

## CHAPTER 7

# Personality in Animals

## *What Can We Learn from a Species-Comparative Approach?*

Alexander Weiss

Whether looking at people or animals, two observations have been made by psychologists, biologists, and lay observers. First, individuals differ consistently in how they behave and react toward, and think about, the world around them. Second, not all these differences are independent of one another: Individuals who are high (or low) on some traits tend to be high (or low) on other traits. In more formal language, individuals can be characterized by stable individual differences in personality traits, and these traits have a structure to them.

Scientific studies of human personality can be traced back at least to the work of Sir Francis Galton (1884) who lived from 1822 to 1911. For a long time, this work was predominantly descriptive (see also John, Chapter 2, this volume). Researchers, for example, would identify and categorize personality traits, whether by studying the natural language of populations (Allport & Odbert, 1936) or by analyzing data derived from questionnaires, naturally occurring behaviors, and behavioral tests (Cattell, 1946). The descriptive flavor of this early research was, and continues to be, criticized by some authors (e.g., Block, 1995; Eysenck, 1992; Uher, 2013). However, gathering de-

tailed, descriptive data is a crucial first step in any scientific discipline (Chamberlin, 1890/1965). In fact, that description should come before theory has been recognized for a long time in the field of animal behavior (Tinbergen, 1959, 1963), and this recognition likely contributed to the emergence of animal personality research in that field.

This chapter examines how the study of personality in nonhuman animals contributes to our understanding of personality in general and of human personality in particular. For one, animal research has helped elucidate the evolutionary bases of personality variation and structure by the method of exclusion (Platt, 1964). In other words, this research has shown that some proposed evolutionary explanations for personality are not likely to be true. In addition, personality research on animals contributes to our understanding of the neuroanatomical bases of personality variation, informs the debate about the origins and magnitude of age differences in personality, and addresses why the personalities of some people predispose them to be happier than others. Readers of this chapter who are familiar with Gosling's (2001) review of the literature will thus see that research in animal personality

is addressing questions that Gosling, and no doubt others, described as being particularly amenable to studies of nonhuman animals.

### The Historical Development of Animal Personality Research

The scientific study of animal personality can be traced to Charles Darwin and to major figures in psychology, including Ivan Pavlov, Robert Yerkes, and Donald Hebb. However, until the 1970s, animal personality research by comparative psychologists was sporadic (Weiss & Gartner, 2016; Whitman & Washburn, 2017).

The burst of research into animal personality that followed came largely from within behavioral ecology, an offshoot of the study of animal behavior in biology. Researchers in this area seek to answer questions about the proximate (physiological, environmental, and developmental) and ultimate (functional and evolutionary) causes of animal behavior (Tinbergen, 1963). A central tenet of behavioral ecology is that species evolve to behave optimally under environmental conditions and that behaviors can be mathematically modeled (Parker & Maynard Smith, 1990). For example, a behavioral ecologist may devise a model to determine the optimal group size for a population. The model's parameters might include greater vigilance against predators (a benefit) and greater competition for resources (a cost). These models can then be tested in various populations.

The behavioral ecologists' approach has been successful at explaining all manner of behaviors in animals and in humans (Krebs & Davies, 1997). However, like humans, not all animals within a species behave as predicted by models. As described elsewhere (e.g., Réale, Reader, Sol, McDougall, & Dingemans, 2007), for a long time, behavioral ecologists' models relegated variation around the optimum behavior (i.e., individual differences) to the error term. According to Réale and his colleagues, the situation changed with the publication of a study on stickleback fish by Huntingford (1976). The fish in that study displayed individual differences in behavior that were consistent across different stages of their breeding cycle and in the presence of different intruders. More-

over, fish that displayed more aggression in the behavioral tests were more likely to explore new environments. This discovery of consistent individual differences led biologists to try to understand why animals do not always exhibit the "optimal" behavior given a set of circumstances (e.g., Wilson, Clark, Coleman, & Dearstyne, 1994) and resulted in a rapid growth in animal personality research.

### Reliability and Validity

As in the study of human personality, there needs to be evidence that the measures of personality under study are reliable and valid. This is true regardless of whether the measures are ostensibly objective measures, such as behavioral observations, or ostensibly subjective measures, such as ratings. Establishing the construct validity of measures in animals is also important, because doing so establishes whether a measure assesses the same construct in different species. It also enables researchers to determine whether species similarities and differences are in line with what one would expect given the natural history of the species.

#### Reliability

Animal personality traits are stable over time. The stability of animal personality traits has been demonstrated in three meta-analyses. The first meta-analysis (Bell, Hankison, & Laskowski, 2009) involved 114 studies of a wide range of species and trait measures classified as belonging to one of 13 categories: migration, mate preference, activity, affiliation, parental, courtship, antipredator, foraging, exploratory, aggression, habitat, mating, and "other." The authors of this meta-analysis found a *mean repeatability*—a type of intraclass correlation coefficient (Boake, 1989; Nakagawa & Schielzeth, 2010)—of .37 across studies. The second meta-analysis was based on estimates of retest reliability from eight studies of nonhuman primates, and found a mean retest reliability of .58 across personality dimensions such as confidence and excitability (Freeman & Gosling, 2010). The third meta-analysis, using a variety of stability

estimates, was based on 31 studies of dogs, and found a mean stability correlation of .43 for traits classified as belonging to one of six personality dimensions, namely activity, sociability, aggression, submissiveness, responsiveness to training, and fearfulness/reactivity (Fratkin, Sinn, Patall, & Gosling, 2013).

Animal personality studies based on behavioral observations or ratings often assess interjudge agreement reliability among the observers or raters. Reviews of the literature on multiple taxa (Freeman & Gosling, 2010; Gartner, 2014; Gartner & Weiss, 2013; Gosling, 2001; Jones & Gosling, 2005) all find interrater or interobserver reliability estimates comparable to those for established measures of human personality, such as the Revised NEO Personality Inventory (Costa & McCrae, 1992).

Studies that examine a broad range of traits have also found that, for a given species, data reduction techniques tend to yield the same personality dimensions, regardless of the method used to collect the personality data (i.e., rating instruments or behavioral observations). For example, studies of chimpanzees show that different rating instruments (Dutton, 2008; Dutton, Clark, & Dickins, 1997; Freeman et al., 2013; King & Figueredo, 1997) and behavioral measures (Koski, 2011b; Massen, Antonides, Arnold, Bionda, & Koski, 2013; van Hooff, 1970) identify the same dimensions or subsets of these dimensions. Similar results have been found in rating-based studies of brown capuchin monkeys that rely on different questionnaires developed on the basis of different principles (Morton, Lee, Buchanan-Smith, et al., 2013; Uher, Addessi, & Visalberghi, 2013). Rating-based studies (Stevenson-Hinde & Zunz, 1978; Weiss, Adams, Widdig, & Gerald, 2011) and observation-based studies (Brent et al., 2014) of rhesus macaques also yield similar sets of dimensions (see Weiss, 2017, for other examples). In short, for a given species, all the different types of personality instruments appear to measure the same set of constructs.

### **Validity**

Attempts to establish the validity of ratings of personality have met with success in

nonhuman primates (Freeman & Gosling, 2010), felids, the taxonomic group that includes cats (Gartner & Weiss, 2013), dogs and other household pets (Gartner, 2014; Jones & Gosling, 2005), and other species (Gosling, 2001). Much of the evidence for validity has been based on studies examining relationships between individual behaviors and ratings of single personality items or personality dimensions. However, recent studies have found associations between animal personality measures, based on either ratings or behaviors, and what would be referred to as “consequential outcomes” (Ozer & Benet-Martínez, 2006) or “life outcomes” (Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007) in studies of humans. In Barbary macaques and barnacle geese, for example, personality traits are related to achieving high rank (e.g., Konečná, Weiss, Lhota, & Wallner, 2012; Kurvers et al., 2009). Moreover, personality traits are related to whether dogs can be successfully trained to for certain “jobs,” such as being a detector dog (e.g., Harvey et al., 2016; Maejima et al., 2007; Sinn, Gosling, & Hilliard, 2010). There are even links between primate personality and cognitive performance measures analogous to “scholastic aptitude” (e.g., Altschul, Wallace, Sonnweber, Tomonaga, & Weiss, 2017; Altschul, Weiss, & Terrace, 2016; Carter, Marshall, Heinsohn, & Cowlishaw, 2014; Hopper et al., 2014; Morton, Lee, & Buchanan-Smith, 2013). For example, chimpanzees that were rated as higher in conscientiousness and openness 3 years earlier performed better on a touchscreen learning task, and higher openness predicted engaging in the learning task even when no reinforcers were delivered (Altschul et al., 2017).

In addition to the aforementioned attempts to validate personality ratings, some researchers have used validity studies to challenge assumptions about measures of personality, such as behavioral tests or behavioral observations. For example, Carter, Marshall, Heinsohn, and Cowlishaw (2012b) examined two purported behavioral measures of boldness (a novel object test and responses to a stuffed snake) in wild chacma baboons. They found that these measures were related to each other only weakly and probably defined separate constructs. As a consequence of these and related findings,

behavioral ecologists now show a greater appreciation of the need to examine the construct validity of behavioral measures (Araya-Ajoy & Dingemanse, 2014; Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2012).

Finally, it is important to show that personality measures are sensitive to expected species differences—an issue that has not yet been discussed much (see, however, Uher et al., 2013, p. 429). For example, among hyenas, females are physically stronger than males and dominate them. Given this sex role reversal in power relations among hyenas compared to humans, it makes sense that female hyenas are higher on assertiveness than males (Gosling, 1998), and lower on neuroticism (Gosling & John, 1999). From a measurement perspective, these findings provide evidence for what might be called the “comparative validity” of the personality measures.

### Evolutionary Explanations for Personality Differences

Biologists and psychologists have advanced several evolutionary explanations to explain the presence of persistent, heritable variation in behavior (for reviews, see, e.g., Dingemanse & Wolf, 2010; Penke, Denissen, & Miller, 2007). Although there is not enough space in this chapter to cover all of these proposed explanations, it is worth discussing those that have received the most attention or support.

The default (or null) hypothesis is that personality variation reflects the accumulation of mutations that do not influence survival or reproduction (i.e., they are “neutral” in terms of selection; Kimura, 1968, 1983, 1986). This hypothesis was advanced by evolutionary psychologists whose main focus was on describing cognitive modules that, they argued, were human universals (Tooby & Cosmides, 1990). However, considerable evidence has come to light that personality is associated with health (Strickhouser, Zell, & Krizan, 2017) and reproductive success (Alvergne, Jokela, & Lummaa, 2010; Eaves, Martin, Heath, Hewitt, & Neale, 1990; Jokela, Alvergne, Pollet, & Lummaa, 2011) in humans. Likewise, evidence in nonhuman

animals shows that personality traits are associated with survival and reproductive success (see, e.g., Smith & Blumstein, 2008, for a review). As such, personality variation in both humans and animals can probably not be attributed to neutral selection.

A second possibility is that balancing selection maintains variation in personality. This possibility is supported by studies of birds, lizards, insects, small mammals, and ungulates, which find that whether and in what direction a personality trait is associated with survival and reproduction varies across environments, time, and/or developmental stages (for reviews, see Dingemanse & Réale, 2013; Dingemanse & Wolf, 2010). For example, Dingemanse, Both, Drent, and Tinbergen (2004) captured wild great tits and measured how often and how rapidly they explored a novel laboratory environment. They then released the birds into the wild and followed them over three winters: Availability of the birds’ preferred food during the first winter was poor, availability of the birds’ preferred food during the second winter was good, and availability of the birds’ preferred food during the third winter was poor. For male birds, exploration in the laboratory was associated with lower survival rates during winters when food was scarce but higher survival rates during the winter when food was abundant; for female birds, the pattern was in the opposite direction.

In another study, Nicolaus, Tinbergen, Ubels, Both, and Dingemanse (2016) found that the association between exploration and fitness in great tits varied as a function of population density: Faster explorers were favored when the population density was low; slower explorers were favored when the population density was high. Critically, although birds changed their behavior as a function of population density, it was in the opposite direction as one would expect if doing so was to maximize fitness: Birds became faster explorers when the population density was high and slower explorers when the population density was low.

A third possibility is that personality variation is maintained by trade-offs related to differences in life-history strategy, a continuum that was originally used to characterize species or populations (MacArthur & Wilson, 1963). At one end of this continuum

are species or populations with a “fast” life-history strategy. Individuals belonging to these species or populations breed early and often, but at the expense of longevity and offspring survival. At the other end of this continuum are species or populations with a “slow” life-history strategy. Individuals belonging to these species or populations breed later and less frequently but have longer lives and more surviving offspring. Life-history strategy has been extended to describe differences between individuals within species and populations (Réale et al., 2010). Because different life-history strategies have similar fitness payoffs (MacArthur & Wilson, 1963), the variation of any personality trait associated with life history should be maintained (Biro & Stamps, 2008; Wolf, van Doorn, Leimar, & Weissing, 2007). Consistent with the life-history strategy perspective, Réale, Martin, Coltman, Poissant, and Festa-Bianchet (2009) tested whether two personality traits (boldness and docility) in bighorn sheep were genetically correlated, and whether genetic tendencies for these traits were associated with survival and reproductive success. *Boldness* was defined as the tendency to enter a baited trap, and *docility* was defined as reactions to being handled by humans. Boldness and docility were associated with life-history trade-offs, heritable, and had a negative genetic correlation with each other. Moreover, the predicted genetic values of boldness and docility were related to a longer lifespan and late-life reproductive success.

A fourth possibility is that personality variation is maintained because of genetically or environmentally mediated correlations between traits (Sih, Bell, Johnson, & Ziemba, 2004). These correlations can occur within contexts, such as the case of brown capuchin monkeys: Individuals high on a personality dimension labeled “assertiveness” tend to be more aggressive, dominant, and independent, but less fearful and cautious (see Table 6 in Morton, Lee, Buchanan-Smith, et al., 2013, for all of the loadings). These correlations can also occur across contexts, for example, in stickleback fish in which more aggressive individuals were more likely to explore a new environment (Huntingford, 1976). In both cases, because the traits are correlated, being at

the optimum level of one trait (assertiveness in monkeys and aggressiveness in fish) is incompatible with being at the optimum level of the other trait (cautiousness in monkeys and the tendency to explore new environments in fish).

It is unlikely that any one of these possible evolutionary mechanisms, or others that are not discussed here, is solely responsible for maintaining personality variation. However, the identification of these mechanisms in several species testifies to how animal personality research can solve problems related to personality evolution. There is more to say about the maintenance of personality variation, but that involves comparing species, a topic that I address later in this chapter. Until then, I describe the search for the physiological bases of animal personality.

### Physiological Underpinnings of Animal Personality Differences

With respect to identifying the physiological bases of animal personality, some of the most convincing work comes from selection studies and studies of animal coping styles. Animal breeders have long known that breeding (selecting) for *physical* traits can lead to changes in *behavioral* traits, and vice versa. In a classic study, Dmitry Belyaev bred foxes for tameness for over 40 years (Trut, Oskina, & Kharlamova, 2009). In several respects, the tame foxes behaved more like domesticated dogs than their wild counterparts; they also differed from wild foxes in their rate of development and neuroendocrine profiles (Trut et al., 2009). Specifically, compared to wild foxes, tame foxes retained youthful features but reached sexual maturity earlier and showed higher levels of reproductive hormones (Trut et al., 2009). Moreover, during development, foxes display a reduction in their exploratory behavior and an increase in glucocorticoids, both of which mark the end of their sensitive socialization period; these changes occurred later in tame foxes than in wild foxes (Trut et al., 2009). It thus seems foxes bred to thrive in captivity had an extended adolescent period, perhaps because they were not selected to survive in a more competitive and stressful environment (the wild).

Another selection study compared birds (great tits) selected to be fast or slow explorers of novel environments (van Oers, Buchanan, Thomas, & Drent, 2011). Fast explorers had better immune functioning and lower testosterone levels than slow explorers. The latter findings surprised van Oers and his colleagues, because fast explorers are more aggressive. However, this difference may mean that, like Belyaev's domesticated foxes, birds selected for lower levels of a trait related to aggression reached sexual maturity more rapidly.

In the animal personality literature, *coping style*<sup>1</sup> refers to a suite of behavioral and physiological tendencies related to how individuals react to stressors (Koolhaas et al., 1999). At one end of this spectrum are *proactive* individuals. At the other end of this spectrum are *reactive* individuals. In behavioral tests, proactive individuals were found to attack more quickly and were more likely to engage in defensive behavior (Koolhaas et al., 1999, Table 2). Animals with a proactive coping style also differ with respect to their hypothalamic–pituitary–adrenal axis activity and reactivity, and their parasympathetic reactivity, both of which are low relative to animals with a reactive coping style (Koolhaas et al., 1999, Table 3). Finally, the sympathetic and testosterone reactivity of individuals with a proactive coping style are high compared to individuals who have a reactive coping style (Koolhaas et al., 1999, Table 3).

Differences in neurophysiology have also been identified as proximate explanations for personality variation. A magnetic resonance imaging study of 74 chimpanzees revealed that the percentage of grey matter in the brain, but not the asymmetry of the brain's subgenual cingulate cortex region, was associated with lower dominance and higher conscientiousness (Blatchley & Hopkins, 2010). Personality measures in that study were derived by questionnaire ratings: Dominance was made up of traits related to boldness, fearlessness, assertiveness, and aggressiveness; conscientiousness was made up of traits related to self-control, predictability, and emotional stability (Weiss, King, & Hopkins, 2007).

A later magnetic resonance imaging study of 107 chimpanzees by Latzman, Hecht,

Freeman, Schapiro, and Hopkins (2015) revealed associations between personality and other brain regions: The volume and asymmetry of the frontal region of the brain's grey matter were associated with higher dominance and extraversion, the latter being related to sociability, activity, and other traits that make up its human counterpart (Freeman et al., 2013). Latzman and his colleagues (2015) also found associations between frontal grey matter volume and higher openness, a personality dimension related to exploratory behavior and curiosity (Freeman et al., 2013), and between frontal grey matter asymmetry and higher reactivity/unpredictability, a personality dimension related to low conscientiousness (Freeman et al., 2013).

### Evolutionary Explanations for Human Personality Variation

The findings reviewed earlier suggest that there is promise in the use of animals to understand the evolutionary and physiological underpinnings of personality variation. Turning again to questions about the evolution of personality, researchers have conducted many studies on the association between human personality and health, survival, and reproductive success (see Lewis & Buss, Chapter 1, this volume). However, researchers have been considerably less successful in answering questions related to human personality evolution than they have been in answering questions about animal personality evolution. Fortunately, studies that compare species provide some of the best tests of some of these hypotheses about the evolution of human personality, and so can help move the study of human personality evolution forward.

The comparative method involves conducting natural experiments by comparing species with different evolutionary histories (see Gosling & Graybeal, 2007, for an overview). To see how one tests evolutionary hypotheses in comparative studies, consider the case of studying two species. These species can either be closely related to one another (e.g., humans and chimpanzees) or distantly related to one another (e.g., chimpanzees and brown capuchin monkeys). In

addition, the species that one compares can either have faced similar challenges in their evolutionary history (e.g., both species live in large groups) or different challenges (e.g., one species lives in an environment in which there are many predators, and the other species lives in an environment in which predators are absent).

There are two comparisons that allow for strong tests about the evolution of personality. The first is the comparison between closely related species that faced different challenges. Here, if the species differ in, for example, the personality dimensions that they possess, the parsimonious explanation is that the personality differences evolved recently in response to the challenges. On the other hand, if these species possess the same set of personality dimensions, the parsimonious explanation is that these personality dimensions were present in the common ancestor of both species.

The second is the comparison between distantly related species that faced similar challenges. Here, if the species are similar to one another, for example, if both possess the same set of personality dimensions, the most parsimonious explanation is that these personality dimensions are an evolutionary product of those challenges. This method has been used to test hypotheses about personality structure, associations between personality traits and other variables, and whether certain features of species led to differences in mean levels of traits.

### Structure

To test hypotheses concerning the evolution of personality structure, researchers have been gathering data on one of several animal personality questionnaires and/or on naturally occurring behaviors (Freeman & Gosling, 2010). These researchers then use factor analysis or principal components analysis to identify personality dimensions in the species. The dimensions identified are typically a combination of (1) those that are human-like (e.g., orangutan neuroticism; Weiss, King, & Perkins, 2006), (2) those that resemble human personality facets (e.g., rhesus macaque anxiety; Weiss et al., 2011), (3) those that combine two or more human dimensions (e.g., brown capuchin monkey

sociability; Morton, Lee, Buchanan-Smith, et al., 2013), (4) those found in multiple primate and primate species, but not in humans (e.g., dominance; Freeman & Gosling, 2010; Gosling & John, 1999), and (5) those specific to a species or taxonomic group (e.g., “opportunistic” in Assamese macaques; Adams et al., 2015).

The way in which animal studies help make sense of personality can be illustrated by describing how they inform hypotheses about the origins of the five-factor model. To begin, consider extraversion and agreeableness. Compared to other primates, humans are intensely social and altruistic (Kurzban, Burton-Chellew, & West, 2015). It is therefore not surprising that some researchers (e.g., Ashton & Lee, 2007; Nettle, 2006) hypothesize that the evolutionary bases of extraversion and agreeableness can be traced to those features of humans. However, personality variation in social traits has been identified in species ranging from the highly social chimpanzee (King & Figueredo, 1997) to the semisolitary orangutans (Weiss, et al., 2006), and to the solitary East Pacific red octopus (Mather & Anderson, 1993). These findings are contrary to the predictions that would be derived from theories based on human sociality and altruism.

There are also problems with tying social traits or their structure to *kin selection*, the tendency of individuals to help related individuals at a cost (Hamilton, 1964). For one, even across primate species, we see great variety in social and mating systems (Crook & Gartlan, 1966), level of paternal care (Fernandez-Duque, Vallengia, & Mendoza, 2009), and other ecological characteristics (Galán-Acedo, Arroyo-Rodríguez, Andresen, & Arasa-Gisbert, 2019). Still, factor-analytic studies of personality in primates (Gold & Maple, 1994; King & Figueredo, 1997; Konečná et al., 2008) have demonstrated that distinct dimensions of extraversion and agreeableness exist in chimpanzees (a species with a promiscuous mating system), as well as in Western lowland gorillas and in Hanuman langurs (both species in which one male monopolizes access to multiple females). Mountain gorillas, curiously, appear to possess a single dimension, namely, sociability, combining traits related to extraversion and agreeableness (Eckardt et al.,

2015). Distinct extraversion and agreeableness dimensions therefore emerge in species that differ with respect to how much information males have about the offspring they are related to, and so these dimensions probably emerged long before modern humans.

Explanations based on *reciprocal altruism*, the tendency to help unrelated individuals because if you do, they are more likely to help you in the future (Trivers, 1971), are beset with similar problems. For one, reciprocal altruism is less likely to evolve in species in which individuals do not regularly encounter one another or species in which individuals would be unable to recognize one another (Trivers, 1971). Nonetheless, separate agreeableness and extraversion dimensions have been found in orangutans (Weiss et al., 2006), but not in brown capuchin monkeys (Morton, Lee, Buchanan-Smith, et al., 2013) or mountain gorillas (Eckardt et al., 2015), the latter two both being social primate species. These findings are not consistent with what one would predict if the evolutionary bases of interpersonal personality dimensions in humans (e.g., extraversion, agreeableness, or honesty–humility) are evolutionary products of reciprocal altruism. An alternative explanation emerged from a study of six macaque species, in which Adams et al. (2015) found that the personality dimensions defined by traits related to assertiveness, social confidence, and aggression differ as a function of the degree to which the species were despotic versus tolerant (see Thierry, 2000, for definitions).

Evolutionary accounts of openness to experience and of conscientiousness also do not appear to withstand this kind of scrutiny. Proposed benefits of openness have included greater creativity, and thus being more attractive to the opposite sex; the proposed costs have included proneness to unusual beliefs and psychotic disorders (Nettle, 2006). However, studies of nonhuman primates suggest that openness evolved independently in several primate lines and possibly for other reasons. For example, there is evidence that openness evolved in species that get some of their food from places that are hard to reach or when effort and ingenuity give access to additional food resources (see, e.g., Adams et al., 2015; Konečná et al., 2008, 2012).

For conscientiousness, one evolutionary explanation that has been advanced is that it enables costly signaling (Buss, 2009) or reflects a balance between delayed mating and longevity (Nettle, 2006). One might therefore predict that conscientiousness should be widespread in the animal kingdom. Yet despite the finding that variation in two aspects of conscientiousness appear to be widespread in the animal kingdom (Delgado & Sulloway, 2017), as was noted in Gosling and John's (1999) review, in animals, personality dimensions such as conscientiousness are rare.

So what selective pressures may have led to the evolution of conscientiousness in our species and those other animals that appear to possess it? Studies of nonhuman primates and other animals suggest that species with a conscientiousness dimension, such as chimpanzees (King & Figueredo, 1997), bonobos (Weiss et al., 2015), brown capuchin monkeys (Morton, Lee, Buchanan-Smith, et al., 2013), and Asian elephants (Seltmann, Helle, Adams, Mar, & Lahdenperä, 2018) tend to have larger brains. Moreover, a study of 36 species, including primates and nonprimates, that adjusted for phylogeny found that greater self-control (which is central to conscientiousness) was associated with a larger absolute brain size and a more varied diet (MacLean et al., 2014). However, the finding that a conscientiousness dimension is absent in the large-brained orangutan (Weiss et al., 2006) but present in the small-brained common marmoset (Iwanicki & Lehmann, 2015; Koski et al., 2017; but see Inoue-Murayama, Yokoyama, Yamanashi, & Weiss, 2018) suggests that brain size may only partly be responsible. For example, the finding of conscientiousness in common marmosets may mean that the need for helpers to rear young (Burkart, Hrdy, & Van Schaick, 2009) may also favor the evolution of dimensions resembling human conscientiousness. Thus, Altschul et al.'s (2018) finding that conscientiousness was not related to mortality in captive chimpanzees should also not be surprising.

In contrast to the previous examples, evolutionary explanations for neuroticism often draw on the animal literature. This may be because traits associated with neuroticism differ from the more visible aspects



of human personality, because dimensions such as neuroticism are found in many species (Gosling & John, 1999), or because it is difficult to come up with a way in which high neuroticism is “beneficial” to humans. For example, Nettle (2006) hypothesized that costs related to higher neuroticism, including poorer health and being at risk of psychological disorders, are offset by increased vigilance. Focusing on the African apes, this explanation is consistent with neuroticism being present in chimpanzees (King & Figueredo, 1997), but not bonobos (Weiss et al., 2015) or mountain gorillas (Eckardt et al., 2015), as the latter two are believed to have evolved in predictable, resource-rich environments. Studies of humans have found further support for this hypothesis in that a part of neuroticism related to worry and feelings of vulnerability is related to better physical health outcomes, including longevity (Gale et al., 2017; Weiss et al., 2019), and that these relationships appear to exist at the level of the genome (Hill et al., 2019). On the other hand, this explanation is not supported by the finding that neuroticism is present in western lowland gorillas (Gold & Maple, 1994), which also live in a predictable, resource-rich environment. It thus appears that the proposed benefits of neuroticism only partly outweigh its costs, and that further study is needed.

### **Development**

In addition to answering questions relating to the maintenance of variation and/or the evolution of personality dimensions, comparative research has enabled researchers to test whether biological factors (McCrae & Costa, 2003) or investing in sociocultural roles (Roberts & Jackson, 2009) are the drivers of personality development. The logic here is that the roles that are hypothesized to influence personality development, such as beginning full-time employment, are absent or very different in other species. In one of these studies, King, Weiss, and Sisco (2008) compared chimpanzees to humans. In another study, Weiss and King (2015) compared chimpanzees to orangutans. The authors of these studies took into account and adjusted for the different rates of development between the great ape

species and the humans. They found that the direction and magnitude of personality age differences were mostly comparable across species, which appears inconsistent with a social roles explanation of personality development (King et al., 2008; Weiss & King, 2015). Moreover, two findings from these studies suggest that personality development is a product of natural selection. First, orangutans declined in agreeableness, suggesting that age-related increases in human and chimpanzee agreeableness may be an adaptation for living among unrelated conspecifics, which orangutans do not do (Weiss & King, 2015). Second, in contrast to humans, orangutans, and female chimpanzees, age-related declines in extraversion leveled off among male chimpanzees (King et al., 2008; Weiss & King, 2015), which may reflect an adaptation for heightened aggression in chimpanzee males (Wrangham, Wilson, & Muller, 2006).

### **Personality, Happiness, and Health**

Human personality dimensions are associated with psychological and physical health. The study of animal personality provides insight into the mechanisms and evolutionary bases that underlie these associations.

In one case, the comparative approach has revealed why people who are lower in neuroticism and higher in extraversion, and, to a lesser degree, higher in the other three human personality dimensions, tend to be happier (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008). These findings grew from a study by King and Landau (2003), who created a four-item questionnaire that allowed raters closely familiar with the animals to assess a construct akin to subjective well-being in chimpanzees. King and Landau’s analyses indicated that the four items defined a single factor, the interrater and retest reliabilities were high, and the factor was related to higher dominance, extraversion, and conscientiousness. Similar relationships have been found in other studies of personality ratings in nonhuman primates (Robinson et al., 2016; Weiss et al., 2009, 2011) and felids (Gartner, Powell, & Weiss, 2016).

King and Landau’s (2003) findings were an initial indication that associations be-

tween personality and subjective well-being predated the emergence of humans and human societies. This study thus led to a search for explanations that would hold across humans, chimpanzees, and possibly other primates. One possible explanation put forward was that common genes were responsible for some aspects of personality (the dominance dimension in this case) and subjective well-being. This notion was initially supported by a quantitative genetic study of chimpanzees (Weiss, King, & Enns, 2002) and later by quantitative genetic studies of personality and subjective well-being in humans and orangutans (see Weiss & Luciano, 2015, for a review). A recent genomewide association study yielded results consistent with these earlier studies (Weiss et al., 2016). In brief, a common set of genes that give rise to individual differences in both personality and subjective well-being may have existed prior to human evolution.

Studies of personality in other species are also informative for those who seek to address why people with certain personalities tend to suffer from poorer physical health (Deary, Weiss, & Batty, 2010; Strickhouser, et al., 2017). Many mechanisms have been proposed, but those that predominate in the literature posit that human behaviors, such as dietary choices, substance use, and physical activity, are responsible (Deary et al., 2010). Studies of nonhuman animals, however, suggest that the mediation models favored in much of the human literature may provide only a partial picture of how personality translates into health. For example, a meta-analysis of studies comparing multiple species revealed that species with higher boldness and higher exploration (i.e., traits that roughly correspond to low neuroticism and high openness, respectively) live longer (Smith & Blumstein, 2008).

Studies of personality and health by comparative psychologists have largely, but not exclusively, been of nonhuman primates. These studies include two that investigated associations between personality and mortality. The first was an 18-year follow-up of zoo-housed western lowland gorillas: higher extraversion was related to mortality, but neuroticism, agreeableness, and dominance were not (Weiss, Gartner, Gold, & Stoiniski, 2013). The second was a study of chim-

panzees housed in zoos, research centers, and a sanctuary. Mortality was assessed 7 to 24 years later. Among males, longevity was related to higher agreeableness; among females, however, openness was related to longer life, but this relationship was tenuous; neither dominance, extraversion, conscientiousness nor neuroticism were related to longevity (Altschul et al., 2018).

Further studies investigated health outcomes other than mortality. The authors of one such study found that lower aggressiveness, lower “mellowness,” and higher excitability were related to morbidity in golden snub-nosed monkeys, and that sociability was related to higher morbidity in younger monkeys but lower morbidity in older monkeys (Jin, Su, Tao, Guo, & Yu, 2013). A study that examined associations between personality ratings and veterinary records revealed that rhesus macaques higher in confidence and anxiety were less likely to be injured; there appeared to be no association between these personality dimensions and illness or between injury and the four remaining dimensions, those being activity, openness, friendliness, and dominance (Robinson et al., 2018). Finally, experimental studies have demonstrated that in rhesus macaques, some common factor or factors underlie personality traits related to sociability and immune system robustness, and that these effects tend to show up in unstable social environments (see review by Capitano, 2011).

These and similar findings (see Mehta & Gosling, 2008, for a review), and especially findings in captive animals whose diets are managed, whose health is monitored, and who receive treatment for health conditions that arise, suggest that studies of human personality and health may benefit from searching for mechanisms that can explain these associations in humans and nonhumans. Differences may be informative, too. For example, the study by Altschul et al. (2018) that did not find an association between conscientiousness and longevity in chimpanzees was based on captive samples. This means the diets of these chimpanzee subjects were controlled, they received regular health checks, and preventative measures and interventions were administered. All of this strongly supports the view that the relationship between conscientiousness and bet-

ter health in humans is mediated by individual health behaviors (Altschul et al., 2018).

In summary, the findings reviewed in this section suggest that studies of personality in animals have revealed weaknesses of some proposed evolutionary and mechanistic explanations of human personality. Studies of animal personality have also pointed to promising alternative explanations. In terms of furthering our understanding of personality, then, the need to study personality in animals can be likened to the suggestion that we study WEIRD (Westernized, educated, industrialized, rich, and democratic) humans (Henrich, Heine, & Norenzayan, 2010).

### Future Directions

The evidence that personality can be measured reliably in animals, and that these measures are capturing real differences among individuals, both within and between species, is hard to dispute. Likewise, the studies described in this chapter show how animal personality research has informed our understanding of human personality, with regard to its proximate causes and consequences, and its evolutionary bases. The research described thus far represents only a small part of the extensive literature on animal personality research conducted by behavioral ecologists, comparative psychologists, and personality psychologists. Further progress could be made by research that answers the growing calls for an integration of these still-distinct research strands (Carter, Feeney, et al., 2012; Koski, 2011a; Nettle & Penke, 2010; Weiss & Adams, 2013).

One set of studies could examine associations between the domains and facets of the five-factor model and behavioral measures such as boldness, exploratory behavior, and so forth (Réale, et al., 2007), using a multitrait–multimethod framework (Campbell & Fiske, 1959). Although animal researchers have examined how personality dimensions assessed by ratings are related to specific behavioral observations (e.g., Pederson, King, & Landau, 2005) and behavioral tests (e.g., Carter, Marshall, Heinsohn, & Cowlshaw, 2012a), no comparable human

work has been done. Such studies could improve the measures and clarify what constructs are being measured by behavioral ecologists.

Future research is also needed on a wider range of species to fill in what one might describe as “phylogenetic gaps.” Next to nothing is known about personality in a vast array of primate and nonprimate species. Carefully selecting which species to study and use of phylogenetic analyses (Nunn, 2011) could lead to new findings.

Finally, there is evidence that human personality structure may differ in societies that more closely resemble those of our early human ancestors (Gurven, Von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013). Likewise, there is evidence that the personality structure of chimpanzees and bonobos in captive environments may differ from their wild counterparts (Garai, Weiss, Arnaud, & Furuichi, 2016; Weiss et al., 2017). However, because of differences in how personality was measured in both sets of studies, it is too early to conclude whether these differences reflect environmental influences or evolved differences brought about, for example, by self-domestication (Hare, Wobber, & Wrangham, 2012). Studies using the same personality measures in both captive and wild environments would help to resolve this question.

### Conclusions

I hope that this chapter has shown the usefulness of studying animal personality, whether by behavioral ecologists or comparative psychologists, without giving the impression that it is the only way to learn about personality. Although an integrative research agenda would be useful for answering some questions, the diverse personality research ecosystem on display in this volume will ensure that other questions are not ignored, and perhaps are answered, too.

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## NOTES

1. Coping styles as discussed here are not the same as those in the work on coping in the human personality literature (see Carver & Connor-Smith, 2010).

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