Personality traits

Journal of Personality 00:00, Month 2017

DOI: 10.1111/jopy.12310

Personality Traits: A View From the Animal Kingdom

Alexander Weiss
The University of Edinburgh

Abstract

Given their backgrounds in classical ethology and in comparative psychology, researchers who study animal personality in biology and psychology, respectively, differ in how they measure personality, what questions they see as important, and how they address these questions. Despite these differences, both comparative psychologists and biologists embrace personality traits. By doing so, they have solved empirical and conceptual problems in animal behavior. Studies of animal personality have provided answers to questions about the evolution of human personality and have presented conceptual and empirical anomalies for sociocognitive theories. Animal personality research does not break from trait theories of personality. Instead, it enriches trait theories by conceiving of traits as not belonging to a species, but as expressed, with some modifications, across species. Broadening trait theory in this way has the potential to further enhance its ability to answer questions related to animal and human personality.

Keywords: Evolution, primate, philosophy of science, history, ape

> The report of my death was an exaggeration.
> —Mark Twain, *New York Journal*, June 2, 1897

The central question of this special issue concerns the status of traits in modern personality science. The purpose of this article is to demonstrate that trait theory excels in solving problems related to personality evolution in animals. To do so, the article begins by reviewing the history of the trait–situation debate, revealing that trait theory has never been a paradigm, in crisis, or overthrown by an interactionist or sociocognitive paradigm. This article then shows how biologists have incorporated trait theory into a research tradition used to understand the evolutionary and mechanistic bases of behavioral variation in nonhuman animals. Following this, the article discusses how this research tradition has been less successful in solving problems about the evolution of human personality, possibly because researchers in the area developed hypotheses without attending to the animal literature, and shows how problems related to the evolution of human personality can be addressed by studies of animal personality. The article concludes by discussing the ability of trait theory and sociocognitive theories of personality to solve conceptual problems and suggests ways in which trait theories from psychology can accommodate animal personality research.

To start, the lore in personality psychology that was passed on to me was that early on in the history of modern personality research, trait theory was the predominant paradigm. During that era, personality researchers failed to take note of, marginalized, or ignored the effects of situations on behavior. The story then goes on to say that in 1968, Walter Mischel's book *Personality and Assessment* exposed the folly of ignoring the effects of the situation in favor of the effects of traits, namely, as traits only weakly affected behavior. Finally, a scientific revolution was said to have taken place, and trait theory was replaced by a new interactionist paradigm, and then, according to some accounts, it returned with the advent of the Big Five or Five-Factor Model.

Based on findings from studies of animal personality, I came to question the above history of personality psychology and the notion that trait theory is inadequate for personality science and should be revised or replaced. In hindsight, I should not have been surprised that such an overly simplistic, Kuhnian history of the field of personality psychology was not an accurate retelling of events. As is true in many scientific disciplines (Brush, 1974), the history presented to students of personality psychology is sanitized. There are many motives for presenting science students with sanitized histories of their field, among them the desire to instill in students the need to be neutral, unbiased observers, and to test hypotheses using the scientific method

Thoughts and insights herein emerged from discussions over the years with, among others, Jake Jacobs, Dick Byrne, Paul Costa, Ian Deary, Sam Gosling, Tim Bates, and Mark James Adams. Their patience, willingness to answer questions, and frank comments and criticism have helped me hone my thoughts. I also wish to thank Jim Coyne for sending me reprints and Jim King and Emily Weiss for their comments and suggestions on earlier drafts.

Correspondence concerning this article should be addressed to Alexander Weiss, Department of Psychology, School of Philosophy, Psychology and Language Sciences, The University of Edinburgh, 7 George Square, Edinburgh EH8 9JZ, United Kingdom. Email: alex.weiss@ed.ac.uk.

(Brush, 1974, p. 1164). Unfortunately, presenting a sanitized history comes at the expense of recognizing other considerations that play a role when scientists evaluate theories, including aesthetics, findings in other fields, and the subjective weighting of existing findings (Brush, 1974, pp. 1168–1169; Chang, 2012).

So how has the history of personality psychology been sanitized? For one, despite claims to the contrary (e.g., Uher, 2013), including by Walter Mischel (2009), the history of personality psychology did not precede in a Kuhnian fashion—that is, it is not one of normal science (the trait paradigm) followed by crisis and revolution (the publication of *Personality and Assessment* and its aftermath) followed by a new paradigm.

To show that the modern history of personality psychology does not fit a Kuhnian narrative, one has to determine whether anything like a paradigm existed in the field. One also has to determine whether there was a crisis (see, e.g., Leahey, 1992).

By *paradigm*, Kuhn (1970) referred to broad assumptions that are universally held by researchers in a field. These assumptions include, for example, how to measure phenomena, what phenomena one should study, and what phenomena one should ignore (Kuhn, 1970). According to Kuhn, during periods in which a paradigm rules a scientific field, there is consensus among researchers. One way in which the consensus is manifested is in a field's textbooks: During periods of normal science, a field's textbooks serve as guides to conducting research within the paradigm and are not compendiums of past and present theories (Kuhn, 1970). Take, as an example, Plomin, DeFries, Knopik, and Neiderhiser's (2013) textbook on behavioral genetics. It begins with chapters on genetic inheritance and similarity among relatives. Next, it describes how to determine, by quantitative and molecular methods, the extent to which genes influence traits. These chapters are followed by examples of how one or more of these methods were used to understand the genetic (and environmental) bases of various traits and disorders. However, at some point, the discovery of a phenomenon or phenomena that are inconsistent with the theories of the normal science leads to a crisis, and it becomes ever more difficult for the theory to explain these anomalies (Kuhn, 1970). This crisis is resolved by the emergence of a new theory, which explains both the anomalies and the observations of the previous theory (Kuhn, 1970).

Throughout its history, personality psychology has been marked by prominent, competing personality theories and a decided *lack* of consensus. For example, prior to the publication of *Personality and Assessment* (Mischel, 1968), there were psychodynamic and trait theories of personality. In addition, although the most prominent among these disagreements was the person–situation debate, which *Personality and Assessment* helped spark (Kenrick & Funder, 1988), there existed (and still exist) disagreements, even among trait theorists, about, for example, the structure of personality (Costa & McCrae, 1992a, 1992b; Eysenck, 1992a, 1992b) and whether personality maturation is attributable to genetic and biological causes (McCrae & Costa, 2003) or a response to taking on societal roles, such as becoming a parent or beginning work (Roberts, Wood, & Smith, 2005). This ongoing lack of consensus in personality psychology is reflected in personality textbooks, which, unlike those in paradigmatic sciences, such as behavior genetics, are not guides to working within a paradigm, but, instead, summaries of various theories and perspectives.

The historical record is also at odds with claims that Mischel's (1968) book led to a crisis. Kenrick and Funder (1988, p. 23) noted that clashes between psychologists who favored trait versus situational approaches to personality were ongoing before 1968. Moreover, contrary to what one might expect if *Personality and Assessment* led to a crisis period in personality psychology, reviews of the book were mostly positive (Aiken, 1968; Beech, 1969; Madison, 1968). In fact, even a review that Mischel (2009, p. 283) claimed "dismissed" his book took the arguments presented in the book seriously (Craik, 1969). This absence of a crisis is consistent with the fact that, for there to be a crisis, there has to be a paradigm (Leahey, 1992), and, as observed here and elsewhere (Eysenck, 1983), personality psychology is a pre-paradigmatic science.

So is there a better description for the history of personality psychology? The many different strands of research inherent in personality psychology (and other social sciences) are better described by pragmatic descriptions of progress in science. Laudan (1977) put forward one such description of scientific progress. He described science as a human activity designed to solve problems, and, instead of seeing theories as being generated by an overarching, dominant paradigm, Laudan proposed that theories, such as trait theory, were generated by and part of research traditions. Successful research traditions, according to Laudan, were those that solved more problems.

Laudan (1977) identified two broad types of problems that are solved by research traditions. Empirical problems are those described by Kuhn (1970) and include problems solved by one or more theories, problems that remain unsolved, and problems solved by one theory but not a competing theory. Importantly, different research traditions attach different weights to different problems (Laudan, 1977). In the case of personality psychology, for instance, trait theorists are less concerned with how traits and situations interact to produce behavior than are social learning theorists. Instead, they are more concerned with, for example, the problem of family resemblances in personality. The other type of problems, conceptual problems, were not identified by Kuhn and are problems with scientific theories (Laudan, 1977). According to Laudan, conceptual problems are as important as are empirical problems, and not addressing these problems can hold back a research tradition. For example, despite its clear ability to answer empirical problems about species diversity and to make novel predictions, conceptual problems, such as a belief in an unchanging natural world, prevented the acceptance of Darwin's evolutionary theory (Mayr, 1972).

An obvious question then is, how well do research traditions that include trait theory solve empirical and conceptual problems about animal behavior? Individual differences in animal behavior were probably apparent to humans ever since we began interacting with animals. Moreover, as others (e.g., Gosling, 2001)

have noted, the origins of the scientific study of animal personality can be traced to Charles Darwin and major figures within psychology, including Ivan Pavlov, Robert Yerkes, and Donald Hebb. However, animal personality research up until the 1970s by comparative psychologists—which included studies of development, learning, behavior genetics, immune responses, and structure—was sporadic (see Weiss & Gartner, 2017).

The burst of research into animal personality that followed these initial investigations came largely from biology, probably because trait theory proved to be an especially good problem solver in behavioral ecology. An offshoot of classic ethology, the study of animal behavior in natural conditions, behavioral ecology seeks answers to Tinbergen's (1963) questions about the proximate (the physiological mechanisms and environmental conditions leading to a behavior and how the behavior develops during the individual's life) and ultimate (what the behavior's function is and how it has evolved) explanations for animal behavior. One core tenet of behavioral ecology is that species evolve to behave optimally under environmental conditions (Parker & Maynard Smith, 1990). For example, a behavioral ecologist may devise models to predict how long birds of a particular species will search for food within a patch. The parameters of this model could include how long they have been exploiting a patch, the energy they will expend and risks they will take in finding a new patch, and how likely the new patch is to be better than the patch they are currently exploiting.

Behavioral ecology had been quite successful at explaining animal behavior (Krebs & Davies, 1997). However, like humans, all animals within a species do not behave as predicted by their models. As described elsewhere (e.g., Réale, Reader, Sol, McDougall, & Dingemanse, 2007), for a long time, the statistical models used by behavioral ecologists relegated the variation around the optimum behavior to the error term. According to Réale and his colleagues, the situation changed with the publication of a study on stickleback fish. The fish in this study displayed individual differences in behavior that were consistent across different stages of their breeding cycle and in the presence of different intruders, and the fish that displayed more aggression in the behavioral tests were more likely to explore new environments (Huntingford, 1976).

These results, and those in other species, did not lead evolutionary biologists (e.g., Wilson, Clark, Coleman, & Dearstyne, 1994) to suggest that the effects of environmental conditions or development were less important than individual differences or that interactions instead of main effects should be studied. Evolutionary biologists also did not describe these findings as leading to a crisis or as causing a paradigm shift. Instead, a research tradition emerged to solve the problem, and its rapid growth testifies to its ability to do so. Personality traits are at the core of this tradition.

One empirical problem that this research tradition addressed is the question of why behavioral variation exists, especially as studies of nonhuman animals have found that additive genetic effects underlie this variation (Van Oers, De Jong, Van Noordwijk, Kempenaers, & Drent, 2005). This phenomenon is puzzling because, as noted by Fisher, directional selection should exhaust the additive genetic variation underlying a trait (see Penke, Denissen, & Miller, 2007, for a discussion). It is also puzzling because, if an animal is to survive and reproduce, the best behavioral strategy would be to be flexible enough so that its behavior can match whatever is optimal for a particular time and environment (Réale et al., 2007; Sih, Bell, Johnson, & Ziemba, 2004).

Several evolutionary mechanisms have been developed to explain the presence of persistent, heritable variation in behavior (Dingemanse & Wolf, 2010; Penke et al., 2007). Although there is not enough space to cover all of these mechanisms, it is worth discussing those that have received the most attention in some detail.

One possibility is that personality variation is maintained by the accumulation of mutations that do not influence survival or reproductive success (Kimura, 1983). However, traits are associated with survival and reproductive success (see Smith & Blumstein, 2008, for a review). Readers familiar with the human personality literature are no doubt familiar with findings of associations between personality and health (Deary, Weiss, & Batty, 2010), and between personality and reproductive success (Alvergne, Jokela, & Lummaa, 2010; Eaves, Martin, Heath, Hewitt, & Neale, 1990; Jokela, Alvergne, Pollet, & Lummaa, 2011).

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 that 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, in one study, 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. Among males, across the three winters, exploration scores were associated with lower, higher, and lower survival rates, respectively; for female birds, the pattern was in the opposite direction. Moreover, female personality was associated with breeding success, though this also fluctuated across years: In winters during which food was scarce, females with high or low exploration scores had poorer breeding success; in the winter during which food was abundant, females with average scores had poorer breeding success.

Nicolaus, Tinbergen, Ubels, Both, and Dingemanse (2016) found that the association between exploration and fitness in great tits also 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 of what 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. The concept of a life-history strategy is that of a continuum, and it was originally used to characterize species or populations (MacArthur & Wilson, 1963). One end of this continuum described the so-called "fast" life-history strategy. Species or populations with a fast life history would breed early and often, but at the expense of longevity and offspring survival. The other end of this continuum described the so-called "slow" life-history strategy. Species or populations with a slow life history would breed later and less frequently, but they had longer lives and more surviving offspring. Life-history strategies have 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).

There is considerable support for the possibility that personality variation is maintained because personality traits are associated with life-history strategy. For example, in a study of bighorn sheep rams, Réale, Martin, Coltman, Poissant, and Festa-Bianchet (2009) tested whether two personality traits, boldness and docility, were genetically correlated and whether genetic tendencies for these traits were associated with survival and reproductive success. Boldness was operationally defined as the tendency of an individual to enter a baited trap. Docility was operationally defined as reactions to being handled by humans. Variation in boldness and docility were associated with life-history trade-offs. Boldness and docility were also heritable and negatively genetically correlated. Moreover, the predicted genetic values of boldness and docility were related to longer life spans and late-life reproductive success. Evidence also comes from a study of crickets. In their study, Niemelä, Dingemanse, Alioravainen, Vainikka, and Kortet (2013) examined whether personality variation was maintained by life-history strategy trade-offs. They found that, although there was an association between a measure related to life history (body size) and a personality trait (de-freezing), there was little evidence for a genetic correlation between the two. Based on these results, the authors concluded that common environmental influences were responsible for the association.

A fourth possibility put forward is that personality variation is maintained because of the existence of genetically or environmentally mediated correlations between traits, which are known as behavioral syndromes to behavioral ecologists (Sih et al., 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 et al., 2013, for all of the loadings). These correlations can also occur across contexts: Recall, for example, the finding that more aggressive stickleback fish were also those more likely to explore a new environment (Huntingford, 1976). In the cases of both brown capuchin monkeys and stickleback fish, because the traits are correlated, being at the optimum level of one trait (dominance in monkeys and aggressiveness in fish) prevents one from 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 mechanisms or others that were not discussed are singularly responsible for maintaining personality variation in nonhuman animals. However, the identification of these mechanisms in several species testifies to this research tradition's ability to 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 will be addressed later. Until then, it is worth highlighting how successful this research tradition has been in solving another problem, namely, identifying the proximate bases of individual differences in animal behavior.

With respect to identifying the physiological bases of animal personality, some of the most convincing work comes from selection studies and studies of coping styles. Animal breeders have long known that breeding (or selecting) for physical traits can lead to changes in behavioral traits or the other way around. In a classic selection 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 wild foxes and also differed from wild foxes in their rate of development and neuroendocrine profiles (Trut et al., 2009). Other findings from this study are also worth highlighting. For one, compared to wild foxes, the tame foxes retained youthful features, but they reached sexual maturity earlier and showed higher levels of reproductive hormones (Trut et al., 2009). Also, 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 their wild counterparts (Trut et al., 2009).

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 et al., as 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 more rapidly reached sexual maturity.

Coping style in the animal personality literature refers to a suite of behavioral and physiological tendencies related to how individual animals react to stressors (Koolhaas et al., 1999). At one end of this spectrum are "proactive" individuals. At the other are "reactive" individuals. In behavioral tests, proactive individuals, for example, attack more quickly and are 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 (HPA) axis activity, HPA axis reactivity, and parasympathetic reactivity, all 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. One MRI study of 74 chimpanzees found that the percentage of gray 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 were derived by questionnaire ratings: Dominance was composed of traits related to boldness, fearlessness, assertiveness, and aggressiveness; conscientiousness was composed of traits related to self-control, predictability, and emotional stability (Weiss, King, & Hopkins, 2007). A later study of 107 chimpanzees by Latzman, Hecht, Freeman, Schapiro, and Hopkins (2015) found associations between personality and other brain regions: The volume and asymmetry of the frontal region of the brain's gray 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). This study also found associations between frontal gray matter volume and higher openness, a personality dimension related to exploratory behavior and curiosity (Freeman et al., 2013), and between frontal gray matter asymmetry and higher reactivity/unpredictability, a personality dimension related to low conscientiousness (Freeman et al., 2013).

Unfortunately, despite the fact that researchers have gathered an enormous amount of data on the association between personality and human survival and reproductive success (see above), one would be at pains to make the case that this research tradition has been successful at solving problems related to the human personality evolution. This may be attributable to a tendency among some evolutionary psychologists and personality psychologists to develop premature theories (Chamberlin, 1890/1965) based on a narrow set of observations (i.e., studies of personality in humans). Among evolutionary psychologists, this takes the form of ascribing functions to human personality dimensions based on the commonsense meanings of their names, which itself may be a holdover from functionalism (Degler, 1991). For example, Nettle (2006) hypothesized that the benefits of extraversion included mating success, having more social allies, and being more willing to explore the environment, and that its costs included physical risks and family instability. This tendency is not limited to evolutionary psychologists. For example, a review argued that kin selection and reciprocal altruism are better captured by the HEXACO model than by the Five-Factor Model or Big Five (Ashton & Lee, 2007). Another possibility is that there is a problem with trait theory; however, comparative personality research has highlighted trait theory's ability to solve problems concerning personality evolution in humans and other animals.

The comparative method involves comparing species and using the evolutionary history of those species to conduct natural experiments (see Gosling & Graybeal, 2007, for an overview). One can apply this method to study personality structure and associations between personality traits and other variables, and to determine whether certain features of species led to differences in mean levels of traits. For example, by comparing differently related species that do or do not face similar evolutionary challenges based on, say, their different systems of social organization or the ecologies in which they live, one can test whether mean levels of a trait and the presence of a personality dimension are features inherited from a common ancestor or are evolved adaptations to that environment or social organization (Gosling & Graybeal, 2007). A strong test of whether some physical or behavioral trait is inherited from a common ancestor involves comparing closely related species that evolved in different habitats, societies, and so on. If these species resemble one another in that trait, the most parsimonious explanation is that the trait was present in a common ancestor. If they differ in that trait, the most parsimonious explanation is that the trait evolved recently. Conversely, a strong test of whether a trait is derived (i.e., evolved recently) is to compare that trait in distantly related species that evolved in similar habitats, societies, and so on. The similarities between these species are most parsimoniously explained as adaptations to those environments. The explanatory or problem-solving power of the comparative method, when applied to evolutionary questions about personality, can be highlighted by some examples.

Compared to other primates, humans are an intensely social, altruistic species (Kurzban, Burton-Chellew, & West, 2015). This salient fact about our species probably explains why some researchers (see the examples of Nettle, 2006, and Ashton & Lee, 2007, above) hypothesize that the evolutionary bases of personality variation can be traced to sociality. However, on a broad level, personality variation in social traits has been identified in species ranging from the highly social chimpanzee (King & Figueredo, 1997) to semi-solitary and solitary species, such as orangutans (Weiss, King, & Perkins, 2006) and octopuses (Mather & Anderson, 1993). These findings are contrary to what one would expect if these traits or their structure were adaptations for life in social groups.

There are also problems with tying social traits or their structure to kin selection, the tendency of individuals within a species to help related individuals at a cost to themselves (Hamilton, 1964). For one, across primate species, social and mating systems (Crook & Gartlan, 1966) and the level of paternal care (Fernandez-Duque, Valeggia, & Mendoza, 2009) vary considerably. Still, factor-analytic studies of personality in chimpanzees, a species with a promiscuous mating system, and studies of western lowland gorillas and Hanuman langurs, both species in which one male monopolizes access to multiple females, reveal distinct extraversion and agreeableness dimensions (Gold &

Maple, 1994; King & Figueredo, 1997; Konečná et al., 2008). Mountain gorillas, curiously, only possess a single dimension, sociability, comprising traits related to extraversion and agreeableness (Eckardt et al., 2015). Extraversion and agreeableness therefore emerge in species that likely differ with respect to how much information males have about who they are related to, and so probably emerged long before the ancestors of modern humans were on the evolutionary stage.

Similar problems mar explanations based on reciprocal altruism, the tendency to help unrelated individuals because doing so might lead them to help you in the future (Trivers, 1971). For one, reciprocal altruism is less likely to evolve in species where individuals do not regularly encounter one another or in species where individuals would be unable to recognize one another. The presence of separate agreeableness and extraversion dimensions in orangutans (Weiss et al., 2006), a semi-solitary species, but not in brown capuchin monkeys (Morton et al., 2013) or mountain gorillas (Eckardt et al., 2015), both social primate species, is not consistent with what one would predict if the evolutionary bases of extraversion, agreeableness, or honesty-humility were evolutionary products of reciprocal altruism. On the other hand, a study of six macaque species by Adams et al. (2015) found that the personality dimensions defined by traits related to assertiveness, social confidence, and aggression are shaped by the degree to which the species were despotic as opposed to tolerant (Thierry, 2000).

Evolutionary accounts of openness to experience (openness) and of conscientiousness dimensions also stand on clay feet. Perhaps this reflects the (probably correct) view that these dimensions are partly responsible for many of the greatest human accomplishments. Insofar as the benefits and costs of openness are framed in terms of creativity, such as being more sexually attractive, but more prone to psychotic disorders (Nettle, 2006), this evolutionary explanation evokes the image of the mad (sexy?) creative person. However, evidence for openness dimensions across several nonhuman primate species, including five macaque species (Adams et al., 2015), white-faced capuchin monkeys (Manson & Perry, 2013), brown capuchin monkeys (Morton et al., 2013), common marmosets (Iwanicki & Lehmann, 2015), and mountain gorillas (Eckardt et al., 2015), but not in other species, including Hanuman langurs (Konečná et al., 2008) and the large-brained orangutans (Weiss et al., 2006), suggests that openness evolved for more prosaic reasons. Given this, the absence of an association between openness and psychosis (Boyette et al., 2013) should not be surprising.

Explanations informed by human personality research for the evolution of conscientiousness have also been put forward. One possibility raised is that conscientiousness enables costly signaling (Buss, 2009) or reflects a balance between delayed mating and longer life (Nettle, 2006). If true, these explanations would predict that conscientiousness should be widespread in the animal kingdom, but this is not the case (Gosling & John, 1999). Studies of nonhuman primates and other animals appear to offer an alternative explanation that is better supported by data. Species that have a conscientiousness dimension, such as chimpanzees (King & Figueredo, 1997), bonobos (Weiss et al., 2015), and brown capuchin monkeys (Morton et al., 2013), tend to have larger brains than species that do not. Moreover, a recent study of 36 primate and nonprimate species that adjusted for phylogeny found that higher self-control was associated with larger absolute brain size and a more varied diet (MacLean et al., 2014). However, the absence of a conscientiousness dimension in the large-brained orangutan (Weiss et al., 2006) and its presence in the small-brained common marmoset (Iwanicki & Lehmann, 2015) suggests that brain size may be only partly responsible for its evolution. For example, the finding of conscientiousness in common marmosets may mean that other conditions, such as the need for helpers to rear young, also favor the evolution of a conscientiousness dimension (Burkart, Hrdy, & Van Schaick, 2009).

In contrast to the above examples, evolutionary explanations for neuroticism often draw on the animal literature. This may be because traits associated with neuroticism are somehow distinct from the more salient, social aspects of human personality; because of the fact that dimensions like neuroticism are found in so many species (Gosling & John, 1999); or because, by focusing solely on humans, it is difficult to come up with a way in which high neuroticism is beneficial. For example, Nettle (2006) suggested that the costs of neuroticism, such as poorer health and being at greater risk of psychological disorders, are offset by increased vigilance. Focusing on just the African apes, this explanation is consistent with neuroticism featuring in the personality structures of humans (Digman, 1990) and chimpanzees (King & Figueredo, 1997), but not bonobos (Weiss et al., 2015) or mountain gorillas (Eckardt et al., 2015), the latter two having evolved in more predictable, resource-rich environments than did humans or chimpanzees. On the other hand, this explanation is not consistent with the presence of neuroticism in western lowland gorillas (Gold & Maple, 1994), which also live in a predictable, resource-rich environment. The proposed evolutionary benefits for neuroticism are thus perhaps wanting, and need to be studied further.

Comparative personality research can be used to solve empirical problems other than those revolving around the maintenance of variation and/or structure. For one, comparative personality research has enabled researchers to test whether investing in sociocultural roles (Roberts & Jackson, 2009) or whether biology processes (McCrae & Costa, 2003) predominate personality development. After all, sociocultural roles of the sort that are hypothesized to influence personality development (e.g., beginning full-time work) are absent or very different in other species. Both a study comparing chimpanzees to humans, which adjusted for different rates of development between these species (King, Weiss, & Sisco, 2008), and a similar study comparing orangutans to chimpanzees (Weiss & King, 2015) found that the direction and magnitude of personality age differences were comparable across species. The findings of both studies, therefore, appear to rule out social roles as a cause of personality development. There were, however, two findings that suggested that personality development is a product of natural selection.

First, unlike humans and chimpanzees, orangutans declined in agreeableness, suggesting that age-related increases in human and chimpanzee agreeableness may be an adaptation for living among unrelated conspecifics, a cross that orangutans do not have to bear (Weiss & King, 2015). Second, unlike humans, orangutans, and female chimpanzees, there was a leveling off of age-related declines in extraversion among male chimpanzees (King et al., 2008; Weiss & King, 2015). This difference may reflect adaptation for heightened levels of aggression in chimpanzee males (Wrangham, Wilson, & Muller, 2006).

The comparative approach has also been used to explain why people who are lower in neuroticism and higher in the other four human personality dimensions tend to be happier (DeNeve & Cooper, 1998; Steel, Schmidt, & Shultz, 2008). Similar associations between personality and subjective well-being have been found in nonhuman primates (King & Landau, 2003; L. M. Robinson et al., 2016; Weiss, Adams, Widdig, & Gerald, 2011; Weiss et al., 2009) and in felids (Gartner, Powell, & Weiss, 2016). These studies, as well as those demonstrating similar genetic associations between personality and subjective well-being in humans, chimpanzees, and orangutans (see Weiss & Luciano, 2015, for a review), suggest that these associations long predate the emergence of humans and our societies.

A third empirical problem concerns identifying mechanisms by which personality influences human health (Deary et al., 2010). An 18-year follow-up of western lowland gorillas found that more extraverted gorillas lived longer, but no associations between mortality and personality dimensions related to agreeableness, neuroticism, or a dominance dimension (Weiss, Gartner, Gold, & Stoinski, 2013). Another prospective study found associations between lower aggressiveness, lower mellowness, and higher excitability, and morbidity in golden snub-nosed monkeys (Jin, Su, Tao, Guo, & Yu, 2013). This same study found that extraversion was related to higher morbidity in younger monkeys but lower morbidity in older monkeys (Jin et al., 2013). Experimental studies have highlighted the likelihood that some common factor or factors underlie personality traits related to sociability and immune system robustness in rhesus macaques, and that these effects are moderated in that they show up in unstable social environments (Capitanio, 2011). These and similar findings (see, e.g., Mehta & Gosling, 2008, for a review) should lead one to search for variables in addition to health behaviors (e.g., smoking, alcohol consumption, and diet) that may explain associations between personality and health.

In addition to showing how a research tradition that includes personality trait theory can solve empirical problems about animal and even human personality, it is worth highlighting how trait theory and its alternatives give rise to and solve conceptual problems. Trait theories clash with the view that with the "right" kinds of environmental inputs, humans can improve their lot and create better societies. Conversely, this belief suggests that our failings, and those of society, can be traced back to the "wrong" kinds of environmental inputs. Sociocognitive theories of personality that "recognize that men can and do reconceptualize themselves and change, and that an understanding of how humans can constructively modify their behavior in systematic ways" (Mischel, 1968, p. 301) solve this problem by marginalizing traits and, in fact, denying their existence outside of environmental contexts. Theories such as these thus win out over trait theory in that they are consonant with the perception that human environments and cultures shape human behavior. However, by adopting these views, these theories are burdened with conceptual problems. Organisms whose behaviors are ever changing will be beyond the reach of evolutionary forces. Thus, these theories deny the continuity between ourselves and other species. On the other hand, trait theories do not clash with evolutionary biology and so do not require humans to have powers over their destinies. Moreover, trait theory is not necessarily incompatible with the values described above. After all, accepting the effects of one variable (traits) does not deny the effects of another (the environment), or that these variables may interact with one another. It does, however, require abandoning the view that "the conceptual split between person and situation" is "absurd" (Mischel, 2009, p. 283), or, speaking statistically, that the presence of an interaction makes main effects uninterpretable.

Research traditions, therefore, that include or give rise to trait theory have been and continue to be excellent at solving problems about personality in animals and in humans. It is for this reason that tinkering with trait theory or, worse, discarding it would be a mistake. That said, to be useful for solving further problems in animal personality, which will yield answers to questions about the evolution of human personality, requires that some features be added to trait theory.

Trait theories, such as the Five-Factor Model, start from basic tendencies, that is, a hierarchically organized set of traits (McCrae & Costa, 1999). This starting point may, however, come too late to be useful when studying animals other than humans. This was not willful. It was merely impossible to foresee the different ways that traits were organized in other species. To deal with the diverse personality structures encountered in nonhuman primates and other animals, trait theorists should acknowledge that basic traits exist within populations and are subject to evolutionary forces, and that, across species, different traits may be more or less important and their organization into higher levels may differ. Another way to think of traits, then, is as elements and compounds (I owe the allusion to chemistry to a 2009 article by McCrae).

Incorporating this view raises new questions about personality evolution: What are the elemental units and how do different species come to be defined by different, though sometimes overlapping, personality domains? Comparative personality research can be used to dissect basic tendencies into their elemental parts. For example, humans and chimpanzees share five domains—neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness—that presumably were present in our common Pan-Homo ancestor some 5 to 6 million years ago. However, in the process of becoming human, we "lost" a

personality dimension related to dominance that modern-day chimpanzees possess (King & Figueredo, 1997). This dominance dimension is made up of traits related to low neuroticism, high extraversion, low agreeableness, and both high and low conscientiousness. These traits thus appear to be elements in that they have combined or split apart over a relatively short period of evolutionary time, either because of genetic drift or because different selection pressures were acting on the personalities of chimpanzees and humans during their evolution (see Weiss et al., 2015, for the case of conscientiousness).

In closing, it is worth reconsidering the absence of a paradigm in personality psychology. Would personality psychology be better off if it adopted a paradigm (see Eysenck, 1983, for a discussion)? My own view is that, at its current stage of development, personality psychology would be better off if it delayed gratification and remained a pluralistic discipline. This would allow other research traditions, such as contemporary accounts of the self that incorporate stable traits (M. D. Robinson & Sedikides, 2009), to emerge and try their hand at problem solving alongside research traditions that emphasize trait theory. This may sound utopian, but the lack of a single paradigm or research tradition in chemistry was arguably responsible for its success and development into a mature science (Chang, 2012). There is no reason why this should not be true, too, for the scientific study of persons, even if they are animals.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author received no financial support for the research, authorship, and/or publication of this article.

References

Adams, M. J., Majolo, B., Ostner, J., Schuelke, O., De Marco, A., Thierry, B., et al. (2015). Personality structure and social style in macaques. *Journal of Personality and Social Psychology*, **109**, 338–353.

Aiken, L. R. (1968). *Book reviews: Personality and assessment by Walter Mischel*. New York: John Wiley & Sons, Inc., 1968. Pp. xii + 365. $8.50. Educational and Psychological Measurement, 28, 968–970.

Alvergne, A., Jokela, M., & Lummaa, V. (2010). Personality and reproductive success in a high-fertility human population. *Proceedings of the National Academy of Sciences*, **107**, 11745–11750.

Ashton, M. C., & Lee, K. (2007). Empirical, theoretical, and practical advantages of the HEXACO model of personality structure. *Personality and Social Psychology Review*, **11**, 150–166.

Beech, H. R. (1969). Book review: Personality and assessment: Walter Mischel. John Wiley & Sons, Inc., London (1968). pp. 365. *Behaviour Research and Therapy*, **7**, 350.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, **23**, 361–368.

Blatchley, B. J., & Hopkins, W. D. (2010). Subgenual cingulate cortex and personality in chimpanzees (*Pan troglodytes*). *Cognitive, Affective and Behavioral Neuroscience*, **10**, 414–421.

Boyette, L. L., Korver-Nieberg, N., Verweij, K., Meijer, C., Dingemans, P., Cahn, W., et al. (2013). Associations between the five-factor model personality traits and psychotic experiences in patients with psychotic disorders, their siblings and controls. *Psychiatry Research*, **210**, 491–497.

Brush, S. G. (1974). Should the history of science be rated X? The way scientists behave (according to historians) might not be a good model for students. *Science*, **183**, 1164–1172.

Burkart, J. M., Hrdy, S. B., & Van Schaick, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, **18**, 175–186.

Buss, D. M. (2009). How can evolutionary psychology successfully explain personality and individual differences? *Perspectives on Psychological Science*, **4**, 359–366.

Capitanio, J. P. (2011). Nonhuman primate personality and immunity: Mechanisms of health and disease. In A. Weiss, J. E. King, & L. E. Murray (Eds.), *Personality, temperament, and behavioral syndromes in nonhuman primates* (pp. 233–255). New York: Springer.

Chamberlin, T. C. (1890/1965). The method of multiple working hypotheses. *Science*, **148**, 754–759.

Chang, H. (2012). *Is water H_2O? Evidence, realism, and pluralism*. Dordrecht: Springer.

Costa, P. T., Jr., & McCrae, R. R. (1992a). Four ways five factors are basic. *Personality and Individual Differences*, **13**, 653–665.

Costa, P. T., Jr., & McCrae, R. R. (1992b). Reply to Eysenck. *Personality and Individual Differences*, **13**, 861–865.

Craik, K. (1969). Personality unvanquished: A review of *Personality and assessment. Contemporary Psychology: A Journal of Reviews*, **14**, 147–148.

Crook, J. H., & Gartlan, J. S. (1966). Evolution of primate societies. *Nature*, **210**, 1200–1203.

Deary, I. J., Weiss, A., & Batty, G. D. (2010). Intelligence and personality as predictors of illness and death: How researchers in differential psychology and chronic disease epidemiology are collaborating to understand and address health inequalities. *Psychological Science in the Public Interest*, **11**, 53–79.

Degler, C. N. (1991). *In search of human nature: The decline and revival of Darwinism in American social thought*. New York: Oxford University Press.

DeNeve, K. M., & Cooper, H. (1998). The happy personality: A meta-analysis of 137 personality traits and subjective well-being. *Psychological Bulletin*, **124**, 197–229.

Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology*, **41**, 417–440.

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 847–852.

Dingemanse, N. J., & Réale, D. (2013). What is the evidence that natural selection maintains variation in animal personalities? In C. Carere & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 201–220). Chicago: University of Chicago Press.

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3947–3958.

Eaves, L. J., Martin, N. G., Heath, A. C., Hewitt, J. K., & Neale, M. C. (1990). Personality and reproductive fitness. *Behavior Genetics*, **20**, 563–568.

Eckardt, W., Steklis, H. D., Steklis, N. G., Fletcher, A. W., Stoinski, T. S., & Weiss, A. (2015). Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology*, **129**, 26–41.

Eysenck, H. J. (1983). Is there a paradigm in personality research? *Journal of Research in Personality*, **17**, 369–397.

Eysenck, H. J. (1992a). Four ways five factors are not basic. *Personality and Individual Differences*, **13**, 667–673.

Eysenck, H. J. (1992b). A reply to Costa and McCrae: P or A and C—The role of theory. *Personality and Individual Differences*, **13**, 867–868.

Fernandez-Duque, E., Valeggia, C. R., & Mendoza, S. P. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology*, **38**, 115–130.

Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, **75**, 1042–1053.

Gartner, M. C., Powell, D. M., & Weiss, A. (2016). Comparison of subjective well being and personality assessments in the clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*). *Journal of Applied Animal Welfare Science*, **19**, 294–302.

Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology*, **13**, 509–522.

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.

Gosling, S. D., & Graybeal, A. (2007). Tree thinking: A new paradigm for integrating comparative data in psychology. *Journal of General Psychology*, **134**, 259–277.

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

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, **7**, 17–52.

Huntingford, F. A. (1976). The relationship between anti-predator behavior and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus. Animal Behaviour*, **24**, 245–260.

Iwanicki, S., & Lehmann, J. (2015). Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, **129**, 205–217.

Jin, J., Su, Y., Tao, Y., Guo, S., & Yu, Z. (2013). Personality as a predictor of general health in captive golden snub-nosed monkeys (*Rhinopithecus roxellana*). *American Journal of Primatology*, **75**, 524–533.

Jokela, M., Alvergne, A., Pollet, T. V., & Lummaa, V. (2011). Reproductive behavior and personality traits of the five factor model. *European Journal of Personality*, **25**, 487–500.

Kenrick, D. T., & Funder, D. C. (1988). Profiting from controversy: Lessons from the person-situation debate. *American Psychologist*, **43**, 23–34.

Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, **31**, 257–271.

King, J. E., & Landau, V. I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality*, **37**, 1–15.

King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: Age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology*, **122**, 418–427.

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., & Pluháček, J. (2008). Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. *Journal of Comparative Psychology*, **122**, 379–389.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., et al. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.

Krebs, J. R., & Davies, N. B. (1997). *Behavioural ecology: An evolutionary approach* (4th ed.). Malden, MA: Blackwell.

Kuhn, T. S. (1970). *The structure of scientific revolutions* (2nd ed.). Chicago: University of Chicago Press.

Kurzban, R., Burton-Chellew, M. N., & West, S. A. (2015). The evolution of altruism in humans. *Annual Review of Psychology*, **66**, 575–599.

Latzman, R. D., Hecht, L. K., Freeman, H. D., Schapiro, S. J., & Hopkins, W. D. (2015). Neuroanatomical correlates of personality in chimpanzees (*Pan troglodytes*): Associations between personality and frontal cortex. *Neuroimage*, **123**, 63–71.

Laudan, L. (1977). *Progress and its problems: Towards a theory of scientific growth*. London and Henley: Routledge & Kegan Paul.

Leahey, T. H. (1992). The mythical revolutions of American psychology. *American Psychologist*, **47**, 308–318.

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of self-control.

Proceedings of the National Academy of Sciences, **111**, E2140–E2148.

Madison, P. (1968). *Personality and assessment. By WALTER MISCHEL*. New York, John Wiley and Sons, Inc., 1968. Pp. xii, 365. $8.50. *American Journal of Psychology*, 81, 609–611.

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

Mather, J. A., & Anderson, R. C. (1993). Personality of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology*, **107**, 336–340.

Mayr, E. (1972). The nature of the Darwinian revolution. *Science*, **176**, 981–989.

McCrae, R. R. (2009). The physics and chemistry of personality. *Theory & Psychology*, **18**, 670–687.

McCrae, R. R., & Costa, P. T., Jr. (1999). A five-factor theory of personality. In L. Pervin & O. P. John (Eds.), *Handbook of personality* (2nd ed., pp. 159–181). New York: Guilford Press.

McCrae, R. R., & Costa, P. T., Jr. (2003). *Personality in adulthood: A five-factor theory perspective*. New York: Guilford Press.

Mehta, P. H., & Gosling, S. D. (2008). Bridging human and animal research: A comparative approach to studies of personality and health. *Brain, Behavior, and Immunity*, **22**, 651–661.

Mischel, W. (1968). *Personality and assessment*. New York: John Wiley and Sons.

Mischel, W. (2009). From *Personality and assessment* (1968) to Personality Science, 2009. *Journal of Research in Personality*, **43**, 282–290.

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

Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist*, **61**, 622–631.

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, **19**, 478–486.

Niemelä, P. T., Dingemanse, N., J., Alioravainen, N., Vainikka, A., & Kortet, R. (2013). Personality pace-of-life hypothesis: Testing genetic associations among personality and life history. *Behavioral Ecology*, **24**, 935–941.

Parker, G. A., & Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature*, **348**, 27–33.

Penke, L., Denissen, J. J. A., & Miller, G. F. (2007). The evolutionary genetics of personality. *European Journal of Personality*, **21**, 549–587.

Plomin, R., DeFries, J. C., Knopik, V., & Neiderhiser, J. N. (2013). *Behavioral genetics*. New York: Worth.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 4051–4063.

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, **22**, 1599–1607.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.

Roberts, B. W., & Jackson, J. J. (2009). Sociogenomic personality psychology. *Journal of Personality*, **76**, 1523–1544.

Roberts, B. W., Wood, D., & Smith, J. L. (2005). Evaluating five factor theory and social investment perspectives on personality trait development. *Journal of Research in Personality*, **39**, 166–184.

Robinson, L. M., Waran, N. K., Leach, M. C., Morton, F. B., Paukner, A., Lonsdorf, E., et al. (2016). Happiness is positive welfare in brown capuchins (*Sapajus apella*). *Applied Animal Behaviour Science*, **181**, 145–151.

Robinson, M. D., & Sedikides, C. (2009). Traits and the self: Toward an integration. In P. J. Corr & G. Matthews (Eds.), *The Cambridge handbook of personality psychology* (pp. 457–472). Cambridge: Cambridge University Press.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, **79**, 241–277.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, **19**, 448–455.

Steel, P., Schmidt, J., & Shultz, J. (2008). Refining the relationship between personality and subjective well-being. *Psychological Bulletin*, **134**, 138–161.

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp. 106–128). Berkeley: University of California Press.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift fur Tierpsychologie*, **20**, 410–433.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.

Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. *Bioessays*, **31**, 349–360.

Uher, J. (2013). Personality psychology: Lexical approaches, assessment methods, and trait concepts reveal only half of the story—Why it is time for a paradigm shift. *Integrative Psychological and Behavioral Science*, **47**, 1–55.

Van Oers, K., Buchanan, K. L., Thomas, T. E., & Drent, P. J. (2011). Correlated response to selection of testosterone levels and immunocompetence in lines selected for avian personality. *Animal Behaviour*, **81**, 1055–1061.

Van Oers, K., De Jong, G., Van Noordwijk, A. J., Kempenaers, B., & Drent, P. J. (2005). Contribution of genetics to animal personalities: A review of case studies. *Behaviour*, **142**, 1191–1212.

Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid

personality and subjective well-being. *Journal of Comparative Psychology*, **125**, 72–83.

Weiss, A., & Gartner, M. (2017). Animal personality. In T. A. Widiger (Ed.), *The Oxford handbook of the five factor model* (pp. 281–300). Oxford: Oxford University Press.

Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2013). Extraversion predicts longer survival in gorillas: An 18-year longitudinal study. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 2012–2231.

Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Udono, S., Ochiai, T., et al. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, **71**, 283–292.

Weiss, A., & King, J. E. (2015). Great ape origins of personality maturation and sex differences: A study of orangutans and chimpanzees. *Journal of Personality and Social Psychology*, **108**, 648–664.

Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology*, **69**, 1264–1277.

Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, **90**, 501–511.

Weiss, A., & Luciano, M. (2015). The genetics and evolution of covitality. In M. Pluess (Ed.), *Genetics of psychological well-being: The role of heritability and genetics in positive psychology* (pp. 146–160). Oxford: Oxford University Press.

Weiss, A., Staes, N., Pereboom, J. J. M., Inoue-Murayama, M., Stevens, J. M. G., & Eens, M. (2015). Personality in bonobos. *Psychological Science*, **26**, 1430–1439.

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, **9**, 442–446.

Wolf, M., Van Doorn, S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–585.

Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates*, **47**, 14–26.