocating*	0.76	0.06
Socially intelligent/good politician vs. *socially inept*	0.85	0.10
Mean	0.81	0.09

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972 *Note.* *Excluded from further analysis; see text.

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975 Table 2. Correlations across age ranges of item scores. $N = 21$.

	Correlation (r)		
Trait	6-8 years/ 8-10 years	8-10 years/ 10-12 years	6-8 years/ 10-12 years
Active	0.40	0.44*	0.31
Aggressive	0.79***	0.76***	0.58**
Meddlesome	0.80***	0.67***	0.47*
Assertive	0.91***	0.78***	0.66**
Reactive	0.31	0.18	-0.30
Impulsive	0.81***	0.62**	0.50*
Popular	0.81***	0.69***	0.57**
Attentive to others	0.41	0.59**	0.12
Fearful	0.69***	0.71***	0.50*
Relaxed	0.58**	0.62**	0.47*
Alert	0.56**	0.27	0.20
Curious	0.61**	0.32	0.36
Neophobic	0.45*	0.47*	0.31
Eccentric	0.40	0.54*	0.45*
Tolerant	0.55**	0.39	-0.04
Solicitous	0.55**	0.78***	0.52*
Opportunistic	0.60**	0.42	0.29
Playful	0.60**	-0.10	0.25
Creative	0.76***	0.58**	0.46*
Sociable	0.68***	0.62**	0.48*
Domineering	0.84***	0.81***	0.74***
Persistent	0.69***	0.63**	0.66**
Reciprocating	0.71***	0.80***	0.70***
Socially intelligent	0.62**	0.80***	0.63**

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977 *Note.* *$p < .05$; **$p < .01$; ***$p < .001$

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