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Subjective Well-being and Its Relationship to Personality in Animals

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Background and Overview

In many societies, and for some time, the lives of most people are no longer characterized by an existential struggle to feed, house, and clothe oneself and one's family, but by a pursuit of happiness (Inglehart, 2018). More recently, in fact in some people's living memory, there has been a growing concern for the happiness and well-being of others, including unrelated individuals living in different countries, and animals (Pinker, 2011, Inglehart, 2018).

The question of how best to ensure the happiness, whether we define it as welfare, subjective well-being, or some other term (see Chapter 2 in this volume for a discussion), of animals under our care is a pressing and relatively recent concern. This development is remarkable considering that the desire to ensure animal happiness extends not just to animals with whom we share a recent common ancestor, such as chimpanzees and the other great apes, or a home, as with pets. The human desire for animals to be happy extends to distantly related species, animals in the wild, animals in the entertainment industry, animals that we use to learn more about ourselves and our world, animals that help us cure diseases, and even to farmed animals that many of us eat.

It is hard to imagine how this strong impulse to care for the well-being of species other than our own could have arisen if it were not possible for us to perceive where individual animals stand on a psychological continuum ranging from suffering to contentedness. Of course, it is possible that we are fooling ourselves. We may be seeing emotions that are not there or mistaking the display of one emotion for another. However, it is our view that the evidence suggests that, when we perceive an animal to be happy, sad, or 'fair to middling', we are more likely than not to be accurate in our appraisal.

In this chapter we will evaluate a subset of the evidence that our perceptions of animal happiness are accurate and that the 'happiness' that we see in other animals is much like the

happiness that we see in other humans or experience ourselves. This evidence consists of work on the relationships between personality traits and subjective well-being, both of which are psychological constructs, a notion that we will define early on. We will then---perhaps too briefly---discuss the implications of these findings with regards to what they say about the evolution of happiness, the practical implications of these findings, and what they say about how one might be able to better understand the physiological bases of happiness. That said, we will *not* engage in a defense of or promote the use of ratings by humans to measure happiness, or personality for that matter, in animals. We will also abstain from cataloging, comparing, or ranking all the ways that one can measure subjective well-being and personality in animals.

Psychological Constructs and Nomological Networks

Determining any given human or animal's level of happiness or standing on some personality trait differs from determining its height or weight. In the latter case, the measure is a more-or-less 'direct' measure of a physical property that is being measured. In the case of happiness, however, there is not a direct correspondence between our measure of happiness and happiness itself. Instead, our measure in this instance is based on a theory of how the thing that we wish to measure is represented by things that we can measure in the world.

The lack of a one-to-one correspondence between measures of any psychological construct and the measure itself is true whether one is interested in studying subjective well-being, personality, or any other psychological trait or state (Cronbach and Meehl, 1955). It is also true regardless of whether the measures we use are behavioral observations, behavioral tests, ratings by knowledgeable informants, or blood tests. Consequently, when measuring any psychological construct, it is important to establish the construct validity of a measure for, by doing so, one is better able to rule out the possibility that one is measuring something other than the construct of interest (Cronbach and Meehl, 1955). This may sound

straightforward, but it is not because in most cases there is no direct measure of the construct that can serve as a criterion. Contrast this with the case for weight; if we wanted to develop a new means of assessing weight, we could check whether it measures weight by examining the relationship between our new measure and the weight indicated by a scale. In short, so-called 'objective' and 'subjective' measures of psychological constructs stand on the same shaky ground.

We expect that it may surprise some people that the degree to which a measure is rooted in what can be seen and counted is not informative with regards to whether it is a good measure of what one wishes to measure. Moreover, the question of how, given this situation, one goes about studying things like subjective well-being or personality in animals (or even humans), is probably vexing to some. It is thus worth illustrating this point with a historical example, particularly because this example points towards a solution.

In the 1940s researchers became interested in locating the part of the brain that made people feel like they had enough to eat. An obvious way to have identified this satiety center would have been an experiment in which human volunteers either experienced some kind of 'sham surgery' control or had a part of their brain removed. After enough studies, one of the experimental groups would report being insatiable when compared to the sham surgery group. Of course, there are ethical problems with this kind of study, and so experimenters turned to the next best thing at the time: rats. These studies of rats eventually did find an area---the ventromedial nucleus of the hypothalamus---that seemed to be the satiety center of the brain. Although the rats could obviously not tell the researchers how hungry or full they felt, compared to rats in the control group, the rats in the experimental group ate constantly, and consequently, became obese. Similar results were produced by lesioning this area of the brain in other animals and similar behavior was described in humans who had tumors affecting that part of the brain (Brobeck, 1946 cited in Miller et al., 1950).

Not surprisingly, these researchers concluded that the ventromedial nucleus of the hypothalamus was the brain's satiety center. Not everybody was convinced, however, that the behavior displayed by subjects with these lesions were expressions of hunger. A series of experiments by Miller et al. (1950) showed that this skepticism was justified. They found that, unlike rats without lesions, rats with lesions did not seem as motivated to eat: their rate of bar pressing to receive food rewards did not increase as much as a function of food deprivation, they did not run down an alley towards a food reward as quickly or pull harder to get a food reward, they consumed less food than the non-lesioned rats when they had to lift a heavy lid to get at a food reward, and they were less likely to eat food that had been made to taste bitter.

This side story from the history of psychology tells us that, to measure something like happiness or a personality trait---entities that do not have corresponding criteria in the physical world---we need to use multiple indicators of multiple traits that we do and do not expect to be manifestations of that which we wish to measure (Campbell and Fiske, 1959). Doing so is a sort of triangulation that enables us to identify whether the psychological construct underlying these measures is the one that we think underlies these measures (see Figure 1). Conversely, this means that we infer the presence of a psychological construct by the relationships among our measures.

We hope that the reader will allow time for one further elaboration. To be able to claim that one's measures do 'tap' the construct of interest requires setting one's measures within a 'nomological network'. This means theoretically deriving and testing predictions about how constructs impinge on measures and other constructs, and testing predictions about the relationships between constructs and things in the 'real world' (Cronbach and Meehl, 1955).

For our purposes, in the next section we will describe a measure of nonhuman animal happiness. Claiming that one has a measure of 'happiness' for a nonhuman species is still controversial. It was thus probably a good thing that this measure was initially developed to measure happiness in chimpanzees, namely as, in our personal experience, people are more willing to forgive studying such fanciful things in our closest nonhuman relatives. We will then show that, although happiness' nomological network started small, its "roots" (Cronbach and Meehl, 1955, p. 291) have since entwined more and more constructs and things in the real world and have spread to other species. Personality played a key role in these developments.

Chimpanzee Happiness

The study of personality in nonhuman primates, including by using ratings, can be traced back to at least the 1930s (Whitman and Washburn, 2017). However, although researchers had developed and studied animal, including primate, models of negative affective states, such as depression (see, e.g., Harlow and Suomi, 1974) for some time, studies of happiness originated much later. The first (so far as we are aware) notable study was by King and Landau. Their subjects were 128 zoo-housed chimpanzees. King and Landau (2003) measured the happiness of their subjects by obtaining ratings on a four-item questionnaire from zoo keepers and staff who knew the individual chimpanzees, often for many years. Versions of this questionnaire can be found at: http://extras.springer.com/2011/978-1-4614-0175-9.

There are multiple definitions of human subjective well-being and each of the items that King and Landau devised was designed to operationalize one of the more common definitions. The first item concerned the balance of positive and negative affect, and asked raters to do the following:

> Estimate the amount of time the chimpanzee is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the chimpanzee is unhappy, bored, frightened, or otherwise in a negative mood.

The second item asked about the degree of positive versus negative affect that a chimpanzee experienced from social interactions:

> Estimate the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the chimpanzee. Use as many social interactions that you can recall as a basis for your judgment.

The third item was less straightforward than the first two. It asked raters to estimate the degree of control that a chimpanzee had over its life:

> Estimate, for this chimpanzee, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each chimpanzee will presumably have its own set of goals that may be different from other chimpanzees.

The last item was an attempt to get raters to gauge the chimpanzee's overall life satisfaction. In a sense, it was asking raters to indicate what one of the English-speaking chimpanzees

from *Planet of the Apes* (the 1968 version, of course) would response if he or she were asked "How happy are you?"

> Imagine how happy you would be if you were that chimpanzee for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, would perceive the world the same way as that chimpanzee, and would feel things the same way as that chimpanzee.

The overarching goal of King and Landau's study was to determine the extent to which chimpanzee happiness, as defined by ratings on this questionnaire, was surrounded by a nomological network like that which surrounds human measures of happiness. They thus addressed five questions, all bearing upon whether a consistent set of findings from the human happiness literature would be present in chimpanzees. These findings from the human literature included the correlation between individuals' self-reported of happiness and reports of their happiness by others; the positive intercorrelations of happiness measures, which suggest the presence of a single underlying factor; the rank order stability of happiness; and the relationships between happiness and personality whereby individuals who are higher in extraversion, lower in neuroticism, and higher in conscientiousness tend to be happier (Sandvik et al., 1993, Pavot et al., 1991, DeNeve and Cooper, 1998). They also asked a fifth question, which was whether their measure of chimpanzee happiness was related to independently assessed behaviors.

King and Landau did find evidence for a human-like pattern of relationships. First, across the four questionnaire items, there was a respectable level of agreement between independent ratings. Second, the four subjective well-being items were intercorrelated and a principal components analysis indicated that a single dimension accounted for just over 70% of their variance. Third, in a subsample of chimpanzees that were rated twice with an average

of 4.6 years separating the ratings, there was very little difference in the level of happiness and the stability of the ratings was high, that is, a chimpanzee's level of happiness relative to other chimpanzees was consistent over time. Fourth, there was a meaningful pattern of correlations between a set of ratings-based personality factors obtained as part of a previous study and happiness. Specifically, the sum of the four items from the subjective well-being scale was related to higher dominance, higher extraversion, and higher dependability (since Weiss et al., 2009, we have referred to this factor as "conscientiousness"). Higher ratings on the balance of positive and negative affect, the pleasure derived from social interactions, and global life satisfaction, the first, second, and fourth items, respectively, were related to higher dominance and extraversion. Higher ratings on the degree of control chimpanzees had over their lives and their ability to achieve their goals, that is, the third item, were related to higher dominance and higher dependability. They also did not find significant associations between any of the items or the total score and either agreeableness, emotionality (since Weiss et al., 2009, we have referred to this factor as "neuroticism"), or openness. Fifth, again in a subsample of chimpanzees, there was a negative correlation between behaviors related to submissiveness, and especially avoidance, which are consistent with the just-described relationship between higher dominance and happiness.

Before moving onwards, it is worth pointing out that, although the personality-happiness relationships mostly resembled those found in humans, there was a clear difference, too. Neuroticism was not significantly related to lower chimpanzee happiness (King and Landau, 2003). Instead, dominance, a personality domain that is apparently not represented by a single factor in humans (Digman, 1990) had the strongest relationship with happiness. This should strike the reader as odd. After all, there is a consistent and strong relationship between human happiness and neuroticism (DeNeve and Cooper, 1998, Steel et al., 2008). Although we will revisit this matter later, the likely explanation has to do with the

items that were defined dominance and neuroticism in chimpanzees. The neuroticism measure was based on the results of an earlier study, which showed that lower ratings on an item denoting stability and an item denoting unemotionality and higher ratings on an item denoting excitability defined chimpanzee neuroticism (King and Figueredo, 1997). Higher dominance, on the other hand, was not just defined by items indicating competitive prowess or agonistic interactions with others, but by lower ratings on items relating to dependence, fearfulness, timidity, cautiousness (King and Figueredo, 1997). Putting it another way, dominance may have possessed more traits related to those aspects of neuroticism related to lower well-being.

Chimpanzee Happiness Revisited

This chimpanzee study described in the previous section was followed by three follow-on studies that also examined the extent to which the nomological network that captured human subjective well-being applied to its chimpanzee counterpart. The first study had two goals. The first was to test whether variation in chimpanzee happiness was partly attributable to genetic differences between chimpanzees. The second was to determine the extent to which genes for personality were also genes for subjective well-being. The goal of the second study was to determine whether features of captive chimpanzees' physical or social environments contributed to their happiness. The goal of the third study was to determine whether the relationship between chimpanzee personality and subjective well-being were present in an independent sample.

The first study was motivated by two previous studies of subjective well-being. This first was Lykken and Tellegen's (1996) classic study of human happiness. In this study twins were administered twice, several years apart, a personality questionnaire that included a subjective well-being scale (the Multidimensional Personality Questionnaire; Tellegen, 1982). This study had three noteworthy findings. First, 44 to 52% of the variability in

subjective well-being was attributable to genetic differences. Second, around 80% of the variability of the stable component of subjective well-being was attributable to genetic differences between individuals. In other words, among these participants, most of the differences in happiness that were not attributable to fluctuations around an individual's average happiness, were genetic in origin. Third, only a small proportion of differences in individuals' subjective well-being was attributable to things shared by people raised in the same family, or demographic indicators, such as socioeconomic status, education level, and marital status. The second study found evidence in 202 zoo-housed chimpanzees that differences among chimpanzees in the personality factor dominance were the result of genetic differences; the other five factors were not 'heritable' (Weiss et al., 2000).

Using the 128 chimpanzees featured in King and Landau's (2003) study, the first of the follow-on studies found that about 40% of the variation in chimpanzee subjective well-being was heritable (Weiss et al., 2002), which is consistent with the average of heritability estimates derived from previous and subsequent studies of human happiness (Bartels and Boomsma, 2009). Moreover, this study found that nearly all the shared variation between chimpanzee dominance and subjective well-being was attributable to common genetic effects. Since the publication of this study, research on happiness in humans (Weiss et al., 2008, Hahn et al., 2016, Hahn et al., 2013, Weiss et al., 2016) and orangutans (Adams et al., 2012) have yielded similar results concerning the genetic bases of the personality-happiness relationship.

The second study found little to no evidence that the physical (e.g., population density) or social (e.g., how related an individual was to group mates) characteristics of the enclosure contributed to subjective well-being over and above the effects of sex, age, and personality (Weiss and King, 2006). Thus, much like Lykken and Tellegen's results, demographic factors relating to the environment did not appear to contribute to chimpanzee

happiness either. Work in humans that has been conducted since these studies suggests that the early pessimism about environmental effects may have been premature. However, because these new findings will take some time to describe and are useful for pointing out new directions for work on animal happiness, we hope the reader will appreciate the need to discuss these matters in the concluding section of this chapter.

The purpose of the third study was to determine whether the personality and subjective well-being relationships described by King and Landau could be found in an independent sample. This study of 146 chimpanzees by Weiss et al. (2009) differed from King and Landau's study in two ways. First, to measure personality, this study used the Hominoid Personality Questionnaire (HPQ; Weiss, 2017), an extended version of the questionnaire developed for King and Figueredo's 1997 study. The HPQ includes 11 additional items to better represent traits related to neuroticism, openness, and conscientiousness. Second, the chimpanzees were housed in either Japanese zoos, the Kyoto University Primate Research Institute, or, what is now known as Kumamoto Sanctuary. As such, this study tested whether the relationships between personality and subjective well-being generalized when raters were from a different culture. The results of this study of chimpanzees in Japan were consistent with those from King and Landau's study of chimpanzees in zoos in the United States and Australia in two ways. First, the four subjective well-being items defined a single component. Second, dominance and extraversion were related to higher ratings on each of the subjective well-being scale's items and the sum of these items, the latter representing the construct. However, there were differences: Conscientiousness was not related to any of the subjective well-being measures; neuroticism, as one would expect based on human studies (DeNeve and Cooper, 1998, Steel et al., 2008), was related to lower ratings on all the measures; agreeableness was related to higher ratings on the items and the sum score; and openness was related to all the measures save the item

relating to the ability to achieve goals. Because of some procedural and data analytic differences between this study and that of King and Landau, it is impossible to determine whether the differences reflect cultural differences in how raters interpreted some questionnaire items or the procedural and data analytic differences mentioned above.

The results of these studies are encouraging and further support to the notion that the 'happiness' construct measured in chimpanzees has a nomological network resembling that of human happiness. One finding that was especially encouraging was the identification of a biological explanation for the relationship between chimpanzee personality and happiness, which was subsequently found in humans and orangutans. Nevertheless, like all psychological constructs, establishing construct validity will continue to be a work in progress. This reflects two characteristics of psychological constructs and nomological networks. First, there are near infinite ways that one can measure a construct. Second, nomological networks grow and their connections may change with new observations and a better understanding of the construct (Cronbach and Meehl, 1955). As we shall discuss in the next two sections, this true for subjective well-being, regardless of the species in which it is measured.

Other Species

As hinted at in the previous section, the work based on the human conception of happiness has included studies of other species. To prevent confusion in this section, it is worth pointing out two things to readers who are not familiar with the animal personality literature. First, the set of personality dimensions possessed by a given species tends to differ to varying degrees from those possessed by other species. Second is the so-called 'jingle jangle' problem: different researchers often have different naming conventions for what are probably the same personality traits and/or affix the same name to what are probably different personality traits (Thorndike, 1904, Kelley, 1927, both cited in Block, 1995). As such,

although we will introduce more than a few different personality domain labels, the reader should bear in mind the degree to which they might be aligned with the human domains that tend to be associated with subjective well-being.

Published research in nonhuman primates has examined at least one species belonging to great apes, Old World monkeys, and New World monkeys (no work has been conducted on prosimians, such as ring-tailed lemurs). As in studies of subjective well-being in humans (Sandvik et al., 1993, Pavot et al., 1991) and chimpanzees (Weiss et al., 2009, King and Landau, 2003, Robinson et al., 2017), the items used to measure subjective well-being items in these studies defined a single subjective well-being factor.

Among great apes, other than chimpanzees, the only report of correlations between personality and subjective well-being was in 140 zoo-housed orangutans (Weiss et al., 2006). Orangutans were found to have five personality domains and of these, higher extraversion, higher agreeableness, and lower neuroticism were associated with being rated higher in subjective well-being.

A study of semi-free ranging rhesus macaques living on Cayo Santiago found correlations between the six personality domains identified in this study and subjective well-being. The relationships between subjective well-being and higher confidence, higher friendliness, and lower anxiety were significant regardless of whether these constructs were measured at the same time or at two different times between 13.9 and 18 months apart (Weiss et al., 2011).

A study of 66 brown capuchin monkeys in research centers also found evidence for prospective, that is, cross-time, associations between personality and subjective well-being. The personalities of these monkeys were assessed as part of an earlier study, which identified five personality dimensions (Morton et al., 2013). Two of these dimensions, assertiveness and sociability, were positively associated with subjective well-being (Robinson et al., 2016).

These associations were also examined in 77 common marmosets, another New World monkey species, housed in a laboratory colony in Japan (Inoue-Murayama et al., 2018). This study identified three personality domains of which two, sociability and neuroticism, were positively and negatively related to subjective well-being.

So far as we are aware, questions about the associations between personality and subjective well-being have only been investigated in one other taxonomic group, that is, felids. These studies found that the four or five subjective well-being items were intercorrelated in such a way as to define a single dimension. The first of these studies was of 25 Scottish wildcats living in zoos (Gartner and Weiss, 2013). This study found that, of three personality domains, self-control was consistently related to higher subjective well-being. The second study examined these associations in 16 clouded leopards, 17 snow leopards, and 21 African lions, all of which lived in zoos (Gartner et al., 2016). In all three species, higher neuroticism was related to lower subjective well-being. Moreover, in the clouded leopards, higher subjective well-being was also related to higher scores on a personality domain that was a blend of agreeableness and openness, and in African lions, impulsiveness was related to lower subjective well-being.

At this point, the perceptive reader may have noticed that, although we noted the relationships between personality and the individual items for the two earlier studies of chimpanzees (Weiss et al., 2009, King and Landau, 2003), we did not do so here. Our reason for not doing so is for the sake of brevity. However, considering what the individual items and the personality domains purportedly measure, these associations were mostly what one might expect to find. Overall, then, these findings indicate that personality domains related to being gregarious, sociable, and active are associated with higher subjective well-being and that those related to being impulsive, fearful, and vigilant are related to lower subjective well-being. In short, the links in the nomological net between subjective well-being and

personality are consistent across distantly-related species of nonhuman primate and between primates and another mammalian order. Readers who wish to learn about these finer-grained associations are invited to read the relevant papers.

The studies reviewed here and in the previous section only focused on a part of the nomological net that supports the construct validity of happiness (and personality, too) as measured in nonhuman primates and felids. In the next section we will discuss other connections in this net, including how and whether they support the construct validity of subjective well-being.

Other Connections

As the reader should know by now, one question when considering the construct validity of the subjective well-being measure is whether it is associated with other purported measures of happiness or similar constructs. Other measures hypothesized to be related to the relative happiness (or unhappiness) of nonhuman animals, and in some cases, humans, include welfare questionnaires, cognitive bias tests, motor stereotypies, and corticosteroid levels. There have been tests for associations between these measures. However, when it comes to tests of associations between subjective well-being ratings and these measures, the research has been sparse. This is regrettable for it means there are few strong tests for the construct validity of subjective well-being ratings and these other measures.

One exception to this lack of studies is the case of welfare and subjective well-being. A broad definition of welfare focuses on the so-called 'five freedoms', that is, freedom from hunger and thirst, freedom from discomfort, freedom from pain, injury, or disease, freedom to express normal behavior, and freedom from fear and distress (Farm Animal Welfare Council, 1979). Using this framework, animal welfare measures have often focused on using behavioral and physiological outputs as indicators of negative welfare states (Broom, 1991). More recently, researchers have recognized the need to focus not just on suffering, but on

thriving, and have put forward ways to measure positive welfare states (Boissy et al., 2007, Yeates and Main, 2008). In addition to the recognition that one needs to study positive welfare states there has been an increasing interest in studying whether the needs that matter to an individual animal are being satisfied, a notion known as the animal's quality of life (McMillan, 2005, McMillan, 2000).

It would be surprising if a measure of subjective well-being was not related to measures of positive welfare or quality of life. If this were found, it would cast doubt upon whether these were measures of these constructs. To examine this, Robinson et al. (2016) developed a 12-item scale, since expanded into a 16-item scale (Robinson et al., 2017), to assess quality of life and a few aspects of the five freedoms in captive nonhuman primates. This scale, available at https://www.drlaurenrobinson.com/surveysdesigned/, targeted people who has been working with individual animals, such as care staff and researchers in laboratories, and was created with the principle that welfare ranges from very bad to very good (Boissy et al., 2007, Yeates and Main, 2008). The key section of this questionnaire included items that reflected traditional conceptions of animal welfare (Broom, 1991, Broom and Johnson, 1993) and factors identified as relating to quality of life (McMillan, 2005). As such, these questions were about mental stimulation, health, social relationships, stress, and the control of the social and physical environment. For example, one question was "How frequently is this individual stressed? Stress being an unpleasant emotional experience in response to a threatening event that potentially harms the individual's health." Another question was "How often does the individual display signs of positive welfare?" In addition to these questions, we included one question that incorporated quality of life into assessments of welfare (see Green and Mellor, 2011):

In this individual's life, would you say he/she experiences:

A. considerably more negative experiences than positive experiences.

B. more negative experiences than positive experiences.

C. equal amounts of negative and positive experiences.

D. more positive experiences than negative experiences.

E. considerably more positive experiences than negative experiences.

In both the brown capuchin monkeys and the chimpanzees studied by Robinson et al. in 2016 and 2017, respectively, ratings on the welfare scale were highly correlated (> .9) with the subjective well-being items scale. Not surprisingly, principal components analyses in these two studies found that all the items from both scales loaded onto a single component. Both studies then examined the relationships between this component and personality. In brown capuchin monkeys, higher component scores were associated with higher sociability and assertiveness and lower neuroticism and attentiveness. In chimpanzees, higher component scores were associated with higher extraversion and lower neuroticism. Finally, the study of chimpanzees also tested for association between this component and several behaviors. In doing so, it found that the component was related to less frequent regurgitation, coprophagy (eating feces), urophagy (drinking urine), and increased proximity to neighboring chimpanzees. These findings provide strong and direct evidence in favor of the construct validity of subjective well-being or happiness in these species. The construct that the subjective well-being scale assesses is nearly identical to that of welfare measured using a very different scale, and the combination of these scales is related to personality and behaviors in ways that one would expect.

Along with this direct evidence, there is indirect evidence for the construct validity of subjective well-being, too. This evidence, some of which we discuss below, is in the form of

associations between other purported measures of well-being or similar constructs, such as positive affect, and personality traits related to subjective well-being.

Cognitive bias tests were developed for use in laboratory rodents (Harding et al., 2004) and have since been applied across animals ranging from honeybees (Bateson et al., 2011) to chimpanzees (Bateson and Nettle, 2015) and animals housed in other different environments, including on farms (Baciadonna and McElligott, 2015) and in zoos (Clegg, 2018). The test procedure is as follows. First, each animal is trained in a discrimination task in which one stimulus signals the presence of a food treat and the other signals the absence of a food treat. For example, a rat would be presented with several trials in which a food is hidden behind a white card and no food is hidden behind a black card. In each trial, the rat is given the treat if it approaches the white card and is not given a treat if it approaches the black card. After several trials the rat learns to only approach the white card. Then comes the crucial test. The rat is then presented with a stimulus that is intermediate in value. In our example, the rat would be presented with a gray card. An animal---our hypothetical rat---that approaches this ambiguous stimulus is said to be “optimistic” in that it is acting as if it expects the food reward to be behind the stimulus. An animal that does not approach this stimulus is said to be “pessimistic”. The construct validity of the cognitive bias test has amassed considerable support and a discussion of the evidence. Among this evidence are findings that indicate that animals reared in poor environments or that are made to experience a stressor are more likely to make pessimistic decisions than those animals reared in good environments (Mendl et al., 2009, Baciadonna and McElligott, 2015). These findings mirror studies of humans that show, for example, that people with major depressive disorder perceive neutral events as more threatening than do people without major depressive disorder (see Gotlib and Joormann, 2010 for a reivew of this literature).

One study which provides evidence that performance on the cognitive bias test may be related to subjective well-being comes from a study of three chimpanzees---one adult female and two adult males---by Bateson and Nettle (2015). Of the three chimpanzees, the more dominant of the males showed the least pessimism, measured by the latency to touch the intermediate stimulus, the other male showed an intermediate amount of pessimism, and the female showed the most pessimism. These findings are consistent with findings from studies based on ratings that show a relationship between higher ratings of dominance and higher subjective well-being in chimpanzees (King and Landau, 2003, Weiss et al., 2009, but see Robinson et al., 2017).

A study of 31 dogs by Barnard et al. (2018) also provides indirect evidence that subjective well-being is related to cognitive bias. Choices reflecting an optimistic bias were associated with dogs that exhibited greater sociability, one of five traits measured by the Dog Mentality Assessment test, a behavioral assay (Svartberg and Forkman, 2002) and owner ratings reflecting higher non-social fear and excitability, two of the six dimensions on the Canine Behavioral Assessment and Research Questionnaire (Hsu and Serpell, 2003). A pessimistic bias was associated with higher dimensions derived by owner ratings: dog-directed aggression, dog-directed fear, and separation-related problems.

Motor stereotypies are seemingly functionless behaviors that are repetitive and unchanging (Mason, 1991, Mason and Latham, 2004). A study of over 4000 rhesus macaques examined whether demographic factors, early rearing, animal housing, and personality traits were associated with motor stereotypies and self-biting (Gottlieb et al., 2013). Personality in this study was measured in infancy using ratings and behavioral tests. The authors found that, along with several demographic, rearing, and housing factors, monkeys who displayed an “active temperament”, that is, those monkeys who were less “gentle”, more likely to display

activity in response to a human intruder, and who made more contact with novel objects, were at greater risk of developing motor stereotypies.

Cortisol (a corticosteroid) levels are related to activation of the hypothalamic-pituitary-adrenal axis, which aids the organism in coping with stress. High cortisol levels may indicate chronic activation of the axis, which can have harmful effects on the organism. There thus should be an association between chronic levels of stress, lower well-being, and cortisol levels. In a review, Koolhaas et al. (1999) described a clustering of behavioral and physiological characteristics in rodents referred to as coping styles. Proactive coping styles were related to low attack latencies, protecting one's territory, and low levels of flexibility. Reactive coping styles were related to more defensive behaviors, withdrawal responses, and higher levels of flexibility. Koolhaas et al. also reported that these coping styles were related to lower and higher hypothalamic-pituitary-adrenal axis activation, respectively.

Work that examines relationships between behavioral traits and cortisol in primates is mostly consistent with the work on coping styles, and offers indirect evidence linking personality and subjective well-being. One of these studies measured brown capuchin monkey personality using behavioral observations and ratings, found that higher basal blood cortisol and cortisol reactivity were associated with an inhibited and fearful personality (Byrne and Suomi, 2002). Another study, this one of basal cortisol levels measured in blood, found that more excitable rhesus macaques had lower levels of cortisol in the afternoon and that more confident macaques had higher levels of cortisol in the morning (Capitanio et al., 2004). A third study did not find a relationship between subjective well-being ratings and hair cortisol (Inoue-Murayama et al., 2018). Moreover, contra to what one might expect given the relationship between higher sociability and higher subjective well-being in this species, that study found a positive association between higher cortisol levels were higher sociability.

What, then, are we to conclude from what has been presented so far, both about the subjective well-being as a construct and its probable genetic association with personality. In addition, and more importantly for some readers, what do these findings lead one to conclude concerning what can or cannot be done to improve the happiness of animals in our care? We discuss these matters, and consider future directions for research, in the final section.

Conclusions

If anything, the research outlined here and that which we did not cite (see other chapters in this volume), on subjective well-being and related constructs in nonhuman primates and other animals should convey a single point. There is *at least* as much scientific evidence to support the existence of something like human subjective well-being or happiness in at least some species of nonhuman animals as there is in support of the existence of this construct in humans. In addition, the parallels between human and animal subjective well-being, including how and why they are related to personality, suggests that the constructs are similar across species. Consequently, the experience of happiness or subjective well-being along with its links to personality are almost certainly evolutionarily old. To test this, that is to rule out alternative evolutionary scenarios, such as convergent evolution, however, requires more work. Large phylogenetic studies, such as those used to study other traits (MacLean et al., 2014) would go some way to achieve this aim.

More critically for captive animals is the question of how do these findings inform best practice? We expect that some may readers will come away pessimistic. After all, subjective well-being in humans, chimpanzees, orangutans, and probably other species is influenced by genes, including those genes related to personality variation. This reflects a misunderstanding about what heritability estimates mean. Heritability estimates indicate the degree to which differences between individuals are influenced by genes and not the degree to which individuals are influenced by genes (Falconer and Mackay, 1996). In other words, if

an environmental intervention, such as a new enclosure, raised every individual's happiness by a roughly equal amount, the heritability of happiness would be roughly the same. That is because the differences between individuals would still be present and likely related to their genetic background.

But is it possible to change happiness by means of environmental interventions? We think so and studies of animals and humans support this view. Contrary to earlier thinking on the matter, human happiness can be adversely affected over long periods of time by events such as divorce, unemployment, or widowhood (Diener et al., 2006). Likewise, animal rearing and husbandry practices can make a difference (Clay et al., 2018). Moreover, a study of happiness in 52 countries found that happiness in 45 countries increased from 1981 to 2007 and that the rate of increase was related to economic development, democratization, and greater tolerance, all of which contributed to a sense that they had free choice (Inglehart et al., 2008). These findings suggest that some current views about role of free choice on animal welfare and the actions to take (e.g., Kagan et al., 2015) are on the right track. More importantly, perhaps, they show just how much we can potentially learn about animal happiness from studying it humans, and vice versa.

Figure Captions

Figure 1. By gathering data on multiple traits, each measured with a set of methods, one can isolate the variance related to the trait from that related to how the trait was measured and vice versa. Circles represent variance related to either traits (e.g., subjective well-being, cognitive ability, and self-control) or the methods used to measure those traits (e.g., behavioral tests, questionnaires, and behavioral observations). Boxes represent observations in a study, such as the score on a behavioral test that purportedly measures subjective well-being. Figure by the authors and licensed under the terms of the Creative Commons Attribution 4.0 International License.

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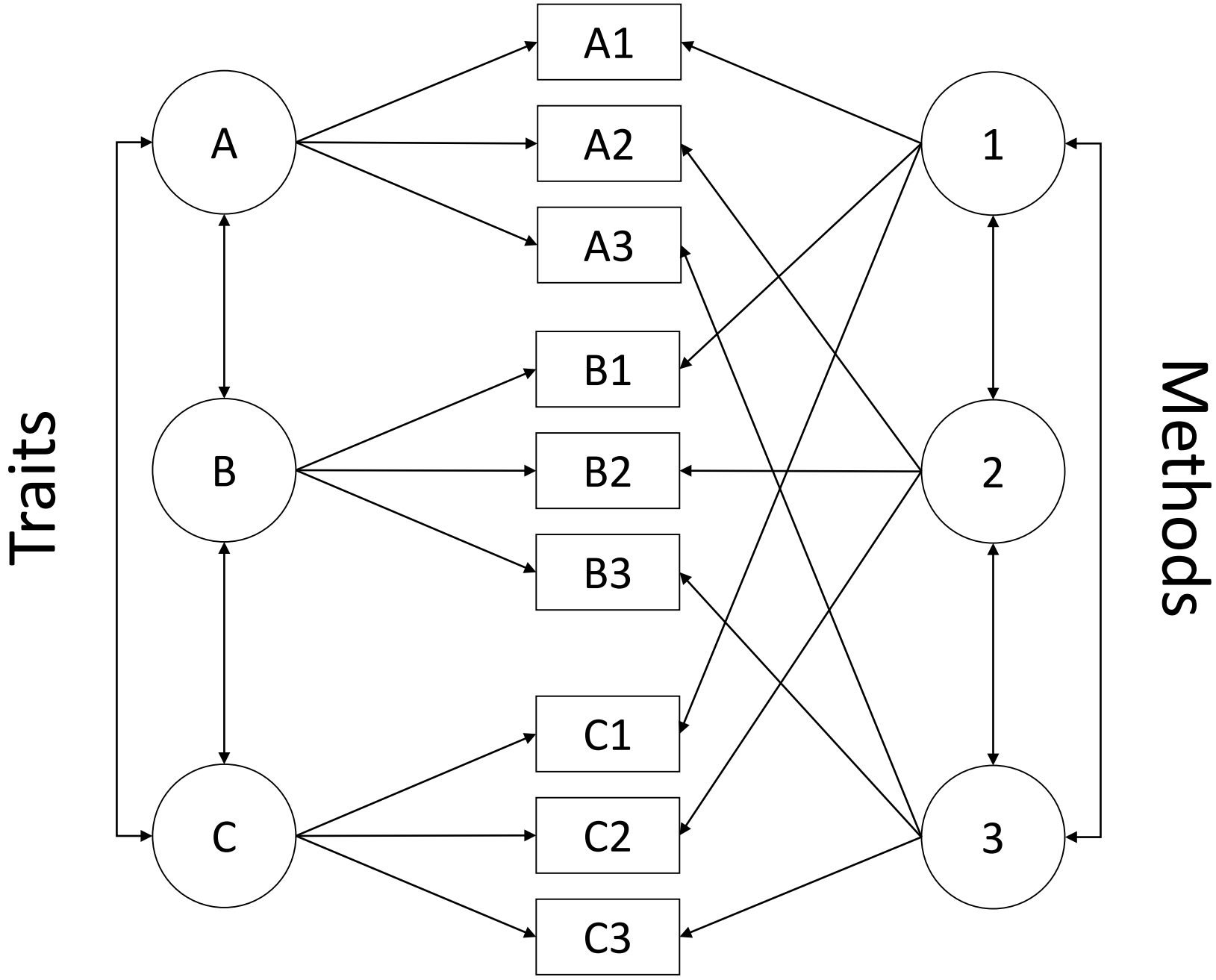
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