Comparative Perspectives on Temperament and Personality in Human and Nonhuman Animals

Kristine Coleman

Introduction

As anyone working with animals is well aware, individuals differ vastly with respect to their behavioral responses to stressful or novel stimuli. Exposed to the same stimulus, some individuals eagerly approach it, while others cower or freeze in response. There are many reasons for these disparate behavioral responses, including past experience, current emotional state, and the stimulus itself. However, one of the major forces underlying these different reactions is biological predisposition, known as personality or temperament. Once considered "noise" around an adaptive mean (Francis, 1990), these individual differences are now generally accepted as interesting and important in their own right (Clark & Ehlinger, 1987).

My own interest in this field started when I was in graduate school. My doctoral research examined individual differences in shyness and boldness in a population of pumpkinseed sunfish (*Lepomis gibbosus*). We found that individual fish living in a single population differed with respect to their propensity to inspect novel objects (Coleman & Wilson, 1998; Wilson, Coleman, Clark, & Biederman, 1993). Further, these differences were consistent and correlated with a host of other traits, including acclimation to laboratory conditions, choice of prey, and microhabitat usage. These studies were among the first to examine individual differences in temperament in a non-primate species.

Since these early studies in animal temperament, similar differences have been found in a variety of diverse taxa, from beetles to octopus to fish to birds and reptiles. Strikingly, individual differences in temperament have been found in every species in which they have been investigated, indicating the conserved nature of this trait. The impact of animal temperament can be seen in the wide range of academic disciplines in which it is now studied. While once studied predominantly by

K. Coleman (✉)
Oregon National Primate Research Center, Beaverton, OR, USA
e-mail: colemank@ohsu.edu

L. A. Schmidt, K. L. Poole (eds.), *Adaptive Shyness*,
https://doi.org/10.1007/978-3-030-38877-5_14

psychologists, personality is now examined by researchers in a wide range of fields, including neuroscience (e.g., Fox et al., 2015; Roseboom et al., 2014), evolutionary ecology (e.g., Réale, Reader, Sol, McDougall, & Dingemanse, 2007), and conservation biology (e.g., McDougall, Réale, Sol, & Reader, 2006). Personality is becoming a common variable in translational studies as well as applied science. Indeed, few traits have been studied as broadly as personality, both in terms of the number of species as well as range of disciplines involved.

In this chapter, I describe animal personality and some of the common tests used to assess it. I then discuss some of the current research in animal personality, with a focus on translational and applied research.

What Is Temperament/Personality?

Broadly speaking, the terms "personality" and "temperament" are defined somewhat similarly as behavioral differences that persist through time (e.g., Stamps & Groothuis, 2010). While the terms are often used interchangeably today (Capitanio, 2011), this has not always been the case. Historically, distinctions were made between the terms, with "temperament" being used to describe behavioral responses in animals and children and "personality" restricted to human adults (Watters & Powell, 2012). Researchers have previously argued that temperament reflects genetic behavioral differences, while personality reflects non-genetic differences (e.g., Buss & Plomin, 1986). Little distinction is made between the terms today; both are used to refer to an individual's basic position toward environmental change and challenge (Lyons, Price, & Moberg, 1988), which emerges early in life and remains relatively consistent throughout development (McCall, 1986). Further, both are used to describe behavioral differences in human and nonhuman animals alike. While temperament or personality are the most commonly used terms, other researchers use "behavioral syndromes" (Sih, Bell, Johnson, & Ziemba, 2004) or "coping style" (Koolhaas et al., 1999) to describe these behavioral differences. The discrepancies in use often reflect the field of study. "Behavioral syndromes," for example, is widely used in behavioral ecology studies, while "coping style" or "temperament" are more common in neuroscience. For the purposes of this chapter, I use the term "personality".

Measuring Animal Personality

There are many methods by which temperament or personality is assessed in both humans and nonhuman animals. Indeed, there are almost as many ways to assess personality as there are research groups assessing it. Even "standardized" tests such as the Human Intruder Test (HIT) for macaques (see below) are performed somewhat differently across laboratories. Still, despite the disparate methodologies utilized to assess personality, the underlying dimensions are usually relatively similar (e.g., Bergvall, Schäpers, Kjellander, & Weiss, 2011; Konecna et al., 2008) and characterize how individuals deal with various challenges.

In humans, information regarding personality or temperament is often derived by interviews or surveys with the individual (or a parent), administration of standardized testing batteries, or from direct behavioral assessments of the individual. In many cases, comparable tests are used with nonhuman animals. The majority of the methodologies used to assess personality in animals rely on direct behavioral coding, either in the home environment (in which little is done to the animal) or in a situation in which the animal is somehow challenged (i.e., presented with a stimulus designed to elicit a response). Behavioral coding involves measuring the duration or frequency of particular variables, for example, the amount of time an individual spends inspecting a novel object or moving about a new enclosure. Personality also may be assessed using observer rating (Freeman & Gosling, 2010) in which care staff or others fill out questionnaires about the subjects. Some of the most common assessment tools are described below. It should be noted that these methods are not mutually exclusive; researchers often employ multiple approaches to assessing personality.

Home Environment Assessments

One way in which personality can be assessed is by observing subjects in their home environment and quantifying their responses to everyday, naturalistic events (e.g., interactions with conspecifics or caretakers, introduction to new situations). Individuals within a population typically vary with respect to many personality traits, including level of sociability, propensity to explore, degree of agitation, etc. This kind of assessment is often done with children, either at home or in the school setting, and has been used for a wide range of animals, including fish (Colléter & Brown, 2011), birds (David, Auclair, & Cézilly, 2011), elephants (Horback, Miller, & Kuczaj, 2013), and rhesus monkeys (Capitanio, 2011). In these studies, researchers quantify the duration and/or frequency of time animals spend in various behaviors such as social behaviors, locomotion, play, aggression, and exploration. Statistical methods such as factor analysis are then used to reduce the data into various clusters of behaviors (often called "traits"). For example, in a recent study examining elephant personality (Horback et al., 2013), researchers used this kind of behavioral coding to assess the amount of time elephants engaged in approximately 20 different behaviors, including play, social behavior, and aggressive behavior. Factor analysis on 480 h worth of data revealed three primary personality traits: "playful," "curious," and "sociable" (Horback et al., 2013).

As described above, observer rating also can be employed to assess personality in the home environment (e.g., Capitanio, 2011; Freeman & Gosling, 2010). Rating instruments typically involve two or more observers, well acquainted with the subjects, who rate them based on a number of predefined traits or adjectives.

For example, in nonhuman primate (NHP) studies, adjectives used often include "apprehensive," "active," "playful," and "curious" (e.g., Stevenson-Hinde & Zunz, 1978). Observers are typically asked to rate individuals on a Likert scale (e.g., "On a scale of 1–7, how curious is this individual?"). As with the behavioral observations, scores are analyzed with factor analysis in order to uncover various dimensions of behavior. Key dimensions in animal studies differ by study, but often include bold/shy, aggression, exploration/avoidance, sociability, and activity (Gosling, 2001). Interestingly, these factors are similar to human personality dimensions referred to as the "Five Factor Model" (Openness, Conscientiousness, Extraversion, Agreeableness, and Neuroticism; Goldberg, 1990). Observer ratings are most commonly used with species that receive a great deal of attention from their caretakers, such as dogs (Jones & Gosling, 2005; Ley, McGreevy, & Bennett, 2009), horses (McGrogan, Hutchison, & King, 2008), nonhuman primates (Freeman & Gosling, 2010), farm animals (Finkemeier, Langbein, & Puppe, 2018), and zoo animals (Tetley & O'Hara, 2012), although these ratings have been used in other species as well (e.g., Gosling & John, 1999).

Home environment personality assessments are ethologically relevant to the animals and highlight naturally occurring variation. Resulting dimensions from these tests are often analogous to human personality traits, which is particularly important for translational studies (see below). However, behavioral observations tend to be highly time intensive and sensitive to potential confounds, such as time of day and time of year (Coleman & Pierre, 2014). Observer ratings tend to take less time, but require observers with a great deal of familiarity with the subjects. In both cases, interpretation of dimensions that result from factor analysis can be somewhat subjective (Réale et al., 2007). See Freeman & Gosling (2010) for a comparison of various approaches to these rating instruments.

Response to Challenge

While home environment assessments, and observer ratings in particular, are becoming more popular, for most species, personality assessments involve evaluating the subject's response to some sort of purposeful environmental perturbation. These stimuli typically involve a degree of novelty and/or risk, such as a new object or situation, or may involve something aversive, such as restraint. Unlike observer ratings, which capture several personality constructs, each test typically measures one or two dimensions, most often shy/bold and exploration/avoidance (Réale et al., 2007). Researchers often use more than one test and may combine them with home environment assessments. I describe some of the most common types of tests below. This review is by no means exhaustive; for any given species, there may be dozens of specific tests used. As an example, a relatively recent review of personality in sheep listed over 15 unique assessment tools (Dodd, Pitchford, Hocking Edwards, & Hazel, 2012).

Novel Object

Perhaps the most commonly utilized tool for assessing personality in animals is a "novel object test," which measures response to unfamiliar items. The novel objects vary with respect to perceived risk, ranging from seemingly innocuous (e.g., novel food, brightly colored toy) to potentially threatening (e.g., toy with big eyes, which can be somewhat threatening to certain species). Because there is inherent risk in inspecting any novel object, these tests typically measure an individual's boldness.

Variables examined in novel object tests often include latency to approach and/or inspect the object and amount of time spent near or with the object. Some studies quantify behavioral variables including distress behavior as well. Animals exhibit a spectrum of responses to these novel stimuli, ranging from "bold" (i.e., short latency to approach) to "shy" (i.e., long latency to approach, Fig. 1). These tests can be performed in the individual's home environment (e.g., Coleman & Wilson, 1998; Herskin, Kristensen, & Munksgaard, 2004) but are often carried out in a novel testing arena (e.g., Colléter & Brown, 2011).

Responses on this test have been ecologically validated in a variety of species (see Réale, Chap. 15 this volume). For example, pumpkinseed sunfish assessed as bold on a novel object test in their home environment had different stomach contents and parasite loads and acclimated faster to the laboratory than shy fish (Wilson et al., 1993). Wild vervet monkeys (*Chlorocebus pygerythrus*) found to be bold with respect to a novel object were more likely to engage in predator inspection behavior toward a model predator than their shy counterparts (Blaszczyk, 2017). Similarly, bold grey mouse lemurs (*Microcebus murinus*) studied in their natural environment were more likely than others to forage in a risky environment (Dammhahn & Almeling, 2012).

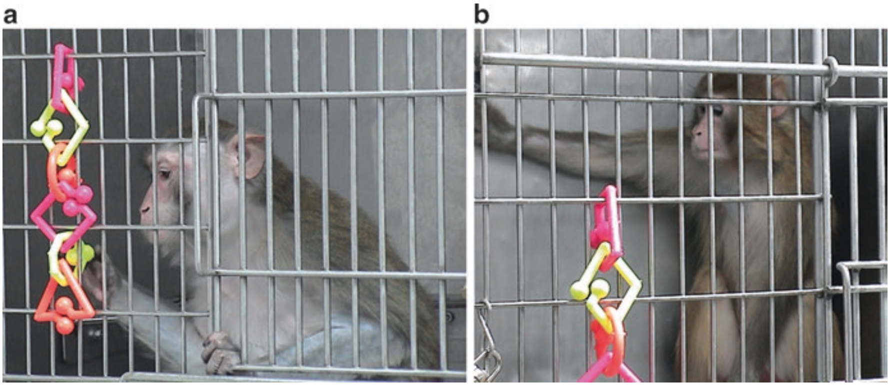

Fig. 1 Example of a rhesus macaque inspecting (Bold; **a**) and avoiding (Shy; **b**) a brightly colored bird toy placed on the cage as part of a novel object test. Republished by permission of Taylor and Francis Group, LLC, a division of Informa plc, from the *The Handbook of Primate Behavioral Management,* S.J. Schapiro (Ed), 2017

As indicated above, novel object tests are common in studies of animal temperament/personality. Variations of this test have been used in just about every species in which personality has been found, including insects (Müller & Juškauskas, 2018; Tremmel & Müller, 2013), hermit crabs (Watanabe et al., 2012), fish (Wilson et al., 1993), birds (Stowe et al., 2006), rodents (Joshi & Pillay, 2016), farm animals (Dodd et al., 2012), and nonhuman primates (Blaszczyk, 2017; Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Coleman, Tully, & McMillan, 2005). A version of this test is utilized in human children as well (Kagan, 1997); indeed, many of the novel object tests used in animal species are based, at least in part, on these human assessments.

Novel Environment

Another relatively common temperament assessment measures response to a novel environment. In these tests, often termed "open field" tests (Walsh & Cummins, 1976), the subject is removed from the home environment and subsequently exposed to an unfamiliar open enclosure. In some versions of this test, the novel environment is divided into "safe" (e.g., has some sort of cover) and "risky" (e.g., exposed) areas. Novel objects may be present in the testing arena as well.

This test measures the personality constructs boldness and/or exploration. Variables assessed in this test typically include one or more of the following: latency to begin exploring (i.e., leave starting place), amount of locomotion in the environment, amount of time spent in the risky environments, and number of times animals move between safe and risky environments. Open field tests are utilized in many species, including fish (e.g., Burns, 2008; White, Wagner, Gowan, & Braithwaite, 2017), rodents (Prut & Belzung, 2003), farm animals (Dodd et al., 2012), and monkeys (Williamson et al., 2003).

Response to Human

One specific intruder test is the Human Intruder Test (Kalin & Shelton, 1989). This test, designed to measure an individual's response to the potentially threatening social stimulus of an unfamiliar human intruder, is one of the most widely used tests to measure temperament in rhesus macaques (*Macaca mulatta*) and related species. Specifically, it was designed to measure behavioral inhibition, defined as behavioral withdrawal from (Kagan, Reznick, & Snidman, 1988) or fearfulness in response to (e.g., Schmidt et al., 1997) novelty. The HIT was originally developed to assess behavior in infant macaques, but has been adapted to other age groups and NHP species (e.g., Costall et al., 1988). In general, the subject is brought to a cage in a novel room and allowed to acclimate for a period of time. The subject is then exposed to a human intruder, with whom it has no prior experience. The intruder first stands by the subject's cage taking care to avoid eye contact (designed to represent a potential social threat), after which the intruder makes direct eye contact, a threatening posture, with the subject. While there have been various iterations of this test, they all have similar components (e.g., an unfamiliar human who makes direct eye contact with the subject). Subjects display a wide range of behavioral responses to this test. Generally, individuals who show excessive freezing behavior when the intruder is not making direct eye contact, and/or those showing excessive anxious behavior (e.g., scratching, distress behaviors) in the presence of the intruder, are considered more behaviorally inhibited than others (see Coleman & Pierre, 2014 for review). One reason for the widespread use of this test is that it has been pharmacologically validated. Behavioral responses to the intruder (including freezing, hostility, etc.) have been reduced with various anxiolytics (Habib et al., 2000; Kalin, Shelton, & Turner, 1991) and increased with anxiogenic compounds (Kalin, Shelton, & Turner, 1992).

Response to unfamiliar humans is also used to assess personality in other species. The human avoidance distance test in cattle and the human approach test in dairy cows measure the response of the animals to a human making direct eye contact (Gibbons, Lawrence, & Haskell, 2011; Parham, Tanner, Wahlberg, Grandin, & Lewis, 2019; Sutherland, Rogers, & Verkerk, 2012). Similar tests have been conducted in pigeons (Santos et al., 2015), pigs (Brown et al., 2009), and horses (Calviello et al., 2016).

Restraint

Personality assessments often measure an individual's response to an aversive stimulus. One experience that is aversive to most animals is manual restraint or handling, which can happen for husbandry or clinical purposes. For example, cattle and dairy cows or other livestock may be restrained in stalls known as cattle crushes or chutes for examinations or veterinary treatment. Some animals become agitated in response to this restraint, while others remain relatively docile (e.g., Parham et al., 2019). Because it elicits this kind of behavioral variation, researchers have utilized this restraint as part of a personality test for these species. In this test, the animal is loosely restrained in the chute for a period of time, and observers assess the animal's response to the restraint (known as chute score) as well as the response to being released from the chute (known as exit score). Responses to both include "docile," "restless," "nervous," and "aggressive" (see Parham et al., 2019). While subjective, these scores have been found to be reliable across both experienced and inexperienced observers (Parham et al., 2019). The flight speed with which the animals exit the chute may also be calculated. A similar test has been developed for pigs. In this test (the backtest), young pigs are put on their backs and gently restrained for a period of time (e.g., Hessing et al., 1993). Researchers measure the degree of struggling as an indicator of coping style (Zebunke, Repsilber, Nürnberg, Wittenburg, & Puppe, 2015), with increased struggling thought of as reactive coping. Restraint tests are also relatively common in bird (Campbell, Hinch, Downing, & Lee, 2016; Fucikova, Drent, Smits, & van Oers, 2009) and fish (Colchen, Faux, Teletchea, & Pasquet, 2017; Ferrari, Benhaïm, Colchen, Chatain, & Bégout, 2014; Magnhagen et al., 2015) species.

Predator

For certain species (i.e., those most vulnerable to predation in the wild), response to a predatory simulation has been used to assess personality. For example, insects such as beetles are often handled with forceps to simulate a predator attack (Müller & Juškauskas, 2018; Tremmel & Müller, 2013). Insects generally respond to such handling with a period of tonic immobility, after which they begin to move again. The latency to move is used as a measure of boldness; bolder individuals spend less time immobile than shyer individuals (Müller & Juškauskas, 2018). The image of a predator (a raptor) displayed on a screen has been used to assess boldness in hermit crabs (Watanabe et al., 2012). In response to the image, most hermit crabs withdraw into their shells. Bold hermit crabs re-emerge sooner than their shy conspecifics (Watanabe et al., 2012). Response to a predator also has been used to assess personality traits in nonhuman primate species. The Predator Confrontation Test (Barros, Boere, Huston, & Tomaz, 2000) was developed to assess response to a predatory threat in marmosets (*Callithrix penicillata*). In these tests, marmosets are exposed to a taxidermized Ocilla cat (*Felis tigrina*), a natural predator, in an open field testing arena. Observers assess response to the "predator," including displacement behavior, vigilance, and exploratory behavior. Similar to the HIT, this test has been pharmacologically validated. Anxiolytics reduced displacement behaviors and increased exploratory behavior in marmosets exposed to the model predator (Barros et al., 2000; Barros, Mello, Huston, & Tomaz, 2001).

Social Isolation

For social species, isolation from the group can be highly aversive to individuals. Isolation tests are therefore used for highly gregarious species, such as sheep or horses (Lansade, Bouissou, & Erhard, 2008; Rice, Jongman, Butler, & Hemsworth, 2016). For example, in the isolation box test, a sheep is put into an opaque box for a set amount of time, and behavior and/or level of agitation is measured (Murphy et al., 1994). In addition, the speed at which animals leave the isolation chamber is also used as a measure of temperament (Plush, Hebart, Brien, & Hynd, 2011). It is worth noting that while these tests quantify response of animals to social isolation, many personality assessments necessitate that animals be removed from their social group for testing. Animals are typically tested individually on the Human Intruder tests, Open Field tests, and restraint tests. This separation from the social group can be an experimental confound and/or a welfare concern and has been used to support the use of home environment assessments (Hopper, Cronin, & Ross, 2018).

Animal Personality Research

Recent years have seen a dramatic increase in publications on the study of animal personality (Fig. 2). A literature search on animal temperament or personality performed with PsychInfo, a database of peer-reviewed literature, revealed over 2200 articles published between 1900 and 2018. Over a third of these papers were published in the past 5 years. Importantly, this increase can be seen across a wide range of scientific fields, including psychology, neuroscience, agricultural sciences, veterinary science, and environmental science. Below, I briefly review some fields of study in which animal personality studies are found. Because animal personality studies in the fields of behavioral ecology and evolution are covered elsewhere in this book (see Réale, Chap. 15), I focus on biomedical/translational and applied ethology studies.

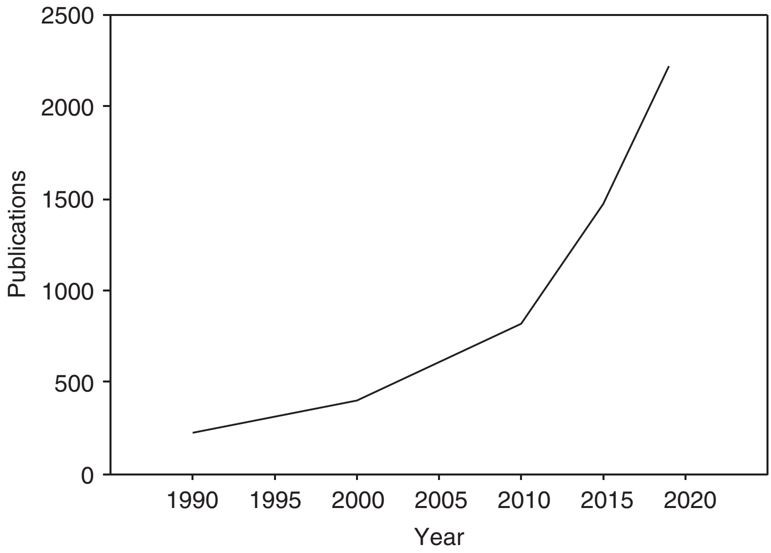

Fig. 2 Cumulative number of peer-reviewed publications on animal personality or temperament published between 1990 and 2019. There were approximately 230 publications prior to 1990. Data taken from PsychInfo

Biomedical Research

One reason for the current increased interest in personality is its role in various behavioral and/or health outcomes in humans (Capitanio, 2011; Deary, Weiss, & Batty, 2010; Mehta & Gosling, 2008; Miller, Cohen, Rabin, Skoner, & Doyle, 1999; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). The link between personality traits, such as behavioral inhibition, and vulnerability to stress-induced behavioral problems in human populations has long been established. Several studies have demonstrated that children who consistently score as inhibited early in life are at a greater risk of developing anxiety, depressive disorders, and other psychopathologies later on in life compared to non-inhibited peers (Hirshfeld et al., 1992; Rosenbaum et al., 1993; Schwartz, Snidman, & Kagan, 1999). Inhibited children are also more likely than others to suffer from allergic disorders (Kagan, Snidman, Julia-Sellers, & Johnson, 1991) and respiratory illnesses (Boyce et al., 1995). This relation is not limited to children; personality traits have been associated with adult health-related outcomes as well (e.g., Schmidt & Fox, 1995). The personality dimension conscientiousness, which includes traits such as reliability, competence, and self-discipline, has been associated with longevity (Kern & Friedman, 2008). Conversely, studies have found a correlation between high levels of neuroticism and premature death (Roberts et al., 2007).

Similar associations between personality and illness have been found in various animal species, including nonhuman primates. Behaviorally inhibited rhesus macaque infants show greater hypothalamic-pituitary-adrenal (HPA) axis activation and behavioral responses to stresses, such as separation from peers, compared to others (Suomi, 1991) and also show impaired immune function (Laudenslager et al., 1993). They are more likely than non-inhibited individuals to develop airway hyperresponsiveness, a characteristic of asthma (Chun, Miller, Schelegle, Hyde, & Capitanio, 2013). Socially inhibited rhesus monkeys have lower antibody response to immunization and social relocation compared to highly sociable monkeys (Capitanio, Mendoza, & Bentson, 1999; Maninger, Capitanio, Mendoza, & Mason, 2003). Nervous monkeys low in confidence are also more likely than others to experience chronic diarrhea, particularly in response to repeated stressors (Gottlieb et al., 2018).

Not only are there behavioral similarities between humans and animals, there are also physiological similarities. Young rhesus macaques identified as behaviorally inhibited on the Human Intruder test show increased activity of the amygdala and bed nucleus of the stria terminalis (Kalin, Shelton, Fox, Oakes, & Davidson, 2005), structures shown to be important in behavioral inhibition in humans as well. Further, these monkeys have higher basal cortisol levels than others (Kalin, Shelton, Rickman, & Davidson, 1998); this finding is congruent with previous work demonstrating that behaviorally inhibited and temperamentally shy children have higher levels cortisol levels (Kagan et al., 1988; Schmidt et al., 1997). Further, similar genes have been found to correlate with personality traits in humans and animals.

For example, a repeat polymorphism of the dopamine D4 receptor (DRD4) has been associated with the trait novelty seeking in both humans and vervet monkeys (Bailey, Breidenthal, Jorgensen, McCracken, & Fairbanks, 2007).

Because of these similarities, animals, particularly nonhuman primate and rodent species, have been used as models for studying the relation between human personality and health outcomes. There are several reasons for why this kind of comparative approach can enhance such studies. In an interesting review, Mehta and Gosling (2008) identify four main benefits of using animal studies to better understand human personality and health, although there may be others. One of the primary benefits is that animal studies allow researchers to control variables that may have confounding effects. Factors such as access to health care, levels of social support, food intake, and exposure to substance abuse have all been found to influence various health outcomes in human populations. While difficult to account for in human studies, these factors can be controlled in animal studies. Animals within a colony tend to get fed the same food items, and most have similar access to clinical care. Controlling for these variables allows researchers to examine factors that might covary with personality to affect health outcomes. Researchers can measure and manipulate biological variables (e.g., hormones or neurotransmitters) in ways that would not be ethically possible in human studies. Further, animal studies allow researchers to observe subjects in their home environment in ways that would not be possible to do in humans. Such observations can enhance the ability to examine the relations among personality, the environment, and health outcomes (Mehta & Gosling, 2008). Finally, the relatively short lifespan of many animal species allows for longitudinal studies examining changes over development that would not be feasible with human studies (Mehta & Gosling, 2008).

Behavioral Management

Attending to the behavioral needs of animals in captivity is an integral part of animal care. Behavioral management is a comprehensive strategy for promoting psychological well-being involving factors such as socialization, nonsocial enrichment, and positive reinforcement training (PRT), as well as facilities design and positive animal-staff interactions (Keeling, Alford, & Bloomsmith, 1991; Weed & Raber, 2005; Whittaker, Laule, Perlman, Schapiro, & Keeling, 2001). The goals of behavioral management plans are to produce animals that are in good physical condition, display a variety of species-typical behaviors, are resilient to stress, and that easily recover (behaviorally and physiologically) from aversive stimuli (Novak & Suomi, 1988). It is well known that an individual's behavioral needs can differ due to a variety of factors, including personality. Therefore, it stands to reason that knowledge about individual differences in personality should help guide decisions about how to manage the care of captive animals.

Behavioral Health

Perhaps not surprisingly, personality traits have been associated with well-being and affect in humans. Studies have shown people high in the trait "extraversion" have higher positive affect compared to those low in the trait (e.g., Burgdorf & Panksepp, 2006). Similar results have been found in animals. For example, personality traits have been associated with subjective well-being in a variety of species including chimpanzees (*Pan troglodytes*) (King & Landau, 2003), orangutans (*Pongo pygmaeus* and *Pongo abelii*) (Weiss, King, & Perkins, 2006), brown capuchins (*Sapajus apella*) (Robinson et al., 2016), rhesus macaques (*Macaca mulatta*) (Weiss, Adams, Widdig, & Gerald, 2011), and Scottish wildcats (*Felis silvestris grampia*) (Gartner & Weiss, 2013). In these studies, researchers use observer ratings to assess both personality and subjective well-being. Subjective well-being ratings usually focus on questions surrounding perceived happiness of the individual, the animal's social relationships, personal control and whether the individual is meeting its goal, and how happy the rater would be if he or she were the specific animal (see King & Landau, 2003, for details). As with personality ratings, there tends to be relatively high inter-rater reliability across observers (e.g., King & Landau). In other words, despite the subjectivity of the measures, individual raters tend to score individuals in the same way.

Cognitive bias testing is another way of assessing emotional states of animals. Cognitive bias refers to the influence of affective state on information processing (Mendl, Burman, Parker, & Paul, 2009). Multiple studies have demonstrated that, in humans, self-reported emotional states can influence cognitive processes, including attention, memory, and judgment. Specifically, individuals in a negative affective state (e.g., anxiety, depression) show increased vigilance to threatening stimuli, are quicker to recall negative memories, and are more likely to have negative assumptions about future events or ambiguous stimuli compared to those in a positive emotional state (Mendl et al., 2009; Paul, Harding, & Mendl, 2005). Researchers have exploited this bias in information processing to develop cognitive bias tests to indirectly measure emotional states in nonhuman animals. These tests have been used to assess both positive and negative affect in multiple species, including rats (Harding, Paul, & Mendl, 2004; Richter et al., 2012), dogs (Mendl et al., 2010), and sheep (Doyle, Fisher, Hinch, Boissy, & Lee, 2010). Studies have shown that personality can influence emotional response to these cognitive bias tests. Pigs with a proactive (e.g., bold) personality as assessed on a novel object test and isolation test responded more optimistically on the cognitive bias tests than others (Asher, Friel, Griffin, & Collins, 2016). Similarly, dogs with a calm as opposed to anxious temperament were more likely to respond optimistically (Mendl et al., 2010). Taken together, these studies support the idea that, as with people, personality can influence well-being and affect in animals.

Although relatively few studies have specifically examined the relation between personality and affect, personality has been shown to play a role in the development of some behavioral problems, including stereotypic behavior. Stereotypies, defined as repetitive, habitual behavior patterns with no obvious function (Mason, 1991;

Shepherdson, 1993), are commonly seen in captive animals in a variety of settings. While there is much to learn about its causes, recent evidence suggests that certain personality types may be more vulnerable. Boldness, as measured by response to a novel object, was found to positively correlate with the development of stereotypic behavior in rhesus macaques, both when the monkeys were tested as infants (Gottlieb, Capitanio, & McCowan, 2013) and as adults (Gottlieb, Maier, & Coleman, 2015). Similar findings have been seen in other species, including striped mice (Joshi & Pillay, 2016), farmed mink (Hansen & Jeppesen, 2006), and horses (Nagy, Bodó, Bárdos, Bánszky, & Kabai, 2010). Further, boldness has been linked to feather damaging behavior in parrots (van Zeeland, van der Aa, Vinke, Lumeij, & Schoemaker, 2013) and certain lines of hens (Uitdehaag, Rodenburg, Komen, Kemp, & van Arendonk, 2008). In these studies, animals that engaged in the behavior were bolder or less reactive than those not displaying the behavior. These results may seem somewhat counter intuitive at first; however, stereotypic behavior and feather damage have been proposed to be a coping mechanism (e.g., van Zeeland et al., 2009). Thus, the bolder, more proactive animals may be engaging in this coping mechanism more than others. This finding is not ubiquitous. Cussen and Mench (2015) found that extraverted parrots had a less pronounced increase in stereotypy following the removal of enrichment compared to those low on the extraversion. However, in that study, authors examined stereotypy in response to a stressful event.

Environmental Enrichment

One of the most commonly utilized strategies for addressing behavioral needs of animals in captivity is to provide them with environmental enrichment, including items such toys and foraging devices (Coleman, Weed, & Schapiro, 2017). These devices are designed to increase the expression of species-typical behaviors and decrease boredom for animals. Enrichment is often provided with a "one size fits all" approach; that is, what is good for one is assumed to be good for all animals. However, personality can influence how individuals respond to various enrichment strategies. For example, Bolhuis, Schouten, Schrama, and Wiegant (2005) found an interaction between personality as measured on the backtest and enrichment use in pigs. While all of the pigs in the study displayed increased play and manipulation behavior in an enriched compared to barren environment, this increase was significantly higher in pigs that had a bolder, more proactive personality (Bolhuis et al., 2005). In other words, the bold pigs were more likely than shy pigs to utilize environmental enrichment when provided. Similar results were found in rhesus macaques given novel apps on iPad as enrichment. Some bold monkeys (as measured on a novel object test) used this enrichment device, but none of the shy monkeys interacted with it (Coleman, 2017).

Other studies have found that enrichment can actually cause stress for individuals with certain personality traits. Because animals tend to lose interest in items with continuous exposure (e.g., Lutz & Novak, 2005), enrichment is often rotated with the goal of promoting novelty. While exposure to novelty has been found to promote well-being for most animals, it can be potentially anxiogenic for highly inhibited individuals. A study of orange-winged Amazon parrots (*Amazona amazonica*) found that highly fearful birds showed increased anxiety in response to rotating enrichment compared to non-fearful birds (Fox & Millam, 2007). Similarly, Yamanashi and Matsuzawa (2010) examined the behavior of chimpanzees while they were performing various cognitive tasks (e.g., Numerical Sequence Task in which the chimpanzee chooses numerals in ascending order and a Masking Task in which the chimpanzees have to memorize numerals). Cognitive tasks such as these have been utilized as enrichment (Washburn & Rumbaugh, 1992). Half of the chimpanzees in the study were labeled as "stress sensitive" because they displayed self-directed behaviors such as scratching while performing the tasks. The stress-sensitive chimpanzees were more likely than others to become agitated when they got an incorrect response on the cognitive tasks (Yamanashi & Matsuzawa, 2010). Together, these studies suggest that enrichment may not confer the same benefits to all individuals and may even increase distress in some individuals.

In addition to promoting species-typical behaviors and reducing boredom, enrichment also can be used as a mitigation strategy to reduce stress in animals. Personality can affect how individuals perceive these mitigation efforts. For example, lavender oil has been found to be anxiolytic in several species (e.g., Cline et al., 2008; Hawken, Fiol, & Blache, 2012), including humans (Woelk & Schlafke, 2010). Researchers investigated the anxiolytic effects of lavender in female sheep selectively bred to have either a "calm" or "nervous" personality (Hawken et al., 2012). In this study, sheep were exposed to a mask containing either lavender oil or a control (peanut oil) for 30 min, after which they were isolated from their group for 5 min. Not surprisingly, calm sheep showed less agitation during the isolation stress than nervous sheep, regardless of whether they received the lavender or the control. However, the authors found an interaction between personality and the effects of the lavender. Lavender had an anxiolytic effect for calm sheep; compared to controls, sheep that received the lavender showed less agitation and lower plasma cortisol concentration. In contrast, nervous sheep given lavender showed higher agitation and plasma cortisol in response to the isolation stress compared to controls (Hawken et al., 2012). Results such as these are not only relevant to behavioral management of sheep, but may adapted to other species, including humans.

Compatibility

Another component of behavioral management is socialization. Socialization, or housing animals with compatible conspecifics, has been shown to be an important factor in promoting psychological well-being of a variety of species (Coleman et al., 2017). However, socialization can result in aggression or even trauma if the partners are not compatible. Therefore, finding compatible partners is important. There is evidence that humans tend to choose partners with similar personalities to their own (Dijkstra & Barelds, 2008). This relation recently has been explored in nonhuman primate species as well. Studies in rhesus macaques (Capitanio, Blozis, Snarr, Steward, & McCowan, 2017; Coleman, 2017) have found that female, but not male, monkeys were more likely to be successfully pair-housed with partners that had similar personality traits. Pairs in which the partners had similar personalities engaged in more affiliative and less aggressive behavior than pairs consisting of partners with dissimilar personalities. Similarly, in capuchins (*Sapajus* sp.), dyads with similar personalities (particularly in the traits Neuroticism and Sociability) had higher quality relationships than those with differing personalities (Morton, Weiss, Buchanan-Smith, & Lee, 2015). The authors also found that monkeys high in Neuroticism and low in Sociability tended to avoid social relationships in general. While more work needs to be done in other species, these results highlight the role of personality in relationships.

Positive Reinforcement Training

Positive reinforcement training (PRT) is another component of many behavioral management programs. PRT is a form of operant conditioning in which the subject is presented with a stimulus (e.g., a verbal command), responds by performing a specific behavior (e.g., present a body part for injection), and is provided with reinforcement (e.g., food treat). Several studies have demonstrated that positive reinforcement training can reduce behavioral and physiological indices of stress associated with common management procedures (Bassett, Buchanan-Smith, McKinley, & Smith, 2003; Schapiro, Bloomsmith, & Laule, 2003). For example, Lambeth and colleagues (2006) found that chimpanzees trained to voluntarily accept an injection of anesthetic (Ketamine HCl) have lower hematological indicators of stress (e.g., neutrophils and white blood cells) than chimpanzees who were not trained for this task.

While positive reinforcement training is generally considered to enhance well-being, there is a great deal of variation among individuals with respect to training. Some subjects are relatively easy to train and learn tasks quickly, while others do not appear to learn tasks as easily. Personality has been found to play a role in training success. For example, in a series of studies (Coleman, 2017; Coleman et al., 2005), we found that shy, fearful macaques were less likely than bold monkeys to successfully learn tasks including touching a target and presenting a body part. Similarly, reactive macaques were found to be less likely to cooperate with voluntary restraint than calm monkeys (Bliss-Moreau & Moadab, 2016).

Results of these studies suggest that personality assessments can identify individuals that may be difficult to train. However, it is not practical, or in many cases desirable, to restrict training to those animals with certain personality traits. Thus, there is a need to develop alternate training techniques for fearful or reactive animals. Nonhuman primates and other animals are known to imitate the actions of others (e.g., Subiaul, Cantlon, Holloway, & Terrace, 2004); thus, one potential alternate training technique is to have subjects watch a conspecific train various tasks, in the hopes that the observer would learn through social learning or imitation, a process by which observers (i.e., subjects) can learn from skilled “teachers” or demonstrators.

There is evidence to suggest that personality may play a role in an individual's propensity to engage in social learning. In an interesting study, Carter, Marshall, Heinsohn, and Cowlishaw (2014) assessed two personality traits, shy/bold (as measured on a novel object test) and anxious/calm (as measured by response to a model predator) in wild baboons (*Papio ursinus*). They then examined the propensity for the animals to engage in social learning to solve a task (finding either a novel or familiar food item). Both boldness and anxiety were found to be associated with social learning. Bold, anxious baboons were more likely to perform the task after watching a conspecific perform that task than shy/calm individuals (Carter et al., 2014). These animals were not necessarily more likely to watch the demonstrators, but rather seemed to have an increased propensity for learning. Studies along these lines could serve as a model for other species.

Farming Community

Another field in which personality is often used as a tool is in agricultural science. Indeed, it is not uncommon for the farming community to selectively breed for particular temperamental traits, including docility in cattle (Haskell, Simm, & Turner, 2014) and reduced aggression in pigs (Turner et al., 2008). This has been done both for the safety of personnel as well as for welfare and productivity reasons. Highly reactive livestock tend to have decreased growth rates and increased susceptibility to illness than less reactive animals (Dodd et al., 2012). In addition, calm personality has been associated with production measure such as meat tenderness in cattle (Coutinho et al., 2017), enhanced milk production in cows (Sutherland et al., 2012), and higher wool growth in sheep (Plush et al., 2011). It is thought that these differences might be due, in part, to the circulating corticosteroids (Plush et al., 2011). Not only do these findings have practical implications, but they can also affect the welfare of the animal. The welfare of stress-sensitive animals may be compromised due, in part, to their inability to cope with stress (Finkemeier et al., 2018; Gibbons et al., 2011; Sutherland et al., 2012). For example, highly reactive cattle may injure themselves in the weigh chutes.

Conclusions

In recent years, there has been a sharp increase in published studies of animal personality. This trend underscores the importance of this trait across a wide range of fields. Studies of animal personality can provide insight into studies of human personality, but are also important in their own right. Personality affects many aspects of animals' lives, including their factors important to welfare and how we can appropriately manage their needs.

Personality also can be an unintended confound in scientific studies. For example, we have shown that it is more challenging to train shy rhesus macaques for various tasks than their bolder counterparts (Coleman et al., 2005). Thus, it is possible that shy animals may be disproportionately removed from studies in which subjects must be trained for a particular task, such as getting blood drawn, leading to sample bias. This kind of sample bias may be particularly problematic for studies in which the animals voluntarily cooperate with tasks. In these scenarios, animals with particular temperamental traits (e.g., shy) may be less likely than others to participate, which could skew resulting data. In a recent study, zoo-housed squirrel monkeys rated on personality assessments as “low caution” and “high gentleness/affection” were more likely than others to voluntarily participate in training (Polgar, Wood, & Haskell, 2017). This bias also may be present in cognitive studies. In a recent study (van Horik, Langley, Whiteside, & Madden, 2017), researchers found that neophobic pheasants (as measured on a novel object test) were less likely to participate in voluntary cognitive assessments than bolder group mates. The authors point out that this differential participation can lead to misinterpretation of cognitive performance. Even if participation in cognitive testing is not voluntary, performance may be affected by personality. This may be particularly valid in situations in which a human tester is present. Inhibited or shy individuals may have more difficulty performing the task not because of diminished cognitive ability, but rather because of an inherent wariness of the human.

Similarly, capture methods can also introduce sample bias in studies in which subjects are removed from the natural environment. Capture methods that involve a degree of novelty seeking may be more likely to attract bold members of the population. For example, Wilson et al. (1993) captured pumpkinseed sunfish from a pond with one of the two methods, a novel object (empty minnow trap) or a seine net. Fish caught in the trap were bolder than those caught in the net in a number of variables (Wilson et al., 1993). In that study, the minnow trap served as a novel object test. However, had the trap had been the sole capture method, the population of fish used in subsequent studies would have been disproportionately bold. In field studies, shy fish may be more likely to hide or flee, while bold animals might be more likely to approach human observers, resulting in sample bias. Researchers should be cognizant of these potential biases and account for them when possible.

Acknowledgments I thank Dr. Daniel Gottlieb for useful comments on the manuscript, as well as Dr. Allison Heagerty, Adriane Maier, and Lisa Houser for their assistance on the studies undertaken at the Oregon National Primate Research Center (ONPRC). Support is acknowledged from the ONPRC, NIH 8P51OD011092.

References

Asher, L., Friel, M., Griffin, K., & Collins, L. M. (2016). Mood and personality interact to determine cognitive biases in pigs. *Biology Letters, 12*(11), 20160402. https://doi.org/10.1098/rsbl.2016.0402

Bailey, J. N., Breidenthal, S. E., Jorgensen, M. J., McCracken, J. T., & Fairbanks, L. A. (2007). The association of DRD4 and novelty seeking is found in a nonhuman primate model. *Psychiatric Genetics, 17*(1), 23–27. https://doi.org/10.1097/YPG.0b013e32801140f2

Barros, M., Boere, V., Huston, J. P., & Tomaz, C. (2000). Measuring fear and anxiety in the marmoset (Callithrix penicillata) with a novel predator confrontation model: Effects of diazepam. *Behavioural Brain Research, 108*(2), 205–211.

Barros, M., Mello, E. L., Huston, J. P., & Tomaz, C. (2001). Behavioral effects of buspirone in the marmoset employing a predator confrontation test of fear and anxiety. *Pharmacology Biochemistry and Behavior, 68*(2), 255–262.

Bassett, L., Buchanan-Smith, H. M., McKinley, J., & Smith, T. E. (2003). Effects of training on stress-related behavior of the common marmoset (*Callithrix jacchus*) in relation to coping with routine husbandry procedures. *Journal of Applied Animal Welfare Science, 6*(3), 221–233. https://doi.org/10.1207/S15327604JAWS0603_07

Bergvall, U. A., Schäpers, A., Kjellander, P., & Weiss, A. (2011). Personality and foraging decisions in fallow deer, *Dama dama*. *Animal Behaviour, 81*, 101–112.

Blaszczyk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal Behaviour, 123*, 91–100. https://doi.org/10.1016/j.anbehav.2016.10.017

Bliss-Moreau, E., & Moadab, G. (2016). Variation in behavioral reactivity is associated with cooperative restraint training efficiency. *Journal of the American Society of. Laboratory Animal Science, 55*(1), 41–49.

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2005). Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. *Applied Animal Behaviour Science, 93*(3–4), 213–228. https://doi.org/10.1016/j.applanim.2005.01.006

Boyce, W. T., Chesney, M., Alkon, A., Tschann, J. M., Adams, S., Chesterman, B., … Wara, D. (1995). Psychobiologic reactivity to stress and childhood respiratory illnesses: Results of two prospective studies. *Psychosomatic Medicine, 57*(5), 411–422.

Brown, J. A., Dewey, C., Delange, C. F. M., Mandell, I. B., Purslow, P. P., Robinson, J. A., … Widowski, T. M. (2009). Reliability of temperament tests on finishing pigs in group-housing and comparison to social tests. *Applied Animal Behaviour Science, 118*(1–2), 28–35. https://doi.org/10.1016/j.applanim.2009.02.005

Burgdorf, J., & Panksepp, J. (2006). The neurobiology of positive emotions. *Neuroscience & Biobehavoiral Reviews*, 30, 173–187. https://doi.org/10.1016/j.neubiorev.2005.06.001

Burns, J. G. (2008). The validity of three tests of temperament in guppies (*Poecilia reticulata*). *Journal of Comparative Psychology, 122*(4), 344–356. https://doi.org/10.1037/0735-7036.122.4.344

Buss, A. H., & Plomin, R. (1986). The ESA approach to temperament. In R. Plomin & A. H. Buss (Eds.), *The study of temperament: Changes, continuities and challenges* (pp. 67–79). Hillsdale, NJ: Lawrence Erlbaum Associates.

Calviello, R. F., Titto, E. A., L., Infante, P., Leme-dos-Santos, T. M., Neto, M. C., Pereira, A. M. F., Titto, C. G. (2016). Proposal and validation of a scale of composite measure reactivity score to characterize the reactivity of horses during handling. *Journal of Equine Veterinary Science*, 47, 62–70. https://doi.org/10.1016/j.jevs.2016.08.009

Campbell, D. L. M., Hinch, G. N., Downing, J. A., & Lee, C. (2016). Fear and coping styles of outdoor-preferring, moderate-outdoor and indoor-preferring free-range laying hens. *Applied Animal Behaviour Science, 185*, 73–77. https://doi.org/10.1016/j.applanim.2016.09.004

Capitanio, J. P. (2011). Individual differences in emotionality: Social temperament and health. *American Journal of Primatology, 73*(6), 507–515. https://doi.org/10.1002/ajp.20870

Capitanio, J. P., Blozis, S. A., Snarr, J., Steward, A., & McCowan, B. J. (2017). Do "birds of a feather flock together" or do "opposites attract"? Behavioral responses and temperament predict success in pairings of rhesus monkeys in a laboratory setting. *American Journal of Primatology, 79*, 1. https://doi.org/10.1002/ajp.22464. e22464.

Capitanio, J. P., Mendoza, S. P., & Bentson, K. L. (1999). The relationship of personality dimensions in adult male rhesus macaques to progression of simian immunodeficiency virus disease. *Brain, Behavior, and Immunity, 13*, 138–154.

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2012). How not to measure boldness: Novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour, 84*(3), 603–609. https://doi.org/10.1016/j.anbehav.2012.06.015

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ, 2*, e283. https://doi.org/10.7717/peerj.283

Chun, K., Miller, L. A., Schelegle, E. S., Hyde, D. M., & Capitanio, J. P. (2013). Behavioral inhibition in rhesus monkeys (*Macaca mulatta*) is related to the airways response, but not immune measures, commonly associated with asthma. *PLoS One, 8*(8), e71575. https://doi.org/10.1371/journal.pone.0071575

Clark, A. B., & Ehlinger, T. J. (1987). Pattern and adaptation in individual behavioral differences. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in ethology* (pp. 1–47). New York: Springer.

Cline, M., Taylor, J. E., Flores, J., Bracken, S., McCall, S., & Ceremuga, T. E. (2008). Investigation of the anxiolytic effects of linalool, a lavender extract, in the male Sprague-Dawley rat. *AANA Journal, 76*(1), 47–52.

Colchen, T., Faux, E., Teletchea, F., & Pasquet, A. (2017). Is personality of young fish consistent through different behavioural tests? *Applied Animal Behaviour Science, 194*, 127–134. https://doi.org/10.1016/j.applanim.2017.05.012

Coleman, K. (2017). Individual differences in temperament and behavioral management. In S. J. Schapiro (Ed.), *The Handbook of Primate Behavioral Management* (pp. 95–113). Boca Raton, FL: CRC Press.

Coleman, K., & Pierre, P. J. (2014). Assessing anxiety in nonhuman primates. *ILAR Journal, 55*(2), 333–346. https://doi.org/10.1093/ilar/ilu019

Coleman, K., Tully, L. A., & McMillan, J. L. (2005). Temperament correlates with training success in adult rhesus macaques. *American Journal of Primatology, 65*(1), 63–71.

Coleman, K., Weed, J. L., & Schapiro, S. J. (2017). Psychological environmental enrichment of animals in research. In P. M. Conn (Ed.), *Animal Models for the Study of Human Disease* (pp. 47–69). London: Academic Press/Elsevier.

Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. *Animal Behaviour, 56*, 927–936.

Colléter, M., & Brown, C. (2011). Personality traits predict hierarchy rank in male rainbowfish social groups. *Animal Behaviour, 81*(6), 1231–1237. https://doi.org/10.1016/j.anbehav.2011.03.011

Costall, B., Domeney, A. M., Gerrard, P. A., Kelly, M. E., & Naylor ,R. J. (1988). Zacopride: anxiolytic profile in rodent and primate models of anxiety. *Journal of Pharmacology*, 40, 302–305.

Coutinho, M., Ramos, P. M., da Luz, E. S. S., Martello, L. S., Pereira, A. S. C., & Delgado, E. F. (2017). Divergent temperaments are associated with beef tenderness and the inhibitory activity of calpastatin. *Meat Science, 134*, 61–67. https://doi.org/10.1016/j.meatsci.2017.06.017

Cussen, V. A., & Mench, J. A. (2015). The relationship between personality dimensions and resiliency to environmental stress in orange-winged amazon parrots (*Amazona amazonica*), as indicated by the development of abnormal behaviors. *PLoS One, 10*(6), e0126170. https://doi.org/10.1371/journal.pone.0126170

Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour, 84*(5), 1131–1139. https://doi.org/10.1016/j.anbehav.2012.08.014

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour, 81*(1), 219–224. https://doi.org/10.1016/j.anbehav.2010.10.008

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*(2), 53–79. https://doi.org/10.1177/1529100610387081

Dijkstra, P., & Barelds, D. P. H. (2008). Do people know what they want: A similar or complementary partner? *Evolutionary Psychology*, 6, 1–10. https://doi.org/10.1177/147470490800600406

Dodd, C. L., Pitchford, W. S., Hocking Edwards, J. E., & Hazel, S. J. (2012). Measures of behavioural reactivity and their relationships with production traits in sheep: A review. *Applied Animal Behaviour Science, 140*(1–2), 1–15. https://doi.org/10.1016/j.applanim.2012.03.018

Doyle, R. E., Fisher, A. D., Hinch, G. N., Boissy, A., & Lee, C. (2010). Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science, 122*(1), 28–34. https://doi.org/10.1016/j.applanim.2009.11.003

Ferrari, S., Benhaïm, D., Colchen, T., Chatain, B., & Bégout, M.-L. (2014). First links between self-feeding behaviour and personality traits in European seabass, *Dicentrarchus labrax*. *Applied Animal Behaviour Science, 161*, 131–141. https://doi.org/10.1016/j.applanim.2014.09.019

Finkemeier, M. A., Langbein, J., & Puppe, B. (2018). Personality research in mammalian farm animals: Concepts, measures, and relationship to welfare. *Frontiers in Veterinary Science, 5*, 131. https://doi.org/10.3389/fvets.2018.00131

Fox, A. S., Oler, J. A., Shackman, A. J., Shelton, S. E., Raveendran, M., McKay, D. R., … Kalin, N. H. (2015). Intergenerational neural mediators of early-life anxious temperament. *Proceedings of the National Academy of Sciences of the United States of America, 112*(29), 9118–9122. https://doi.org/10.1073/pnas.1508593112

Fox, R. A., & Millam, J. R. (2007). Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonic*a). *Applied Animal Behaviour Science, 104*(1–2), 107–115. https://doi.org/10.1016/j.applanim.2006.04.033

Francis, R. C. (1990). Temperament in a fish: A longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. *Ethology, 86*, 311–325.

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology, 72*(8), 653–671. https://doi.org/10.1002/ajp.20833

Fucikova, E., Drent, P. J., Smits, N., & van Oers, K. (2009). Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology, 115*(4), 366–374. https://doi.org/10.1111/j.1439-0310.2009.01618.x

Gartner, M. C., & Weiss, A. (2013). Scottish wildcat (Felis silvestris grampia) personality and subjective Well-being: Implications for captive management. *Applied Animal Behaviour Science, 147*(3–4), 261–267. https://doi.org/10.1016/j.applanim.2012.11.002

Gibbons, J. M., Lawrence, A. B., & Haskell, M. J. (2011). Consistency of flight speed and response to restraint in a crush in dairy cattle. *Applied Animal Behaviour Science, 131*(1–2), 15–20. https://doi.org/10.1016/j.applanim.2011.01.009

Goldberg, L. R. (1990). An alternative 'description of personality': The Big-Five factor structure. *Journal of Personality and Social Psychology*, 59, 1216–1229.

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., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8, 69–74.

Gottlieb, D. H., Capitanio, J. P., & McCowan, B. (2013). Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta)*: Animal's history, current environment, and personality. *American Journal of Primatology, 75*(10), 995–1008. https://doi.org/10.1002/ajp.22161

Gottlieb, D. H., Del Rosso, L., Sheikhi, F., Gottlieb, A., McCowan, B., & Capitanio, J. P. (2018). Personality, environmental stressors, and diarrhea in rhesus macaques: An interactionist perspective. *American Journal of Primatology, 80*(12), e22908. https://doi.org/10.1002/ajp.22908

Gottlieb, D. H., Maier, A., & Coleman, K. (2015). Evaluation of environmental and intrinsic factors that contribute to stereotypic behavior in captive rhesus macaques (*Macaca mulatta*). *Applied Animal Behaviour Science, 171*, 184–191. https://doi.org/10.1016/j.applanim.2015.08.005

Habib, K. E., Weld, K. P., Rice, K. C., Pushkas, J., Champoux, M., Listwak, S., … Gold, P. W. (2000). Oral administration of a corticotropin-releasing hormone receptor antagonist significantly attenuates behavioral, neuroendocrine, and autonomic responses to stress in primates. *Proceedings of the National Academy of Sciences of the United States of America, 97*(11), 6079–6084.

Hansen, S. W., & Jeppesen, L. L. (2006). Temperament, stereotypies and anticipatory behaviour as measures of welfare in mink. *Applied Animal Behaviour Science, 99*(1–2), 172–182. https://doi.org/10.1016/j.applanim.2005.10.005

Harding, E. J., Paul, E. S., & Mendl, M. (2004). Animal behaviour: Cognitive bias and affective state. *Nature, 427*(6972), 312. https://doi.org/10.1038/427312a

Haskell, M. J., Simm, G., & Turner, S. P. (2014). Genetic selection for temperament traits in dairy and beef cattle. *Frontiers in Genetics, 5*, 368. https://doi.org/10.3389/fgene.2014.00368

Hawken, P. A., Fiol, C., & Blache, D. (2012). Genetic differences in temperament determine whether lavender oil alleviates or exacerbates anxiety in sheep. *Physiology & Behavior, 105*(5), 1117–1123. https://doi.org/10.1016/j.physbeh.2011.12.005

Herskin, M. S., Kristensen, A.-M., & Munksgaard, L. (2004). Behavioural responses of dairy cows toward novel stimuli presented in the home environment. *Applied Animal Behaviour Science, 89*(1–2), 27–40. https://doi.org/10.1016/j.applanim.2004.06.006

Hessing, M. J. C., van Beek, J. A. M., Wiepkema, R. P., Schouten, W. G. P., Hagelsø, A. M., & Krukow, R. (1993). Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science, 37*(4), 285–295.

Hirshfeld, D. R., Rosenbaum, J. F., Biederman, J., Bolduc, E. A., Faraone, S. V., Snidman, N., … Kagan, J. (1992). Stable behavioral inhibition and its association with anxiety disorder. *Journal of the American Academy of Child and Adolescent Psychiatry, 31*(1), 103–111.

Hopper, L. M., Cronin, K. A., & Ross, S. R. (2018). A multi-institutional assessment of a short-form personality questionnaire for use with macaques. *Zoo Biology, 37*(5), 281–289. https://doi.org/10.1002/zoo.21439

Horback, K. M., Miller, L. J., & Kuczaj, S. A. (2013). Personality assessment in African elephants (*Loxodonta africana*): Comparing the temporal stability of ethological coding versus trait rating. *Applied Animal Behaviour Science, 149*(1–4), 55–62. https://doi.org/10.1016/j.applanim.2013.09.009

Jones, A. C., & Gosling, S. D. (2005). Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. *Applied Animal Behaviour Science, 95*(1–2), 1–53. https://doi.org/10.1016/j.applanim.2005.04.008

Joshi, S., & Pillay, N. (2016). Association between personality and stereotypic behaviours in the African striped mouse *Rhabdomys dilectus*. *Applied Animal Behaviour Science, 174*, 154–161. https://doi.org/10.1016/j.applanim.2015.11.021

Kagan, J. (1997). Temperament and the reactions to unfamiliarity. *Child Development, 68*(1), 139–143.

Kagan, J., Reznick, J. S., & Snidman, N. (1988). Biological bases of childhood shyness. *Science, 240*(4849), 167–171.

Kagan, J., Snidman, N., Julia-Sellers, M., & Johnson, M. O. (1991). Temperament and allergic symptoms. *Psychosomatic Medicine, 53*(3), 332–340.

Kalin, N. H., & Shelton, S. E. (1989). Defensive behaviors in infant rhesus monkeys: Environmental cues and neurochemical regulation. *Science, 243*(4899), 1718–1721.

Kalin, N. H., Shelton, S. E., Fox, A. S., Oakes, T. R., & Davidson, R. J. (2005). Brain regions associated with the expression and contextual regulation of anxiety in primates. *Biological Psychiatry, 58*(10), 796–804. https://doi.org/10.1016/j.biopsych.2005.05.021

Kalin, N. H., Shelton, S. E., Rickman, M., & Davidson, R. J. (1998). Individual differences in freezing and cortisol in infant and mother rhesus monkeys. *Behavioral Neuroscience, 112*(1), 251–254.

Kalin, N. H., Shelton, S. E., & Turner, J. G. (1991). Effects of alprazolam on fear-related behavioral, hormonal, and catecholamine responses in infant rhesus monkeys. *Life Sciences, 49*(26), 2031–2044.

Kalin, N. H., Shelton, S. E., & Turner, J. G. (1992). Effects of beta-carboline on fear-related behavioral and neurohormonal responses in infant rhesus monkeys. *Biological Psychiatry, 31*(10), 1008–1019.

Keeling, M. E., Alford, P. L., & Bloomsmith, M. A. (1991). Decision analysis for developing programs of psychological Well-being: A bias-for-action approach. In M. A. Novak & A. J. Petto (Eds.), *Through the looking glass* (pp. 57–65). Washington, D.C.: American Psychological Association.

Kern, M. L., & Friedman, H. S. (2008). Do conscientious individuals live longer? A quantitative review. *Health Psychology*, 27, 505–512.

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. https://doi.org/10.1016/S0092-6566(02)00527-5

Konecna, M., Lhota, S., Weiss, A., Urbanek, T., Adamova, T., & Pluhacek, J. (2008). Personality in free-ranging Hanuman langur (Semnopithecus entellus) males: Subjective ratings and recorded behavior. *Journal of Comparative Psychology, 122*(4), 379–389. https://doi.org/10.1037/a0012625

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., … Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews, 23*(7), 925–935.

Lansade, L., Bouissou, M.-F., & Erhard, H. W. (2008). Reactivity to isolation and association with conspecifics: A temperament trait stable across time and situations. *Applied Animal Behaviour Science, 109*(2–4), 355–373. https://doi.org/10.1016/j.applanim.2007.03.003

Laudenslager, M. L., Rasmussen, K. L., Berman, C. M., Suomi, S. J., & Berger, C. B. (1993). Specific antibody levels in free-ranging rhesus monkeys: Relationships to plasma hormones, cardiac parameters, and early behavior. *Developmental Psychobiology*, 26, 407–420.

Ley, J. M., McGreevy, P., & Bennett, P. C. (2009). Inter-rater and test–retest reliability of the Monash canine personality questionnaire-revised (MCPQ-R). *Applied Animal Behaviour Science, 119*(1–2), 85–90. https://doi.org/10.1016/j.applanim.2009.02.027

Lutz, C. K., & Novak, M. A. (2005). Environmental enrichment for nonhuman primates: Theory and application. *ILAR Journal, 46*(2), 178–191. https://doi.org/10.1093/ilar.46.2.178

Lyons, D. M., Price, E. O., & Moberg, G. P. (1988). Individual differences in temperament of domestic dairy goats: Constancy and change. *Animal Behaviour, 36*, 1323–1333.

Magnhagen, C., Backstrom, T., Overli, O., Winberg, S., Nilsson, J., Vindas, M. A., & Brannas, E. (2015). Behavioural responses in a net restraint test predict interrenal reactivity in Arctic charr *Salvelinus alpinus*. *Journal of Fish Biology, 87*(1), 88–99. https://doi.org/10.1111/jfb.12691

Maninger, N., Capitanio, J. P., Mendoza, S. P., & Mason, W. A. (2003). Personality influences tetanus-specific antibody response in adult male rhesus macaques after removal from natal group and housing relocation. *American Journal of Primatology, 61*(2), 73–83. https://doi.org/10.1002/ajp.10111

Mason, G. J. (1991). Stereotypies: A critical review. *Animal Behaviour, 41*(6), 1015–1038.

McCall, R. B. (1986). Issues of stability and continuity in temperament research. In R. Plomin & J. Dunn (Eds.), *The study of temperament: Changes, continuities and challenges* (pp. 13–25). Hillsdale, NJ: Lawrence Eribaum Associates.

McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal temperament: Causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation, 9*, 39–48. https://doi.org/10.1111/j.1469-1795.2005.00004.x

McGrogan, C., Hutchison, M. D., & King, J. E. (2008). Dimensions of horse personality based on owner and trainer supplied personality traits. *Applied Animal Behaviour Science, 113*(1–3), 206–214. https://doi.org/10.1016/j.applanim.2007.10.006

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*(5), 651–661. https://doi.org/10.1016/j.bbi.2008.01.008

Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., Blackwell, E., & Casey, R. (2010). Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. *Current Biology, 20*(19), R839–R840. https://doi.org/10.1016/j.cub.2010.08.030

Mendl, M., Burman, O. H. P., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science, 118*(3–4), 161–181. https://doi.org/10.1016/j.applanim.2009.02.023

Miller, G. E., Cohen, S., Rabin, B. S., Skoner, D. P., & Doyle, W. J. (1999). Personality and tonic cardiovascular, neuroendocrine, and immune parameters. *Brain, Behavior, and Immunity, 13*(2), 109–123. https://doi.org/10.1006/brbi.1998.0545

Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. *Animal Behaviour, 105*, 163–171. https://doi.org/10.1016/j.anbehav.2015.04.013

Müller, T., & Juškauskas, A. (2018). Inbreeding affects personality and fitness of a leaf beetle. *Animal Behaviour, 138*, 29–37. https://doi.org/10.1016/j.anbehav.2018.02.002

Murphy, P. M., Purvis, I. W., Lindsay, D. R., Le Neindre, P., Orgeur, P., & Poindron, P. (1994). Measures of temperament are highly repeatable in merino sheep and some are related to maternal behaviour. *Australian Society of Animal Production Proceedings, 20*, 247–250.

Nagy, K., Bodó, G., Bárdos, G., Bánszky, N., & Kabai, P. (2010). Differences in temperament traits between crib-biting and control horses. *Applied Animal Behaviour Science, 122*(1), 41–47. https://doi.org/10.1016/j.applanim.2009.11.005

Novak, M. A., & Suomi, S. J. (1988). Psychological well-being of primates in captivity. *American Psychologist, 43*(10), 765–773.

Parham, J. T., Tanner, A. E., Wahlberg, M. L., Grandin, T., & Lewis, R. M. (2019). Subjective methods to quantify temperament in beef cattle are insensitive to the number and biases of observers. *Applied Animal Behaviour Science, 212*, 30. https://doi.org/10.1016/j.applanim.2019.01.005

Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience & Biobehavioral Reviews, 29*(3), 469–491. https://doi.org/10.1016/j.neubiorev.2005.01.002

Plush, K. J., Hebart, M. L., Brien, F. D., & Hynd, P. I. (2011). The genetics of temperament in Merino sheep and relationships with lamb survival. *Applied Animal Behaviour Science, 134*(3–4), 130–135. https://doi.org/10.1016/j.applanim.2011.07.009

Polgar, Z., Wood, L., & Haskell, M. J. (2017). Individual differences in zoo-housed squirrel monkeys' (*Saimiri sciureus*) reactions to visitors, research participation, and personality ratings. *American Journal of Primatology, 79*(5). https://doi.org/10.1002/ajp.22639

Prut, L., & Belzung, C. (2003). the open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: A review. *European Journal of Pharmacology*, 463, 3–33.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society, 82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rice, M., Jongman, E. C., Butler, K. L., & Hemsworth, P. H. (2016). Relationships between temperament, feeding behaviour, social interactions, and stress in lambs adapting to a feedlot environment. *Applied Animal Behaviour Science, 183*, 42–50. https://doi.org/10.1016/j.applanim.2016.07.006

Richter, S. H., Schick, A., Hoyer, C., Lankisch, K., Gass, P., & Vollmayr, B. (2012). A glass full of optimism: Enrichment effects on cognitive bias in a rat model of depression. *Cognitive, Affective, & Behavioral Neuroscience, 12*(3), 527–542. https://doi.org/10.3758/s13415-012-0101-2

Roberts, B. W., Kuncel, N. R., Shiner, R., Caspi, A., & Goldberg, L. R. (2007). The power of personality: The comparative validity of personality traits, socioeconomic status, and cognitive ability for predicting important life outcomes. *Perspectives on Psychological Science, 2*(4), 313–345. https://doi.org/10.1111/j.1745-6916.2007.00047.x

Robinson, L. M., Waran, N. K., Leach, M. C., Morton, F. B., Paukner, A., Lonsdorf, E., … Weiss, A. (2016). Happiness is positive welfare in brown capuchins (*Sapajus apella*). *Applied Animal Behaviour Science, 181*, 145–151. https://doi.org/10.1016/j.applanim.2016.05.029

Roseboom, P. H., Nanda, S. A., Fox, A. S., Oler, J. A., Shackman, A. J., Shelton, S. E., … Kalin, N. H. (2014). Neuropeptide Y receptor gene expression in the primate amygdala predicts anxious temperament and brain metabolism. *Biological Psychiatry, 76*(11), 850–857. https://doi.org/10.1016/j.biopsych.2013.11.012

Rosenbaum, J. F., Biederman, J., Bolduc-Murphy, E. A., Faraone, S. V., Chaloff, J., Hirshfeld, D. R., & Kagan, J. (1993). Behavioral inhibition in childhood: A risk factor for anxiety disorders. *Harvard Review of Psychiatry, 1*(1), 2–16.

Santos, C. D., Cramer, J. F., Parau, L. G., Miranda, A. C., Wikelski, M., & Dechmann, D. K. (2015). Personality and morphological traits affect pigeon survival from raptor attacks. *Scientific Reports, 5*, 15490. https://doi.org/10.1038/srep15490

Schapiro, S. J., Bloomsmith, M. A., & Laule, G. E. (2003). Positive reinforcement training as a technique to alter nonhuman primate behavior: Quantitative assessments of effectiveness. *Journal of Applied Animal Welfare Science, 6*(3), 175–187. https://doi.org/10.1207/S15327604JAWS0603_03

Schmidt, L. A., & Fox, N. A. (1995). Individual differences in young adults' shyness and sociability: Personality and health correlates. *Personality and Individual Differences, 19*(4), 455–462.

Schmidt, L. A., Fox, N. A., Rubin, K. H., Sternberg, E. M., Gold, P. W., Smith, C. C., & Schulkin, J. (1997). Behavioral and neuroendocrine responses in shy children. *Developmental Psychobiology, 30*(2), 127–140.

Schwartz, C. E., Snidman, N., & Kagan, J. (1999). Adolescent social anxiety as an outcome of inhibited temperament in childhood. *Journal of the American Academy of Child and Adolescent Psychiatry, 38*(8), 1008–1015.

Shepherdson, D. (1993). Stereotypic behaviour: What is it and how can it be eliminated or prevented? *Journal of the Association of British Wild Animal Keepers, 16*, 100–105.

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An intergrative overiew. *Quarterly Review of Biology, 79*(3), 241–277. https://doi.org/10.1086/422893

Stamps, J., & Groothuis, T. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews of the Cambridge Philosophical Society, 85*(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Stevenson-Hinde, J., & Zunz, M. (1978). Subjective assessment of individual rhesus monkeys. *Primates, 19*, 473–482.

Stowe, M., Bugnyar, T., Loretto, M. C., Schloegl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes, 73*(1), 68–75. https://doi.org/10.1016/j.beproc.2006.03.015

Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation in rhesus macaques. *Science, 305*(5682), 407–410. https://doi.org/10.1126/science.1099136

Suomi, S. J. (1991). Uptight and laid-back monkeys: Individual differences in the response to social challenges. In S. E. Brauth, W. S. Hall, & R. J. Dooling (Eds.), *Plasticity of development* (pp. 27–56). Cambridge, MA: MIT Press.

Sutherland, M. A., Rogers, A. R., & Verkerk, G. A. (2012). The effect of temperament and responsiveness towards humans on the behavior, physiology and milk production of multi-parous dairy cows in a familiar and novel milking environment. *Physiology & Behavior, 107*(3), 329–337. https://doi.org/10.1016/j.physbeh.2012.07.013

Tetley, C. L., & O'Hara, S. J. (2012). Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals. *Animal Welfare, 21*(4), 463–476. https://doi.org/10.7120/09627286.21.4.463

Tremmel, M., & Müller, C. (2013). Insect personality depends on environmental conditions. *Behavioral Ecology, 24*(2), 386–392. https://doi.org/10.1093/beheco/ars175

Turner, S. P., Roehe, R., Mekkawy, W., Farnworth, M. J., Knap, P. W., & Lawrence, A. B. (2008). Bayesian analysis of genetic associations of skin lesions and behavioural traits to identify genetic components of individual aggressiveness in pigs. *Behavior Genetics, 38*(1), 67–75. https://doi.org/10.1007/s10519-007-9171-2

Uitdehaag, K. A., Rodenburg, T. B., Komen, H., Kemp, B., & van Arendonk, J. A. (2008). The association of response to a novel object with subsequent performance and feather damage in adult, cage-housed, pure-bred Rhode Island red laying hens. *Poultry Science, 87*(12), 2486–2492. https://doi.org/10.3382/ps.2008-00059

van Horik, J. O., Langley, E. J., Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural Processes, 134*, 22–30. https://doi.org/10.1016/j.beproc.2016.07.001

Van Zeeland, Y. R. A., Spruit, B. M., Rodenburg, T. B., Riedstra, B., van Hierden, Y. M., Buitenhuis, B., … Lumeij, J. T. (2009). Feather damaging behaviour in parrots: A review with consideration of comparative aspects. *Applied Animal Behaviour Science, 121*, 75–95. https://doi.org/10.1016/j.applanim.2009.09.006

van Zeeland, Y. R. A., van der Aa, M. M. J. A., Vinke, C. M., Lumeij, J. T., & Schoemaker, N. J. (2013). Behavioural testing to determine differences between coping styles in Grey parrots (*Psittacus erithacus erithacus*) with and without feather damaging behaviour. *Applied Animal Behaviour Science, 148*(3–4), 218–231. https://doi.org/10.1016/j.applanim.2013.08.004

Walsh, R. N., & Cummins, R. A. (1976). The open-field test: A critical review. *Psychological Bulletin, 83*(3), 482–504.

Washburn, D. A., & Rumbaugh, D. M. (1992). Testing primates with joystick-based automated apparatus: Lessons from the language research Center's computerized test system. *Behavior Research Methods, Instruments & Computers, 24*(2), 157–164.

Watanabe, N. M., Stahlman, W. D., Blaisdell, A. P., Garlick, D., Fast, C. D., & Blumstein, D. T. (2012). Quantifying personality in the terrestrial hermit crab: Different measures, different inferences. *Behavioural Processes, 91*(2), 133–140. https://doi.org/10.1016/j.beproc.2012.06.007

Watters, J. V., & Powell, D. M. (2012). Measuring animal personality for use in population management in zoos: Suggested methods and rationale. *Zoo Biology, 31*(1), 1–12. https://doi.org/10.1002/zoo.20379

Weed, J. L., & Raber, J. M. (2005). Balancing animal research with animal Well-being: Establishment of goals and harmonization of approaches. *ILAR Journal, 46*(2), 118–128. https://doi.org/10.1093/ilar.46.2.118

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*(1), 72–83. https://doi.org/10.1037/a0021187

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. https://doi.org/10.1037/0022-3514.90.3.501

White, S. L., Wagner, T., Gowan, C., & Braithwaite, V. A. (2017). Can personality predict individual differences in brook trout spatial learning ability? *Behavioural Processes, 141*(Pt 2), 220–228. https://doi.org/10.1016/j.beproc.2016.08.009

Whittaker, M., Laule, G., Perlman, J., Schapiro, S., & Keeling, M. (2001). *A behavioral management approach to caring for great apes.* Paper presented at the The Apes: Challenges for the 21st Century Conference Proceedings, Brookfield.

Williamson, D. E., Coleman, K., Bacanu, S., Delvin, B. J., Rogers, J., Ryan, N. D., & Cameron, J. L. (2003). Heritability of fearful-anxious endophenotypes in infant rhesus macaques: A preliminary report. *Biological Psychiatry, 53*(4), 284–291. https://doi.org/10.1016/S0006-3223(02)01601-3

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology, 107*(3), 250–260.

Woelk, H., & Schlafke, S. (2010). A multi-center, double-blind, randomised study of the lavender oil preparation Silexan in comparison to lorazepam for generalized anxiety disorder. *Phytomedicine, 17*(2), 94–99. https://doi.org/10.1016/j.phymed.2009.10.006

Yamanashi, Y., & Matsuzawa, T. (2010). Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: Individual differences in self-directed 25 behaviours during cognitive tasks. *Animal Welfare, 19*(1), 25–30.

Zebunke, M., Repsilber, D., Nürnberg, G., Wittenburg, D., & Puppe, B. (2015). The backtest in pigs revisited – An analysis of intra-situational behaviour. *Applied Animal Behaviour Science, 169*, 17–25. https://doi.org/10.1016/j.applanim.2015.05.002