

Exploring Factor Space (and Other Adventures) with the Hominoid Personality Questionnaire

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Abstract

In this chapter, I describe a research tradition for investigating the evolutionary origins of the personalities of different species of primates, including humans. To that end, I describe the tradition's origins and methods, set out its assumptions, and evaluate its ability to solve empirical problems related to personality. In doing so, I will clear up misconceptions and assuage critics of the approaches that define this research tradition. After surveying the literature that originated from this research tradition, I conclude that it solves many problems as well as other research traditions do. I then identify its limitations and the need for further studies of wild populations, and propose a new direction for the study of personality and behavior.

Finally: It was stated at the outset, that this system would not be here, and at once, perfected. You cannot but plainly see that I have kept my word. But I now leave my cetological system standing thus unfinished, even as the great Cathedral of Cologne was left, with the crane still standing upon the top of the uncompleted tower. For small erections may be finished by their first architects; grand ones, true ones, ever leave the cope-stone to posterity. God keep me from ever completing anything. This whole book is but a draught—nay, but the draught of a draught. Oh, Time, Strength, Cash, and Patience!

—Herman Melville, *Moby-Dick*; or, *The Whale*, 1851

Although the study of personality in nonhuman animals is not new (see Whitham and Washburn,

this volume), it has, in the past 20 years or so, migrated from the fringes of the psychological and biological sciences into the mainstream. The genetic and evolutionary forces that maintain variation in personality traits, the limited plasticity of behavior, personality development, and the covariation of personality traits are now recognized by many as key to understanding the

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evolution of animal behavior. Reviews of work in these and other areas are widely available (e.g., Dingemanse and Wolf 2010; Réale et al. 2007; Sih et al. 2004; Weiss and Adams 2013), including in the present volume. You will excuse me then, I hope, for taking a different tack for, although I will discuss some of the literature, I have set as my goal to describe what I think of as the research habits that have guided my work on personality structure in nonhuman primates. To this end, I will explore the origins of these habits, what this work does and does not assume, the thorny question of anthropomorphism, what empirical problems have been solved, and what problems remain. I will conclude by discussing how methodological and statistical advances that are benefiting human personality research may benefit the study of personality and behavior in nonhuman primates and other species.

Before moving on to this exercise in introspection, it will benefit the reader if I define what I mean by “research habits” and also explain why I am taking this unconventional approach in writing this chapter. Research habits here refer to how I collect animal personality data and, more importantly, what I do with those data; that is, how I analyze them and interpret the results after they have been collected. What I have just described may sound like a paradigm (Kuhn 1970), and the work that I do and similar work on personality ratings by others, has been labeled such in the earlier chapter by Whitham and Washburn. However, my research habits (I cannot speak for others who conduct similar research) are not unthinking and automatic, but follow from pragmatic constraints, accidents of history, learning from experience, and otherwise. In this sense, and this is arguably true for research in psychology more generally (Leahey 1992), my research habits are probably better characterized as part of a research tradition (Laudan 1977) than as a Kuhnian paradigm. In other words, these research habits have been adopted as part of an approach to studying the question of animal personality because they lead to the solution of certain empirical problems.

Having spelled out what I mean by research habits, the question remains as to why I am

taking the time to lay them out in this chapter. The overarching goal of my research on personality is to develop a taxonomy of personality structure in nonhuman primates, mammals, and other species for which these methods are appropriate. Doing so, in my view, is crucial to establishing the functional bases of personality traits. However, comparing species requires comparable methods. As such, I would like this chapter to serve as a guide for future comparative studies of personality structure, whether carried out by me and my colleagues or by others, including those who come along after I am dead, no longer able to carry out research, or have moved on to other things, whichever comes first. That way, if there is a need to deviate from these methods, for example to address a reviewer comment or because of a particular characteristic of the species or sample under study, or a wish to pursue some more exploratory analyses, these deviations or explorations will be clear. Another purpose that I hope this chapter will serve is to inform colleagues, including young investigators and often reviewers, why either I or my colleagues have decided to pursue a particular analysis or interpret results in one way instead of another. In doing so, I hope that this chapter will bring forth discussions that enable me and others to cultivate research habits that are more effective at solving problems concerning personality evolution.

Origins

Speaking broadly, the habits in question involve obtaining ratings on a large number of personality traits (typically 40 or more), and then using data reduction to find out what traits cluster together. As is clear from the introduction to this volume and elsewhere (Stevenson-Hinde and Hinde 2011), there is nothing novel or innovative about assessing animal personality using questionnaires. My own work began in 1997 or 1998, at around the time when animal personality research was being increasingly recognized as serious scientific business. I was a Ph.D. student and Jim King, who would soon become my Ph.

D. supervisor, and A. J. Figueredo, who was my Ph.D. supervisor at the time, recently published a paper describing their study of 100 zoo-housed chimpanzees (*Pan troglodytes*) that had been rated on 43 trait descriptive adjectives by keepers, volunteers, and researchers (King and Figueredo 1997).

Around the time that Jim King and A. J. Figueredo were about to study chimpanzee personality, there was a growing consensus that human personality could be described by five dimensions collectively known as “the Big Five” or “Five-Factor Model” (Digman 1990; Goldberg 1990; McCrae and John 1992). As such, when developing what would be known as the Chimpanzee Personality Questionnaire or CPQ, Jim King sampled 41 items from Goldberg’s (1990) paper describing the taxonomy of the human Big Five. Jim King’s reason for doing so was to determine the extent to which the Five-Factor Model domains were present in chimpanzees, a finding that would lend support to the Big Five or Five-Factor Model; and to ensure that the questionnaire items measured traits characterizing not just behavioral differences among chimpanzees, but also differences in emotional reactivity and stability, interactions with conspecifics, and differences in cognitive domains, such as self-control and curiosity (James E. King, Personal Communication).

To achieve these goals, when selecting trait descriptive adjectives, Jim King made sure to select adjectives from as many of the clusters or facets that defined each of the five human personality domains—neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness (King and Figueredo 1997). In addition, when selecting trait descriptive adjectives, he made sure that the adjectives would be applicable to chimpanzees and did his best to sample positive and negative markers for a given domain (King and Figueredo 1997). The top panel of Table 2.1 shows that he was fairly successful in achieving these goals. Unfortunately, as is also clear from the top panel of Table 2.1, it proved difficult or impossible to find trait descriptive adjectives, such as “unimaginative,” to take an example from Goldberg’s taxonomy,

related to the low pole of openness, that is, being “closed to experience.” As a result, the only openness markers represented the positive pole of this domain. The questionnaire also included two trait descriptive adjectives (“clumsy” and “autistic”) based on descriptions of chimpanzee behavior. Finally, Jim King came up with one to three sentences for each of the 43 trait descriptive adjectives. These sentences defined each item in terms of chimpanzee behavior, but in a manner consistent with the common dictionary definition. For example, the description for the item “fearful” is: “Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress.” Including these sentences was important as it reduced the degrees of freedom that raters can use when deciding what a trait means and where, on the scale for a trait, to place a particular chimpanzee.

In the end, King and Figueredo (1997) found that the chimpanzee personality traits defined six mostly uncorrelated factors. Remarkably, they did find evidence for five factors that were analogs or homologues of the five human domains. The other factor they found was the first and largest factor and comprised of trait markers of multiple domains in such a way to suggest that it was related to competitive prowess or dominance. They thus named this factor “dominance.” Importantly, they found that the consistency between raters was on par with what had been found in studies of personality in humans (Costa and McCrae 1992; McCrae and Costa 1987; 1989; all cited in King and Figueredo 1997).

My work in this heady milieu began with the suggestion that I study the heritability of the CPQ domains in a dataset consisting of the original 100 chimpanzees and 45 additional individuals. I found considerable evidence that at least the dominance domain was heritable; none of the personality variation appeared to be attributable to shared zoo environments (Weiss et al. 2000). The heritability findings were later supported by quantitative and molecular genetic studies of orangutans, *Pongo spp.* (Adams et al. 2012), chimpanzees (Hopkins et al. 2012; Latzman et al. 2015a, b; Wilson et al. 2016), bonobos, *Pan*

Table 2.1 Origins of the 54 traits comprising the Hominoid Personality Questionnaire

	Location in Human Five-Factor Model									
	Neuroticism		Extraversion		Openness		Agreeableness		Conscientiousness	
	+	-	+	-	+	-	+	-	+	-
<i>CPQ traits</i>										
Dominant										
Submissive										
Dependent/follower										
Independent										
Fearful										
Decisive										
Timid										
Cautious										
Intelligent										
Persistent										
Bullying										
Stingy/greedy										
Solitary										
Lazy										
Active										
Playful										
Sociable										
Depressed										
Friendly										
Affectionate										
Imitative										
Impulsive										
Defiant										
Reckless										
Erratic										
Irritable										
Predictable										
Aggressive										
Jealous										
Disorganized										
Sympathetic										
Helpful										
Sensitive										
Protective										
Gentle										
Stable										
Excitable										
Unemotional										
Inventive										
Inquisitive										
Manipulative										
<i>n</i> traits	4	3	5	4	4	0	7	6	4	4
<i>OPQ add-ons</i>										
Anxious										
Vulnerable										
Cool										
Curious										
Conventional										
<i>n</i> traits	6	4	5	4	5	1	7	6	4	4

Table 2.1 continued

	Location in Human Five-Factor Model									
	Neuroticism		Extraversion		Openness		Agreeableness		Conscientiousness	
	+	–	+	–	+	–	+	–	+	–
<i>HPQ add-ons</i>										
Thoughtless										
Distractible										
Quitting										
Individualistic										
Innovative										
Unperceptive										
<i>n</i> traits	6	4	5	4	7	2	7	6	4	7

Note CPQ traits are found in the original Chimpanzee Personality Questionnaire (King and Figueredo 1997). OPQ add-ons are traits found in the Orangutan Personality Questionnaire (Weiss et al. 2006). HPQ add-ons are traits found in the Hominoid Personality Questionnaire (Weiss et al. 2009). Filled boxes under “+” indicate that the item is a marker of the positive pole of the human personality domain. Filled boxes under “–” indicate that the item is a marker of the negative pole of the human personality domain

paniscus (Staes et al. 2016), rhesus macaques, *Macaca mulatta* (Brent et al. 2014), and of non-primates (van Oers et al. 2005; Van Oers and Sinn 2013).

Shortly afterwards, I addressed whether the association between the chimpanzee dominance domain and a measure of subjective well-being described in a paper by King and Landau (2003), who developed and validated this measure, was attributable to shared genes. For me, this study was more exciting than my original heritability study. It marked the first time that I used chimpanzee data to address a question about individual differences in humans, namely why do people who are emotionally stable and extraverted report being happier than people who are neurotic and introverted? Although I focused on dominance, because it was the only domain in my previous study that I found to be heritable, this new study had the ability to inform the human debate. This was because several loadings on dominance (see Table 2.1 in King and Figueredo 1997) were associated with high extraversion (e.g., the positive loading of “assertive”) and low neuroticism (e.g., the negative loading of “fearful”), and so dominance captured trait variance related to higher subjective well-being in humans. The analyses were conducted using data from 128 chimpanzees on which we had personality and subjective well-being data, and the results were stark.

Variation in dominance and subjective well-being were both attributable to the same additive genetic effects, which accounted for about 60% of the variation in dominance and 40% of the variation in subjective well-being (Weiss et al. 2002).

At about the same time that I was watching the maximum likelihood models of this study converge, I began to collect my own data for a side project on orangutan personality. Perhaps because I was working on my doctoral research, I decided to take the easy road and more or less used the same personality questionnaire as was used in the previous chimpanzee studies. In fact, initially, I made only two changes to the CPQ. The first was to add three items—“anxious”, “vulnerable”, and “cool”—related to the Five-Factor Model neuroticism domain; the first two items were based on two neuroticism facets (Costa and McCrae 1992); the last had no specific origins in human or animal personality studies, but its descriptive sentence, that is, “Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.” clearly makes it a marker of the low pole of neuroticism (Weiss et al. 2006). The second change was to add two items—“curious” and “conventional”—related to the Five-Factor Model openness domain; these items were based on another Five-Factor Model questionnaire (McCrae and Costa 1985) and were chosen to represent high and low openness, respectively.

However, this questionnaire, the Orangutan Personality Questionnaire, was short-lived, for at a late stage in that study, I created six more items (Weiss et al. 2009). These additional trait adjectives were derived from a bipolar adjective measure of the Five-Factor Model (McCrae and Costa 1985) and included “thoughtless,” “distractable,” and “quitting,” which were related to the low pole of conscientiousness, “individualistic” and “innovative,” which were related to the high pole of openness, and “unperceptive,” which was related to the low pole of openness. I christened the revised questionnaire the “Hominoid Personality Questionnaire” (or HPQ), a name that I now admit was rather grandiose given that I was studying only chimpanzees and orangutans.¹

The preceding paragraph naturally leads to the question of why I augmented the questionnaire with those particular items instead of leaving the questionnaire alone or choosing a different set of items? The decision to add the first five items followed the results of a study by Jim King, myself, and Kay Farmer. In this study, which was published many years later (King et al. 2005), we used targeted orthogonal Procrustes rotation (McCrae et al. 1996) to compare the personality factors obtained (i.e., the personality structure) from ratings of 74 zoo-housed chimpanzees that were not part of King and Figueredo’s (1997) study and those obtained from ratings of 43 chimpanzees living in a naturalistic sanctuary in the Republic of the Congo. To our delight, the dominance, extraversion, conscientiousness, and agreeableness domains were identified in both samples, and there was considerable similarity across all of the factor loadings. On the other hand, neuroticism and openness domains clearly comparable to those found in zoo-housed

chimpanzees were not found in their sanctuary-housed counterparts. However, the factor loadings from the targeted rotation suggested that those domains were present (see Table 5 in King et al. 2005); a follow-up analysis found similar results when comparing the personality structure found in the 74 zoo-housed chimpanzees to that found in the 100 zoo-housed chimpanzees from King and Figueredo’s original study (King, et al. 2005, pp. 401–402).²

The findings of our study of chimpanzees in zoos and in the naturalistic sanctuary led us to suspect that, although chimpanzee variants of neuroticism and openness are present, these domains were not as robust because neuroticism was represented by only three items and openness was represented by only two items. In hindsight, I suspect that neuroticism and openness were represented by so few items because King and Figueredo did not anticipate that so many items representing these traits would cluster into the broad dominance domain. Our interpretation of the results was later vindicated by two studies of chimpanzees, each using a different questionnaire, and developed based on different principles, that found evidence for neuroticism and openness domains (Dutton 2008; Freeman et al. 2013). However, at the time, Jim King and I pursued what we thought was the simplest solution, which was to increase the number of items, especially for openness, that might tap these domains.

Turning to the decision to include three new items for conscientiousness, this was motivated by two observations. The first was that, at the time, conscientiousness domains had reportedly been found only in humans and in chimpanzees, suggesting that this domain evolved recently (Gosling and John 1999, p. 71). The second was the surprising finding that orangutans did not appear to possess a conscientiousness domain. Instead, orangutan personality structure was defined by extraversion, dominance, neuroticism,

¹Readers can go to <http://extras.springer.com/2011/978-1-4614-0175-9/> to obtain the HPQ for chimpanzees, orangutans, and rhesus macaques at. Filenames prefixed by “weiss” are English-language versions of the HPQ. Filenames prefixed by “weissmurayama” are Japanese-language versions of the HPQ. The HPQ is also available in Dutch, German, Chinese, French, and Spanish. Until I develop a website, please contact me if you wish to obtain any of these other versions or the LaTeX code should you wish to adapt the HPQ for your own purposes.

²Similar studies of the chimpanzee personality conducted after the HPQ was developed that used the original 43 CPQ items yielded similar results (Weiss et al. 2009, 2007).

and agreeableness domains, which resembled those found in chimpanzees, and an intellect domain, which combined aspects of openness and conscientiousness. In the resulting paper, published 2 years later, we speculated that this finding, the absence of a distinct conscientiousness domain, may be attributable to the fact that the OPQ did not include items suitable for measuring conscientiousness in a semi solitary species (Weiss, et al. 2006, p. 508). As noted in the paper, we thought that a straightforward way to test this possibility would be to include items related to less social aspects of conscientiousness in our questionnaire, which is exactly what Jim King and I did when developing the HPQ. In addition, although we did not raise the possibility in the paper, we thought that a straightforward way to test Gosling and John's hypothesis about the recent emergence of conscientiousness would be to use the HPQ to assess other species of primates. I will describe these studies later.

Throughout this period and up to 2007, when I was analyzing data that I collected with Miho Inoue-Murayama on chimpanzees living in Japan, I adopted the remaining research habits that flavor this research tradition. Because this period of time included my 3 years of postdoctoral training, studying human personality with Paul Costa, I adopted some habits from human personality research. Since that time, I have been surprised by the extent to which some of these habits, which I continue to adhere to and teach, have caused me and my students' grief. I hope that by describing them and their rationale in the next section will spare myself, my students, and future researchers from further suffering.

Habits

So to put the question plainly, how do I analyze HPQ data on some new species? The first step is to estimate the interrater reliabilities of the HPQ items. To do so, like King and Figueredo (1997), I use two of the intraclass correlation coefficients (ICCs) described in Shrout and Fleiss (1979). The first, $ICC(3,1)$, is an estimate of how reliable an individual rater's rating is likely to be, and

therefore can be used to compare reliabilities across studies that differ in how many raters are used. The second, $ICC(3,k)$, is an estimate of the reliability of the average (mean) score across raters (k refers to the number of raters per target). Because later analyses are conducted after aggregating scores across raters, $ICC(3,k)$ is informative with respect to the reliability of the measures used in these analyses. To compute these, ICCs requires treating raters as fixed effects. This makes sense because, in studies of nonhuman animals housed in zoos, research facilities, sanctuaries, and even in human homes, the raters have expertise in working with non-human animals and/or know these animals better than anybody else. They are not a random sample drawn from the entire universe of possible raters. One question that often arises when estimating interrater reliabilities in samples derived from multiple facilities, as is often the case in these studies, is whether to obtain variance components with or without taking into account the fact that targets (and raters) are nested within facilities. Although I began by taking this nesting into account (Weiss et al. 2006, 2009), I no longer do so (e.g., Morton et al. 2013). This change in habit came about following an insight: so long as each animal and each rater have a unique ID, when zookeepers and other personnel at a facility rate only the animals at their facility, the nesting is already taken into account. Of course, if some animals have lived in and have been rated at two or more facilities, one should take nesting into account.

The second step is to screen out items with interrater reliabilities that are zero or negative. I do not test whether the interrater reliabilities are significantly different from zero or use some higher interrater reliability as a cut-off point. This is a shockingly liberal criterion to some, and it has been the source of criticism by reviewers. So why use such a liberal cut-point? The main reason for being such 'wide-eyed liberals' when it comes to interrater reliabilities is that intraclass correlations are ratios of the true score variance, which comes from the subject, to the total variance, which comprises the subject variance and the error variance, the latter being the subject \times rater

interaction (Shrout and Fleiss 1979). As such, it is possible that these low interrater reliabilities indicate that the trait assessed by an item is rare, i.e., something seen infrequently in few animals, and not that it is unimportant (see Stevenson-Hinde and Hinde 2011 for a discussion). An example taken from another field illustrates this point. Researchers in genetic epidemiology often estimate the heritability of various diseases. Heritability estimates are ratios of the amount of variation attributable to genetic effects over the total amount of variation, and so resemble interrater reliabilities. In fact, both are special cases within generalizability theory (Shavelson et al. 1989). The heritability of stomach cancer is $\sim 1\%$ (Czene et al. 2002). The authors of the paper did not take this to mean that genetic variation does not contribute to this trait. In fact, this study, which comprised ~ 9.6 million people (the whole of Sweden, in fact), found that the heritability was statistically significant. Thus, because of the fact that, without very large sample sizes, it is impossible to determine whether low interrater reliabilities are statistically significant, it is probably best to retain these items until they are shown to be otherwise and to not throw out possibly meaningful traits at this early stage. Another reason to accept such low interrater reliabilities is that, if they are random error, they are unlikely to load onto any domains derived via principal components analysis or factor analysis in a meaningful way. A third reason is that a key determinant for how many subjects are needed in principal components analyses or factor analyses to obtain a stable structure is the ratio of items to factors: the higher the ratio, the fewer subjects are needed (see Table 2.1 in MacCallum et al. 1999). As such, setting a low cut-point ensures that principal components analyses and factor analyses of the HPQ and related questionnaires will reveal stable structures.

Another habit deserving of mention and explanation is our use of principal components analysis as our primary means of data reduction. This practice is (rightly I suspect) frowned upon by psychometricians because principal components analysis does not reduce the dataset by modeling the correlations between variables as

being caused by one or more latent variables, but by finding linear composites of the variables in the analysis (Widaman 2007). I began using principal components analysis based on advice I received from a senior researcher at a poster session in 1999. It became a habit after I began using an additional method to determine how many factors or components were present in a sample. Specifically, I initially used a scree plot and my judgement of whether factors or components “made sense” to determine how many dimensions to extract. Of course, this widespread practice is somewhat subjective, and has led to disagreements about the number of human personality domains (see the exchange in Eysenck 1992; Zuckerman et al. 1991). To get around this subjectivity, I began to use parallel analysis in addition to these other methods to determine the number of dimensions. In parallel analysis, one conducts factor analyses or principal components analyses on several sets of randomly generated datasets that are identical to the real dataset in terms of the number of items and the number of subjects (Horn 1965). The eigenvalues, which indicate how much variance each factor or component accounts for, derived from the real data are then compared to the distribution of eigenvalues generated from the randomly generated data (Horn 1965). Factors or components with eigenvalues that fall below a cut-off (usually the 95th percentile) are discarded. Early on I noticed that, parallel analysis, conducted using code provided by O'Connor (2000), when applied to factor analysis, typically recommended one or two more factors than did the scree plot. These factors were also not interpretable, for instance, they included only a single item. This did not happen when I used principal components analyses. Little did I know then that I was not the first person to observe this phenomenon, nor that it was attributable to a specific method for extracting dimensions in factor analysis (Buja and Eyuboglu 1992). Since discovering that, using the `fa.parallel` function in the `psych` package (Revelle 2015) and setting the option “SMC” (estimate communalities by using squared multiple correlations) to “False,” I can avoid the problem of trivial factors, I have begun

leaning toward factor analysis as my primary method for data reduction. However, I plan to still report the results of principal components analyses, which, in any event, tend to be similar to those derived from factor analyses (Velicer 1977).

My final habit deserving of mention concerns how I interpret the personality domains, that is, how do I decide what they mean and what to label them? To do so, I first apply an orthogonal (usually varimax) and oblique (usually promax) rotation to the factors or components. In a promax rotation, factors or components are allowed to correlate. If the correlations between factors or components are high and/or lead to loadings on one or more factors or components that differ from loadings derived from a varimax rotation, where the correlations are fixed at zero, I interpret the results of the promax rotation. I otherwise interpret the results of the varimax rotation. In all of the HPQ-based studies that I have conducted to date, the mean of the absolute correlations between factors or components has been low (less than 0.2). Moreover, the factors or components that result from these different rotations are close to identical. Nonetheless, I now present or provide the results of both rotations. Next, depending on the study species, when interpreting the factors or components and assigning labels to them, I rely on all available information, including, but not limited to, what is known about the species' socioecology and the personality structures of closely related species (e.g., Weiss et al. 2015) or of species where there is evidence of convergent evolution in behavior (e.g., Morton et al. 2013). Also, where available, correlations of the personality domains with behaviors are another source of information that I use to label personality domains (e.g., Morton et al. 2013). Finally, as a principle, I avoid labels that are too specific and, whenever possible, use the same label for factors or components that are similar to those of other species, and especially other closely related species. I follow these principles because they acknowledge the fact that personality dimensions and similar constructs do not have clearly defined boundaries (Adams et al.

2015; King and Weiss 2011) and because I want to avoid the confusion generated in a literature where many different terms are used to refer to what is possibly the same construct.

After interpreting and labeling factors, I estimate the interrater and, if data are available, retest reliabilities of these domains. I then turn my attention to addressing the questions described in other chapters within this volume. Before describing the results of attempts of my research tradition to solve empirical problems, I will spell out what this research tradition does and does not assume, which I hope will clarify some misconceptions.

Assumptions and Non-assumptions

The first assumption is that the factors or components derived from the HPQ (or any other set of traits, regardless of how measured) are biologically relevant and can be used to better understand the functions of those traits. It follows, then, that the factors or components revealed in rating studies are believed to not be implicit theories of personality based on folk psychology, artifacts of the questionnaire, such as the semantic similarity of the items (see Kenrick and Funder 1988 for a summary of these criticisms) or, because we are studying animal personality, anthropomorphic projections (Uher 2011).

This assumption and its antecedents, and especially that concerning anthropomorphic projection, has been used as a bludgeon by reviewers and, more gently (and genteelly), and usually over drinks, by other researchers, to criticize animal personality research based on ratings. From what I can gather, this criticism stems from two sources. The first is the HPQ's origins in the Big Five or Five-Factor Model traditions of human personality research. The second is an aversion to studying animal behavior by means other than observation that is held by ethologists and learning theorists. This aversion is often framed in terms of preferring measures that are "objective" to those that are "subjective." The origins of this aversion can be

traced to the founders of modern ethology and learning theory who reacted against the relative lack of rigor of their predecessors (Wynne 2005).

However, inspection of the bases of this criticism suggests that this criticism is lacking. Let us examine the concerns raised by the origin of the HPQ and related instruments. First, there appears to be a lack of awareness or a deliberate ignoring of the reasons for the HPQ's origins and the fact that care was taken to insure that it was appropriate for assessing nonhuman primate personality (both described earlier in this chapter).

Second, large studies of human personality find that the personality factors measured by questionnaires are found in many human cultures (Eysenck and Eysenck 1985; Ion et al. 2017; McCrae et al. 2005; Schmitt et al. 2007) and that the factors or components that emerge from questionnaires are attributable to common genetic influences on sets of traits and not implicit biases about the associations between traits (McCrae et al. 2001; Yamagata et al. 2006) or their semantic similarity (Rowe 1982). Closer to the theme of this chapter, a study of dogs, *Canis familiaris* (Kwan et al. 2008), and a study of chimpanzees and orangutans (Weiss et al. 2012) found no evidence that anthropomorphic projection adversely influenced ratings.

Third, studies using the CPQ and the HPQ have not yielded the Five-Factor Model, even in our closest animal relations, chimpanzees and bonobos (King and Figueredo 1997; Weiss et al. 2009; Weiss et al. 2007; Weiss et al. 2015). A study of spotted hyenas (*Crocuta crocuta*) that used an adaptation of a questionnaire based on a human personality scale (the Big Five Mini-markers) also failed to find the human Big Five (Gosling 1998).

Fourth, like other human observations, behavioral codings are susceptible to error and bias. For example, the meaning of behaviors can be misinterpreted (Carter et al. 2012a, b). The distinction between the objective and subjective is therefore a false dichotomy. This statement should not be controversial. Researchers in animal behavior acknowledge that their measures are not without bias or error and take steps to

mitigate the problem, such as video recording subjects, asking independent observers to code videos, and computing interobserver reliabilities. There have also recently been recommendations for further steps that researchers should take to avoid misinterpreting behavioral traits (Carter et al. 2012a, b).

Given that interrater or interobserver reliability estimates reflect the degree to which traits or behaviors are easy or difficult to assess, it should be possible to determine whether one approach is more "objective" than another. I do not have data in hand that would enable me to compare behavioral observations and ratings directly. However, analyses of interrater reliability estimates reported in a study of crab-eating macaques (*M. fascicularis*) measured at two time points (Uher et al. 2013a, b) and from a study of brown capuchin monkeys (*Sapajus apella*) measured once (Uher and Visalberghi 2016) are informative. In both studies, the researchers measured personality traits via so-called "trait-adjective items" or so-called "behavior-descriptive verb items." The behavior-descriptive verb items, although not being direct observations of behavior, were generated from behavioral observations and so were designed to be "less colloquial" than trait adjectives (Uher et al. 2013a, b, p. 429). To highlight the differences between these types of items, for example, impulsiveness in crab-eating macaques was measured by the trait-adjective item "*Name* is impulsive." (Uher 2016d, p. 2) and by the behavior-descriptive verb item "When he/she does not like something, *Name* shakes trees or jumps on or slaps others." (Uher 2016c, p. 2). The results of my analyses did not support the view that behavioral observations are more objective than trait ratings. Briefly, for crab-eating macaques at time 1, the mean ICC (3,1) of behavior-descriptive verb ratings (0.43) was higher than that of trait-adjective ratings (0.39), but Welch's *t* test revealed that the difference was not significant, $t_{32,279} = -0.72$, $p = 0.48$ (Uher 2016c, d). For the macaque ratings at time 2, the mean ICC (3,1) of behavior-descriptive verb ratings (0.40) was lower than that of trait-adjective ratings (0.43), but this difference was also not significant, $t_{33,651} = 0.50$, $p = 0.62$

(Uher 2016c, d). Finally, for brown capuchin monkeys, the mean $ICC(3,1)$ of behavior-descriptive verb ratings (0.39) was also lower than that of trait-adjective ratings (0.43), and, once again, this difference was not significant, $t_{37,922} = 0.62$, $p = 0.54$ (Uher 2016a, b). The code and ICC data for these analyses can be found at https://github.com/alexweissuk/uher_icc_comparison.

Another assumption of the research tradition that I described is that similar behaviors in closely related species serve similar functions and have similar genetic, physiological, and developmental underpinnings. This assumption is central to research that seeks to understand animal behavior, and has yielded insights into, the evolutionary bases of, among other things, human culture (Whiten et al. 1999).

In addition to holding these (and probably) other assumptions, there are things that this tradition does not assume. For one, it does not assume that personality traits or domains serve similar functions, or have similar genetic, physiological, and developmental bases, even in closely related species. In other words, we do not assume that the same traits or domains in different species are homologues. After all, if we did, research on a species would stop after determining that species' personality structure, and the research tradition would be a descriptive enterprise (Braithwaite 1968). What we have instead is research examining this question, which has yielded encouraging results with respect to whether similar personality domains in closely related species are, in fact, homologues.

In describing these studies and their results I will first return to the findings on personality domains and subjective well-being. To recap, there is a trend across primate species, including humans, for more emotionally stable and social individuals to experience higher levels of subjective well-being compared to those who are less emotionally stable and less social. Furthermore, in chimpanzees, this association is largely attributable to common genetic effects (Weiss

et al. 2002). Starting in 2008, studies of human twins (Weiss et al. 2008) and siblings (Hahn et al. 2013), and a study of interrelated orangutans (Adams et al. 2012) all found that personality and measures related to subjective well-being share common genetic underpinnings. Finally, in humans, polygenic scores (weighed sums indicating how many single nucleotide polymorphisms for a trait an individual has) for extraversion were associated with higher life satisfaction and subjective well-being and polygenic scores for neuroticism were associated with lower subjective well-being (Weiss et al. 2016).

Additional evidence comes from neurophysiological and molecular genetic studies. MRI studies of chimpanzees rated on the CPQ and a related questionnaire identified associations between areas of the chimpanzee brain and personality domains that are similar to the associations expected based on human findings (Blatchley and Hopkins 2010; Latzman et al. 2015a, b). Concerning molecular genetic evidence, CPQ and HPQ studies of arginine vasopressin 1a receptor polymorphisms and personality in chimpanzees (Hopkins et al. 2012; Wilson et al. 2016) and in bonobos (Staes et al. 2016) are consistent with human findings (Bachner-Melman et al. 2005; Pappa et al. 2016) and point to an association between arginine vasopressin 1a receptor polymorphisms and socially appropriate behaviors.

Studies of development also support the likelihood that similar personality domains are homologous. Specifically, with some exceptions, which I will discuss in the next section, at least in the case of chimpanzees (King et al. 2008) and orangutans (Weiss and King 2015), sex and age differences in similar domains are similar to one another and to sex differences (Costa et al. 2001) and age differences (Roberts et al. 2008) found in comparable human personality domains.

Some things that this research tradition does not assume have not been studied. Although I will not present an exhaustive catalog here, some

are worth noting. For one, the research tradition that I described does not assume that different domains or traits in distantly related species have different functions. In other words, different personality domains in different species could serve the same function in those two species. Second, this work does not assume that personality traits are isomorphic with behaviors, that is, there is no assumption that each trait that makes up a personality domain corresponds to a single behavior. A third matter concerns personality structure. Specifically, there is no assumption as to what the personality structure of a given species will be or should be.

Finally, this research tradition does not assume that the labels or even definitions of the components or factors are immutable. Instead, they are better characterized as hypotheses. Data collected in the future on revised versions of the HPQ, behavioral observations, or on the genetics, physiology, and development of these domains, will test these hypotheses, and some revisions will no doubt be necessary. One area in which this might happen would involve the domains related to competitive prowess that have been identified in nonhuman primates but not in humans. In particular, to recognize species differences in social organization, my collaborators and I have labeled domains similar to the chimpanzee dominance “assertiveness” in brown capuchin monkeys (Morton et al. 2013) and in bonobos (Weiss et al. 2015). Should future studies not support this distinction by, for example, showing that all such domains underlie similar behaviors and are related to genes with similar functions, then, depending on these findings, it would make sense to rename the capuchin and bonobo domains, the chimpanzee domains, or both.

Evaluating This Research Tradition

Having discussed what this research tradition does and does not assume, it is worth asking whether it has been successful in solving empirical problems important to personality research. This is an important question as

research traditions stand or fall on this criteria, and even a technically sophisticated research tradition will be abandoned or changed if it cannot solve the problems in its domain (Laudan 1977).³

When it comes to characterizing species' personalities, a straightforward question is whether the structure of the traits measured using the above-described approach resembles the structure of traits measured using other approaches. As I noted earlier, questionnaires developed based on other conceptions of personality (e.g., Dutton 2008) or by other approaches (Freeman et al. 2013) yield chimpanzee personality structures similar to those found using the CPQ and HPQ. More striking evidence comes from a study of brown capuchin monkeys rated on trait-adjective items and behavior-descriptive verb items, the latter, recall, being identified from observations of naturally occurring behaviors (Uher and Visalberghi 2016). A factor analysis of these ratings yielded personality domains similar to those identified from principal components analysis or factor analysis of HPQ ratings (Morton, et al. 2013).

Other evidence suggests that scales such as the CPQ, OPQ, and HPQ characterize biologically meaningful relations between traits. The first comes from a factor analysis of ratings of crab-eating macaques on trait adjective descriptors and behavioral verb descriptors identified from observations of naturally occurring behaviors. The analysis yielded dimensions labeled playful-active-curious, aggressive-competitive, prosocial-gregarious, and assertive-nonanxious (Uher et al. 2013a, b, p. 657). There has not yet been, at least to my knowledge, a study of crab-eating macaques using the HPQ. However, crab-eating macaques are a relatively despotic macaque species (Thierry 2000) and, in an earlier paper, my colleagues and I reported on the personality structures of Japanese (*M. fuscata*), Assamese (*M. assamensis*), Barbary macaques

³The question of whether this research tradition is as good, better, or poorer at solving conceptual problems (Laudan 1977) than some other research tradition is beyond the scope of this chapter.

(*M. sylvanus*), Tonkean macaques (*M. tonkeana*), and crested (*M. nigra*) macaques, all rated using the HPQ (Adams et al. 2015). One of the species investigated, Assamese macaques, have a level of despotism similar to that of crab-eating macaques (Thierry 2000). Analysis of the HPQ ratings found personality domains labeled confidence, activity, openness, friendliness, and opportunism (Adams, et al. 2015), and so, with the exception of the separate activity and openness domains, the Assamese macaque structure was similar to that found in crab-eating macaques by Uher (2013b). Finally, a study of Hanuman langurs (*Semnopithecus entellus*) compared the personality structure based on ratings on an offshoot of the CPQ to that based on behavioral observations, and found them to be similar (Konečná et al. 2008).

Moreover, as I noted in detail earlier, in addition to identifying similar personality structure to other methods, the research tradition described here has led to greater understanding of the genetic and neurophysiological mechanisms that underpin personality in chimpanzees and bonobos. Likewise, as also discussed in detail earlier in this chapter, this research found that the associations between personality traits and affect described in humans, nonhuman primates, and in other species likely reflect their genetic architecture.

Moving to the ability to solve other problems, studies of sex and age differences in chimpanzees and in orangutans have contributed to the understanding of the evolutionary origins of these differences. In addition, these studies have informed debates concerning whether biological or sociocultural processes drive age differences in human personality.

Personality sex differences actually differ some between chimpanzees, humans, and orangutans. Cross-cultural studies of humans have found that, although the magnitude of the difference varies across countries, compared to men, women are higher in neuroticism, extraversion, openness, agreeableness, and conscientiousness (Costa et al. 2001). In chimpanzees, however, the only sex differences consistent with the human pattern were for

conscientiousness and agreeableness; males and females did not differ in extraversion or in openness and males were higher in neuroticism than females (King et al. 2008). This finding together with findings suggesting that an activity facet of extraversion was higher in males than in females, and so also differing from the human pattern, and a pattern of age differences suggesting that males but not females exhibit a prolonged period of aggression, led us to hypothesize that chimpanzee personality differences partly reflect the higher levels of aggression in male chimpanzees than in humans (King et al. 2008). Later findings that, in orangutans, sex differences in neuroticism were like those in humans (Weiss and King 2015), supported this hypothesis as male orangutans do not display the same intensity of aggression that is found in male chimpanzees.

With respect to age differences, among humans, lifetime changes in personality suggest that individuals become more mature as they age, with individuals declining in neuroticism, extraversion, and openness, but increasing in agreeableness and conscientiousness (Roberts et al. 2008). This appears to be a universal phenomenon, having been found in several cultures (Bleidorn et al. 2013; McCrae et al. 2005). One explanation for these trajectories is that they are products of biological maturation (McCrae and Costa 2003). An alternative explanation for these trajectories is that they are products of social and cultural forces, such as the need for increased responsibility when entering the workforce or increased desire for caretaking when having children (Roberts et al. 2005). A study of chimpanzee personality found that the pattern of age differences for the five human-like domains is conserved, although, among males, there is a less consistent decline of neuroticism and extraversion (King et al. 2008). This finding, too, was attributed to the pattern of aggression among male chimpanzees. Moreover, among orangutans, extraversion, neuroticism, and agreeableness, domains that orangutans share with humans and chimpanzees, the age differences were like those of humans except for agreeableness, which was lower in older individuals (Weiss and King

2015). Finally, both studies found that, despite differences in how their societies are structured, after adjusting for the different rate of development in humans and the two great ape species, the magnitudes of age differences were similar across all three species (King et al. 2008; Weiss and King 2015).

The findings concerning age differences in two species that differ in many ways from humans are more consistent with what one would expect if the development of personality resembled that of height and other physical characteristics than what one would expect if human sociocultural forces were responsible. However, this research also highlights the possible functions of some of these traits in these species. As noted above, the pattern of development for extraversion and neuroticism in male chimpanzees is consistent with the higher aggression noted in male chimpanzees. Furthermore, the decline in orangutan agreeableness suggests that the increases found in humans and chimpanzees may be adaptive for individuals that live in large groups of, at best, distantly related individuals (Weiss and King 2015). In other words, among species that are solitary or semisolitary such as orangutans (Galdikas 1985), there is no selection for age-related rises in agreeableness.

Studying personality and reproductive success among captive individuals is problematic because, in these settings, reproduction is controlled so as to prevent inbreeding and overpopulation and to maximize the genetic diversity of the species (see Watters et al., this volume). The HPQ has also only seldom been deployed to study wild populations, and these studies have, for the most part, been cross-sectional. As such, there is no definitive answer to whether these personality domains are related to reproductive success. However, studies have examined the association between personality domains assessed using the HPQ and related measures, and dominance rank, an important asset in the social lives of nonhuman primates that is associated with fitness outcomes, including reproductive success (see, e.g., Pusey et al. 1997).

Evidence that the HPQ and related measures capture precursors of dominance rank includes

the ubiquity of domains related to dominance rank in nonhuman primates that the HPQ, like other rating scales, unveils. Further evidence includes findings that the social organization of nonhuman primate species is reflected in the make-up of personality domains related to dominance rank. For example, a study of six macaque species revealed that the degree of despotism that characterizes each species is associated with the structure of personality traits related to aggression (e.g., “bullying”) and social competence (e.g., “independent”) in those species (Adams et al. 2015). There is some suggestion for a similar phenomenon among African apes. Specifically, if one examines the cardinal CPQ, OPQ, or HPQ traits associated with dominance rank, i.e., “dominant” and “submissive,” one sees that they are more strongly related to the dominance-like domains in captive chimpanzees (King and Figueredo 1997; Weiss et al. 2009, 2007) and captive western lowland gorillas, *Gorilla gorilla gorilla* (Schaefer and Steklis 2014), than they are in captive bonobos (Weiss, et al. 2015) or in wild Virunga mountain gorillas, *G. beringei beringei* (Eckardt et al. 2015).

Moreover, consistent with the fact that, unlike other great apes, female bonobos exhibit so-called “partial female dominance” (see, e.g., Furuichi 2011), female bonobos score higher than males in assertiveness (Staes et al. in press) whereas in chimpanzees (King et al. 2008; Weiss et al. 2009, 2007),⁴ orangutans (Weiss and King 2015), and mountain gorillas (Eckardt et al. 2015), males score higher. The previously discussed study of spotted hyenas, another species in which females are higher ranking than males, also found that females were more assertive (Gosling 1998).

This research tradition has also identified direct evidence of the role of dominance-like personality domains. A study of provisioned, semi-free-ranging Barbary macaques that assessed personality using an offshoot of the CPQ found that the temporal stability of dominance

⁴In the Weiss et al. 2009 study, the sex effect was not significant ($p = .0694$), but the direction of the effect was comparable to what had been found in the other studies.

rank was attributable to the personality domain, confidence (Konečná et al. 2012). In addition, among wild Virunga mountain gorillas, the dominance domain was associated with dominance strength and spending less time staring at other gorillas (Eckardt et al. 2015), and in zoo- and laboratory-housed brown capuchin monkeys, individuals who were higher in assertiveness were groomed more often, less often solitary, and less likely to be targets of aggression (Morton et al. 2013). Similarly, among bonobos, individuals higher in assertiveness were groomed more often, less likely to be targets of aggression, and less likely to retreat from agonistic encounters (Staes et al. in press).

One area that perhaps illustrates the effectiveness of this research tradition more than any other is its ability to uncover the phylogenetic origins of personality traits (Gosling and Graybeal 2007). The best example comes from work on conscientiousness. As I previously mentioned, an early review noted that, of the species studied, conscientiousness was found only in chimpanzees. Based on this, the authors of the review reasonably hypothesized that conscientiousness emerged relatively recently in African apes (Gosling and John 1999). However, with the exception of King and Figueredo's 1997 study of chimpanzees, the personality measures used in the other studies cited by Gosling and John did not include many traits related to self-control, behavioral predictability, persistence, and other markers of conscientiousness. Fortunately, testing these hypotheses is a simple matter of assessing multiple related species using the HPQ. Doing so revealed that conscientiousness and/or a related trait, attentiveness, exists in captive western lowland gorillas (Schaefer and Steklis 2014), captive bonobos (Weiss et al. 2015), and possibly exists in wild Virunga mountain gorillas (Eckardt et al. 2015). Using the HPQ to unearth the phylogenetic origins of domains like conscientiousness or attentiveness has also revealed an attentiveness domain in brown capuchin monkeys (Morton et al. 2013) and, using a modified version of the HPQ, in common marmosets, *Callithrix jacchus* (Iwanicki and Lehmann 2015), but not in Old World monkeys

(Adams et al. 2015; Konečná et al. 2008; Konečná et al. 2012).⁵ These studies therefore indicate that, conscientiousness-like domains emerged in the African apes, but also independently emerged in some species of platyrrhines. Moreover, because conscientiousness was found in common marmosets, there is a need to re-evaluate whether domains like conscientiousness emerge only in species that are cognitively and socially complex (King and Weiss 2011).

All in all, then, these studies have uncovered personality domains that appear to be species-specific adaptations, highlight the functional significance of traits, and allow one to address questions about their proximate and ultimate origins. In a real sense, then, in the case of personality, this research tradition is capable of addressing Tinbergen's four questions about animal behavior (2005).

Conclusion

Before I conclude I want to stress that, as I have noted elsewhere (Weiss and Adams 2013) I do not think of this research tradition as fixed or the only way to study animal personality. It will change with the advent of problems that its present form has difficulties solving and other research traditions are bound to be equally good at solving problems. As I stated from the outset, I merely wanted to describe my own tradition and to evaluate it. Others will probably differ in their judgement.

Ultimately, the approach used should be suitable for the questions researchers seek to address. For example, Brent et al. (2014), Sussman et al. (2014) have, to good ends, used ethological approaches to address questions concerning the genetics, evolution, and development of macaque personality. It is thus important to remember that it would be foolhardy to use the HPQ without modifications (or at all) to address questions about species other than haplorrhine primates (see Koski 2011 and

⁵In my mind, whether orangutans have something like a conscientiousness or attentiveness domain is unresolved.

references therein). Moreover, given recent findings on wild bonobos (Garai et al. 2016), it is unclear whether HPQ traits are defined by the same structure in wild and captive populations (see also Gurven et al. 2013 for the case of humans). As such, until more is known, or a revision of the HPQ addresses any discrepancies, it would be premature to draw strong conclusions about species differences when they are confounded by whether the samples live in the wild, are semi-free-ranging, or are housed in captivity.

Finally, the study of Hanuman langurs found very strong correlations between personality domains and behavioral indices generated from the raw behavioral observation data (see Table A1 in Konečná, et al. 2008). Similarly, recent research on humans has shown machine learning algorithms can be used to measure personality via individuals' Facebook "Likes" (Youyou et al. 2015). These findings suggest that each questionnaire item or personality domain does not necessarily correspond to a single discrete behavior. They also recommend the possible gains that can be made by using machine learning approaches to study associations between personality and behavior provided the sample sizes are large enough.

As I noted at the beginning of this chapter, this research tradition has met with criticism, especially with regards to its origins in the traditions of human personality research. However, the history of animal behavior includes prominent examples of successful research traditions that directly sprung from human psychology (e.g., Harding et al. 2004). As such, the admonishment from some that human personality research is an inappropriate starting place for studying the personalities of other members of our primate lineage strikes me as not just shortsighted, but downright fanciful.

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