

Handbook of Personality

Theory and Research

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CHAPTER 12

Personality in Animals

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Consider the following hypothetical study of personality. A set of individuals, whose genetic lineage is known, is monitored from conception to birth and observed at regular intervals from birth to death. Because maternity and paternity are known for certain, a subset of the individuals can be cross-fostered at birth so that the effects of maternal postnatal social environment can be distinguished from the effects of biological inheritance and prenatal effects. The environments in which the individuals live can be carefully monitored and, if the researchers wish, manipulated. Numerous physiological measures can be taken, including regular blood samples, and samples of body and brain tissue can be collected at autopsy. On top of all this, several generations could be examined in the course of 10 years.

Although such a study could never be conducted on human participants, if it were done, it would permit investigators to address numerous foundational questions about the genetic, neurochemical, physiological, and environmental bases of personality. However, many of the features of this hypothetical study could be implemented in nonhuman animal research—indeed, many of them already are. There is now compelling evidence that personality traits can be assessed in nonhuman animals (Gosling & Vazire, 2002;

Vazire, Gosling, Dickey, & Schapiro, 2007), opening the way for animal studies to augment human personality research on such basic questions.

To illustrate the opportunities that animal research can bring to personality science, consider some features of one ongoing animal personality research program (the findings are presented in greater detail later in the chapter). One of us (J. P. C.) has collected personality data on over 175 rhesus monkeys since 1993. The animals' personalities were assessed at 5–10 years of age, and a four-factor structure was derived by factor analysis using one subsample and confirmed on a separate subsample using confirmatory factor analysis. Some of the animals were removed from the living situation in which personality was measured, and were tested in a variety of situations, both nonsocial and social (including with both familiar and unfamiliar companions). Behavioral and physiological measures were obtained in these situations for up to several years following the initial assessments. Persisting relationships were found between the personality factors and measures of social behavior and emotionality, plasma cortisol concentrations, tetanus- and herpes-virus-specific antibody responses, heart rate, and central nervous system functioning. One personality factor,

Sociability, reflecting a tendency to affiliate, was found to be related to variation in patterns of neural innervation of lymph nodes, to moderate the response to a social stressor and influence expression of genes associated with innate immune responses, and to relate to individual differences in progression of immunodeficiency virus disease (Capitanio, 1999, 2002, 2004; Capitanio, Mendoza, & Baroncelli, 1999; Capitanio, Mendoza, & Bentson, 2004; Capitanio & Widaman, 2005; Capitanio et al., in press; Maninger, Capitanio, Mendoza, & Mason, 2003; Ruys, Capitanio, & Mendoza, 2002; Sloan, Capitanio, Tarara, & Cole, in press).

As we shall see, providing animal models for human personality research is only one application of studies of animal personality. Animal research can also illuminate the evolutionary processes that shaped personality structure and promoted individual differences in personality. In addition, the assessment of personality in animals has numerous practical applications that can contribute to human and animal welfare. In this chapter, we provide an overview of the emerging field of animal personality, summarizing the major issues and findings, and pointing to the potential contributions to be made by this emerging cross-disciplinary field.

HISTORY

Over the past three decades, personality research in nonhuman animals has become increasingly common in the scientific literature, with particularly fast growth in the last 5 years. As a mark of the widespread interest in, and broad applicability of, animal personality research, studies have been conducted across a wide range of disciplines, including biological psychiatry, behavioral ecology, applied ethology (or animal welfare), animal behavior, primatology, behavioral genetics, and comparative psychology. Indeed, the strongest interest in individual differences in animal behavior has come from fields outside mainstream personality research. For example, the field of applied ethology has produced many studies examining personality in a broad range of domestic species, including cattle, pigs, sheep, dogs, and mink. In their attempts to solve practical issues (e.g., which individuals tend to become agitated when

handled), applied ethologists have made great progress in developing methods for assessing individual differences in behavior.

Although many personality psychologists are just now becoming aware of the relevant nonhuman literature, historically there were closer ties between researchers studying individual differences in human and nonhuman species. In the formative days of social and personality psychology, investigators believed that studies of animals could inform research on the psychological processes underlying individual differences in social behavior in the same way animal research had informed most other areas of psychology (Domjan & Purdy, 1995). One early landmark in animal personality research was Nobel Laureate Ivan Pavlov's series of studies at the beginning of the 20th century (e.g., Pavlov, 1906); this research program identified four basic types of canine personality based on three properties of the nervous system: force, equilibrium, and mobility. Interest in animal personality continued with Yerkes's and Crawford's ape studies in the 1930s and with those of Hebb in the 1940s. At the time, such work was considered relevant to researchers in human social and personality psychology. Indeed, in the 1935 *Handbook of Social Psychology*, more than a third of the chapters were devoted to work on nonhuman subjects. But two decades later, in the 1954 handbook, the attention to nonhuman studies had faded significantly; already, Hebb and Thomson saw cause to draw attention to the importance of animal studies, warning in their chapter that social psychology will "be dangerously myopic if it restricts itself to the human literature" (p. 532). Fifteen years later Zajonc's text *Animal Social Psychology* (1969) again highlighted the value of research on nonhuman social behavior, revealing a large animal literature that was "entirely surprising in scope, quality, and significance" (p. v). Unfortunately, during the subsequent 30 years, with few notable exceptions (e.g., Buss, 1988), personality theory and research based on nonhuman animals largely disappeared from contemporary social and personality psychology—none of the chapters in the latest *The Handbook of Social Psychology* (Gilbert, Fiske, & Lindzey, 1998) or either *Handbooks of Personality* (Hogan, Johnson, & Briggs, 1997; Pervin & John, 1999) focused on nonhuman

animals, and studies of nonhuman animals rarely appeared in mainstream personality journals. Yet there are myriad ways in which animal studies can inform human personality psychology research. This chapter reviews the basic issues in the recently reinvigorated field of animal personality and illustrates the varied and unique contributions that animal studies can make to our understanding of personality.

DEFINITIONS

What is meant by “personality”? There is no single definition of personality that would satisfy all personality psychologists, and most would be satisfied by only a very broad definition. For example, one way to define personality that captures most phenomena studied by personality psychologists is as those characteristics of individuals that describe and account for consistent patterns of feeling, cognition, and behaving. The phenomena studied by human personality psychologists include temperament and character traits, dispositions, goals, personal projects, abilities, attitudes, physical and bodily states, moods, and life stories. The vast majority of animal personality studies focus on just a subset of these constructs: behavioral traits. Although researchers do not rule out the possibility that behavioral traits are associated with characteristic patterns of cognition and affect, they tend to focus on cross-situational and cross-temporal patterns of behavior, which are easier to measure. Focusing on overt measures of consistency in behavioral patterns, rather than on underlying emotional processes, is often done to avoid inviting criticisms about anthropomorphism and lack of objectivity.

In animal personality research, terms such as “temperament” and “behavioral syndrome” or “style” are often used instead of “personality” for the very reason of avoiding the anthropomorphic connotations of the “*p*-word.” In human research, temperament is considered a construct closely related to personality; it has often been defined as the inherited, early-appearing tendencies that continue throughout life and serve as the foundation for personality. This definition is not adopted uniformly by animal or even human researchers (McCrae et al., 2000), but

a similar definition of temperament that has gained acceptance among nonhuman primate researchers is that proposed by Clarke and Boinski (1995), who stated that temperament refers to behavioral styles or tendencies that show continuity over time and can be identified in early infancy, and which are reflected in the degree and nature of responsivity to novel or stressful stimuli. The term “behavioral syndrome” has gained recent popularity in the field of behavioral ecology (Sih, Bell, Johnson, & Ziemba, 2004). Behavioral syndromes are defined as suites of correlated behaviors expressed either within a given behavioral context or across different contexts. Clearly, this definition very closely matches the concept of personality in humans.

We prefer the term “personality” for three reasons. First, it is confusing to create new terms without a compelling conceptual reason to do so. Second, using the term “personality” facilitates connections with the enormous existing research on personality in humans. Third, we do not think it is useful, as some have suggested, to adopt the term “temperament” for nonhumans because to do so would entail a priori assumptions (e.g., about traits being inherited and appearing early) that may or may not be appropriate; for example, it is increasingly clear that individual differences in adult animal behavior are a function of both biological tendencies and experience, as is the case with humans.

METHODS

Methods for assessing personality in animals can be split into two broad categories: codings of overt behaviors and ratings of broader traits by knowledgeable observers. Behavior codings and trait ratings reflect different solutions to the apparent tradeoff between quantifying personality in terms of objective behaviors and using humans to record and interpret information more subjectively. Many animal behavior researchers regard behavior codings as intrinsically superior to global personality ratings. Historically, rating data obtained from observers have been derided as subjective and inappropriate for the objective requirements of scientific measurement. In contrast, many human researchers would argue that behavior codings actually deserve the closest scrutiny. They would point to

research on human personality, where consensual observer ratings are often considered to be the *sine qua non* of personality traits (Gosling, Kwan, & John, 2003). Animal personality researchers who have chosen to sacrifice the objectivity supposedly gained from detailed behavior codings do so in favor of obtaining more comprehensive ratings on traits such as confidence, curiosity, and playfulness by people who are familiar with individual animals.

Behavior codings have been used widely in animal personality studies. In a comprehensive review, one of us (Gosling, 2001) found that 74% of the animal personality studies to that date had used behavior codings to assess personality. Behavior codings often require repeated observations of individuals, and thus can be performed only with animals whose behavior is easily visible or recorded. It is surprisingly difficult to summarize the specific methods and procedures used in the typical behavior coding study because the details are often not reported; for example, researchers seldom report how many observers coded each animal, who the observers were (e.g., experts vs. undergraduate research assistants), how the observers were trained, how many hours of observation were collected for each animal, or the interobserver reliabilities of the codings.

The choice of which behaviors to code is largely driven by the goals of the study, and much variation across studies exists with respect to the specific behaviors chosen to code. Once the behaviors have been chosen, the observers must be trained to recognize and record these behaviors. This can be done with basic paper-and-pencil techniques or by using more sophisticated computer-based data collection systems (e.g., Noldus, 1991). To facilitate the process of deciding which behaviors to code, researchers typically refer to published ethograms, which are lists of species-typical behaviors.

Trait ratings are used less commonly than behavior codings in animal personality studies. In Gosling's 2001 review, only 34% of the studies used trait ratings to measure animal personality; most of these examined dogs, cats, or primates. Typically, researchers have quantified impressions by asking observers who were familiar with the animals to rate each one on a number of personality traits. Usually these ratings were made

by more than one observer, and occasionally they were made at several points in time.

Both codings and ratings can be based on three possible sources of information: experimenter-defined behavioral tests, naturalistic behavior, and observers' knowledge of the animals. Behavioral tests involve exposing an individual to a specific situation or stimulus believed to elicit meaningful individual differences in behavior. For example, in study of social responsiveness in rhesus monkeys, one of us (Capitanio, 2002) exposed 12 adult males to videotapes of unfamiliar animals displaying aggressive, affiliative, or nonsocial behaviors. Wide variation in behavioral responses to the videotapes were seen, with individuals differing in the frequencies of behaviors such as yawning (which reflects tension), lipsmacking (which reflects appeasement), as well as durations of looking at the displayed images.

In typical studies of naturalistic behaviors, trained observers record the behavior of one animal at a time in "focal animal samples," in which frequencies and/or durations of virtually all (or, sometimes, a focused subset of) behaviors displayed are collected (Altmann, 1974). The number of observers for each animal varies across studies, but is usually as low as one or two. Focal samples can vary in duration from study to study (e.g., from 10 seconds to 30 minutes), as does the number of times each animal is sampled.

Personality assessments can also draw upon observers' familiarity with particular animals. For example, in the video playback study described above (Capitanio, 2002), personality assessments had been made on the animals using the rating methodology nearly 4 years prior to the playback experiment. Six of the twelve animals had been rated high in "Sociability," a dimension reflecting a tendency to affiliate, and the remaining six animals had been rated low on this dimension. The variation in responses that were found in this study was strongly related to the prior personality rating: Animals that were low in Sociability showed higher frequencies of yawning and lower frequencies of lipsmacking, and tended to have higher durations of looking at the videotapes. Importantly, when both high- and low-sociable animals saw a social signal (threat, lipsmack) displayed on the videotape, their most common response was to avert their gaze. High-sociable ani-

mals, however, gaze-averted in about half the time compared to low-social animals. Given the threatening nature of direct eye contact in this species, this suggested that high Sociability reflected greater social skill in managing potentially dangerous situations.

In theory, coding or rating methods could be applied to any of the three sources of information outlined above. In practice, however, the information available in behavioral tests and naturalistic observations is almost always gathered using coding methods, and the information accumulated by observers about individuals is almost always recorded using rating methods.

Vazire and colleagues (2007) compared codings and trait ratings in a study of chimpanzees that implemented both methods, evaluating each in terms of its reliability, subjectivity, and practicality. Their analyses showed that the widely supposed advantages of codings over trait ratings are often not borne out in practice. Specifically, trait-rating methods were more reliable and practical than behavior-coding methods and were not as subjective as many researchers believe. Trait ratings are reliable and hence well suited for detecting consistencies in animals' behavior, the very foundation of personality. Behavior codings, in contrast, can be difficult to measure reliably, particularly when observations are made across different times of day or under varying conditions. Even when behaviors are measured at the same time of day or under the same conditions, they may reflect other characteristics of the environment (e.g., situational influences), not just personality. Behavior can be used to infer personality, but personality and behavior are not the same thing (Capitanio, 2004): An individual's traits, dispositions, or proclivities combine with elements of the situation or environment to promote expression of particular behaviors. But those same behaviors can be expressed in very different situations and can be prompted by different proclivities. For example, in some contexts, a monkey's sexual presentation posture (rump elevated, legs braced, orientation toward another individual) can reflect friendliness, appeasement or subordination, or an invitation for sexual behavior. Behavior-coding methods may be better suited for experimental manipulations, where researchers are concerned with detecting the effects of situational variables on behavior.

Vazire and colleagues' (2007) findings indicate that researchers (1) cannot assume that behavior codings are reliable and (2) should compute and report reliabilities for behavior codings as they do with trait ratings. In addition, researchers using either method should take steps to improve the reliability of their measures. For example, behavior codings can be made more reliable by increasing the number and length of observation, providing specific definitions of the behaviors to be coded, and training observers extensively. Trait ratings can also be made more reliable by increasing the number of observers, ensuring that all observers are well-acquainted with the animals they are rating, and providing specific definitions of the traits being rated.

To estimate and reduce the effects of observer bias on both trait-rating and behavior-coding methods, researchers can perform variance-partitioning analyses such as intraclass correlations or the social relations model (Kenny, 1994). These analyses allow researchers to measure and statistically control for "perceiver effects," which are systematic idiosyncrasies in observers' ratings (Kwan, Gosling, & John, 2008).

An important additional advantage of trait ratings over behavioral codings is their relative practicality. In fact, the efficiency with which ratings can be applied suggests that studies of personality could be carried out in many contexts where researchers may be discouraged by the efforts associated with coding methods. These findings further suggest that rating studies of personality can piggyback on the many animal studies already underway.

Ultimately the choice of whether to use rating or coding methods should be driven by theoretical concerns because the two methods measure different things. Rating methods assess broader psychological traits, whereas behavioral-coding methods assess the observable results of these traits interacting with contextual factors.

SPECIES STUDIED

In the most comprehensive review to date, one of us (Gosling, 2001) identified 187 personality studies of one kind or another in 64 different species. It should be noted that these studies varied a great deal in quality,

with some of them, especially the early studies, consisting of little more than a series of field observations. Furthermore, the species studied were far from representative of the species in existence. Eighty-four percent of the studies in Gosling's review focused on mammals (29% primates, 55% nonprimates), 8% focused on fish, 4% focused on birds, and the remaining 4% were divided among reptiles, amphibians, arthropods, and mollusks.

TRAITS STUDIED

This review (Gosling, 2001) also summarized the traits studied in past animal research. There are numerous conceptual challenges to defining traits and determining their equivalence across studies and across species. However, a number of dimensions have appeared consistently across multiple species. Many of the papers identified a dimension reflecting an individual's characteristic reaction to novel stimuli or situations. This dimension has been referred to with terms such as Reactivity, Emotionality, or Fearfulness, and has been measured by behavioral indicators such as defecation rate in open field tests and by ratings on traits such as "nervous." A second recurring dimension is the propensity to seek out novel stimuli or situations in the first place, and has been identified in several articles as Exploration. This dimension has been measured by behaviors such as approach to novel objects and by ratings on traits such as "curious." Several studies identified a dimension differentiating those individuals who sought out social interactions from those who preferred to remain solitary. This dimension, usually referred to as Sociability, has been measured by behaviors such as frequency of social encounters and by ratings on traits such as "affiliative." A number of studies identified an Aggression dimension derived from such behavioral measures as latency to attack another individual and by ratings of traits such as "aggressive." A fifth dimension to appear in several studies referred to an animal's general activity level and has been measured by behaviors such as the amount of enclosure covered by the animal's roaming and by ratings on traits such as "energetic." Several studies also identified a Dominance or Assertiveness dimension, which was usually related to the individual's

rank in the dominance hierarchy (e.g., Gosling, 1998; King & Figueredo, 1997; Sapolsky & Ray, 1989).

Most studies in the review (Gosling, 2001) had a narrow scope, focusing on only one or two dimensions. To get a better idea of the personality structures associated with different species, exploratory studies with a broader focus are needed. One of us (Gosling & John, 1999) reviewed 19 such studies, using the five-factor model (FFM; John, 1990; see also John, Naumann, & Soto, Chapter 4, this volume; McCrae & Costa, Chapter 5, this volume) as an organizing framework for the findings. The FFM dimensions of Extraversion, Neuroticism, and Agreeableness showed considerable generality across the 12 species included in their review. Of the 19 studies, 17 identified a factor closely related to Extraversion, capturing dimensions ranging from Surgency in chimpanzees; Sociability in pigs, dogs, and rhesus monkeys; Energy in cats and dogs; Vivacity in donkeys; to a dimension contrasting bold approach versus avoidance in octopuses. Of course, the way these personality dimensions are manifested depends on the species: Whereas the human scoring low on Extraversion stays at home on Saturday night or tries to blend into a corner at a large party, the octopus scoring low on Boldness stays in its protective den during feedings and attempts to hide itself by changing color or releasing ink into the water.

Factors related to Neuroticism appeared almost as frequently, capturing dimensions such as Fearfulness, Emotional Reactivity, Excitability, and low Nerve Stability. Factors related to Agreeableness appeared in 14 studies, with Affability, Affection, and Social Closeness representing the high pole, and Aggression, Hostility, and Fighting representing the low pole. Factors related to Openness were identified in all but 4 of the 12 species. The two major components defining this dimension were Curiosity-Exploration (interest in new situations and novel objects) and Playfulness (which is associated with Extraversion when social, rather than imaginative, aspects of play are assessed). Chimpanzees were the only species with a separate Conscientiousness factor, which was defined more narrowly than in humans but included the lack of attention and goal-directedness and erratic, unpredictable, and disorganized behavior typical of the low pole. Dominance emerged as a clear separate factor in 7 of the

19 studies reviewed (Gosling & John, 1999). A separate Activity dimension was identified in only two of the studies.

Overall, the past 10 years of research have shown that it is viable to assess at least some elements of personality in animals. This fact raises the question of whether animal research can be used to inform the field of personality psychology. In the following section we discuss examples of animal personality studies that, in our opinion, firmly establish the importance of animal research in the field of personality.

WHY STUDY ANIMAL PERSONALITY?

Animal personality research is useful in three broad domains, all of which are relevant to humans, although in very different ways. The first domain involves understanding a species for its own sake. All animals, including humans, must accomplish certain tasks in order to survive and reproduce, such as obtain food, protect themselves from predators, and secure a mate. At a fundamental level, understanding the personality structure within a species helps us understand the different strategies that animals employ in accomplishing these tasks. In this way, personality research in nonhuman animals parallels that in humans, by focusing on how individual-difference factors facilitate or constrain an animal's ability to solve the problems with which it is faced daily. Taking a comparative perspective on personality can, for example, highlight common solutions that different species have taken to solve common problems. Just as human personality research has enriched the field of animal personality research, this "behavioral ecology" approach to personality research may suggest novel ways of thinking about human personality. A second domain in which animal personality research is valuable concerns its utility in "animal model" research. The greater experimental control of both environmental and genetic factors in animal research, coupled with a greater ability to manipulate independent variables and assess dependent variables, provides a powerful way of exploring issues that are of fundamental importance to humans. Finally, there are practical applications of animal personality research relating to the interaction between humans and animals, including the welfare of animals used

in scientific experiments, animals as pets, and conservation of endangered species. Below, we describe examples in each of these three domains.

STUDYING ANIMALS TO ADDRESS SPECIES-SPECIFIC QUESTIONS OF BEHAVIOR

The primary goal of behavioral ecology studies of animal personality is to gain a better understanding of how individuals of a given species vary in their day-to-day behaviors, and to explore the adaptive function of such variation. Historically, behavioral ecologists, like many psychologists, have viewed individual differences in behavior as representing nonadaptive, random variation surrounding a presumably adaptive population mean. Recently, however, the notion that the differences themselves may represent nonrandom and possibly adaptive solutions to the challenges of survival and reproduction has become more widely accepted (Dall, Houston, & McNamara, 2004; Nettle, 2006). The existence of suites of correlated behaviors (i.e., behaviors that co-occur) could reflect variation in adaptive strategies among individuals within a population. Correlations among behaviors may be expressed either within a given context (e.g., correlations between activity and exploratory behaviors in a foraging context) or across different contexts (e.g., correlations among feeding, antipredator, and mating behaviors); as noted, in the field of behavioral ecology, these suites of behaviors are commonly referred to as behavioral syndromes (Sih et al., 2004). Such syndromes presumably reflect underlying genetic or physiological mechanisms and constrain the flexibility of individuals' behaviors. This constraint in behavioral flexibility can generate tradeoffs, in which a certain personality characteristic may prove advantageous for an animal in one situation but not another. For example, highly aggressive individuals of a given species may be successful in defending their territories and monopolizing valuable food sources against conspecifics, but these same individuals may act inappropriately aggressively toward predators, approaching them when fleeing might actually result in a greater probability of survival; the reverse would hold true for less aggressive individuals. The existence of variation in environments may thus have helped maintain

individual differences in behavior during the course of evolution, because the fitness benefits associated with different personality characteristics change as environmental conditions fluctuate (Wilson, 1998). To continue the example, when predator densities were low, high aggressiveness may have been adaptive, and when predator densities were high, aggressiveness may have been less useful for individuals.

Compelling evidence supporting this idea is provided by a Netherlands research group that has been conducting long-term studies of personality in a natural population of a passerine bird species, the great tit, *Parus major*, over the last several years (see Groothuis & Carere, 2005, for a review). Birds have been found that differ consistently in exploratory behavior when placed in a novel environment, and these differences have been correlated with variation in a wide range of social and nonsocial behaviors (specific examples are discussed below). Notably, differences in exploratory tendency between individuals were related to variation in their annual survival as well as to survival of their offspring; the direction of the relationship, however, depended on the distribution and availability of food during the winter (Dingemanse, Both, Drent, & Tinbergen, 2004). Thus, fluctuations in environmental conditions may have led to fluctuations in competition for space and food, which in turn affected the survival and reproductive success of different personalities (reflecting alternative strategies); such variation in selection pressures is one mechanism that can maintain individual differences in personality in a population.

The understanding of how individuals differ in the behaviors they use to deal with the challenges of survival and reproduction, the constraints or tradeoffs that animals experience with respect to behavioral flexibility, and why evolution may have favored the maintenance of individual differences in personality in a given population or species are the key issues that behavioral ecologists seek to explore through the study of personality. Animals must accomplish many tasks in their daily lives. Although the specific challenges they encounter often depend on the species or population in question, common tasks include acquisition of food and territory, avoidance of predation, competition for mates, the rearing of offspring, and integration into a

social group (which often includes establishing dominance rank among a hierarchy of individuals). Below we describe examples of studies that address how personality influences the way in which animals solve some of these challenges. As noted in our discussion above, animal studies primarily use the coding approach in order to assess individual variation in personality, and most behavioral ecology studies of personality have done so by measuring animals' responses to novel or threatening stimuli. As a result, much attention has been paid to the "shy–bold continuum," which comprises behaviors such as exploration, activity, and aggression (Wilson, Clark, Coleman, & Dearstyne, 1994).

Anti-Predator Behavior

Some studies of anti-predator behavior have demonstrated negative consequences associated with possessing certain personality traits. Quinn and Cresswell (2005) measured personality in wild chaffinches (*Fringilla coelebs*) by assessing activity level, and then related variation in activity level to anti-predator behavior when birds were presented with a model hawk. Anti-predator behavior was assessed in two situations: a low-risk or indirect threat situation, in which the model hawk flew 2 meters to the side of the chaffinch, and the presumed optimal response was to freeze to avoid detection; and a high-risk or direct threat situation, in which the model flew directly overhead, and the presumed optimal response was to escape. Activity level in the absence of a predator was negatively correlated with freezing behavior in both the low- and high-risk predator situations. Thus, individuals low in activity experienced a tradeoff in which they were more likely to perform the correct anti-predator response in the low-risk situation (i.e., to freeze), but were less likely to perform the correct response in the high-risk situation, where fleeing, rather than freezing, was presumed optimal. The opposite tradeoff occurred in highly active birds.

Competition for Mates

In many species of birds and fish, females prefer to mate with brightly colored males rather than males with duller coloration. One hypothesis that has been proposed to explain this phenomenon states that if the

expression of preferred traits in males (such as conspicuous colors) is indicative of males' overall quality, females will choose to mate with males that express these traits in order to gain benefits such as access to a better territory or for transmission of better genes to their offspring. Godin and Dugatkin (1996) showed that in the Trinidadian guppy (*Poecilia reticulata*), the conspicuousness of males' coloration correlated positively with boldness toward a cichlid fish predator as well as their escape distance—that is, more colorful males approached a fish predator more often than did drab males, but when the predator began “stalking” them, the brightly colored males fled sooner, and from a greater distance, compared to the drab males. Godin and Dugatkin concluded from their experiments that bold males were more informed about nearby predators and more likely to survive encounters with them. In addition, they found that though females preferred more colorful males as mates, females actually preferred bolder males irrespective of coloration when given the opportunity to observe males' behavior toward a potential fish predator. By preferentially mating with colorful males, female guppies were thus choosing relatively bold, and perhaps more viable, individuals. If such viability is heritable, females may potentially gain fitness benefits from mating with these males by producing more viable offspring.

Parental Care/Reproductive Success

Some studies of personality and parental care have found behavioral inhibition, or shyness, to be associated with lower levels of parental behavior. One such example is demonstrated by Budaev, Zworykin, and Mochek's (1999) study of a captive group of convict cichlids, *Cichlasoma (Archocentrus) nigrofasciatum*. They assessed fish behavior in a novel area and in the presence of a novel fish. Individuals varied along an activity–inhibition dimension, such that active/uninhibited cichlids were quicker to enter the novel area and approach the novel fish, whereas inhibited individuals typically “froze” in the presence of the novel fish. Male cichlids that were more inhibited also engaged in less food provisioning of their brood. Females that were most inhibited spent the least amount of time near offspring when their broods were youngest,

and both males and females that were inhibited spent less time near their offspring during later brood stages.

Similarly, Reale, Gallant, Leblanc, and Festa-Bianchet (2000) found that in bighorn sheep, ewes that were bolder (i.e., those that were most likely to approach and remain for longer periods of time at a salt lick associated with the experimenters' trap) were most likely to start reproducing earlier and to have higher weaning success than shy ewes. Reale and colleagues' results suggest that ewes that were more willing to spend time feeding in a risky area may be obtaining important nutrients that enable them to reproduce earlier and have healthier offspring. In both of these examples, inhibition may be a safer, more effective strategy in novel, potentially dangerous situations, but in the context of parental care it is boldness that appears to be associated with behaviors that lead to increased offspring survival.

Behavioral inhibition (or shyness) is not always associated with poorer parental care, however. Both, Dingemanse, Drent, and Tinbergen (2005) measured exploratory behavior in a wild population of great tits during temporary capture and placement in a novel environment, which was a room consisting of five artificial trees. Exploration was measured using the number of movements between branches during the first 2 minutes after the individual entered the room; individuals were classified as either slow or fast explorers. Fledgling condition (as measured by mass) was affected by the interaction between both parents' exploratory behavior, with assortative pairs (i.e., slow–slow and fast–fast pairs) producing fledglings in the best condition. Offspring of both of these sets of parents may have been in similarly good condition because parents were able to specialize in one of two different behavioral strategies that each led to the same end result of heavier offspring: fast-exploring pairs may have been better able to obtain or defend a high-quality territory, whereas slow-exploring pairs may have been better parents (e.g., engaged in more food provisioning).

The three examples above demonstrate that any given trait, such as behavioral inhibition, is not uniformly “good” or “bad”—what is important is how that trait affects functioning in the environments that the individuals experience.

Dominance Rank/Integration into the Social Hierarchy

Becoming integrated into a social group, which usually involves establishing a place in the hierarchy, is a crucial task for socially living animals. Dominance rank has important consequences for fitness because it can affect territory acquisition, access to food, mating success, and survival of offspring. Data from the Netherlands great tit research program suggest that personality influences dominance interactions in complex ways. Verbeek, Boon, and Drent (1996) showed that in pairwise confrontations of juvenile male great tits, fast explorers started and won more fights than slow explorers. However, when tits were formed into aviary groups (which better modeled natural social dynamics than simple pairwise interactions), the relationship between personality and dominance rank varied according to the stability of the hierarchy (Verbeek, De Goede, Drent, & Wiepkema, 1999). That is, during the first day in the aviary, when dominance ranks had not yet stabilized, fast explorers averaged higher dominance ranks and initiated more fights than slow explorers. During this period of social instability, fast explorers took more risks in their fighting behavior (while slow explorers were more cautious), and also had more difficulty coping with defeat than slow explorers. Once the hierarchy stabilized, fast explorers either won or lost all fights with slow explorers—the end result being that slow explorers typically had intermediate dominance ranks, but on average were actually higher in dominance rank than fast explorers. These studies suggest that high levels of boldness or aggression, though often associated with success in agonistic encounters, may not always lead to high dominance rank if individuals are not able to cope with defeat or do not sufficiently temper risky behavior with caution.

Nonhuman primate researchers have found that the relationship between personality and dominance rank is similarly complex and dynamic. Fairbanks and colleagues (2004) administered an intruder challenge test to adolescent male vervet monkeys. In this test, a caged, unfamiliar adult male was placed at the periphery of the target individual's home enclosure. Individuals were found to differ in social impulsivity, reflecting

variation in the tendency to approach rapidly, examine (by touching or sniffing), and challenge (through threats or displays) the intruder. Males with the highest impulsivity scores were most likely to become the alpha male upon introduction into a new group. However, impulsivity declined in all males from adolescence to adulthood. Interestingly, the decline in dominant males was most marked, such that their adult impulsivity scores equaled those of subordinate males 1 year following introduction into new groups. According to Fairbanks and colleagues, increased impulsivity during adolescence may motivate males to leave their natal groups and face the challenges of emigration and immigration. Upon entering a new group, however, the most successful males were the ones that responded with bold overconfidence during the intense initial competition, and then became more measured and conservative in their behavior as alpha males. This study provides additional support for the idea that high levels of aggression or boldness may initially benefit an individual in agonistic encounters, but in order for status to be maintained, caution must be exercised in the long term. The results of such studies of personality and dominance rank suggest new ways of examining normative patterns of personality development and change in many species, including humans.

Finally, an extensive research program conducted by Sapolsky and colleagues on wild olive baboons (*Papio anubis*) has shown that among males, reactivity to stressors (as measured by glucocorticoid function) does not relate to dominance rank in a straightforward manner (Ray & Sapolsky, 1992; Sapolsky & Ray, 1989; Virgin & Sapolsky, 1997). That is, the traditional notion that subordinate males are more stressed than dominant males does not necessarily hold true. Rather, it is styles of dominance (i.e., personality) that best predict glucocorticoid function. For example, high-ranking males that demonstrated behaviors suggesting high degrees of social skillfulness, control, and predictability over social contingencies appeared to be the least physiologically stressed in their daily lives (Sapolsky & Ray, 1989). Dominant males lacking these behavioral features, in contrast, had cortisol concentrations that were as high as those of subordinate males. Virgin and Sapolsky (1997) conducted a sim-

ilar analysis of subordinate males and found that personality differences in these animals were also associated with variation in glucocorticoid function. One subset of subordinate males had significantly high rates of consortships (a behavior usually shown only by high-ranking males) and glucocorticoid responses to stress that were similar to those of dominant males. These animals turned out to be significantly more likely than other subordinates to move to the upper half of the hierarchy in subsequent years.

Population/Species Differences

A final important goal of behavioral ecology research on animal personality is to determine the taxonomic distribution of various personality traits, and to examine how personality differs between populations of a species according to variation in ecological factors (Fraley, Brumbaugh, & Marks, 2005). Employing such a comparative approach to personality research can help us (1) understand how certain traits may have evolved by looking at phylogenetic continuities, and (2) identify common traits across a variety of unrelated taxa that may have evolved independently in response to similar environmental conditions.

Interspecies differences in personality are thought to result from differences in population density, sex ratio, group composition, susceptibility to predation, and habitat and temporal differences in food distribution and availability during the course of evolution (Clarke & Boinski, 1995; Gosling & John, 1999). Mettke-Hofmann, Ebert, Schmidt, Steiger, and Stieb (2005) showed that the correlation between two behaviors typically indicative of boldness can differ between two closely related species of warbler. They compared neophobic and exploratory behaviors between the species at two different times of year: once at the end of the breeding season, and again 10 months later, at the beginning of the following breeding season. Nonmigratory Sardinian warblers showed consistency in personality over time, and neophobia and exploration were negatively related to one another. In contrast, the migratory garden warblers neither behaved consistently over time nor showed a correlation between neophobia and exploration. These results suggest that behavior is more flexible across

time and context in one species of warbler than in the other, and that such increased flexibility is likely necessitated by the variety of challenges presented by migration. In individuals of migratory species, the dimensions of personality so far studied may exert less of a constraining effect on behavior and therefore result in fewer tradeoffs. This lower constraint in turn may predispose individuals to be better able to survive the long migratory journey and subsequently make the rapid behavioral adjustments necessary to adapt to a new environment. In contrast, behavioral consistency or predictability may benefit individuals of nonmigratory species, for example, by facilitating the maintenance of long-term social relationships. If nonmigratory birds are more likely to encounter the same individuals regularly across their lifespan (whereas migratory birds may be more likely to experience frequent turnover in their associations), behavioral predictability will better allow individuals to remember and appropriately respond to one another, facilitating social stability.

Many studies of personality among nonhuman primates have compared different populations or species. Clarke and Boinski (1995) compared personality in three species of macaque—rhesus, bonnet, and long-tailed—and found that long-tailed macaques were the most behaviorally responsive, but also rather fearful; bonnets were the most passive; and rhesus were the most active and hostile. de Waal and Luttrell (1989) compared the differing styles of social organization of rhesus and stump-tailed macaques (*Macaca arctoides*) and showed again that rhesus monkeys were more aggressive and less relaxed, tolerant, and socially cohesive than the stump-tails. One of us suggested that the marked behavioral and social organization differences between macaque species are not a result of differences in personality structure, per se, but of differences in where each species' modal "location" is along the dimensions that make up the structure (Capitanio, 2004). In the case of de Waal's data, for example, both stump-tailed and rhesus macaques may demonstrate the dimension Agreeableness, but stump-tails as a species may have a higher modal value for Agreeableness compared to rhesus. Within the genus *Macaca*, for example, evolution of the various species may have resulted from

natural selection operating on a relatively fixed set of traits in the ancestral species. Complex species differences in personality and social organization may have resulted from straightforward differences in ecological pressures. If, for example, a group of animals occupied a habitat in which it was advantageous for individuals to exercise a high degree of vigilance and protectiveness in their daily actions (perhaps due to heavy predation pressure), the resulting social structure of the group may very likely exhibit stylistic differences compared to that of a group of individuals whose tendencies toward vigilance and protectiveness were less strong. With reproductive isolation, the different groups may eventually have evolved into different species.

Evidence for this phenomenon in nonhuman primates comes from intraspecific studies relating population differences in environment to those of personality. Johnson and Southwick (1984) found that maternal style of free-ranging rhesus macaques varied among three populations and was affected by the level of environmental risk for infant mortality, such that mothers in higher-risk environments were more protective of their infants than were mothers in lower-risk areas. Similarly, Hauser and Fairbanks (1988) found that in wild vervet monkeys, mothers that lived in groups with a higher-quality food supply were more rejecting toward, and had more conflict with, their infants than mothers in neighboring groups with poorer food quality. Given that nonhuman primate mothers exert a large degree of control over their infants' social interactions early in life, and variation in maternal style has been shown to have long-term consequences for a variety of behaviors exhibited by offspring (Fairbanks, 1996), it is not difficult to imagine how relatively simple differences in predation risk or food availability could lead to the differences in personality and social organization that distinguish different species.

The studies discussed above highlight the importance of considering ecological factors when attempting to relate personality to functionally important consequences. A particularly important consideration when interpreting individual differences in personality is that such differences are highly dependent on the ecological and social environment of the study population (Clarke & Boinski,

1995). In the following discussion of the use of animals in modeling personality traits of humans, we urge the reader to bear in mind the salient differences between humans and model species, as well as the importance of examining other (especially closely related) species in order to better understand the evolution of human personality.

ANIMAL MODEL RESEARCH

Since virtually the beginning of modern psychology, nonhuman animals have been used to model psychological and physiological processes, with a goal of elucidating analogous or homologous (Campbell & Hodos, 1970) processes in humans. Of course, in any area, a model is not exactly the same as the thing being modeled, so care must be taken to ensure the validity of the model (Crnic, Reite, & Shucard, 1982). While we recognize the value and importance of studying personality/temperament in a variety of species, in this section we review data from nonhuman primate studies that demonstrate some of the questions that have been asked in trying to understand psychological and physiological processes from an "animal model" perspective. Other chapters in this volume address many of these issues in human studies. We recognize that this review is not comprehensive, although it does summarize data from several laboratories that have long-standing research programs in primate personality. Other important research programs not covered in detail in this review include those by J. R. Kaplan, N. H. Kalin, and J. E. King and their colleagues (e.g., Kaplan, Manuck, Fontenot, & Mann, 2002; Nelson, Shelton, & Kalin, 2003; Pederson, King, & Landau, 2005).

Prenatal Contributions to Personality

The prenatal period is often overlooked when one considers the role of "experience" in shaping personality. In one sense this is odd, because inasmuch as personality is an emergent property of brain activity, the prenatal period is the principal time in an organism's life when brain development proceeds most rapidly, and developmental trajectories are most likely to be impacted by particular experiences. In another sense, however, the

lack of attention paid to the prenatal period is not surprising, given the logistical difficulties in studying this developmental period in humans. Nonhuman primate studies have been important in understanding the role of prenatal experience in personality, owing not only to the ability to experimentally manipulate conditions and to obtain samples (both behavioral and physiological) more regularly, but also because of the ability to follow animals longitudinally in a time frame that is considerably accelerated compared to that for humans.

Schneider developed a paradigm for inducing prenatal stress in pregnant rhesus monkey females that was simple yet produced dramatic results. During mid- to late-gestation, pregnant females were relocated to a cage in an adjacent room for a 10-minute period, during which they experienced three randomly distributed noise bursts of 1-second duration each. This simple procedure was repeated 5 days per week for a few weeks. In comparison to control animals whose mothers were not exposed to this stressor during pregnancy, prenatally stressed (PNS) animals showed impaired neuromotor development and attentional deficits at birth (Schneider, 1992a); more disturbance and less exploratory behavior in a playroom setting at 6 months of age (Schneider, 1992b); continued deficits in exploration and increased disturbance behavior, as well as excessive clinging under stressful conditions assessed at 18 months of age (Clarke & Schneider, 1993); and impaired adaptability and sociability (as indexed by greater inactivity and less proximity) in a social setting at 4 years of age (Clarke, Soto, Bergholz, & Schneider, 1996). Behaviorally, these results suggested to the authors that prenatal stress appeared to result in an "inhibited" personality (Clarke & Schneider, 1997). Further results by this group suggested the neural substrates that might be involved. Specifically, this paradigm for inducing prenatal stress has been shown to result in persisting alterations in functioning of the hypothalamic-pituitary-adrenal axis (a major stress-response system; Clarke, Wittwer, Abbott, & Schneider, 1994), elevations in cerebrospinal fluid concentrations of dopamine and norepinephrine metabolites (Schneider et al., 1998), and reduced neurogenesis in the dentate gyrus (Coe et al., 2003). Finally, these prenatal stress-induced

biobehavioral changes have also been linked to impaired immune system function (Coe, Kramer, Kirschbaum, Netter, & Fuchs, 2002), suggesting possible health implications.

The Importance of Early Postnatal Social Experience

Many readers of this chapter are already aware of the contributions of nonhuman primate research to the study of personality: We refer to the studies of Harlow and Mason, dating from the 1950s, that examined the role of early social experience in the development of social and emotional competence. Although these studies were not framed as investigations into "personality," per se, the pervasive deficiencies in emotionality, social abilities, and overall responsiveness resulting from adverse early experience reflect psychological processes that are fundamental to personality (see Capitanio, 1986, for a comprehensive review of this literature). In the parlance of the FFM, adult rhesus monkeys that were reared with limited or no social opportunities (and in a restricted laboratory environment) for the first year of life could be described as showing little social interest and competence (very low Extraversion, Agreeableness, and Conscientiousness) as well as low adaptability and high volatility (high Neuroticism, low Openness).

Gene × Environment Interactions

While the above research suggests an important role for experience in the development of personality, even extreme reductions in socioemotional opportunities, exemplified by the studies of isolation rearing early in life, did not always produce uniform results. With recent advances in molecular genetic techniques, interest has grown in documenting how different patterns of responsiveness can result, even within the same environments, depending on the individual's genotype. The gene that has been studied most frequently is associated with the central nervous system monoamine neurotransmitter serotonin. Once released into the synaptic cleft, serotonin is drawn back inside the neuron in a process known as "reuptake." The gene that codes for the protein responsible

for reuptake has a promoter region upstream of the gene itself that controls the transcription of the gene. The promoter has two forms (alleles) in both humans and rhesus monkeys. The short allele results in reduced efficiency in transcription of the reuptake protein, compared to the long form of the gene (Heils et al., 1996). Thus, three genotypes are possible: long-long, long-short, or short-short.

Research with humans has demonstrated personality correlates of variation in the serotonin transporter promoter polymorphism. For example, a meta-analysis revealed that possession of a short allele is associated with Neuroticism, as measured by the NEO Personality Inventory (Sen, Burmeister, & Ghosh, 2004). Moreover, interactions of genotype and life stress have been reported for depression and suicidality, such that individuals possessing a short allele who encounter life stress are at greater risk than those possessing two long alleles (Caspi et al., 2003). Experimental research with non-human primates has begun to explore such genotype-by-environment interactions, with much of the published data emerging from the National Institute of Health (NIH) laboratories of Suomi and Higley. The animal model permits exploration not only of the behavioral phenomena, but also the neural substrates of the behavior. In these studies, animals are typically reared either with their mothers (usually in a social group) or with peers in a nursery setting (Shannon, Champoux, & Suomi, 1998). On a neonatal assessment battery modeled after the Brazelton scale, nursery-reared (NR) infants showed higher scores on an Orientation cluster, reflecting better visual orientation and attention, than did mother-reared (MR) animals. Genotype interacted with rearing environment, however: A short allele was associated with lower Orientation scores, but only for NR animals, not for MR infants (Champoux et al., 2002). As juveniles, NR monkeys with a short allele also showed higher rates of aggressive behavior, compared to MR monkeys with a short allele (Barr et al., 2003). Impulsive aggressiveness has been associated with reduced concentrations in cerebrospinal fluid of the serotonin metabolite 5-HIAA in rhesus monkeys (Higley et al., 1992; similar results have been found for low serotonin function in humans: see Carver & Miller, 2006), and

in fact Bennett and colleagues (2002) reported that, although the serotonin genotype was not related to 5-HIAA concentrations in MR animals, there was an effect in NR animals: Possession of a short allele was associated with reduced 5-HIAA concentrations. Finally, in a study of alcohol consumption by adolescent female monkeys, genotype was again found to interact with early rearing experience, in that the greatest alcohol consumption was found for heterozygous animals that had been peer reared (Barr, Schwandt, Newman, & Higley, 2004). Together, these data demonstrate clearly the phenomenon of genotype-by-environment interactions, as well as the value of an experimental approach to studying the nature of such interactions on behavioral traits and later outcomes.

Health-Related Outcomes

The relationship between personality and health has been of interest for decades. Non-human primate personality research has explored both correlates of, and mechanisms associated with, health outcomes. Attention has focused on the trait Sociability. This is one of four personality dimensions identified in adult male rhesus monkeys (Capitanio, 1999; Capitanio & Widaman, 2005), using the rating methodology (see above). The emphasis in this research program has been on conducting the initial personality assessments in the familiar social groups into which the animals had been born, and then measuring behavioral and physiological outcomes in very different contexts and at time points that could be many years after the initial personality assessments. In these studies, Sociability has been found to reflect a tendency to affiliate, as indexed by greater frequencies of approaches, higher durations of social grooming, and lower durations of time spent alone (Capitanio, 1999). Centrally, Sociability is associated with greater sensitivity in dopaminergic function, a result reminiscent of data from humans for the trait Extraversion (e.g., Depue & Collins, 1999; Netter, 2006).

The first indication that Sociability might be associated with health-related outcomes was from a post hoc analysis of personality and immune measures taken from a study of simian immunodeficiency virus (SIV) disease progression (Capitanio et al., 1999). SIV

infection in rhesus monkeys is widely considered the best animal model for AIDS, and results in a disease course that closely mimics the human disease, although at a more accelerated rate. In SIV-infected monkeys, animals higher in Sociability had a greater decline in SIV ribonucleic acid (RNA), which is a measure of viral load and is a strong predictor of survival in both humans and monkeys. Once humans or monkeys are infected with their respective immunodeficiency viruses, the ability of their immune systems to control already-present (i.e., latent) infections with herpesviruses can become impaired. We found that a decline in antibody to the latent herpesvirus cytomegalovirus (CMV) was associated with faster disease progression (Baroncelli et al., 1997), and it was animals that had been rated lower in Sociability years earlier that showed the greatest decline in the CMV antibody response (Capitanio et al., 1999).

The result that Sociability might be associated with disease-related outcomes prompted further prospective studies of animals selected as being high or low in Sociability. We assessed personality of adult male rhesus monkeys while they lived in their familiar outdoor social groups, and then relocated them to indoor housing. Our first hypothesis was that such a change in social environment might have a greater "meaning" to high- versus low-sociable animals, and result in different immune responses. Shortly after the move, we vaccinated the animals with tetanus toxoid, using a veterinary preparation of the same vaccine that humans receive about every 10 years. High-sociable animals had significantly higher tetanus-specific antibody responses to vaccination compared to low-sociable animals (Maninger et al., 2003), confirming our expectation. Later (Capitanio et al., in press), animals were inoculated with SIV to study disease progression; half of the animals experienced stable social conditions, and the other half unstable, stressful social conditions. Personality differences were again found. Within the first few weeks following infection, low-sociable monkeys showed indications of faster disease progression, but only if they were in the unstable social conditions—a personality-by-situation interaction. Specifically, low-sociable animals displayed a greater innate immune response compared to high-sociable monkeys. This

immune response was an increase in the transcription of genes in immune system white blood cells that are associated with antiviral proteins called interferons. Normally, such an immune response would be beneficial, but in the context of SIV or HIV infection, it is not; this response reflects greater viral replication, and in fact is associated with higher viral load, itself a strong predictor of more rapid disease progression. Examination of the behavioral and hormonal responses of the animals again revealed personality-by-situation interactions. Low-sociable animals in unstable conditions coped by showing more sustained submissive behavior, and also displayed a plasma cortisol profile indicative of social stress, compared to high-sociable animals in unstable conditions. All of the relationships between Sociability and outcome measures (gene expression, submissive behavior, and cortisol) were statistically significant for animals in unstable social conditions; none of these relationships was significant for animals in stable conditions. Thus, these data demonstrate that early in immunodeficiency virus infection, personality factors can be influential in the body's ability to develop an immune response to the virus, and this action appears to be mediated by the effect of personality on coping processes, in particular (Capitanio et al., in press).

Personality was also found to be related to a potentially important mechanism that could mediate the effects on disease. Lymph nodes are structures dispersed throughout the body, and many of the body's immune responses take place there. Lymph nodes are innervated by fibers of the sympathetic nervous system, which secrete norepinephrine, and norepinephrine can have a significant adverse impact on immune function, especially in the context of HIV infection (e.g., Cole, Korin, Fahey, & Zack, 1998). This innervation provides one way in which the brain can communicate its state to the body's immune system. Working with lymph nodes from uninfected monkeys, Sloan and colleagues (in press) found that high- and low-sociable animals have lymph nodes that are "wired" differently. Specifically, low-sociable animals had a 2.8-fold greater density of catecholamine-secreting nerves compared to high-sociable monkeys. Because norepinephrine can accelerate HIV replication *in vitro* (Cole et al., 1998), these results provide a

plausible mechanism for why SIV-infected animals that are low-sociable and that experience stressful circumstances should have evidence of accelerated disease progression (Capitanio et al., in press).

These studies demonstrate the range of questions that can be asked in an animal modeling context that would either be very difficult or impossible to perform with humans, yet, given the similarity in personality dimensions between monkeys and humans, also show direct relevance to human physical and mental health and suggest new avenues of research.

PRACTICAL APPLICATIONS OF ANIMAL PERSONALITY RESEARCH

There has been a growing interest in how an individual-differences approach can inform practical solutions to common challenges in working with animals. Here we briefly review some selected applications.

Training of Animals

In a nonhuman primate research laboratory, there are many situations in which training of animals is essential for their effective use in experimental research. For example, rhesus monkeys can be trained to extend their arms for phlebotomy, a practice that results in a substantial reduction in stress to the animal, compared to blood sampling that involves the more usual physical restraint or chemical immobilization. Coleman, Tully, and McMillan (2005) used a simple assessment of temperament to identify animals that were more easily trained to perform a simple instrumental task. A human observer stood in front of the animal's cage and placed a novel food item within the animal's reach. Animals were classified as "exploratory" (inspected the novel food within 10 seconds), "moderate" (inspected the food within the 3-minute trial but not within the first 10 seconds), or "inhibited" (did not inspect the food within the 3-minute trial). Over 85% of the exploratory monkeys, and 75% of the moderate monkeys learned the instrumental task of touching a target. In contrast, only 22% of the inhibited monkeys performed the task consistently. While the authors readily acknowledged the caveat that excluding poten-

tial research subjects based on temperament can create problems for generalizability of results, the project does provide a quantitative approach to a phenomenon that everyone who has ever trained a rhesus monkey (or any animal) has experienced—namely, that some individuals learn tasks more readily than others.

Well-Being of Laboratory Animals

Just as there are individual differences in trainability that depend on personality processes, so too do such differences relate to other aspects of well-being in a laboratory environment. As described above, animals that display an inhibited temperamental style show deficiencies in social abilities and general adaptability. Boyce, O'Neill-Wagner, Price, Haines, and Suomi (1998) reported that such animals are also at greater risk for injuries. Owing to reconstruction of a rhesus monkey troop's outdoor 5-acre habitat, animals were confined for a 6-month period to a large (1,000 square feet) indoor enclosure. Veterinary records were examined and comparisons were made of preconfinement, confinement, and postconfinement periods. Approximately one-third of the animals were rated high on inhibition, and it was these animals that sustained the greatest increase in injuries during the confinement period.

An interesting approach to great ape personality has been taken by King and colleagues, who have developed an instrument based on the FFM. Recently, this approach was extended to the much understudied ape, the orangutan (Weiss, King, & Perkins, 2006). Five factors (Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect) were found. In addition to conducting personality ratings, the zoo keepers also rated animals on a measure of "subjective well-being," which reflected items such as how pleasurable and satisfying the social interactions were for the target orangutan, and how happy the rater would be if he or she were the target orangutan for a week. The measure of well-being was positively correlated with Extraversion and Agreeableness and negatively correlated with Neuroticism.

Together, these data suggest that knowledge of an animal's personality characteristics could be valuable for management of an animal colony, a recognition that has prompted

two laboratories to implement broad-based assessment programs aimed at quantifying personality for just this reason (Capitanio, Kyes, & Fairbanks, 2006; Fairbanks, 2001).

Personality-Based Selection for Working-Dog Occupations

It has been well documented in the field of personnel selection that some personalities are better suited than others to certain jobs (Hogan, Hogan, & Roberts, 1996). Selecting the right personality for the job improves the effectiveness with which the job is performed and the well-being and satisfaction of the individual in the job. The principles of personnel selection can also be applied to the animal domain. A dog that is fearful is not well suited to bomb detection, where it will be required to work in environments that are unusual, unpredictable, and noisy. Training a working dog requires a substantial investment of resources, so organizations that raise and place working dogs have a keen interest in directing those resources to the individuals best suited to the job. As a result, the vast majority of personality studies of dogs have been done by these organizations on the two most widely used breeds, Labrador retrievers and German shepherds (Jones & Gosling, 2005). One study of 2,655 German Shepherds and Belgian Tervurens showed that boldness assessed in a series of behavioral tests between 12 and 18 months of age predicted success in subsequent working-dog trials (Svartberg, 2002); although there were breed differences in boldness, these differences accounted for only part of the variance in performance. This study showed that some personalities are better suited than others to work-relevant tasks, and it demonstrated that these personalities can be identified through a reasonably straightforward battery of tests.

Personality assessments of domestic animals have also been developed to help potential owners identify a pet that matches their needs (Coren, 1998) and to assist with adoption decisions at animal shelters (Ledger & Baxter, 1996). In one study Ledger and Baxter (1996) showed that the behavioral responses of animal-shelter dogs to an unfamiliar person entering their kennel correlated 0.64 with ratings of excitability subsequently made by their new owners after adoption. Clearly, such information would be very use-

ful in setting realistic owner expectations about their new dog and in matching dogs to suitable homes, both of which would reduce the rate of unsuccessful adoptions.

CONCLUSIONS

The review above has described three broad domains in which personality research in nonhumans is flourishing. Several points emerge from this review. First, there is now a reasonably broad base of personality research on animals, with much of it emanating from fields other than mainstream personality. This research base reflects a diversity of species and is notable in that many of the personality dimensions that have been studied are not only similar across species, but are remarkably similar to those found in our own species. Second, just as in other fields of psychology that have turned to animal models, animal personality researchers are studying animals because they make it possible to address questions that would not be possible to address in human studies. Advantages of studying nonhuman species include more rapid development, shorter generation time, greater experimental control, and greater access to tissue samples. Third, the studies conducted to date are just beginning to scratch the surface of the questions that can be addressed using animal subjects. There are many more questions pertaining to central nervous system function, health outcomes, the role of genetics, the importance of prenatal experience, and so on, that can be explored in nonhumans and that are relevant to similar questions that are being, or could be, asked about humans. Finally, animal personality research is providing links to fields hitherto unconnected to the field of human personality, such as behavioral ecology. Why is there something called "personality" in humans, and where did it come from? Certainly, it is more than just coincidental that human and nonhuman primates share many personality characteristics as well as underlying brain substrates. Does it make sense to think about human personality from the perspective of tradeoffs, as behavioral ecologists do? The study of nonhuman personality provides a rich context for understanding the natural world and humans' own place in it.

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