From Mice to Men: What Can We Learn About Personality From Animal Research?

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The author explores the viability of a comparative approach to personality research. A review of the diverse animal-personality literature suggests that (a) most research uses trait constructs, focuses on variation within (vs. across) species, and uses either behavioral codings or trait ratings; (b) ratings are generally reliable and show some validity (7 parameters that could influence reliability and 4 challenges to validation are discussed); and (c) some dimensions emerge across species, but summaries are hindered by a lack of standard descriptors. Arguments for and against cross-species comparisons are discussed, and research guidelines are suggested. Finally, a research agenda guided by evolutionary and ecological principles is proposed. It is concluded that animal studies provide unique opportunities to examine biological, genetic, and environmental bases of personality and to study personality change, personality–health links, and personality perception.

What are the major research challenges facing personality psychology? As we enter the new millennium, it is likely that investigators will increasingly turn their attention to the genetic, biological, and environmental influences on personality (Little, 2001; Pervin & John, 1999). They will search for genes that govern the expression of personality. They will attempt to understand how the genes and environment interact to determine the biological roots of personality. Researchers will also continue to investigate such issues as how personality develops, how personality is linked to health, and how personality impressions are formed in everyday life. The basic aim of this article is to consider whether studies of nonhuman animals[1] can help address such issues.

Animal research has played and continues to play a central role in many areas of psychology, including learning, perception, mem-

ory, and psychopathology (Domjan & Purdy, 1995). Perhaps animal research can play a similar role in personality. Like their colleagues in other areas of psychology, personality researchers may find that animal studies can help tackle questions that are difficult or impossible to address by relying on human studies alone. Indeed, some of psychology's most respected pioneers, such as Pavlov, Yerkes, and Hebb, examined personality in animals and envisioned a field with strong bridges linking human and animal research. Although some subsequent personality researchers used animal models and some animal researchers used personality constructs, the pioneers' vision was largely unrealized: A comparative research program that specifies how animal studies can inform personality research has yet to be articulated.

In this article, I aim to consider the benefits afforded by a comparative approach to personality psychology as well as the obstacles impeding it. In the first section, I start by bringing together research on animal personality, which is dispersed across the fields of agricultural science, animal behavior, anthropology, psychology, veterinary medicine, and zoology. This is the first major review of animal-personality research, and it integrates several perspectives on a multitude of species ranging from octopuses to chimpanzees. By pulling these studies together, I can address some basic questions about the state of the field. Which species have been studied? What elements of personality have been examined? What methods have been used?

I next consider measurement in animal-personality research, focusing on the two related issues of reliability and validity. Researchers must be able to address both issues before they can move on to more substantive questions. I conclude my review by asking what we have learned from the research and what we can do to learn more.

In the second section of the article, I discuss the conceptual issues associated with making cross-species comparisons. I weigh arguments that have been made for and against generalizations

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[1] Henceforth I simply use the term *animals* to refer to nonhuman animals.

across species, and I offer guidelines to promote the judicious use of cross-species comparisons.

In the third section, I outline a preliminary research agenda composed of three general principles and six specific research questions. I discuss the potential role that animal studies may play in helping us understand the genetic, biological, and environmental bases of personality and illuminate research on personality change, links between personality and health, and personality perception processes. Finally, I ask how this agenda can fit in with current research on human personality.

Review of Animal-Personality Research

Establishing what has been learned about animal personality is a difficult task. A considerable number of publications on animal personality exist, but they are dispersed across a wide range of fields and are hard to find. A person hoping to learn about rhesus monkeys would need to scour journals in primatology, anthropology, animal behavior, and psychology. Moreover, the journals publishing reports on monkey personality are not necessarily the journals in which one would find information about pig or dog personality; a researcher hoping to learn about pigs might find relevant information in applied agricultural journals, and someone interested in dogs would need to look in veterinary or anthrozoological journals. Thus, before any general conclusions can be made about research on animal personality, there is clearly a need to bring these isolated reports together.

Selection of Studies

The purpose of this review is to bring together the extraordinarily diverse range of research on personality in animals. This review surveys which species have been studied, which personality constructs have been used, and which methods have been used. With these three goals in mind, I have reviewed publications that purport to study animal personality, ranging from large-scale, methodologically rigorous investigations to rather informal observations. Given the nascent status of the field, I included some studies that would, by today's standards, be considered methodologically weak; even reports that do not make specific empirical contributions may offer unique theoretical insights and can provide an impetus for subsequent, more focused research. For example, Kolozsvary's (1928) observations of ants and Gerould's (1927) field notes on butterflies provide some interesting thoughts about how one might start to conceptualize personality constructs in these species, even though these articles offer few specific empirical findings. In short, the goal of this review is to provide a basic resource to which researchers can turn when they want to know the species and constructs that have been studied and the methods used.

Definition of personality. The first task is to determine what is meant by "personality." Most theoretical and empirical research on personality has been done in the human domain. Human-personality psychologists come in a variety of orientations and often differ in the personality constructs they emphasize. The phenomena studied by personality psychologists include temperament and character traits, dispositions, goals, personal projects, abilities, attitudes, physical and bodily states, moods, and life stories (Angleitner, Ostendorf, & John, 1990; John & Gosling,

2000; Little, 1996; McAdams, 1996). There is no one specific definition of personality that would satisfy all personality psychologists. Only a very broad (and thus somewhat vague) definition would satisfy most. For example, personality can be defined as those characteristics of individuals that describe and account for consistent patterns of feeling, thinking, and behaving (Pervin & John, 1997), a definition broad enough to capture most phenomena studied by personality psychologists.

Temperament is a construct closely related to personality. In human research, temperament has been defined by some researchers as the inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality (A. H. Buss, 1995; Goldsmith et al., 1987). Although this definition is not adopted uniformly by human researchers (McCrae et al., 2000), animal researchers agree even less about how to define temperament (Budaev, 2000). In some cases, the word *temperament* appears to be used purely to avoid using the word *personality*, which some animal researchers associate with anthropomorphism. Thus, to ensure that my review captured all potentially relevant reports, I searched for studies that examined either personality or temperament.

I did not search for specific personality descriptors such as "aggressive" or "affiliative" because almost all human and animal behavior can be described as related to some domain. To include all such research would have cast my net much too broadly, capturing a vast number of articles that were not really focused on personality constructs but had merely included behaviors related to personality domains. I reasoned that if a study did not even mention personality or temperament in the title, list of keywords, or abstract (i.e., the fields scanned in a keyword search), it was highly unlikely that it would have sufficiently broad focus to be relevant to this review.

By reviewing research on animal personality and temperament, it is possible to see what kinds of phenomena are included in animal studies. Are some conceptions of personality particularly prevalent? Are others neglected?

Literature search procedures. My literature search involved two basic procedures: generating a pool of potentially relevant articles and selecting a subset of articles for inclusion in the final review. These two procedures were used iteratively, such that one cycle generated a pool of potential articles and selected a subset of them for review, and this preliminary pool provided the starting point for a subsequent cycle.

In the initial search cycle, I conducted searches in the PsycINFO and Biosis databases for all articles containing the keywords *animal* and *personality* or *animal* and *temperament*. This step yielded 787 references from PsycINFO and 102 from Biosis. After eliminating duplicates, I examined the abstracts of the remaining reports. Although most articles could be easily classified as clearly relevant or clearly irrelevant, there were a number of peripheral reports that were only distantly or obliquely related to personality and did not fall neatly into the core set of clearly relevant papers. I eliminated the clearly irrelevant reports and read the methods and results sections of the remaining 233 clearly relevant and peripheral articles.

This review cannot include every vaguely relevant reference, so only the most important peripheral studies were retained. Recall that the basic goal of this article is to consider what, if anything, personality researchers can learn from animal studies. Thus, my

decision to include or exclude a peripheral study was based on whether the research had conceptualized and operationalized personality as it is conceptualized in contemporary personality research; the papers needed to do more than describe specific situations and conditions that influence the expression of a single trait or narrow range of behaviors. For example, I did not retain an investigation of agonistic behavior in 12 free-ranging dogs (Pal, Ghosh, & Roy, 1998) because it merely examined the frequencies of agonistic encounters as a function of season and the sex and age of the dogs. Instead of focusing on enduring patterns of behavior across time and situations, the article focused on specific situational determinants of aggressive behavior; it was more like a social psychological study than a study of personality. Other peripheral studies that were not added to the review included those on rat-strain differences in learning and a narrow set of brain-lesion studies done in the 1960s. In short, the selection of peripheral studies was guided from the perspective on contemporary personality research that emphasizes consistent patterns of behavior across situations and deemphasizes narrow, isolated responses to specific situations.

Another criterion guiding selection of peripheral studies was minimizing redundancy. In line with Beach's (1950) plea to base comparative psychology on a diverse range of species, my inclusion threshold was higher for frequently studied species (such as the ubiquitous laboratory rat), and it was lower for research involving rarely studied species. For example, I included one narrow, peripheral study of newts (Halliday, 1976) because it was the only study to examine this species. In other words, I included peripheral reports if the species, methodology, or construct was not already well represented by the clearly relevant articles in the review.

The biggest set of studies not included here according to the preceding criteria is the large number of reports based on Hall's (1934) open-field test. This test was originally designed to provide a standardized index of emotionality in rats and mice. The test involves placing an animal in a novel open space and observing its behaviors, such as its level of activity and its rate of defecation. Hall's test spawned a narrow but abundant field of research on emotionality in rats and mice.[2] Another reason why these reports are not included here is that several major reviews have summarized this literature (Archer, 1973; Boissy, 1995; Eysenck & Broadhurst, 1964; Garcia-Sevilla, 1984; Royce, 1977; Walsh & Cummins, 1976), and inclusion here would unnecessarily duplicate these efforts. However, I did not blindly exclude all research based on the open-field test; I retained articles that raised relevant conceptual issues or presented methods, scales, or constructs not sufficiently represented by the clearly relevant articles.

As noted earlier, studies of animal personality are scattered across a wide range of disciplines and can be hard to find; some of the papers are easy to obtain only when one knows where to look. Thus, in the interest of rescuing potentially interesting research from obscurity, I retained some peripheral reports published in places, such as veterinary journals, that psychologists might otherwise overlook. However, because of the challenges of translation, I added few peripheral studies that were not published in English.

As I retrieved new articles, I examined the references section to identify potentially relevant articles that I might have missed in my previous searches. In addition, because my search procedures and

judgments are far from fallible, I circulated my review to numerous colleagues who checked it for completeness and nominated additional studies for inclusion.

These selection procedures identified 180 of the entries in Table 1, representing personality research on more than 60 species. However, because the keyword *animal* is rather general, my searches could have overlooked publications that mentioned the species by name without using the broader label "animal." Thus, I used the results of my initial search as the starting point for a second cycle of database searches in PsycINFO and Biosis. Specifically, for each of the 64 species identified so far, I conducted a new search, replacing the generic term *animal* with species names (e.g., "bear") in conjunction with the keyword *personality* or *temperament*. After exclusion of the references identified in the previous database searches, this cycle provided a total of 870 new references from the PsycINFO database and 108 references from the Biosis database. Again, after eliminating duplicates, I examined the abstracts to determine which ones were relevant. The vast majority of the articles were irrelevant and could be excluded; for example, many of the articles that included "bear" or "ferret" were not referring to animals but were using these words as verbs. This left 118 potentially relevant articles in the pool. After repeating the selection procedures followed for my initial cycle of searches, I ended up with 17 articles that had not been identified in the previous database searches (12 from PsycINFO and 5 from Biosis). However, 10 of these 17 articles had already been identified by the earlier supplementary steps (e.g., nominations from colleagues) such that this step identified only 7 new studies that would have otherwise been overlooked. This was a reassuring finding, cross validating the effectiveness of the earlier search procedures.

The final summary of research is represented by the 187 entries presented in Table 1. The entries in Table 1 are ordered in terms of the taxonomy shown in Figure 1, which represents the phylogenetic relationships among the species reviewed. The relationships shown visually in Figure 1 are represented by the headings in Table 1. In the figure, a species' ancestry can be determined by studying the branching points in its evolutionary history. In the table, a species' ancestry can be determined from the headings, which provide the names of the clades containing a given species (a clade is a taxonomic group consisting of an ancestor and all its descendants). The headings specify the nested structure of the clades with the most recent clades listed last in the heading. For example, sheep (and goats) are in the clade Caprinae, contained within the older clade Bovidae, in turn contained within the even older clade Ruminantia, and so on. Thus, the heading for sheep includes the major nested clades of which it is a member, starting with Tetrapoda (four-legged vertebrates): Tetrapoda (four-legged

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[2] The open-field test has also been used to examine other traits (e.g., timidity, fearfulness, activity, and exploration) and other species, including guppies (e.g., Budaev, 1997b), paradise fish (e.g., Gervai & Csányi, 1985), quail (e.g., Jones, Mills, & Faure, 1991), domestic chickens (e.g., Jones & Andrew, 1992), gerbils (e.g., Oldham & Morlock, 1970), hamsters (e.g., Jarrard & Bunnell, 1968), ferrets (e.g., Ehrlich & Burns, 1958), foxes (e.g., Harri, Rekilä, & Mononen, 1995), dogs (e.g., Royce, 1955), cattle (e.g., R. Kilgour, 1975), sheep (e.g., Moberg & Wood, 1982), and pigs (e.g., Taylor & Friend, 1986).

Table 1

Summary of Research on Animal Personality: Species, Sample Size, Variables, Method, and Focus of Study

Species	Study	Sample size	Example of Coding (C) or rating (R)	Example of Broader dimension	Focus of study

VERTEBRATES

Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Hominidae (gorilla, chimpanzee, human)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
Chimpanzee	Bard & Gardner (1996)	29	Body motion (C)	Activity	Influence of early maternal environment on temperament and cognition
	Buirski et al. (1978)	23	Belligerent (R)[a]	Aggression	Assess reliability of subjective ratings of personality. Relate personality to dominance rank and sex
	Buirski & Plutchik (1991)	1	Belligerent (R)	Aggression	Test personality instrument's ability to detect psychological well-being
	Crawford (1938)	9	Friendliness (R)		Assess reliability of subjective ratings
	Dutton et al. (1997)	24	Enthusiastic (R)	Sociability	Compare structure underlying personality ratings made by different observers
	Hebb (1949)	30	Response to humans (C)	Friendliness	Determine feasibility of measuring complex individual differences in temperament
	King & Figueredo (1997)	100	Excitable (R)	Emotionality	Assess reliability of subjective ratings. Identify broad personality dimensions
	Lilienfeld et al. (1999)	34	Confident (R) Bluff display (C)	Psychopathy	Develop psychopathy measure and relate it to sex, personality variables, and behavior codings
	Murray (1998)	59	Tense (R)[b]	Confidence	Identify broad dimensions of personality and relate them to group size and rearing conditions
	van Hooff (1973)	25	Embracing (C)	Affinity	Identify broad dimensions of social behavior
	Yerkes & Yerkes (1936)	29	Response to snake (C)	Fearfulness	Describe fear responses to novel objects
Gorilla	Gold & Maple (1994)	298	Tense (R)[b]	Fearfulness	Identify broad personality dimensions. Provide normative personality ratings

Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Cercopithecidae, *Cercopithecus* (vervet monkey)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
Vervet monkey	Fairbanks & McGuire (1993)	83	Grooming (C)	Maternal protectiveness	Relate early maternal protectiveness to subsequent responses to novel objects
	McGuire et al. (1994)	97	Assertive (R)	Social ability	Assess reliability of subjective ratings. Identify broad personality dimensions. Relate personality to sex, age, social status, and group composition

Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Cercopithecidae, Unnamed clade, *Macaca* (macaques)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
Japanese macaque	J. A. French (1981)	3	Contact play (C)	Playfulness	Identify individual differences in play behavior
	Martau et al. (1985)	14	Belligerent (R)[a]	Rejection	Assess reliability of ratings
Stumptailed macaque	Figueredo et al. (1995)	13	Tense (R)[b]	Confidence	Assess reliability, stability, and validity of personality dimensions
	Nash & Chamove (1981)	13	Relaxed (R)		Identify broad personality dimensions. Relate personality to dominance rank and self-aggression
Longtailed macaque	Heath-Lange et al. (1999)	3	Response to capture (C)		Describe developmental trends and cross-species differences in temperament
Lion-tailed macaque	Clarke & Lindburg (1993)	5	Frequency of foraging (C)		Describe cross-species differences in behavior
Cynomolgus macaque	Clarke & Lindburg (1993)	5	Frequency of foraging (C)		Describe cross-species differences in behavior
Pig-tailed macaque	Caine et al. (1983)	10	Aggressive (R)[b]	Confidence	Assess reliability of ratings. Relate personality ratings to dominance rank and early separation experience

Table 1 (*continued*)

Species	Study	Sample size	Example of Coding (C) or rating (R)	Broader dimension	Focus of study
			Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Cercopithecidae, Unnamed clade, *Macaca* (macaques) (*continued*)		
Pig-tailed macaque (*continued*)	Heath-Lange et al. (1999)	7	Response to capture (C)		Describe developmental trends and cross-species differences in temperament
	Reite & Short (1980)	21	Area of enclosure animal travels (C)	Activity	Relate behavioral codings to physiological measures
	Westergaard et al. (1999)	30	Open-mouth threats (C)	Aggression	Relate behavioral codings to biochemical measures
Rhesus monkey	Bolig et al. (1992)	22	Excitable (R)[b]	Confidence	Assess reliability and validity of subjective ratings of reactivity and personality Identify broad personality dimensions Relate personality to reactivity, dominance rank, age, and sex
	Capitanio (1984)	12	Cage shaking (C)	Social ability	Relate early rearing experience to subsequent social ability
	Capitanio (1999)	42	Excitable (R)[b] Initiate threat (C)	Equable	Identify broad personality dimensions Relate personality dimensions to behavior codings over time and across situations
	Capitanio et al. (1999)	18	Playful (R)[b]	Sociable	Relate personality to physiological indexes of disease progression
	Chamove (1974)	91	Withdrawal behavior (C)	Hostility	Develop a device and system for scoring social behavior Identify broad behavioral dimensions
	Chamove et al. (1972)	168	Social play (C)	Affiliation	Identify broad personality dimensions
	Clarke & Snipes (1998)	48	Anxious (R)		Relate temperament to rearing experience, sex, and age
	Freedman & Rosvold (1962)	7	Attack (C)	Aggression	Relate aggression and anxiety to sexual behavior
	Kalin et al. (1998)	50	Response to human (C)	Fearfulness	Relate fearfulness behaviors to brain activity and cortisol levels
	Locke, Locke et al. (1964); Locke, Morgan et al. (1964)	12	Approach behaviors (C)	Dominance	Develop series of behavioral tests and assess their reliability Identify broad dimensions of social behavior
	Maestripieri (2000)	10	Scratching behaviors (C)	Emotionality	Develop behavioral measure of emotionality and examine stability over time and across situations
	Schneider et al. (1991)	23	Fearfulness (R) Response to cuddling (C)		Relate temperament ratings to behavioral codings over time and to environmental enrichment in infancy
	Spencer-Booth & Hinde (1969)	16	Response to novel objects (C)		Develop series of behavioral tests and assess their reliability Examine relations between tests and temporal stability
	Stevenson-Hinde et al. (1980a)	25–31	Response to novel objects (C)		Examine consistency in behaviors over time and across situations
	Stevenson-Hinde et al. (1980b)	45	Aggressive (R)[b]	Confidence	Assess reliability and validity of subjective ratings of personality Identify broad personality dimensions Examine temporal stability of dimensions
	Stevenson-Hinde, Zunz, & Stillwell-Barnes (1980)	25	Time off mother (C) Fearful (R)[b]	Confidence	Examine consistency in behaviors over time and across situations Relate behaviors to broad personality dimensions
	Stevenson-Hinde & Zunz (1978)	45	Aggressive (R)[b]	Confidence	Assess reliability of subjective ratings of personality Identify broad personality dimensions
	Suomi (1987)	12	Area of enclosure animal travels (C)	Reactivity	Describe behavioral and physiological characteristics of reactivity Examine environmental and genetic influences on reactivity

(*table continues*)

Table 1 (*continued*)

Species	Study	Sample size	Example of Coding (C) or rating (R)	Example of Broader dimension	Focus of study
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Cercopithecidae, Unnamed clade, *Macaca* (macaques) (*continued*)				
Rhesus monkey (*continued*)	Suomi (1991)	24	Heart rate (C)	Reactivity	Describe behavioral and physiological characteristics of reactivity Examine environmental and genetic influences on reactivity
	Suomi et al. (1996)	8	Chasing, wrestling (C)		Examine consistency in behaviors over time and across situations
	Westergaard et al. (1999)	31	Open-mouth threats (C)	Aggression	Relate behavioral codings to biochemical measures
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Catarrhini, Cercopithecidae, Unnamed clade, *Papio* (baboon)				
Baboon	Buirski et al. (1973)	7	Belligerent (R)[a]	Rejection	Assess reliability of subjective ratings of personality Relate personality to dominance rank
	Heath-Lange et al. (1999)	4	Response to capture (C)		Describe developmental trends and cross-species differences in temperament
	Martau et al. (1985)	6	Belligerent (R)[a]	Rejection	Assess reliability of ratings
	Sapolsky & Ray (1989)	30–45	Threats (C)	Dominance	Identify individual styles of dominance Relate dominance style to endocrine levels and dominance tenure
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Platyrhini, Cebinae, *Cebus* (capuchin)				
Tufted capuchin	Byrne & Suomi (1995)	17	Exploration of food (C)	Exploration	Examine development of social and exploratory behaviors and activity
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Unnamed clade, Platyrhini, Cebinae, *Saimiri* (squirrel monkeys)				
Gothic-arch squirrel monkey	Martau et al. (1985)	5	Belligerent (R)[a]	Rejection	Assess reliability of ratings
Roman-arch squirrel monkey	Martau et al. (1985)	8	Belligerent (R)[a]	Rejection	Assess reliability of ratings
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Primates, Strepsirhini (bushbaby)				
Small-eared bushbaby	Watson & Ward (1996)	45	Area of enclosure animal travels (C)	Activity	Assess reliability of behavioral codings Examine consistency of behaviors across situations Identify broad dimensions of behavior Relate dimensions to age, sex, handedness, and problem-solving
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Ursidae (bear)				
Brown bear	Fagen & Fagen (1996)	7	Travel (C) Solitary (R)[b]	Irritable	Assess reliability of subjective ratings Relate personality to behavioral codings
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Mustelidae (ferret, mink)				
Ferret	Gosling & Bonnenburg (1998)	126	Anxious (R)		Provide sample ratings
Mink	Hansen (1996)	3,636	Reaction to stick inserted in cage (C)	Fearfulness	Determine feasibility of modifying temperament using selective breeding
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Felidae (lion, cheetah, cat)				
Lion	Heinsohn & Packer (1995)	34	Leading or assisting attacks (C)	Cooperation	Examine consistent individual differences in response to aggression
Cheetah	Wielebnowski (1999)	44	Calm (R)[b]	Tense–Fearful	Assess reliability of subjective ratings Identify broad personality dimensions Relate personality to breeding status, sex, and rearing experience

Table 1 (*continued*)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
			Example of		
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Felidae (lion, cheetah, cat) (*continued*)				
Cat	Adamec (1975)	44	Response to unfamiliar conspecific (C)		Examine consistency in behaviors over time and across situations
	Durr & Smith (1997)	22	Response to unfamiliar conspecific (C)		Test cross-situational stability of responses to novel objects Relate behaviors to dominance rank
	Feaver et al. (1986)	14	Chasing another cat (C) Active (R)[b]		Assess reliability of personality ratings Test validity of ratings by relating them to behavioral codings
	Gosling & Bonnenburg (1998)	440	Anxious (R)		Provide sample ratings
	Gosling & John (1998)	382	Warm (R)	Affection	Identify broad personality dimensions
	Meier & Turner (1985)	62	Response to human (C)	Trust	Assess shy and trusting animals
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Canidae (wolf, dog, fox)				
Wolf	Fentress (1967)	1	Response to stranger (C)	Reaction to novelty	Chart the behavioral development of a hand-reared wolf
	Fox (1972)	18	Response to humans (C)	Fearfulness	Relate individual differences in behaviors to social rank
	MacDonald (1983)	5	Response to novel object (C)		Examine consistency of behaviors over time and across situations
Dog	Cattell & Korth (1973)	101	Activity in response to bell (C)	Emotionality	Identify broad dimensions of behavior
	Coren (1998)	133[c]	Friendliness to strangers (R)	Sociability	Identify broad personality dimensions Identify clusters of breeds on basis of personality dimensions
	Diederich (1995)	31	Time spent resting (C)	Activity	Chart development of individual differences in activity
	Freedman (1958)	32	Ability to inhibit eating (C)		Determine impact of rearing style on subsequent ability to inhibit behavior
	Goddard & Beilharz (1983)	887	Nervousness (R)		Assess reliability of subjective ratings Identify broad personality dimensions Relate dimensions to guide-dog suitability
	Goddard & Beilharz (1984a, 1984b, 1985, 1986)	102	Response to stranger (C)	Fearfulness	Identify broad dimensions of behavior Relate dimensions to sex, age, and experience Assess ability of puppy tests to predict adult behavior
	Goodloe & Borchelt (1998)	2,018	Friendly tail wagging (C)	Friendliness	Identify behavioral dimensions
	Gosling & Bonnenburg (1998)	1,022	Anxious (R)		Provide sample ratings
	Gosling & John (1998)	382	Warm (R)	Affection	Identify broad personality dimensions
	Hart & Hart (1985a, 1985b, 1988); Hart & Miller (1985); Draper (1995)	56[c]	Demand for affection (R)	Reactivity	Identify broad personality dimensions Identify clusters of breeds on basis of personality dimensions
	J. A. Murphy (1995)	89	Temperament (R)		Assess reliability of subjective ratings Relate temperament to guide-dog suitability
	J. A. Murphy (1998)	89	Ears back (C)	Anxiety	Identify behavioral markers of temperament categories
	Netto & Planta (1997)	112	Response to being rapidly surrounded by 3 strangers (C)	Aggression	Identify behavioral tests to predict aggression in dogs
	Royce (1955)	53	Timidity (C)	Emotionality	Identify broad dimensions of behavior
	Serpell (1983)	57	Playfulness (R)		Identify set of descriptors Compare ratings of actual and ideal dogs
	Slabbert & Odendaal (1999)	167	Response to sudden appearance of a stranger (C)	Temperament	Predict success as a police dog
	Topál et al. (1998)	51	Response to separation from owner (C)	Anxiety	Identify broad dimensions of behavior

(*table continues*)

Table 1 (continued)

Species	Study	Sample size	Example of Coding (C) or rating (R)	Example of Broader dimension	Focus of study
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Canidae (wolf, dog, fox) (continued)					
Dog (continued)	Wilsson & Sundgren (1997)	2,107	Affability (R)		Determine feasibility of using subjective evaluations of behavior in tests to predict subsequent work performance Identify sex and breed differences Identify major behavioral dimensions
Fox	Harri et al. (1995)	158	Open field activity (C)[d]	Activity	Identify broad dimensions of behavior and relate them to environmental conditions
	Pedersen & Jeppesen (1990)	78	Response to novel stimuli (C)[d]		Examine effects of early handling on subsequent stress levels
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Carnivora, Hyaenidae (hyena)					
Spotted hyena	Gosling (1998)	34	Bold (R)[b]	Assertiveness	Assess reliability of subjective ratings Identify broad personality dimensions Relate personality to dominance rank, appearance, age, and sex
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Lagomorpha (rabbit)					
Rabbit	Gosling & Bonnenburg (1998)	29	Anxious (R)		Provide sample ratings
	Meijsser et al. (1989)	118	Exploring environment (C)[d]	Boldness	Identify broad dimensions of behavior
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Murinae, Rattus (rat)					
Rat	Billingslea (1940, 1941, 1942)	24–46	Response to novel environment (C)	Emotionality	Relate emotionality to other traits, behaviors, and physical characteristics
	Blanchard et al. (1986)	55	Response to humans (C)	Defensive	Compare defensive behaviors of wild and laboratory rats
	Dellu et al. (1993, 1996)	14–40	Exploration of maze (C)	Novelty seeking	Relate novelty responses to responses to environments, food, and drugs and to neuroendocrinology
	Farris & Yeakel (1945)	73	Open-field defecation (C)[d]	Emotionality	Compare emotionality of gray Norway and Wistar albino rats
	Gray (1965)	48	Exploratory behavior (C)	Emotionality	Describe individual differences and sex and strain differences in behavior
	Gray & Lalljee (1974)	32	Open-field defecation (C)[d]	Emotionality	Examine sex differences in emotionality
	Hall (1938)	75	Open-field defecation (C)[d]	Emotionality	Examine heritability of emotionality
	Hall & Klein (1942)	30	Retaliatory attacks	Aggression	Demonstrate individual differences in aggression Assess reliability of behavioral codings Examine consistency in behaviors across situations
	Maier et al. (1988)	65	Open-field activity (C)[d]	Exploration	Identify broad dimensions of behavior and relate them to spatial behavior
	Negrão & Schmidek (1987)	37	Time spent exploring (C)	Exploration	Identify individual differences in behavior and consistency over time
	Ostaszewski et al. (1992); Ostaszewski & Pisula (1994)	48–99	Open-field activity (C)[d]	Reactivity	Examine genetic contribution to, and sex and strain differences in temperament
	Pellis & McKenna (1992)	224	Susceptibility to apomorphine[e]	Boldness	Relate boldness to play fighting
	Pisula (1994)	54	Open-field activity (C)[d]		Demonstrate importance of examining sequence in which behavior is performed
	Utsurikawa (1917)	28	Tendency to bite (C)	Savageness	Compare behaviors of inbred and outbred strains
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Murinae, Mus (mouse)					
Mouse	Benus & Röndigs (1997)	42	Latency to attack (C)	Aggression	Examine contribution of maternal environment to subsequent aggression
	Dawson (1932)	1,232	Time to run a set distance (C)	Wildness	Compare wildness–tameness of wild and domesticated mouse strains

Table 1 (*continued*)

Species	Study	Sample size	Example of		Focus of study
			Coding (C) or rating (R)	Broader dimension	
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Murinae, Mus (mouse)					
Mouse (*continued*)	Durand (1961)	2		Temperament	Present naturalistic observations
	Flint et al. (1995)	879	Open-field activity (C)[d]	Emotionality	Identify genetic basis of emotionality
	Gershenfeld et al. (1997)	514	Open-field activity (C)[d]	Emotionality	Identify genetic basis of emotionality
	Lindzey et al. (1960, 1963)	259–271	Open-field defecation (C)[d]	Emotionality	Examine effects of infantile trauma on personality development
	Royce & Poley (1975)	Not reported	Open-field activity (C)[d]	Emotionality	Examine replicability of emotionality facets across testing conditions, strains, and in response to injections with psychoactive drugs
	Royce et al. (1975)	775	Open-field activity (C)[d]	Emotionality	Examine heritability of facets of emotionality
	Terranova & Laviola (1995)	256	Digging activity (C)	Exploration	Relate individual differences in behaviors to weaning age and sex
	Whitney (1970)	256	Response to noise (C)	Timidity	Compare behaviors of two inbred strains
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Sciurinae, Spermophilus (ground squirrel)					
Ground squirrel	Coss & Biardi (1997)	90	Response to snakes (C)		Examine consistency in antipredator behaviors over time and across situations
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Sciurinae, Marmota (marmot)					
Yellow-bellied marmot	Armitage (1986a)	31	Maze activity (C)	Dispersion	Relate individual differences in behaviors to dispersion from natal group
	Armitage (1986b)	59	Response to mirror (C)	Sociability	Relate mirror responses to sociability and reproductive success
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Glires, Rodentia, Sciurinae, Cynomys (prairie dog)					
Prairie dog	Loughry & Lazari (1994)	203	Time in social interactions (C)		Chart age differences in distinctiveness of behavioral profiles
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Cetacea, Odontoceti (dolphin)					
Dolphin	Kellerman (1966)	3	Cautious (R)[a]	Exploration	Determine feasibility of subjectively rating dolphins
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Suidae (pig)					
Pig	Andersen, Bøe, Fœrevik, Janczak, & Bakken (2000)	84	Exploration of maze (C)	Anxiety	Identify broad dimensions of behavior
	Erhard & Mendl (1997, 1999); Erhard et al. (1997, 1999)	29–219	Response to unknown conspecific (C)	Aggression	Assess viability of assessing individual differences in aggressiveness
	Forkman et al. (1995)	110	Response to novel objects (C)	Exploration	Relate behavioral responses to coping patterns and aggression Identify broad personality dimensions
	Hessing et al. (1993)	218	Social confrontation (R)	Aggression	Examine consistency in behaviors over time and across situations
	Lawrence et al. (1991)	62	Resistance to restraint (R)	Responsivity	Identify broad dimensions of behavior and relate them to social and nonsocial tests
	Mount & Seabrook (1993)	26	Aggressive behaviors (C)		Examine consistency in behaviors over time
	Ruis et al. (2000)	128	Response to human (C)		Examine consistency in behaviors over time and across situations
	Spoolder et al. (1996)	208	Response to novel objects (C)	Exploration	Examine consistency in behaviors over time and across situations Identify broad personality dimensions

(*table continues*)

Table 1 (*continued*)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
			Example of		
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Ruminantia, Cervidae (deer)					
Deer	Pollard et al. (1994)	86	Response to human (C)	Exploration	Examine consistency in behaviors over time and across situations Identify broad personality dimensions
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Ruminantia, Bovidae, Bovinae (cow)					
Cow	Becker & Lobato (1997)	40	Responses to humans (C)	Aggression	Relate early rearing experience to subsequent aggression and escape behavior
	Boissy & Bouissou (1988)	40	Response to feeding in unfamiliar pen (C)	Fearfulness	Relate early rearing experience to subsequent fearfulness
	Boissy & Bouissou (1995)	14	Response to feeding in unfamiliar pen (C)	Fearfulness	Examine consistency in behaviors within and across situations
	Dickson et al. (1970)	1,017	Temperament (docility; R) Bunting (C)		Relate temperament to dominance behaviors, milk yield, age, and size and determine heritability of temperament
	Grandin (1993)	155	Response to restraint (C)	Agitation	Examine consistency in behaviors over time and across situations
	Grandin et al. (1995)	1,500	Response to restraint (C)		Relate behaviors to position of hair whorl on animal's face
	Kerr & Wood-Gush (1987)	20	Response to human touch (C)	Temperament	Examine consistency in temperament over time Relate behaviors to measure of temperament
	R. Kilgour (1975)	50	Open-field activity (C)[d] Temperamental (R)	Temperament	Examine consistency in temperament over time and across situations Relate behaviors to ratings of temperament
	Randle (1998)	57	Response to novel object (C)		Relate behaviors to position of hair whorl on animal's face
	Tulloh (1961)	72	Response to restraint (C) Temperamental (R)	Temperament	Relate behaviors to ratings of temperament and examine breed differences
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Ruminantia, Bovidae, Caprinae, Capra (goat)					
Goat	Lyons et al. (1988)	30	Response to humans (C)	Timidity	Examine consistency in temperament over time and across situations Assess genetic and biological bases of temperament
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Ruminantia, Bovidae, Caprinae, Ovis sheep					
Sheep	R. J. Kilgour (1998)	142	Response to human (C)		Examine consistency in behaviors over time and across situations
	Markowitz et al. (1998)	96	Response to humans (C)	Timidity	Relate early rearing experience to subsequent timidity
	Moberg & Wood (1982)	29	Open-field activity (C)[d]		Relate early rearing experience to subsequent behavior and physiological indexes
	Scott (1942)	18	Looking at other sheep (C)	Investigation	Describe social behaviors of sheep
	Torres-Hernandez & Hohenboken (1979)	164	Response to tethered dog (C) Emotional behavior (R)	Emotionality	Assess viability of assessing emotionality and identify breed differences
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Perrisodactyla, Equidae (donkey, horse)					
Donkey	J. M. French (1993)	45	Friendly (R)	Obduracy	Assess reliability of subjective ratings Identify broad personality dimensions
Horse	Anderson et al. (1999)	103	Friendly (R) Response to novel object (C)	Reactivity	Predict suitability for therapeutic riding programs from trait ratings, behavior codings, and physiological measures
	Estes (1952)	100	Affection toward humans (R)	High-spirits	Identify relation between temperament and racing ability

Table 1 (*continued*)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
			Example of		

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Perrisodactyla, Equidae (donkey, horse) (*continued*)					
Horse (*continued*)	Gosling & Bonnenburg (1998)	10	Anxious (R)		Provide sample ratings
	Le Scolan et al. (1997)	72	Response to novel object (C) Nervous when ridden (R)	Emotionality	Relate behaviors to ratings
	McCann et al. (1988)	32	Activity (C) Nervous (R)	Emotionality	Assess reliability of subjective ratings Relate emotionality to behavioral and physiological measures
	Mills (1998)	20	Affectionate (R)		Assess reliability of subjective ratings
	Molina et al. (1999)	1,273	Temperament (R)		Estimate heritability of temperament
	Morris et al. (2000)	10	Tense and jittery (R)	Neuroticism	Assess reliability of subjective ratings in terms of human personality dimensions
	Wolff et al. (1997)	42	Response to familiar environment (C)	Emotionality	Develop tests to measure individual differences in temperament
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Perrisodactyla, Rhinocerotidae (rhino)					
Rhinoceros	Carlstead et al. (1999)	60	Anxious (R)[a] Response to novel object (C)	Fearful	Assess reliability of behavioral ratings Identify behavioral dimensions Test validity of dimensions by relating them to behavioral codings Relate dimensions to origin (wild vs. captive born), age, sex, and breeding success
Tetrapoda (four-legged vertebrates), Amniota, Mammalia (mammals), Insectivora (hedgehog)					
Hedgehog	Gosling & Bonnenburg (1998)	13	Anxious (R)		Provide sample ratings
Tetrapoda (four-legged vertebrates), Amniota, Diapsida (reptiles and birds), Archosauromorpha, Aves (birds), Galliformes (chicken)					
Chicken	Hasuo (1935)	11	Response to other animals (C)	Nervousness	Relate individual differences in nervousness to maternal environment and behavior of conspecifics
	Jones (1988)	15	Response to novel object (C)	Fearfulness	Assess repeatability of behavioral tests
	Webster & Hurnik (1990)	273	Open-field activity (C)[d]	Fearfulness	Examine consistency of behaviors over time
Tetrapoda (four-legged vertebrates), Amniota, Diapsida (reptiles and birds), Archosauromorpha, Aves (birds), Passeriformes (quail, great tit, zebra finch, oystercatcher)					
Japanese quail	Jones et al. (1991)	168	Open-field activity (C)[d]	Fearfulness	Identify single dimension underlying various fear responses
Great tit	Verbeek et al. (1994, 1996)	67–72	Response to novel environment (C)	Exploration	Examine consistency of behaviors over time and across situations
Zebra finch	Figueredo et al. (1995)	5	Tense (R)[b]	Confidence	Assess reliability, stability, and validity of personality dimensions
Oystercatcher	Goss-Custard et al. (1982)	28	Aggressive encounters (C)		Relate aggression to success of feeding strategies
Tetrapoda (four-legged vertebrates), Amniota, Diapsida (reptiles and birds), Lepidosauromorpha (garter snake)					
Garter snake	Herzog & Burghardt (1988)	38	Attacks test stimulus (C)	Defensive temperament	Assess temporal consistency in responses to threats
	Herzog et al. (1989)	98	Attacks test stimulus (C)	Defensive temperament	Assess interspecies and intraspecies consistency in responses to threats
Tetrapoda (four-legged vertebrates), Amphibia, Caudata, Salamandridae (newt)					
Newt	Halliday (1976)	5	Response to female (C)	Libidinousness	Assess individual differences and temporal consistency of males' sexual responses to females

(*table continues*)

Table 1 (continued)

Species	Study	Sample size	Example of Coding (C) or rating (R)	Example of Broader dimension	Focus of study
Osteichthyes (fish), Acanthopterygii, Perciformes, Centrarchidae (pumpkinseed sunfish)						
Pumpkinseed sunfish	Coleman & Wilson (1998)	138	Response to novel objects (C)	Boldness	Examine context specificity of boldness
	Wilson et al. (1993)	50–411	Response to novel objects (C)	Boldness	Examine temporal stability of boldness and relate it to diet, predator risk, and parasite load
Osteichthyes (fish), Acanthopterygii, Perciformes, Labroidae, Labridae (wrasse)						
European wrasse	Budaev (1997a)	16	Response to novel environment (C)	Boldness	Relate boldness to schooling tendency
Osteichthyes (fish), Acanthopterygii, Perciformes, Labroidae, Cichlidae (cichlids, cichlasoma)						
Midas cichlid	Francis (1990)	41	Exposure to mirror (C)	Aggression	Relate tests of aggression to social rank and sex
Convict cichlid	Budaev et al. (1999b)	46	Exposure to mirror (C)	General activity	Identify broad dimensions of behavior
Lion-headed cichlid	Budaev et al. (1999a)	12	Exposure to mirror (C)		Identify behaviors that are consistent over time and across situations
Firemouth	Shaklee (1963)	13	Light avoidance (C)	Fearfulness	Assess interspecies differences in temperament
Osteichthyes (fish), Acanthopterygii, Perciformes, Belontiidae (paradise fish)						
Paradise fish	Gervai & Csányi (1985)	120	Open-field activity (C)[d]	Exploration	Identify broad dimensions of behavior
Osteichthyes (fish), Acanthopterygii, Cyprinodontiformes, Poecilliidae (guppy)						
Guppy	Budaev (1997b)	29	Open-field activity (C)[d]	Exploration	Examine individual differences in exploratory and social behavior
	Warren & Callaghan (1975)	15	Open-field activity (C)[d]		Examine individual differences in activity over time and relate to sex and ovarian cycle
Platy variatus	Shaklee (1963)	18	Light avoidance (C)	Fearfulness	Assess interspecies differences in temperament
Osteichthyes (fish), Gasterosteiformes, Gasterosteidae, Gasterosteus (three-spined stickleback)						
Three-spined stickleback	Huntingford & Giles (1987)	120	Duration in weed (C)	Boldness	Identify broad dimensions of behavior underlying responses to predators
Osteichthyes (fish), Ostariophysi, Cypriniformes, Leuciscinae (chub)						
Dark chub	Katano (1987)	72	Size of home range (C)		Relate social structure to behavioral and physical characteristics
Osteichthyes (fish), Ostariophysi, Cypriniformes, Rasborinae (zebrafish)						
Zebra fish	Shaklee (1963)	11	Light avoidance (C)	Fearfulness	Assess interspecies differences in temperament
Osteichthyes (fish), Ostariophysi, Cypriniformes, Cyprininae (goldfish)						
Goldfish	Shaklee (1963)	10	Light avoidance (C)	Fearfulness	Assess interspecies differences in temperament
INVERTEBRATES						
Unnamed Clade, Arthropoda (ant, butterfly)						
Ant	Bonavita-Cougourdan & Morel (1988)	141	Response to nestmate (C)		Measure individual differences in behavior
	Kolozsvary (1928)	35	Nervousness (R)		Describe individual differences in escape behavior
	Retana & Cerda (1991)	75–400	Care of cocoons (C)		Measure individual differences in behavior

Table 1 (*continued*)

Species	Study	Sample size	Coding (C) or rating (R)	Broader dimension	Focus of study
			Example of		
		Unnamed Clade, Arthropoda (ant, butterfly) (*continued*)			
Butterfly	Gerould (1927)	11	Gregariousness (R)		Describe behavioral and physical characteristics of several species of butterfly
			Unnamed Clade, Mollusca (octopus)		
Octopus	Mather & Anderson (1993)	44	Ink squirt (C)	Reactivity	Identify broad personality dimensions
	Sinn et al. (2000)	73	Ink squirt (C)	Active engagement	Identify broad temperament dimensions, and examine their development and heritability

Note. The entries are ordered in terms of the phylogenetic relationships depicted in Figure 1. To save space, the table does not include the more than 100 species in which Glickman and Sroges (1966) examined curiosity-related behaviors. The fifth column lists examples of the broader dimension to which the more specific behavioral tests or trait ratings were statistically or conceptually related. For example, Boldness was one of the traits loading on the Assertiveness principal component in Gosling's (1998) study of hyenas. Some studies did not link the behaviors or traits to broader dimensions.
[a] Rating instrument wholly or partially based on the Emotions Profile Index (Plutchik & Kellerman, 1974). [b] Rating instrument wholly or partially based on Stevenson-Hinde and Zunz's (1978) instrument. [c] Subjects were breed prototypes (e.g., the prototypical Labrador), not individuals. [d] The open-field test (Hall, 1934) is a widely used procedure in which an animal is placed in an open area and its reaction (e.g., ambulatory activity, exploration, defecation) is monitored. [e] Physiological measure used instead of trait rating or behavior coding.

vertebrates), Amniota, Mammalia (mammals), Cetartiodactyla, Artiodactyla, Ruminantia, Bovidae, Caprinae, Ovis (sheep).

Whether readers consider the overview comprehensive or even representative will depend on where they draw the line on the issues discussed here and on the definition of personality they choose to adopt. Although I have made every effort to represent all major research on animal personality, readers will inevitably be able to come up with alternative search criteria or point to absent
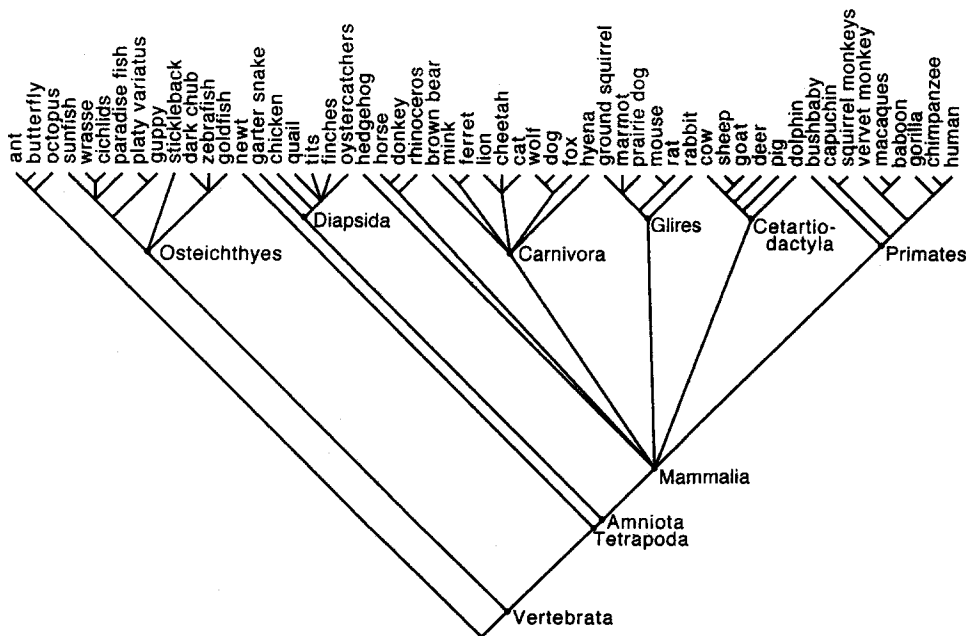
Figure 1. Phylogenetic relationships among the species reviewed in Table 1. Branch divergences represent speciation events, in which an ancestral species gives rise to two or more descendant species. Thus relationships among species are depicted by the branching pattern of the tree. For example, sheep and goats share a common ancestor with each other more recently than either do with pigs, meaning that sheep are more closely related to goats than to pigs.

publications that they would have included, and this review is limited to the extent it has missed such studies.[3]

Content of the Review

An examination of Table 1 invites a number of observations about the field of animal-personality research. First, as one might expect, the personality phenomena studied in animals are only a subset of the personality phenomena studied in humans. Most animal research has focused on traits, behaviors, and abilities, but no research has examined personal projects, identity, attitudes, and life stories. Presumably, this discrepancy between the domains of human and animal personality is largely driven by the nature of the latter concepts, which require participants to articulate their internal motives, feelings, and beliefs. Clearly, any phenomena dependent on self-reports by the research participants cannot be examined in nonhuman populations. More fundamentally, constructs such as projects, identity, and life stories may depend on complex mental representations of the self, some of which may be uniquely human (Gallup, 1977; Robins, Norem, & Cheek, 1999). It is not surprising, then, that empirical research on animal personality is essentially composed of studies of traits.

Second, almost all research on animal personality has focused on within-species comparisons rather than cross-species comparisons. The distinction between within- and cross-species comparisons is important, and I return to it later. Third, many of the studies focused on broad dimensions of personality (e.g., Sociability) and examined how they related to other characteristics of the individuals (e.g., age) and their environments (e.g., level of maternal care). For example, Wilson, Coleman, Clark, and Biederman (1993) examined shyness in pumpkinseed sunfish, comparing shy fish with bold fish in terms of their diet (measured in terms of stomach contents) and how quickly they acclimated to captivity. Example dimensions are shown in the fifth column of Table 1.

Fourth, many of the studies in Table 1 attempted to relate the broad dimensions to specific behaviors or to relatively narrow traits, examples of which are shown in the fourth column of Table 1. Fifth, the studies in Table 1 illustrate a wide variety of research objectives, with personality serving as the primary focus for some studies but being less central to others (the sixth column in Table 1 briefly summarizes how personality relates to the goals of the studies). Indeed, much of the research reviewed here was conducted by investigators whose primary interests were not in personality. Over the course of their investigations into other phenomena, the researchers apparently notice personality characteristics in their nonhuman subjects: "When observers spend hours recording behavior, they end up not only with behavioral data, but also with a clear impression of individuals" (Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980b, p. 66; also see Hebb, 1946). It would seem that animal researchers come to use personality constructs to refer to consistent individual differences in animal behavior in much the same way that humans use personality constructs to describe one another. For example, researchers working with hyenas might describe individuals that consistently use novel ways to approach situations and address problems (e.g., by finding many different ways to escape their enclosures) as more creative than hyenas that do not behave this way.

To provide a conceptual structure for the diverse research, I next describe two frameworks by which the studies in Table 1 can be classified. The first framework is based on the type of comparison being made, distinguishing studies that concentrate on differences among individuals within the same species from those that focus on cross-species differences. The second framework is based on the method used, dividing the studies into those based on assessments of animals over a series of behavioral tests and those based on ratings of the animals. Next I summarize the evidence regarding the reliability of personality assessments of animals, in terms of interobserver agreement and test–retest reliability. I use this evidence as a basis for raising questions about seven parameters that may influence interobserver agreement. The answers to these questions will serve as a practical guide to animal researchers. I next consider the evidence regarding the validity of animal-personality assessments along with four potential challenges to validity that must be addressed by future research. To conclude my review of the literature, I ask what can be learned from current research on animal personality. I identify several personality dimensions that appear to enjoy some degree of cross-species generality, but I also highlight some steps that need to be taken to permit a fuller integration of the animal research.

Framework 1: Within-Species and Cross-Species Comparisons

Most of the articles in Table 1 focus on differences among individuals of a single species and are, therefore, within-species comparisons. Within-species (or intraspecies) comparisons are what people normally mean when they talk about personality comparisons, such as comparing Jill's level of friendliness with John's, where Jill and John are members of the same species. In contrast, some of the articles in Table 1 compare the personality characteristics of one species as a whole with the personality characteristics of another species; these studies are cross-species (or interspecies) comparisons. Cross-species comparisons are sometimes made in terms of a trait common to both species; for example, firemouth fish are more fearful than goldfish (Shaklee, 1963), and lion-tailed macaques are more curious than cynomolgus macaques (Clarke & Lindburg, 1993). Other cross-species comparisons concern the existence or nonexistence of a trait in different species; for example, a dimension of curiosity appears to be present in meerkats but absent in Cuban ground iguanas (Glickman & Sroges, 1966).

In human-personality research, the distinction between within-species and cross-species comparisons does not arise, because studies are performed on a single species: humans. However, in the realm of animal personality, the distinction is important, because the type of comparison made drastically changes the meaning of the comparison. To illustrate, consider the following scenario. I tell you a black mamba is trapped in the room next door, and you ask me whether it is aggressive. If I adopt a within-species framework, I may respond, "No, it is very unaggressive," because it has attacked only two people in the last hour, well below the norm for

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[3] To provide a resource for readers who consider my selection criteria too narrow, I have created a bibliography Web site that lists even the animal-personality research that was beyond the focus of the present review; the bibliography is located on the World Wide Web at http://homepage.psy.utexas.edu/HomePage/Faculty/Gosling/bibliography.htm.

this species of snake. If, on the other hand, I adopt a cross-species framework, I may respond, "Yes, of course it's aggressive," because it is a black mamba, a highly aggressive species of snake. Thus, the framework I adopt will determine whether I answer yes or no to your question about the black mamba's level of aggression. In the field of animal personality, where one can easily switch between the within-species and cross-species frameworks, it is particularly important to consider what kind of comparison is being made (Podberscek & Gosling, 2000).

The specific question under examination determines which of the frameworks should be adopted. If I want to examine the link between hormone levels and aggression in black mambas, I would want to know whether snakes with more of the hormone were more aggressive than snakes with less of the hormone, so I would adopt the within-species framework. However, if I want to know whether or not to go into the next room, it is sufficient for me to know that it is occupied by an aggressive species, so I would adopt a cross-species framework.

It is important to understand within-species variation because it is the raw material of evolution (Mather, 1998). Understanding individual differences in traits enables us to ask questions about the selective benefits of those traits (Mather & Anderson, 1993). For example, do shy fish have a higher selective advantage in rivers with bare banks that are vulnerable to aerial predation but bold fish have a selective edge in rivers protected by overhanging trees (Wilson, Clarke, Coleman, & Dearstyne, 1994)?

It is important to understand cross-species variation because cross-species comparisons can be used to examine the origins and adaptational significance of specific traits (Hodos & Campbell, 1969; Tooby & Cosmides, 1989). For example, has curiosity evolved to promote foraging in species subject to changeable and diverse food sources (Glickman & Sroges, 1966)? I discuss these issues in greater depth later. In the meantime, I turn to the second framework that can be used to classify the studies in Table 1.

Framework 2: Methods Used in Animal-Personality Research

The studies listed in Table 1 used two main methods for obtaining information about individual animals: behavioral codings of the animals' behaviors and subjective ratings of traits. These two methods reflect different resolutions to the trade-off between quantifying personality in terms of objective behaviors and using humans to record and collate information more subjectively (Block, 1961; Stevenson-Hinde, 1983; Stevenson-Hinde et al., 1980b).

Some researchers have tried to take an objective stance by coding narrowly defined behaviors and assessing individual animals over a series of behavioral tests, such as coding an animal's response to a novel object or a new environment (e.g., Hinde, Leighton-Shapiro, & McGinnis, 1978; Mather & Anderson, 1993; Spencer-Booth & Hinde, 1969). These coding studies are identified in the fourth column of Table 1. Other researchers have chosen to sacrifice the objectivity supposedly gained from such detailed behavioral codings in favor of obtaining ratings by people who are familiar with individual animals on traits such as confident, curious, and playful (e.g., Bolig, Price, O'Neill, & Suomi, 1992; Buirski, Plutchik, & Kellerman, 1978; Gosling, 1998; Stevenson-Hinde et al., 1980b). These rating studies are also

identified in the fourth column of Table 1. I next illustrate these two methods using examples representative of each.

Coding behaviors. One method for studying animal personality has been to code how individuals respond to behavioral tests. In a seminal article, Hall and Klein (1942) examined individual differences in aggressiveness by placing pairs of rats together in a cage under a variety of conditions (e.g., thirsty) and coding their aggressive behaviors. In another study, Mather and Anderson (1993) captured 44 wild octopuses and subjected them to three experimental conditions every other day for 2 weeks. The conditions, designed to represent a range of situations with which octopuses are faced in their everyday lives, were alerting (in which the experimenter brought his or her head close to the tank where the octopus could see it clearly), threat (in which the experimenter prodded the octopus with a test-tube brush), and feeding (in which a crab was dropped into the tank for the octopus to eat). In each test, the experimenters rated the octopuses on task-related activities (e.g., in the feeding condition, "capture technique" was rated as 2 if the octopus made a jet-assisted leap through the water, 1 if it walked along the aquarium bottom using sucker-lined arms, and 0 if it waited for capture until the crab walked up to it). Despite the difficulties associated with coding specific behaviors (Gosling, John, Craik, & Robins, 1998), this method has been used in the majority of animal-personality studies, although only rarely with noncaptive animals.

Rating traits. The second method for studying animal personality involves observers as data recording instruments. Historically, data obtained from observers have been derided as subjective and inappropriate for the objective requirements of scientific measurement. However, Buirski et al. (1978) claimed that when applied to animals, terms such as " 'gregarious,' 'timid,' 'depressed,' and 'aggressive' are fundamentally no more subjective or less useful than most terms currently used in psychology or ethology" (p. 127). Block (1961) argued that aggregated observations composed of ratings by several independent observers meet the standards required of any measurement instrument; that is, aggregates composed of multiple observers are reliable and are largely independent of the idiosyncrasies of individual observers (see also Epstein, 1983). Indeed, in research on human personality, consensual observer ratings are often considered to be the sine qua non of personality traits (Hofstee, 1994; McCrae, 1982; Wiggins, 1973).

Most of the animal studies to use subjective impressions of personality examined dogs, cats, or primates. Typically, researchers quantified subjective 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.

Stevenson-Hinde et al.'s (1980b) research on rhesus monkeys is a classic example of the trait-rating method in nonhuman populations. Open-ended descriptions of the monkeys were used to create a list of 25 adjectives, each of which was defined behaviorally (e.g., *active* was defined as "moves about a lot," and *insecure* was defined as "hesitates to act alone; seeks reassurance from others"). Once a year, the monkeys were rated on these adjectives by two observers familiar with the monkeys. This design enabled the researchers to assess observer agreement and to track personality change over time. Gosling's (1998) study of spotted hyenas also relied on impressions by people familiar with the animals. Indi-

vidual researchers made ratings on behaviorally defined adjectives (e.g., *excitable* was defined as "readily roused into action; responsive to stimuli") for each animal based on their observations of the animals over more than 6 years.

This method of collecting information about animals is very efficient because it allows observers to draw on their experiences of animals over time and across contexts without having to dedicate many hundreds of hours to systematic behavioral codings. However, the relative efficiency of the rating method is unimpressive unless the ratings can be shown to be reliable and valid.

Reliability of Personality Assessments of Animals

Reliability is the first psychometric requirement that must be met by any assessment instrument. To determine whether personality assessments of animals meet this fundamental criterion, the present section summarizes and considers the evidence regarding their reliability. Interestingly, with few exceptions (e.g., Byrne & Suomi, 1995; Chamove, 1974; Hall & Klein, 1942; Jones, 1988; R. J. Kilgour, 1998; Netto & Planta, 1997; Watson & Ward, 1996), researchers have largely ignored reliability issues when using behavioral-coding methods, perhaps assuming that such codings are reliable. Instead, when questions about reliability are raised, it is usually in the context of trait ratings, presumably because ratings are considered more subjective. Thus, trait ratings are the focus of the present section.

Animal studies have examined the reliability of ratings from a wide variety of perspectives. Studies differ in how they compute reliability, in the statistical indexes used, and in the types of reliability assessed. Table 2 summarizes the reliability findings reported in these articles. The table is divided into the two types of reliability that have been assessed: interobserver agreement and test–retest reliability. Within each of these types, the studies are further divided into those that computed reliability in the conventional manner, across subjects, and those that computed reliability within subjects. The first column shows the species, and the second through fourth columns show the mean levels of interobserver agreement for each study and the 95% confidence intervals for the mean. The fifth through eighth columns show correlations and labels (where appropriate) for the indicators with the maximum and minimum levels of agreement obtained in each study. The last three columns list the number of animals studied, the number of indicators used, and the relevant citation. I excluded articles that reported incomparable or unique measures of reliability. For example, although J. A. Murphy's (1995) study of dogs aimed to assess the consistency with which guide dogs' temperament could be rated, no quantitative index was provided.

Interobserver agreement, shown in the top two sections of Table 2, is an index of the degree to which two or more observers agree in their personality ratings. Across-subjects agreement correlations are computed across animals and reflect the observers' ability to differentiate the animals. For example, do observers A and B agree that dog X is more nervous than dog Y? A quantitative summary of all studies of interobserver agreement is difficult because a number of different statistical indexes have been used. Moreover, some of the mean reliabilities reported in Table 2 are inflated to an unknown degree because some studies excluded unreliable items during the development of their rating instruments.

However, one can obtain a rough estimate of the magnitude of interobserver reliability by computing the grand mean of the 21 mean correlations in the first section of Table 2. This estimate is rough because it summarizes a set of reliability correlations that were computed at both the item and scale levels, based on a variety of methods, derived from observers who varied in their acquaintance with the animals, based on animals observed across diverse situations, and often based on suboptimal sample sizes. Nevertheless, the grand mean of the 21 means reported in Table 2 comprises more than 375 separate reliability estimates and is probably the best estimate to date of the level of pairwise (dyadic) agreement between observers making personality ratings of animals. The weighted grand mean correlation thus obtained is .52.[4] This correlation is substantial and compares favorably with equivalent interobserver correlations in the human personality literature (e.g., Funder, Kolar, & Blackman, 1995; John & Robins, 1993). It is worth noting that each interobserver correlation represents agreement among judgments of the same construct (e.g., anxiety or playfulness) and, therefore, represents the amount of variance that is shared between two judges (Kenny, 1998); such interobserver agreement correlations are "coefficients of determination," which may be directly interpreted as the variance explained without being squared (Moffitt et al., 1997; Ozer, 1985). In short, the accumulated evidence suggests that animal-personality ratings can be made reliably.

Within-subject reliability analyses take an ipsative approach by computing the interobserver agreement correlations across traits within an animal. For example, do observers A and B agree that a particular baboon is more trustful than it is timid? Within-subject correlations, which have been computed for nine species, are shown in the second section of Table 2. Again, the mean of these correlations is substantial; the weighted grand mean of the 11 within-subject mean correlations in Table 2 is .64. This grand mean, based on more than 130 reliability estimates, again suggests that observers agree in their appraisals of the personalities of the animals they are rating. However, these within-subject correlations should be interpreted cautiously because they do not show that observers are discriminating among the individuals being rated. Strong within-subject reliabilities would be obtained even if observers based their judgments on stereotypical views of the animals, with each observer giving each animal the same stereotype-based ratings. To show that the observers are discriminating among the individuals they are rating, it is necessary to compare the within-subject correlations with the "off diagonal" cases. For example, is the correlation between observer A's rating of animal X and observer B's rating of animal X higher than the correlation between observer A's rating of animal X and observer B's rating of animal Y?

Test–retest reliability, shown in the third and fourth sections of Table 2, is a measure of the degree to which temporally separated measures converge. For example, does an observer's rating of a chimpanzee's personality at Time 1 correlate with her or his ratings of the chimpanzee at Time 2? Crawford (1938) computed test–retest reliability in ratings of chimpanzees, once for a 4-month interval and once for a 10-month interval, obtaining test–retest

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[4] All means were computed with Fisher's *r*-to-*z* transformation when appropriate.

Table 2

How Reliable Are Personality Ratings of Animals? Interobserver Agreement and Test–Retest Reliability in 17 Species

Species	Mean cor	95% confidence interval Lower	Upper	Maximum cor	Item label	Minimum cor	Item label	Sample size	No. of indicators	Study	Retest interval
Interobserver agreement computed for each variable across subjects											
Chimpanzee	.51[a,b]	.45	.57	.70	Dominance	.36	Cleanliness	9	16	Crawford (1938)	
	.86	.78	.92	.90	Friendly to staff	.75	Friendly to "timid man"	30	6[c]	Hebb (1949)	
	.33	.29	.37	.61	Dominant	.10	Erratic	100	43	King & Figueredo (1997)	
Vervet monkey						.55		97	12	McGuire et al. (1994)	
Japanese macaque	.69	.52	.81	.86	Aggressive	.38	Gregarious	14	8[c]	Martau et al. (1985)	
	.61	.43	.74	.82	Aggressive	.24	Distrustful	12	8[c]	Martau et al. (1985)	
Rhesus monkey	.53[d]	.49	.58	.70	Dominant	.17	Sensitive	45	33	Stevenson-Hinde & Zunz (1978); Stevenson-Hinde et al. (1980b)	
	.08	−.01	.18	.42	Sociable	−.45	Opportunistic	42	25	Capitanio (1999)	
Baboon	.75	.66	.81	.84	Rejection	.54	Exploration	7	8[c]	Buirski et al. (1973)	
	.68	.46	.83	.85	Dyscontrolled	−.01	Gregarious	6	8[c]	Martau et al. (1985)	
Gothic-arch squirrel monkey	.71	.35	.88	.92	Timid	.01	Depressed	5	8[c]	Martau et al. (1985)	
Roman-arch squirrel monkey	.76	.61	.85	.86	Aggressive	.35	Dyscontrolled	8	8[c]	Martau et al. (1985)	
Brown bear	.55	.46	.63	.96	Curious about other bears	−.58	Responsive	7	69	Fagen & Fagen (1996)	
Cheetah	.67[e]	.60	.72	.82	Active	.48	Playful	44	15	Wielebnowski (1999)	
Cat	.66	.57	.74	.91	Sociable with people	.31	Solitary	14	18	Feaver et al. (1986)	
Dog	.47	.33	.58	.70	Nervousness	.00	Willingness	9	14	Goddard & Beilharz (1983)	
Spotted hyena	.39[a]	.34	.43	.69	Aggressive	.01	Curious	34	44	Gosling (1998)	
Sheep[f]	.43	.30	.55	.44	Curiosity	.42	Emotionality	164	2	Torres-Hernandez & Hohenboken (1979)	
Donkey[g]	.95	.79	.99	.99	Easy to handle	−.61	Staid vs. playful	24	8	J. M. French (1993)	
Horse	.93							32	4	McCann et al. (1988)	
	.34	.19	.46	.70	Flighty	−.11	Lazy	20	14	Mills (1998)	
	.38[e]	.17	.55	.58	Neuroticism	.17	Openness to experience	10	5[c]	Morris et al. (2000)	
Mdn	.61			.82		.17		17	10		
Interobserver agreement computed within subjects, across variables											
Chimpanzee	.75	.57	.86	.98	NA	.20	NA	14	8[c]	Buirski et al. (1978)	
	.57[h]	.44	.67	.78	NA	.33	NA	8	15	Crawford (1938)	
Japanese macaque	.72	.59	.81	.90	NA	.07	NA	14	8[c]	Martau et al. (1985)	
	.51	.29	.69	.81	NA	−.14	NA	12	8[c]	Martau et al. (1985)	
Rhesus monkey	.81							12	28	Locke, Locke et al. (1964); Locke, Morgan, & Zimmerman (1964)	
Baboon	.71	.33	.89	.90	NA	.20	NA	6	8[c]	Martau et al. (1985)	
Gothic-arch squirrel monkey	.78	.66	.86	.85	NA	.67	NA	5	8[c]	Martau et al. (1985)	
Roman-arch squirrel monkey	.82	.55	.93	.97	NA	.15	NA	8	8[c]	Martau et al. (1985)	
Cheetah	.41	.27	.53	.79	NA	−.30	NA	18	12	Carlstead (2000a)	
Maned wolf	.61	.50	.70	.84	NA	.10	NA	20	10	Carlstead (2000b)	
Rhinoceros	.48[e]	.35	.59	.82	NA	−.03	NA	21	9–14	Carlstead et al. (1999)	
Mdn	.71			.85		.13		12	8		
Test–retest reliability computed for each variable across subjects											
Chimpanzee	.71	.62	.78	.85	Confidence	.21	Cleanliness	9	16	Crawford (1938)	4 months
	.81	.72	.87	.98	Cheerfulness	.12	Destructiveness	8	22	Crawford (1938)	10 months
Donkey	.90	.70	.97	.97	Calm vs. nervous	−.03	Staid vs. playful	3	8	J. M. French (1993)	10 days
Rhinoceros	.31	.17	.43	.59	Urine spray	−.04	Patrols	44	13	Carlstead et al. (1999)	2 years
Test–retest reliability computed within subjects, across variables											
Japanese macaque	.92	.83	.96	.98	NA	.17	NA	12	8[c]	Martau et al. (1985)	12 months

Note. No. of indicators refers to the number of items or scales on which the summaries are based; some studies reported reliabilities for single items, and other studies reported reliabilities for multi-item scales. Some item/scale labels have been slightly abbreviated. The study authors' definitions of personality have been used, so I have not excluded items that would not ordinarily be considered personality constructs (e.g., masturbation). Within-subject correlations are computed across items, and the maximum and minimum reliability correlations refer to individual animals, not items; therefore, the item labels are denoted NA (not applicable) for the within-subject studies. All means have been computed or recomputed using Fisher's *r*-to-*z* transformation when appropriate. cor = correlation.
[a] Pairwise correlations computed from alpha reliability using the Spearman–Brown prophesy formula. [b] Ratings were made on three occasions. The three occasions did not yield similar patterns of interobserver agreement, only correlating .11, on average, across the 16 traits. To obtain the most stable interobserver agreement estimates, I took the mean of the three sets of agreement correlations, and these combined correlations are the data reported here. [c] Data reported for scales (i.e., aggregates of multiple items), not single items. [d] Mean of three annual sets of ratings. [e] Pairwise correlations transformed from Kendall coefficients of concordance (Howell, 1987). [f] Both ratings (curiosity and emotionality) were made in two situations. The averages of the ratings across the situations are reported here. [g] Six of the donkeys were rated by one group of three observers, and 18 donkeys were rated by a second group of two observers. The two groups of observers showed similar patterns of interobserver agreement, correlating .55 across the eight traits. To obtain the most stable interobserver agreement estimates, I took the weighted mean of the two sets of agreement correlations, and these combined correlations are the data reported here. [h] These figures probably offer inflated estimates, because Crawford (1938) only reported agreement among the three observers showing strongest agreement.

correlations of .71 and .81, respectively. Carlstead, Mellen, and Kleiman (1999) examined test–retest reliability over a much longer period—2 years—and obtained a substantially lower reliability estimate of only .31. Unfortunately, it is not possible to use other test–retest findings to tease apart the reasons for the wide discrepancy between the Crawford (1938) and Carlstead et al. (1999) estimates because the other studies used too few subjects (J. M. French, 1993) or estimates were computed within, rather than across, subjects (Martau, Caine, & Candland, 1985). However, four of the five studies found strong test–retest correlations irrespective of the retest interval, providing further evidence, albeit tentative, that traits can be rated reliably in animals. Although initial indications are promising, research on test–retest reliability has been sparse, and further examination of this issue is needed.

Overall, the studies in Table 2 show that it is possible to assess personality traits in animals reliably. However, the generally strong reliabilities obscure a more complex picture in which reliability varies considerably across traits, species, and studies. Some of the pairwise agreement correlations reported in the first section of Table 2 are exceptionally high, but others are unacceptably low. Such variability may prompt researchers to wonder what kind of agreement correlations they can expect from their ratings of animal personality and what they can do to improve the agreement. I next identify seven parameters that could influence agreement, and, when possible, I discuss data pertinent to these influences. I hope to prompt researchers to consider how the parameters could affect their findings, as well as to stimulate researchers to test the effects of the parameters in their data. The results of these tests are needed to serve the practical purpose of guiding future assessments of animal personality.

Parameter 1: Does interobserver agreement improve with acquaintance? It is reasonable to suppose that the longer two observers have known an animal, the more they will agree about the personality of that animal. This supposition has been widely supported by research on humans (Funder & Colvin, 1988; Kenny, Albright, Malloy, & Kashy, 1994; D. Watson & Clark, 1991; D. Watson, Hubbard, & Wiese, 2000). For example, Funder et al. (1995) found that a target will elicit stronger agreement about his or her personality when judged by acquaintances than when judged by strangers who had viewed the target only on videotape. Judgments of animal personality may also be subject to this acquaintanceship effect.

Only a single animal study directly tested the effect of acquaintanceship. Martau et al. (1985) compared personality ratings made by observers who had watched Japanese macaques for 2 hr per day for a month with ratings made by observers who had less than 5 hr experience with the monkeys. Agreement improved slightly with acquaintance; average interobserver correlations (computed at the scale level) were .69 for the relatively acquainted observers and .61 for the relatively unacquainted observers.

Martau et al. (1985) reported only within-subject interobserver agreement correlations and examined only 12 animals, so their findings should be interpreted cautiously. Nevertheless, given the human findings, one might wonder why this study did not produce stronger acquaintanceship effects. One potential explanation could be that interobserver agreement started out high, so there was little room for it to improve with increased acquaintance. This interpretation is supported by studies in humans that have shown minimal effects of acquaintanceship; such studies tend to reveal strong

levels of interobserver agreement after minimal contact with the target individuals (Ambady & Rosenthal, 1992; Blackman & Funder, 1998; Kenny et al., 1994; Paulhus & Bruce, 1992; Robins, Gosling, & Donahue, 1997). According to Kenny (2000, 1994), one reason why such strong agreement is obtained after brief exposure to targets could be that observers are basing their judgments on shared stereotypes. Could the generally high levels of interobserver agreement in Table 2 be inflated by the stereotypes that humans hold about animal species? The characters portrayed in Disney movies such as *The Jungle Book, Bambi,* and *The Lion King* cleverly show the widespread appeal of animal stereotypes (Glickman, 1995). However, interobserver agreement (computed across targets) depends on observers differentiating target individuals and would not be inflated by species-level stereotypes, which would predispose observers to describe all of the animals as alike.[5] Thus, species-level stereotypes are probably not giving a short-term boost to interobserver agreement.

In sum, it has yet to be determined whether observer acquaintance influences the reliability of personality ratings of animals. However, it should be relatively easy to examine this issue, because most studies have already collected ratings by well-acquainted observers and need only to obtain ratings from observers relatively unacquainted with the animals and then compare the two estimates.

Parameter 2: Does communication among observers inflate interobserver agreement? Communication among observers about target animals could inflate the correlation among observers' ratings (Kenny, 1991, 1994). In one study (Goodloe & Borchelt, 1998), each of 22 dogs was rated by two members of their household. Strong levels of interobserver agreement were obtained, but it is easy to see how agreement could have been inflated by communication among the observers. Several of the studies listed in Table 2 attempted to reduce the influence of interobserver communication by instructing observers not to discuss their ratings and to make their ratings independently. However, it is unlikely that all communication about the animals could be eliminated, and such steps do not rule out the influence of communication that occurred prior to the ratings. It would be naive to suggest that observers could eliminate communication about the animals altogether. Fortunately, research on this issue in humans has shown that communication among observers does not severely affect interobserver agreement (Funder et al., 1995). Moreover, communication among observers may pass on legitimate personality-relevant information, such as if observer *A* tells observer *B* that an animal performed a rare but highly diagnostic act during observer *B*'s day off. Nevertheless, studies examining the extent to which communication among observers influences interobserver agreement would be useful.

Parameter 3: Does differential exposure to animals diminish interobserver agreement? The degree to which different observers are exposed to different behaviors by an individual will influence the degree to which the observers agree about the individual's personality (Kenny, 1991, 1994). For example, if observer *A* is the

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[5] Stereotypes could inflate agreement among judges if the observers shared multiple stereotypes within a species. This explanation requires that observers agree on which stereotypes applied to which animals.

person responsible for feeding the animals, whereas observer B is responsible for performing cognitive experiments on the animals, the different sets of behaviors to which the observers are exposed may diminish the degree to which they agree with one another. Studies of humans have shown that although agreement is strongest among observers who know the target in a similar context (e.g., between two college acquaintances), substantial agreement can still be obtained among observers from different contexts (e.g., between a college acquaintance and a parent; Funder et al., 1995). This is an issue that has not been studied systematically in animals but warrants empirical investigation.

Parameter 4: Can very young animals be rated with acceptable levels of interobserver agreement? Observers in some animal studies have claimed to be unable to rate the personality of infants or have felt uncertain about their ratings (Crawford, 1938; Martau et al., 1985). Perhaps ratings are difficult to make because the behavioral repertoire of very young animals is limited in some species. Species whose infants require a great deal of maternal care or protection and spend most of their early life in the arms of a parent might be less free to express their individuality than more precocious species whose infants have the freedom and ability to socialize, play, and explore their environment. On the other hand, some evidence shows that individual differences in infants' behaviors can be assessed successfully, at least in terms of test–retest reliability (Byrne & Suomi, 1995) and interobserver agreement (Clarke & Snipes, 1998; Heath-Lange, Ha, & Sackett, 1999). Future research needs to investigate the age at which the personality of individuals can be distinguished and how this limit may vary across species and methods.

Parameter 5: Are some species more easily judged than others? Different species may vary in the ease with which they can be observed. Some species may be more difficult to observe than others because their behavior is difficult to track. For example, it would be a challenge to track individual bats in the wild because they move quickly and travel long distances in the dark. Observations could also be impeded for species that live in inaccessible or inhospitable environments. Deep-sea squid, Antarctic penguins, and fish that inhabit crocodile-infested rivers all present obstacles to observation. Unfamiliar species may perform behaviors that are less well understood or are more difficult to interpret than those of species that humans know well (L. B. Murphy, 1978). Finally, some animals may simply perform a relatively narrow range of behaviors relative to other animals. This restriction of behaviors may be imposed by transitory environmental conditions (Golani, Kafkafi, & Drai, 1999) or may simply reflect species-typical restrictions in behavioral repertoire. For example, it may be more difficult to behaviorally distinguish two crocodiles that spend the whole afternoon sunning themselves on a riverbank than to distinguish two chimpanzees that engage in a far wider variety of tasks over the same period. Craik (1993) observed that judgments of human personality are often based on critical, behaviorally rich episodes and neglect ordinary humdrum activities; if this pattern is found in animals, it may be easier to judge relatively active versus inactive species.

Parameter 6: Are some traits easier to judge than others? Research in humans has shown that some traits are easier to judge than others (Funder & Dobroth, 1987; John & Robins, 1993). To examine whether this effect pertains to animals, I identified four studies that (a) used similar traits and (b) assessed interobserver

agreement correlations at the trait level. The four studies were of rhesus monkeys (Stevenson-Hinde et al., 1980b), spotted hyenas (Gosling, 1998), cats (Feaver, Mendl, & Bateson, 1986), and chimpanzees (King & Figueredo, 1997). Table 3 lists item labels for each trait included in at least two of the four studies, along with their interobserver agreement correlations. The seventh column shows the mean interobserver agreement correlations for each trait, averaged across the studies that assessed it. The magnitude of these mean correlations was used to determine the order in which the traits were listed, with traits eliciting strongest agreement at the top. These mean correlations provide benchmark levels of interobserver agreement that may be useful for future researchers who want to estimate the levels of agreement they can expect for specific traits.

I first tested whether traits associated with high interobserver agreement in animals tend to be associated with high interobserver agreement in humans. To do this, I correlated the mean animal interobserver correlations (column 7 in Table 3) with human interobserver correlations (column 9), obtained from personality judgments of humans (John & Robins, 1993). The two columns correlated strongly ($r = .59$), suggesting that some traits are generally easier to judge than others.

To see whether some traits were systematically associated with relatively high levels of interobserver agreement across the nonhuman species, I next correlated the columns of pairwise agreement correlations for the four animal species. Strong between-columns correlations would indicate that those traits associated with high interobserver agreement in one species are also associated with high interobserver agreement in another species. The weighted mean of the six between-columns correlations was .47. The range varied from a minimum of $-.40$, computed across the 10 traits common to rhesus monkeys and cats, to a maximum of .70, computed across the 13 traits common to rhesus monkeys and chimpanzees. Four of the six between-columns correlations were .60 or above, again suggesting that, across species, some traits are easier to judge than others.

What makes a trait easy to judge? Research on humans has shown that some personality domains are easier to judge than others; John and Robins (1993) showed that interobserver agreement was highest for traits related to the Five-Factor Model (FFM; John & Srivastava, 1999) domain of Extraversion and lowest for traits related to Agreeableness, with traits related to Neuroticism, Intellect, and Conscientiousness falling in between. To examine whether these findings from human research would extend to interobserver agreement about animals, it was necessary to classify each of the traits into the broad FFM personality domains. The traits were independently classified by seven personality researchers with expertise in the FFM. Traits were assigned to FFM dimensions on the basis of these expert classifications (see Gosling & John, 2001, for details of the rating procedures). Agreement among the seven judges was substantial, with alpha coefficients (computed across the descriptors) of .92 for Extraversion, .96 for Agreeableness, .94 for Conscientiousness, .92 for Neuroticism, and .96 for Intellect. The consensual expert classifications are shown in the second column of Table 3.

Consistent with other research that has classified animal descriptors into the FFM framework (Lilienfeld, Gershon, Duke, Marino, & de Waal, 1999), the majority of descriptors were related

Table 3

Variation in Pairwise Interobserver Agreement: 34 Traits Rated in at Least Two Species

Trait	FFM classification	Animal research						Human[e]
		Rhesus monkey[a]	Hyena[b]	Cat[c]	Chimpanzee[d]	M	SD	
Sociable with humans	E/A		.46	.91		.77	.62	
Dominant	E	.70	.74		.61	.69	.12	.41
High strung, tense	N	.46	.57	.78		.62	.28	.31
Active	E	.52	.55	.76	.60	.62	.19	.30
Confident	N	.65	.57			.61	.09	
Aggressive	A	.61	.69	.61	.48	.60	.13	
Nervous, anxious	N	.66	.47			.57	.20	.23
Submissive	E	.69	.53		.46	.57	.18	.33
Playful	E	.67	.42	.58	.54	.56	.15	.13
Calm, equable	N	.53	.31	.71		.54	.28	
Vocal	E		.32	.68		.52	.34	
Fearful	N	.62	.46	.52	.38	.50	.14	
Slow	E	.56	.43			.50	.12	
Strong	—	.51	.43			.47	.07	
Curious	I	.41	.01	.79		.47	.49	.18
Nurturant	A	.52	.38			.45	.12	
Sociable with conspecifics	E	.43	.25	.64	.35	.43	.21	.15
Solitary	E	.49		.31	.47	.43	.12	
Lazy	C		.43		.40	.42	.03	.18
Eccentric	I	.42	.37			.40	.04	
Protective	A	.52			.22	.38	.24	
Excitable	E	.55	.32	.35	.26	.38	.15	
Gentle	A	.44			.26	.35	.14	
Persistent	C		.42		.28	.35	.11	.21
Irritable	A/N	.41	.33		.27	.34	.08	
Intelligent	I		.32		.35	.34	.02	.31
Opportunistic	E	.38	.27			.33	.09	
Jealous	A		.38		.26	.32	.09	.22
Warm, affectionate	A		.37		.21	.29	.12	.16
Friendly, not hostile	A		.34		.24	.29	.08	
Exploratory, inquisitive	I		.06		.45	.27	.29	
Careful, cautious	C		.08		.31	.20	.17	.12
Impulsive	E		.13		.25	.19	.09	.24
Sensitive	N	.17			.15	.16	.01	

Note. Some item labels have been slightly abbreviated. See source articles for full item definitions. E = Extraversion; A = Agreeableness; N = Neuroticism; I = Intellect; C = Conscientiousness. Dash indicates classified as unrelated to Five-Factor Model (FFM) domains. Two studies were not consistent with the overall pattern reported here; the agreement correlations reported in Fagen & Fagen's (1996) study of bears correlated negatively with the agreement correlations for hyenas ($r = -.45$, N of common traits = 17), chimpanzees ($r = -.34$, $N = 11$), and rhesus monkeys ($r = -.47$, $N = 14$) but positively with the correlations for cats ($r = .42$, $N = 9$). Similarly, Capitanio's (1999) study of rhesus monkeys did not correlate with Stevenson-Hinde et al.'s (1980b) study of the same species ($r = -.06$, $N = 13$) and was correlated negatively with hyenas ($r = -.37$, $N = 12$), chimpanzees ($r = -.46$, $N = 8$), and cats ($r = -.13$, $N = 10$). Given the somewhat contradictory findings for Fagen & Fagen's (1996) study of bears and Capitanio's (1999) study of rhesus monkeys, the best general estimate of agreement between two observers of each trait is given without these studies, and they are not reported here.
[a] Unpublished data from research by Stevenson-Hinde et al. (1980b).   [b] Gosling (1998).   [c] Feaver et al. (1986).   [d] Unpublished data from research by King & Figueredo (1997).   [e] Unpublished data from research by John & Robins (1993).

to the Extraversion, Agreeableness, and Neuroticism domains. Specifically, 11 of the traits in Table 3 were classified as most related to Extraversion, 7 as most related to Agreeableness, and 6 as most related to Neuroticism; of the 10 remaining traits, 4 were classified as most related to Intellect, 3 as most related to Conscientiousness, 2 as straddling two FFM categories, and 1 as unrelated to the FFM.

To compare the present findings from animal studies with previous research on humans, I divided Table 3 into the 17 traits with the highest interobserver agreement (top half) and the 17 traits with the lowest interobserver agreement (bottom half). The top half of the table is composed almost entirely of traits from the Extraversion and Neuroticism domains, including 7 of the 11 (64%) Extraversion traits and 5 of the 6 (83%) Neuroticism traits. The bottom half is composed of a mixture of traits, including 5 of the 7 (71%) Agreeableness traits. To provide an alternative index of this effect, I also computed the point-biserial correlations between the interobserver agreement correlations and each of three new variables that coded for membership in the Extraversion, Neuroticism, and Agreeableness domains. Consistent with the percentage figures just reported, interobserver agreement correlated positively with membership in Extraversion ($r = .24$) and Neuroticism ($r = .27$) but negatively with membership in Agreeableness ($r = -.19$).

Thus, as in humans, animal traits related to Extraversion are associated with high levels of interobserver agreement, and traits related to Agreeableness are associated with low levels of interobserver agreement. Unlike research in humans, however, traits related to Neuroticism are associated with high levels of interobserver agreement in animals.

One reason why some personality domains are easier to judge than others could be that behaviors associated with the different domains differ in their observability (or visibility). Research on humans supports this idea, showing a positive relation between interobserver agreement and observability in judgments of traits ($r = .34$, Funder & Dobroth, 1987; $r = .36$, John & Robins, 1993), behaviors ($r = .38$, Gosling et al., 1998), and emotions ($r = .55$, D. Watson & Clark, 1991). To test for this effect in the present data, I obtained observability ratings from seven experts on animal behavior. The experts' observational experiences represent a broad range of species including wolves, spotted hyenas, sea anemones, aquatic hermit crabs, fiddler crabs, leopard sharks, rhesus monkeys, patas monkeys, vervet monkeys, common marmosets, bushbabies, cynomolgus monkeys, and chimpanzees. The experts independently rated the observability of the traits using instructions adapted from Gosling et al. (1998) and D. Watson and Clark (1991). Given that the experts were basing their judgments on species as diverse as fiddler crabs and chimpanzees, they showed surprisingly strong agreement, and their composite ratings had an alpha reliability of .76. Their combined ratings were used as an index of observability. I correlated this observability index with the interobserver agreement correlations. Consistent with previous research on humans, observability correlated strongly ($r = .57$) with interobserver agreement, suggesting that observable traits elicit higher levels of interobserver agreement than do less observable traits.

These observability findings could shed some light on the discrepancy between the FFM findings in the human and animal domains. Humans, but presumably not animals, are socialized to inhibit overt signs of neuroticism, in which case neurotic behavior could be relatively visible in animals but hard to detect in humans. Indeed, past research in humans has shown that traits central to Neuroticism are negatively correlated ($r = -.27$) with trait observability (Funder & Dobroth, 1987). But do we see the opposite effect in animals? To test this idea, I correlated the FFM experts' ratings of Neuroticism with the animal-behavior experts' ratings of trait observability. Contrary to expectations, Neuroticism showed the same (human) pattern in animals, correlating negatively ($r = -.18$), albeit weakly, with observability. Thus, observability did not mediate the effects of Neuroticism; instead, observability served as a suppressor variable such that the correlation between Neuroticism and interobserver agreement increased (from .27 to .54) when observability was controlled. This finding can be contrasted with the relationship between interobserver agreement and Extraversion, which was almost entirely explained by observability.

In short, some traits appear to be systematically easier to judge than other traits. Some of this variability is related to the personality domain with which the traits are associated, and some variability is related to the observability of traits.

Finally, recall that although four of the six between-columns correlations in Table 3 were .60 or greater, the other two were zero or less. This variability raises the possibility of a Trait × Species

interaction. That is, observers may agree about curiosity in cats but disagree about curiosity in hyenas. This makes intuitive sense: Different species engage in a variety of different behaviors and provide different sources of personality-relevant information. Focused investigations of interspecies differences in interobserver agreement are needed to test this possibility.

Parameter 7: Do some situations promote more agreement than others? Different situations permit and promote different behaviors; an animal's behavior will vary drastically depending on whether it is playing, sleeping, courting, hunting, or fleeing. Behaviors manifested in different situations may vary in their observability or some other quality that influences interobserver agreement. Thus, it is likely that some situations generally elicit more interobserver agreement than others (e.g., sleep vs. social interaction), but it is also probable that there is a Trait × Situation interaction such that some traits will be best judged in some situations and other traits best judged in other situations. The idea that different situations provide windows onto different traits is not new, but it has yet to be directly explored in animal research. The issue is of particular importance in animal research because many of the studies of animal personality are based on wild animals in captivity, which inevitably constrains an animal's behavior and its exposure to a natural array of situations.

Summary. Together, these unresolved issues might appear rather daunting. However, one strong recommendation does emerge from this review: Measure and report reliability! It is somewhat frustrating to realize that many of the issues that remain to be resolved could already have been answered if the studies in Table 1 had measured and reported the reliability of the personality ratings. Such data will enable the field to better understand what determines the reliability of personality ratings and to use this information to improve reliability in future research.

In the meantime, it is advisable for researchers to follow a few general measurement guidelines to optimize the reliability of the ratings they obtain (John & Benet-Martinez, 2000). First, studies of animal personality should use sufficient numbers of observers to obtain reliable estimates of the constructs being rated and, when interobserver agreement is low, add more observers (Block, 1961); for example, if one conservatively estimated that pairwise interobserver agreement would be approximately .30, then (using the Spearman–Brown prophesy formula) one should obtain an alpha reliability of .72 for a composite of six judges. Second, studies should use rating scales that allow observers to express the full range of variability they detect without being so wide that observer biases obscure the ratings. Third, researchers should ensure that there are enough items to provide a reliable estimate of each anticipated dimension (i.e., start with at least three or four items per dimension and preferably more; Goldberg & Digman, 1994). Finally, researchers should make sure the items selected to tap a common construct actually appear to be doing so. In addition, to obtain stable reliability estimates, researchers should collect ratings on as many animals as is feasible. In short, animal-personality researchers should adopt the principles of personality assessment that have been developed over many years of research on human participants.

The issues that remain to be addressed and the measurement guidelines for future research should not obscure the generally promising reliability findings obtained so far. Overall, the levels of interobserver agreement for ratings of personality in animal targets

are high, with agreement correlations at least as high as those in most human research. Although the variability in the findings suggests that reliability is not guaranteed, the findings are consistent enough, converging across traits, species, and independent studies, to suggest that it is possible to rate personality traits reliably in animals.

Validity of Personality Ratings of Animals

Once the reliability of an assessment instrument has been established, the next step is to evaluate the instrument's validity. Validity is an index of how well the instrument is measuring what it is meant to be measuring.

Evaluating the validity of a personality measure is a conceptually and methodologically challenging task regardless of whether the targets are humans or animals. The conceptual challenge is to establish the ultimate criterion against which validity should be gauged. For example, what should serve as the ultimate measure of individuals' personality: what individuals say about themselves, what their friends say about them, what behaviors they perform, their neurotransmitter levels, their DNA, or what? After identifying a validity criterion, researchers are then faced with a methodological challenge: How can we be sure that the instrument with which we are measuring the validity criterion is itself valid? Although these challenges have yet to be fully resolved in personality research (see Funder, 1995; Hofstee, 1994; John & Robins, 1994; Robins & John, 1997), the preferred solution draws on principles of construct validation (Cronbach & Meehl, 1955; John & Benet-Martinez, 2000), that is, search for convergence across independent measures of the same construct (convergent validity) and for divergence across independent measures of different constructs (discriminant validity; Campbell & Fiske, 1959).

Few studies of animal personality have focused on assessing the construct validity of their measures. However, some studies have provided evidence for the construct validity of personality ratings by correlating personality ratings with behavioral codings or with other conceptually related constructs (Bolig et al., 1992; Lilienfeld et al., 1999). For example, in a study of spotted hyenas, in which there is a strong matriarchal dominance hierarchy, the Assertiveness dimension was strongly correlated with rank in the dominance hierarchy and with sex (Gosling, 1998). Moreover, four other personality dimensions, which were conceptually unrelated to dominance, did not show sex differences, and none of the five dimensions correlated with age or the appearance of the animals. In a study of cats, Feaver et al. (1986) validated personality ratings using behavioral codings of each cat's behaviors. For example, did a cat rated as aggressive actually hit, chase, and stare at other cats more than a cat rated as unaggressive? The correlations between the personality ratings and the behavioral codings supported the convergent validity of the ratings, ranging from .60 for "playful" to .85 for "aggressive." A similar pattern was found for cheetahs (Wielebnowski, 1999), such that animals rated as aggressive toward conspecifics engaged in more growls and hisses ($r = .59$) in response to their reflection in a mirror than did animals rated low on aggression; cheetahs rated as self-assured approached the mirror relatively quickly ($r = -.50$), whereas those rated as relatively tense had longer approach times ($r = .53$). Likewise, rhinoceroses rated as fearful interacted less frequently with a novel object ($r = -.30$) than less fearful animals; however, fearfulness was not

related ($r = .13$) to the time taken to touch the novel object (Carlstead et al., 1999).

In a study of vervet monkeys, McGuire, Raleigh, and Pollack (1994) used three overt behavioral measures (exploration, grooming, and initiating submissive gestures) to validate personality dimensions that had been derived from personality ratings and behavioral codings of monkeys. In support of the construct validity of the dimensions, monkeys that performed many exploratory behaviors were high on the dimension labeled "Playful/Curious" ($r = .80$) but neither high nor low on the Socially competent ($r = -.02$) and Opportunistic ($r = .16$) factors. Similarly, the dimension labeled Social competence correlated positively with grooming ($r = .36$) and negatively with the initiation of submissive behaviors ($r = -.53$), but these behaviors were unrelated to the Playful/Curious ($rs = .12$ and $-.20$, respectively) and Opportunistic ($rs = .14$ and .15, respectively) dimensions.

Studies of rhesus monkeys have also used behavioral codings to validate personality measures at the trait and dimension levels (Stevenson-Hinde, 1983; Stevenson-Hinde et al., 1980b). For example, ratings of "aggressive" were validated with occurrences of hits, threats, and chases toward other group members ($r = .49$), and ratings of "fearful" were validated with occurrences of fear grins and avoidance of others ($r = .57$). All six of the ratings assessed by Stevenson-Hinde et al. (1980b) yielded significant validity correlations ranging from .45 for "excitable" to .73 for "effective." At the dimension level (Stevenson-Hinde, Zunz, & Stillwell-Barnes, 1980), the monkeys' personality scores correlated with their behaviors in test situations. For example, male infants' Confidence scores predicted the duration that they voluntarily spent in a cage out of reach of their mother ($r = .68$). However, other validity correlations made less sense; for example, infants with high excitability scores made fewer distress calls than infants with low Excitability scores when mothers and infants were removed from their colony ($r = -.72$). Research on horses (Anderson, Friend, Evans, & Bushong, 1999; Le Scolan, Hausberger, & Wolff, 1997) has also produced mixed evidence for the validity of personality ratings, with only some of the personality ratings correlating with the horses' performance on related behavioral tests.

The most systematic study to validate personality ratings with behavioral codings was performed on 42 male captive rhesus monkeys (Capitanio, 1999). The goal of the study was to test the predictive validity of personality ratings, that is, the degree to which the measures could predict conceptually related, subsequent outcomes. Specifically, Capitanio (1999) attempted to determine whether personality dimensions, identified in adult monkeys living in half-acre cages, predicted behavior in situations different from the one from which the dimensions were originally derived at time points up to 4.5 years after the original assessments. Although the results were somewhat mixed, the predictive validity of the personality dimensions was generally supported. For example, Sociability measured when the monkeys were in their natal groups was positively associated with earlier codings of the number of approaches initiated ($r = .38$) and received ($r = .27$) and was negatively associated with codings made about 3 years later of agonistic signaling (e.g., threats, $r = -.39$, and lipsmacks, $r = -.29$) in response to affiliative stimuli (videotapes of affiliative monkey behavior).

In a related article (Capitanio, Mendoza, & Baroncelli, 1999), personality dimensions were used to predict physiological measures associated with survival in monkeys that had been experimentally inoculated with the simian immunodeficiency virus (SIV). As is the case with research on extraversion in humans (e.g., Miller, Cohen, Rabin, Skoner, & Doyle, 1999), Capitanio et al. (1999) found evidence that sociability in animals was related to immune parameters. Specifically, they found that after inoculation with SIV, animals higher in Sociability showed a greater immune response (i.e., a more rapid decline in plasma cortisol concentrations, elevations in the anti-RhCMV IgG response, and a decline in viral load) than animals lower in Sociability. In terms of the present discussion, this research is important for two reasons. First, the obtained associations between personality and immunity show a pattern that is consistent with human research in this area. Second, the study shows how behaviorally based personality dimensions can predict criterion measures that are not based on behavior.

Another potential source of information about the validity of personality trait ratings is provided by studies of personality structure. Most animal studies of personality structure are based on personality ratings; however, a small number of studies have used behavioral tests and carefully recorded ethological observations instead of ratings. For example, Forkman, Furuhaug, and Jensen (1995) studied individual differences in piglets by recording their behavior in specific situations; a Sociability factor was defined by number of vocalizations, nose contacts, and location in the pen, and an Aggression factor was defined by number of bites, immediacy of attack, and approach to the feeding trough. Also, van Hooff (1973) carefully observed the naturally occurring expressive behavior of chimpanzees; a Social Play factor was defined by such behavior patterns as "grasp and poke" (boisterous but relaxed contact), "pull limb" (playful social contact), and "gymnastics" (exuberant locomotory play, such as swinging, dangling, rolling over, and turning somersaults), and an Affinity factor was defined by behavior patterns indicating social closeness, such as touching (gentle contact, such as stroking another over the head), grooming, and embrace. Each of the factors obtained from behavioral codings resembled factors obtained from rating data, suggesting that rating data are as valid as codings of behavior (Gosling & John, 1999).

In summary, the few studies that have correlated personality ratings or dimensions with behavioral codings or other validity criteria appear to provide support for the validity of personality ratings of animals. However, there are several potential challenges to validity that must be addressed by future research. I next outline these challenges and how they might be addressed.

First, many of the validity findings are based on post hoc interpretations of the analyses, with relatively little attention paid to the constructs' discriminant validity. Ideally, researchers should articulate nomological networks in which they predict how the constructs under examination should and should not be related to one another (Cronbach & Meehl, 1955).

The second problem with previous validation research is that the reliability of the behavioral codings (against which personality ratings are validated) is often assumed rather than tested. Although behavioral codings may appear to be more objective than personality ratings, research on humans has shown substantial variability in coding reliability (Gosling et al., 1998). Thus, future validation

research should be sure to assess and report the reliability of the criterion measures against which validity is estimated.

The third problem with previous validation research is that personality ratings and behavioral codings were usually not made independently. For example, to test the predictive validity of personality ratings of guide dogs, Goddard and Beilharz (1983) correlated personality ratings made before a training program with a series of outcome criteria. The personality measures predicted whether the dogs were considered suitable for training, whether the dogs were rejected from the training program, and their performance evaluations (e.g., "ease of control") at the end of the training program. However, the predictor and criterion scores were not independent because they were all determined by the dog's trainer. Similarly, the observers who made the behavioral codings in Feaver et al.'s (1986) investigation of cats also made the personality ratings. To limit the degree to which the coding procedure would affect the personality ratings, Feaver et al. (1986) did not analyze the data until the codings and ratings had been collected. However, it would have been preferable to obtain the ratings and codings from different sets of observers (Le Scolan et al., 1997).

The fourth problem with previous validation research occurs when the same types of data are used to assess both the predictor and criterion measures. For example, in Gosling's (1998) study of hyenas, the behaviors used to judge traits loading on the assertiveness dimension (the predictor) may also have served as the basis for the dominance assignations (the criterion). When such operational overlap occurs, validity correlations could be inflated by the shared method variance and should be interpreted cautiously. The strongest evidence for validity was provided by the studies in which the predictor being validated and the criterion were maximally independent (e.g., Capitanio et al., 1999). Such independence can be achieved in studies of predictive validity in which the criterion measure is assessed at a different time, by different observers, using different methods. In line with these principles, Carlstead and colleagues (Carlstead & Kleiman, 1998; Carlstead et al., 1999) validated zookeepers' ratings using behavioral codings made from a series of standardized testing sessions; after the keepers had made their ratings, a specially trained team of researchers visited the zoos to conduct the tests and videotape them for subsequent coding.

Overall, the limited evidence to date provides some support for the validity of personality ratings of animals. However, further research remains to be done. Establishing the validity of personality ratings of animals should be a top priority for animal-personality research over the next few years.

What Have We Learned From Research on Animal Personality?

Ideally, one would conclude a review of the animal-personality literature with a list of personality dimensions that have emerged across studies and a quantitative comparison of the various findings. Unfortunately, the diversity of traits examined, species studied, methods used, and analyses performed makes a definitive list impossible to construct and a quantitative comparison impossible to perform. For example, how could we quantitatively compare the duration an individual avoided a lighted area of a fish tank (sup-

posedly a measure of fearful behavior in zebra fish; Shaklee, 1963) with subjective ratings of "insecure" (a trait loading on the fearfulness dimension in gorillas; Gold & Maple, 1994)?

The studies in Table 1 varied greatly in the specificity of the trait or behavior examined, ranging from very broad descriptors (e.g., "active") to very narrow descriptors (e.g., "snapping at children"). Moreover, a single trait was sometimes operationalized differently. For example, "excitable" has been operationalized both as "readily roused into action, responsive to stimuli, impatient, high-strung" (McGuire et al., 1994, p. 4) and as "overreacts to any change" (Stevenson-Hinde & Zunz, 1978, p. 481), and "vigilant" has been defined as "aggressing, fence shaking, or displaying to another group or to another stimulus outside the enclosure" (McGuire et al., 1994, p. 4) and as "alert, ready, attentive, watchful, notices with special attention, not oblivious to surroundings" (Gosling, 1998, p. 118). Similarly, shyness has been variously associated with Emotionality, Curiosity, and Assertiveness (Wilson et al., 1994). This practice of using the same label to refer to different constructs has been termed the jingle fallacy (Block, 1995; Kelley, 1927).

The jangle fallacy, on the other hand, is the practice of using different names to refer to the same construct (Block, 1995; Kelley, 1927). A careful reading of the studies in Table 1 reveals that some traits that appear to have similar operational definitions are referred to differently in different studies. For example, the behavior "readily explores new situations" is described as curious in one article (Stevenson-Hinde & Zunz, 1978), whereas the similar description "seeking out or investigating novel situations" is used to define inquisitive in another article (Buirski et al., 1978, p. 124). Similarly, the responses animals exhibit when they are placed in a novel open space, the "open field test" (Hall, 1934, 1938), have variously been thought to reflect Fearfulness, Extraversion, Exploration, and Activity (Archer, 1973; Gershenfeld et al., 1997). Even at the level of broader dimensions, there is considerable overlap. For example, Gosling's (1998) Assertiveness scale overlaps with Stevenson-Hinde and Zunz's (1978) Confidence-Fearfulness scale, which is, in turn, conceptually related to the dimension of Emotionality. Emotionality, in turn, is operationalized in some studies with tests that are used to measure Exploration in other studies. Similarly, facets of the trait Sensation Seeking can be associated with Reactivity, Curiosity, Sociability, and Dominance (Zuckerman, 1996).

There is clearly a need for researchers to develop a common framework with which to describe animal personality. Without such a framework, it will continue to be difficult to compare studies, and, as shown later, such comparisons are the key to using animal studies to learn about personality.

Developing a common language. The fragmented field of animal personality resembles the early stages of human-personality research when there was widespread disagreement concerning which personality terms to adopt. Recently however, some consensus has emerged in the field regarding a unifying framework: the FFM. This framework suggests that most individual differences in personality can be classified into five broad, empirically derived domains (John & Srivastava, 1999). The FFM has not been universally accepted as the ultimate model of personality (Block, 1995). However, it has provided a common language for human-personality researchers and has unified a field that was in danger

of disintegrating as each researcher invented his or her own system for classifying personality.

It is important that the nascent field of animal personality develop a common language rather than repeat the mistakes made in human-personality research. Researchers should carefully select which variables they study to ensure that they are both comparable and comprehensive.

To ensure comparability, animal-personality researchers should use a standardized set of characteristics translated into species-typical behaviors. Researchers should not render their interesting findings uncomparable by using idiosyncratic terms. This is of particular concern in animal research, which is more vulnerable than human research to the danger of using inconsistent trait concepts because there is typically much more variability across species (e.g., between rats and chimpanzees) than across groups of humans (e.g., between University of Oregon students and University of London students). Nevertheless, researchers should make every effort to ensure that their item pool is as comparable as possible to other research (e.g., by using variables that have been used in other studies).

To ensure comprehensiveness, the range of personality traits studied in a species must fully represent the behavioral repertoire of that species. Research on animal personality often does not use systematic item-generation procedures, exposing animal studies to the danger of overlooking important features of a species' personality. Too often, item pools are generated on the basis of the intuitions of one or two people who know the animals. Care should be taken to account for all of the relevant domains of individual differences. For example, interactions with humans often play a large part in the lives of captive animals, but this realm of behavior is often overlooked in research on captive populations. Therefore, in addition to the within-species social interactions that are typically studied in animal-personality research, studies should also examine facets of human–animal interactions.

Unfortunately, a natural tension exists between the demands of comparability and comprehensiveness. In capturing the idiosyncrasies of a particular species, researchers may be forced to use traits that are not applicable to other species. A balance should be reached in which a basic set of standardized descriptors (operationally defined in species-appropriate terms) is supplemented by important species-specific descriptors. Ultimately, a standard taxonomy of terms and scales may be available from which animal-personality researchers can choose their items and find citations to previous studies that have used these items and scales.

Cross-species personality dimensions. Despite the difficulties associated with comparing the studies in Table 1 quantitatively, a number of dimensions that have appeared repeatedly across multiple species are worth noting. 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 (see Higley & Suomi, 1989, p. 154) and has been measured by behavioral measures such as defecation rate in open-field tests and rated on traits such as nervous. A second recurring dimension is the propensity to seek out novel stimuli or situations in the first place, and this has been identified in several articles as Exploration. This dimension has been measured by behaviors such as approach to novel objects and rated on traits such as curious. Several studies identified a dimension differentiating those individuals seeking out

social interactions from those preferring to remain solitary. This dimension, usually referred to as Sociability, has been measured by behaviors such as frequency of social encounters and rated 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 ratings of traits such as aggressive. A fifth dimension to appear in several studies referred to an animal's general activity level; this has been measured by behaviors such as the amount of enclosure covered by the animal's roaming and rated on.traits such as energetic. Several studies also identified a Dominance or Assertiveness dimension that 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 Table 1 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. Gosling and John (1999) recently reviewed 19 such studies, using the FFM 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; and Vivacity in donkeys. Also, there was a dimension contrasting bold approach and avoidance in octopuses. The way these personality dimensions are manifested, however, depends on the species. For example, whereas a 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 by Gosling and John (1999). A separate Activity dimension was identified in only 2 of the studies.

Overall, the review of animal personality summarized in Table 1 and discussed in this section suggests that it is viable to assess at least some elements of personality in animals. This raises the question of whether animal-research findings can be used to inform personality research. The next section of the article considers this question.

How Can Animal Research Be Used to Inform Research on Personality?

Can questions about personality be addressed using the animal studies summarized in Table 1? The value of cross-species comparisons will be determined by their ability to solve basic problems in the field of personality; for example, can cross-species generalizations help us understand how personality develops, and can animal models shed light on the links between personality and health? In other areas of psychology, much has already been learned about humans from studies of animals (Domjan & Purdy, 1995). Pavlov, Tolman, and Skinner, to name a few, all relied on animals in their seminal studies of learning; Thorndike and Köhler performed important experiments on problem-solving using cats and chimpanzees; and Harlow's research on attachment was based on monkeys. Mehlman (1967) noted that "virtually no limits exist on the forms of life studied and the types of problems set. Studies with animals are presumed to have implications for principles of learning, for understanding of perception, developmental psychology, social interactions, and psychotherapy" (p. 67). However, with few exceptions (e.g., Arnold Buss, Solomon Diamond, Jeffrey Gray, Robert Sapolsky, Stephen Suomi, and Marvin Zuckerman), researchers have not turned to animals to elucidate questions about human personality. In fact, most of the studies included in Table 1 did not explicitly relate their findings to human research.

Researchers vary in their attitudes toward cross-species comparisons, ranging from those who argue that all comparisons between humans and other animals are misguided anthropomorphism to those who strongly favor the use of animal models in research on humans. Disagreements also arise when researchers are pressed to specify exactly how much they can learn from cross-species comparisons (Harlow, Gluck, & Suomi, 1972). For example, can research on timidity in mice inform our understanding of timidity in humans? Can our understanding of the interrelation of personality traits within humans inform our understanding of the interrelationship of personality traits within dogs? Next I describe basic arguments against human–animal comparisons and responses to these arguments before settling on an intermediate view along with some suggested guidelines to promote judicious use of cross-species comparisons.

Arguments Against Comparing Humans With Animals

On one side of the debate are those who claim that, in one way or another, humans are fundamentally different from other animals (e.g., Simpson, 1949). Although people undeniably attribute psychological characteristics to animals, it is unclear whether these attributions are justified. Mitchell and Hamm (1997) found that people use the same psychological processes (e.g., jealousy or trying to hide feelings) to account for behaviors described in a narrative regardless of whether the behaviors were engaged in by a human, chimpanzee, dog, elephant, bear, or otter. Such indiscriminate attributions may raise suspicions about whether the attributions have any grounding in reality. Other research has shown that people do vary their attributions according to the species they are describing (J. L. Rasmussen, Rajecki, & Craft, 1993); nevertheless, some reports of complex psychological processes in animals stretch the limits of plausibility. For example, Best (1963) claimed to have found behavior resembling anxiety or

caution in planarian worms and posed the question "If one finds that planarian behavior resembles behavior that in higher animals one calls boredom, interest, conflict, decision, frustration, rebellion, anxiety, learning, and cognitive awareness, is it permissible to say that planarians also display these attributes?" (p. 62). Such statements have prompted some researchers to dismiss descriptions of psychological states in animals as anthropomorphic projections and to consider animals as unlikely models for complex human processes.

Important differences surely exist between humans and animals. Advanced psychological processes, such as complex representations of the self, may depend on uniquely human features of the brain (Robins et al., 1999). Perhaps humans are so different from other animals in terms of physiology, culture, and experience that extrapolating from animals to humans is a waste of time. Hilgard (1956) stated: "The price to be paid for overmuch experimentation with animals is to neglect the fact that human subjects are brighter, and are able to use language—and probably learn differently because of these advances over lower animals" (p. 329).

Humans' unique ability for complex language and the concomitant social interactions and formation of culture that are facilitated by that ability mean that only humans can sensibly be thought to possess culture-dependent traits (e.g., ethical and artistic). An individual can be thought of as ethical only with respect to a framework of values and morality, and an individual can be thought of as artistic only within the context of a cultural aesthetic. By this logic, animal analogs of such traits will never be identified.[6] Likewise, there is presumably no hope of discovering human analogs of the animal traits that may depend on uniquely bestial faculties. For example, some personality traits might be manifested only by individuals with highly sensitive echolocation sensory systems or with the ability to spontaneously change sex if the conditions favor such a change (Munday, Caley, & Jones, 1998).

More generally, humans and animals have different anatomical structures; few animals have opposable thumbs or sophisticated vocalization equipment, and humans do not have antennae or beaks. Insofar as anatomy constrains what an organism can and cannot do, animals may not be able to engage in some of the personality-relevant behaviors in which humans engage, and vice versa.

Finally, Nagel (1980) has suggested that, in principle, humans cannot know "what it is like to be" an animal; human experiences and animal experiences are incommensurable (Martin & Bateson, 1993; Varela, Thompson, & Rosch, 1991). Specific internal experiences are essential to certain conceptualizations of personality. For example, "cheerful" people do more than behave cheerfully; they feel happy with the present and optimistic about the future. Similarly, malicious or spiteful individuals must engage in their negative behaviors with evil intent. Even if people behave in an extraverted manner, they can still be considered shy if social situations make them feel anxious or uncomfortable. If Nagel is right, humans can never, in principle, be sure that an animal has a trait, at least for those elements of personality that assume the existence of inner experience.

Arguments in Favor of Comparing Humans With Animals

In contrast to the view that humans and animals are fundamentally different, Dethier (1964) maintained that the reluctance to ascribe "higher" characteristics to distantly related organisms is speciesist and scientifically remiss:

> The farther removed an animal is from ourselves, the less sympathetic we are in ascribing to it those components of behavior that we know in ourselves. There is some fuzzy point of transition in the phylogenetic scale where our empathizing acquires an unsavory aura. Yet there is little justification for this schism. If we subscribe to an idea of a lineal evolution of behavior, there is no reason for failing to search for adumbrations of higher behavior in invertebrates. (pp. 1138–1139)

Unconvinced that the reluctance to ascribe characteristics to animals has any empirical justification, Dethier (1964) suggested that proclivities to treat lower animals as qualitatively different are "founded as much on a fear of anthropomorphism, however well disciplined, as on a paucity of data" (p. 1145).

But the fear of anthropomorphism may not be justified. Gosling and John (1999) presented three lines of evidence suggesting that personality descriptions of animals are not merely anthropomorphic projections. First, as noted earlier, across a range of species from cheetahs to chimpanzees, independent observers can agree about the relative ordering of individuals on a trait; the idea that the observers are basing their judgments on real characteristics of the animals offers the most parsimonious explanation for these data.

Second, Gosling and John (1999) found that factor structures showed meaningful differences across species, suggesting that general rating biases in observers did not drive the ratings. For example, Gosling and John (1998) found the familiar FFM dimensions for humans but only four factors for dogs, even when personality ratings were collected with the same instrument for both species; specifically, the items defining a clear conscientiousness factor in humans failed to form a separate factor in dogs.

The third argument against anthropomorphism provided by Gosling and John (1999) is based on comparisons between studies of personality structure based on ratings and those based on behavioral codings. Presumably, studies that used behavioral tests are less vulnerable to anthropomorphic concerns than studies involving personality ratings. Yet, as described in the earlier discussion of validity, these two types of research have yielded similar factor structures. The fact that such similar factors have been discovered using such diverse methods suggests that anthropomorphism is not the major mechanism underlying personality ratings.

One potential criticism of the rating studies—and, to a lesser extent, the behavioral studies—is that by providing observers with rating or behavioral dimensions, the researchers are predisposing observers to project preconceived characteristics onto the animals and to make distinctions they otherwise might not make. A recent study tested this question using generalized Procrustes analyses to quantitatively compare observers' spontaneous free descriptions of pigs (Wemelsfelder, Hunter, Mendl, & Lawrence, 2000). Generalized Procrustes analysis is a multivariate statistical technique that determines congruence among different observers' patterns of ratings and does not depend on observers using a common set of descriptors. Wemelsfelder et al. (2000) showed that even when observers were free to select their own traits to characterize the

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[6] Note, however, that de Waal (1996) has argued that the framework of morality necessary for ethical behavior is not unique to humans.

behavior of pigs, independent observers still showed agreement in their personality descriptions; moreover, the words the observers used to describe the pigs were just the kinds of trait descriptors that have been used in studies based on ratings (e.g., friendly, confident, inquisitive, nervous, and cautious). These findings suggest that the rating procedures used in animal-personality research are not forcing the observers to use constructs they would not ordinarily use.

Defining the Middle Ground: Profiting From the Arguments for and Against Comparative Research

In 1946, Hebb noted that "the true objection to anthropomorphism is . . . inventing similarities that do not exist" (p. 88). Many similarities do exist between humans and animals. The crucial issue is to determine which similarities are relevant for any given comparative analysis.

When generalizing between humans and animals, scientists must consider the ways in which the animals are similar to and different from humans. The vital issue is to determine which of the differences are important enough to invalidate a cross-species comparison and which ones are irrelevant. As a rule, researchers making cross-species comparisons should consider the species' environmental and social ecologies, their biology, and their phylogenetic relationships with other species, and the importance of these criteria should be weighed according to what phenomenon is being examined. For example, Sapolsky (1990) used Serengeti baboons to examine the links between stress and personality in humans; he noted that unlike many animals whose experience of stress is typically sudden and severe (e.g., escaping from an attacking predator), Serengeti baboons are relatively free from predation and have a plentiful supply of food, so their main stressors are social in nature and are relatively chronic. This chronic form of stress is similar to the kinds of stressors to which humans are exposed, making baboons a good species to model the relations between stress and personality in humans.

Likewise, to investigate some social phenomena associated with group living in humans, scientists may find it more useful to focus on a social species such as lions or hyenas rather than a less social species such as orangutans, despite the fact that orangutans are more closely related to humans and are more similar to humans in terms of biology. In short, the species studied should depend on the question being addressed, with consideration paid to the species' environmental and social ecologies, their biology, and their phylogenetic relationships.

Fortunately, the biological, phylogenetic, and social similarities of species are often correlated. Thus, chimpanzees may be the best choice to investigate group-based social phenomena because they are more similar to humans in social terms than lions, and they are more similar to humans than orangutans in phylogenetic and biological terms. However, as Beach argued in 1950, there are good reasons for casting a wider net. According to Beach (1950), a truly comparative psychology would rely on findings from a great diversity of animals. Alarmed by the growing proportion of animal studies performed on the Norway rat, he warned comparative psychologists against focusing on a narrow range of species. Over a period spanning from 1911 to 1948, Beach estimated that more than 50% of the studies surveyed relied on Norway rats as their subjects (but see Dewsbury, 1998). Between the years 1956

and 1959, Best (1963) observed that "fewer than 3% of all animal-behavior experiments were performed on invertebrates, although invertebrates constitute 12 of the 13 animal phyla" (p. 55). Personality research on animals has not been limited to rats, but it has been limited to a relatively narrow range of species; almost all of the studies reported in Table 1 were performed on mammals, and a large proportion of these were performed on primates.

The logic of studying multiple species parallels the practice of supporting or qualifying findings from studies of humans according to how well they replicate in different human populations. In a parallel fashion, examining the extent to which animal-personality findings replicate across other species makes sense. Researchers can then try to determine what is common to the species in which the results replicate and what is different about the species in which they do not. For example, by studying sociability in species with different social systems and by examining the different ways sociability is manifested across those species, we can learn far more about the social, biological, and phylogenetic mechanisms underlying sociability than if we had just relied on a single (albeit closely related) species.

Two Kinds of Cross-Species Comparison

In broad terms, two kinds of cross-species comparisons are made in the service of learning more about humans. Zuckerman (1984, 1996) has called these the "top-down" and "bottom-up" approaches to comparative psychology. The approach used by Zuckerman (and Eysenck) is the top-down approach: using animal studies to examine in more detail what is already known about humans. D. G. Freedman (1958) took a top-down approach by experimentally testing in dogs Levy's (1943) human-based hypothesis that overindulgent rearing leads to an inability of children to inhibit their impulses. In a similar vein, Zuckerman's research (1984, 1995, 1996) has focused on a concept (sensation seeking) that first arose from attempts to find individual differences in how human participants would respond to sensory deprivation experiment (Zuckerman, 1969, 1984). To further understand the role of monoamine systems in this trait, Zuckerman supplemented his investigations of humans with investigations performed on animal populations. Although extrapolating back and forth between humans and animals raises problems (e.g., it is difficult to simulate all facets of human sensation seeking in animals), this comparative approach has major advantages over research relying purely on humans. For example, animal researchers can examine monoamine levels in the brain rather than relying on indirect measures, as one must in human populations.

The second approach to comparative psychology is the bottom-up approach. This entails examining behavior of animals in their own right and then using the animal models to generate hypotheses about humans. For example, Suomi (1987, 1991) has drawn links from his research examining Reactivity in rhesus monkeys to research examining individual differences in temperament in humans. Similarly, Gorenstein and Newman (1980) proposed that models derived from animals with septal lesions could be used to generate specific hypotheses about psychological processes underlying disinhibition in humans. The bottom-up approach allows investigators to examine phenomena and generate hypotheses in a context that is relatively free from the cultural

complexities of human life and to subsequently test their predictions with human participants.

Thus, both the top-down and bottom-up approaches can be used to integrate research in human and animal populations, and together the approaches highlight the benefits of studying humans and animals in tandem. In practice, researchers often adopt both approaches, going back and forth between research on humans and animals. Researchers such as Gray (1982, 1987a, 1987b) epitomize this dual approach. Beginning with the dimension of anxiety in humans, Gray (1978) performed animal studies to further understand the psychological functions and biological bases of anxiety. He then proposed a model of the neuropsychology of anxiety based on analyses of the behavioral effects of antianxiety drugs on animals (Gray, 1982). Similarly, Sensation Seeking has been examined through both top-down (e.g., Siegel & Driscoll, 1996) and bottom-up (e.g., Dellu, Piazza, Mayo, Le Moal, & Simon, 1996) approaches (Zuckerman, 1996). In the next section, I focus on how cross-species generalizations can be used to tackle issues of interest to personality psychologists.

A Preliminary Research Agenda for a Comparative Approach to Personality Psychology

The embryonic field of animal personality has yet to develop into a coherent, multidisciplinary research enterprise. Personality is rarely the primary interest of animal researchers; the majority of studies appear to be side interests of researchers, motivated by an intuition that their animal subjects are individuals with their own personalities. Consequently, animal-personality research has been sporadic rather than programmatic. A research agenda drawing together the potential benefits of animal-personality research has yet to be proposed. Thus, the remainder of this article is devoted to articulating a preliminary research agenda for a comparative approach to personality psychology.

I start by outlining some general principles to guide this agenda. I suggest that an evolutionary approach is important, but I also note that some important questions can be addressed without explicit reference to evolution. I also emphasize the utility of applying an ecological approach to understand how humans perceive personality in animals. Next, I briefly outline several specific research avenues that stand to benefit from a comparative approach. I suggest that eventually animal research can contribute to an understanding of the genetic, biological, and environmental bases of personality, as well as personality change, links between personality and health, and personality perception processes. Finally, I consider areas of research in personality that have little to gain from animal studies.

Some General Principles for a Comparative Approach to Personality Psychology

Take an evolutionary approach. Most scientists of human and animal behavior accept Darwin's (1859/1964) theory of evolution by natural selection as a basic assumption, and they accept that humans are linked to animals via descent from common ancestors. However, the phenomena thought to be subject to evolutionary processes are rather limited; even though researchers readily accept that the anatomy and physiology of humans is similar to that of animals, many of them have been reluctant to ascribe person-

ality traits, emotions, and cognitions to animals. But there is nothing in evolutionary theory to suggest that only physical traits are subject to selection pressures. Indeed, Darwin (1872/1998) himself argued that emotions exist in both humans and animals, and the field of evolutionary psychology has used theories from evolutionary biology to understand the origins of human psychology and behavior (Barkow, Cosmides, & Tooby, 1992; D. M. Buss, 1991; Daly & Wilson, 1999) and how psychological characteristics vary across and within species (D. M. Buss, 1984). Thus, we should not be surprised if personality traits are not as uniquely human as once was thought (A. H. Buss, 1988; Diamond, 1957).

Cross-species comparisons of species-typical traits, along with principles of evolutionary biology, can help elucidate the origins of personality traits. By examining what is similar about species sharing similar traits and what is different about species that do not share traits, scientists can begin to understand whether a trait originated as an evolved solution to a common adaptive problem (i.e., convergent evolution) or was inherited from an ancestral species (i.e., homology; Hodos & Campbell, 1969; Tooby & Cosmides, 1989). For example, the existence of a particular trait, such as scapegoating, in several different social species combined with the absence of that trait in solitary species suggests that this aspect of personality may be an adaptation to social living (convergent evolution). Alternatively, the existence of scapegoating behaviors in a group of closely related species combined with the absence of the trait in species distantly related to the group suggests that the trait is an inherited feature that may or may not have relevance to the species' modern-day ecologies (homology).

To illustrate this process further, consider the very simple hypothetical example represented in Figure 2. Species B and C are closely related to one another (via ancestral species A) and species E and F are closely related to one another (via ancestral species D), but species B and C are only distantly related to species E and F. Species B and E share similar ecologies, and species C and F share ecologies, but the ecology shared by B and E is quite different from that shared by C and F. Suppose that we find personality trait X in species B. Broadly speaking, we may follow two lines of evolutionary reasoning, depending on the evidence. If we also found trait X in species C, but not in species E or F, this would suggest that trait X is a modern relic of a trait present in an ancestor common to species B and C, such as species A; the possession of traits derived from a common ancestor is known as homology. Alternatively, if we also found trait X in species E, but not in species C or F, this would suggest that convergent evolution had occurred, with X appearing as an adaptation to the ecology shared by species B and E. Just as wings evolved independently in bats and birds to facilitate flight, perhaps scapegoating appears across several social species as a means of regulating social tension and maintaining status hierarchies.

Although this example is simplified, it illustrates how testable hypotheses can be derived about the origins of species-level personality traits: One hypothesis predicts trait X in species C, and another hypothesis predicts trait X in species E. Applying this logic, one could examine a trait such as curiosity in several species and then, using known phylogenetic relations among the species, test whether similarities in levels of curiosity were linked to phylogenetic relatedness (Glickman & Sroges, 1966); if humans' curiosity has been inherited from their ancestors (rather than
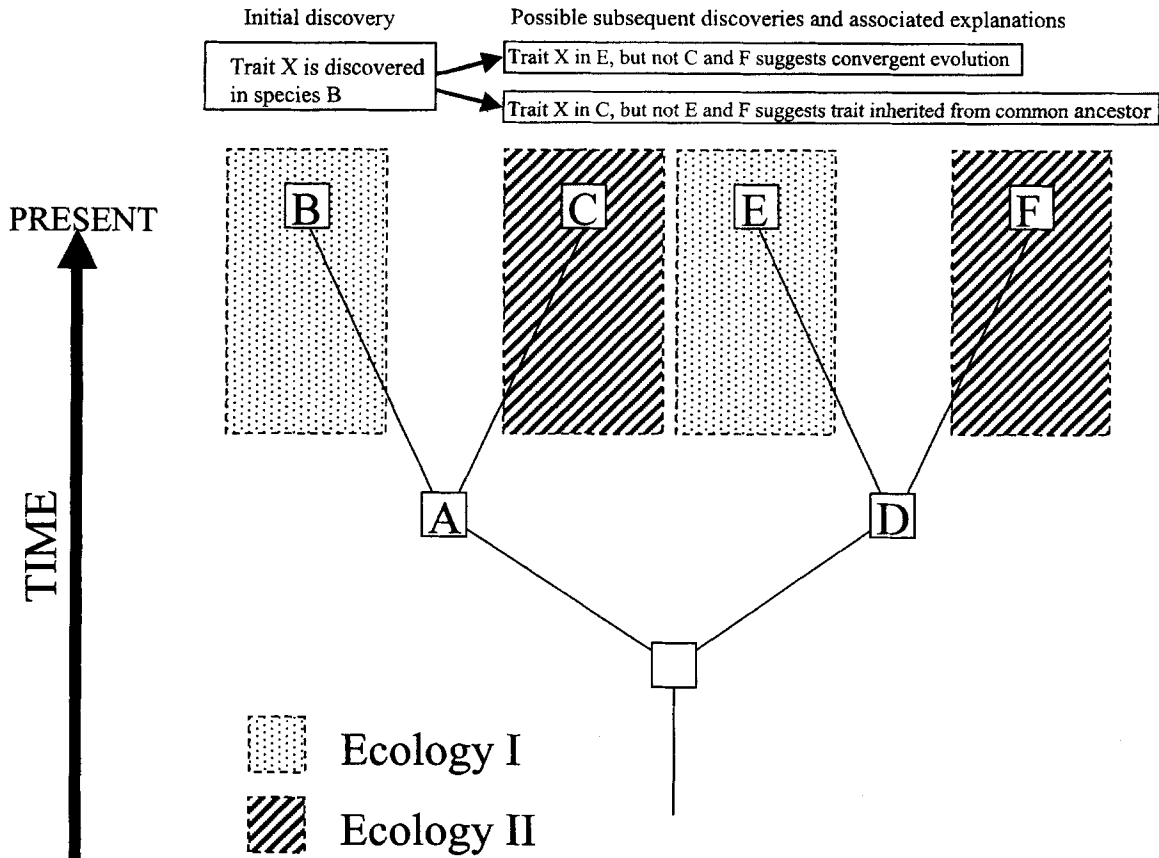
Initial discovery   Possible subsequent discoveries and associated explanations

Trait X is discovered in species B

Trait X in E, but not C and F suggests convergent evolution

Trait X in C, but not E and F suggests trait inherited from common ancestor

PRESENT

TIME

B   C   E   F

A   D

Ecology I

Ecology II

Figure 2. Generating evolutionary hypotheses. Suppose Trait X is discovered in species B. If Trait X is also found in species E but not in species C or F, this suggests that Trait X can be attributed to convergent evolution. If Trait X is also found in species C but not in species E or F, this suggests Trait X can be attributed to a common ancestor (e.g., species A).

emerging as a recent adaptation), such a procedure could enable us to pinpoint when curiosity emerged in humans' evolutionary history. Although the prospect of estimating phylogenies on the basis of behavioral traits may seem daunting, a review of the literature (de Queiroz & Wimberger, 1993) showed that phylogenies based on behavior were just as useful as those based on physical traits. Another possibility is to examine the evolution of gene sequences already associated with personality traits. For example, Lesch et al. (1997) examined genetic information across a range of mammals including tree shrews, rhesus monkeys, chimpanzees, and humans; using this information along with the known phylogenetic relations among the species, they estimated that a gene sequence associated with anxiety (the serotonin transporter gene-linked polymorphic region, known as 5-HTTLPR) was probably introduced into the genome about 40 million years ago.

Recent advances in knowledge about the phylogenetic relations among species, along with methodological developments and computer software (e.g., PAUP [1998] or MacClade [1998]), have greatly enhanced our ability to trace the phylogenetic history of species-level traits (Brooks & McLennan, 1991; McLennan, 1994). I believe that personality psychologists will take advantage of these developments to understand when and how personality traits evolved. To do so, however, researchers will have to study

species for which hypothesized phylogenetic relationships are available, and they will need to consider elements of the social and environmental ecologies that are shared and are unique to the species examined.

The principles of evolutionary biology can also be used as a framework for understanding processes underlying the development and persistence of within-species individual differences (D. M. Buss & Greiling, 1999; Slater, 1981). For example, the process of frequency-dependent selection is based on the idea that the selective advantage of a characteristic is determined by the prevalence of the characteristic in the population. When a characteristic is widespread in a population, its adaptive value may be lower than when it is rare (Maynard Smith, 1972). For example, an animal with a preference for nuts over berries will experience little competition for nuts if that preference is rare in the population, thereby favoring the nut preference until it becomes more widespread and increases the competition for nuts. Similarly, because predators tend to evolve hunting strategies based on the prey species' typical behaviors, individuals of the prey species that exhibit atypical (i.e., rare) behaviors will experience less predation until the behaviors become frequent enough to warrant a change in the predators' hunting strategies. In each case, the rare behaviors offer an adaptive edge by virtue of being rare; this edge promotes

the survival of the rare characteristic, thereby maintaining multiple characteristics in the population. Thus, frequency-dependent selection explains how individual differences can persist in a population. However, before researchers can test such mechanisms, they must first demonstrate the adaptive significance of characteristics and determine the conditions under which various characteristics increase an individual's fitness (Suomi, 1997).

As noted earlier, heritable individual differences are the raw ingredients of evolution (Herzog & Burghardt, 1988). Clarke and Boinski (1995) have used evolutionary reasoning to predict how personality structure will vary across species. They hypothesized a more differentiated personality structure in species that have sophisticated social structures than in species that are less social. A species composed of individuals that rarely interact with conspecifics is less likely than social species to have evolved behaviors related to social traits such as sociability and interpersonal warmth. Thus, one might expect to find fewer personality dimensions in a solitary primate species, such as orangutans, than the six factors of personality identified in the social species of chimpanzees (King & Figueredo, 1997). Similarly, one might expect to find a curiosity or investigatory dimension in a species subject to changeable and diverse food sources, whereas no such dimension might be selected in species with constant, plentiful sources of food (Glickman & Sroges, 1966; Gosling & John, 1999).

One intriguing domain in which to examine adaptation processes in personality research is in domesticated species for which the selection is no longer natural; indeed, in many domesticated species, breeding is carefully controlled and is recorded meticulously and extensively. For such species, adaptation pressures can be experimentally manipulated to test evolutionary hypotheses about personality traits. For example, after many generations, does a curiosity or investigatory dimension emerge in animals exposed to changeable and diverse food sources, as compared with animals exposed to constant plentiful food sources? Of course, researchers need to be aware that genetic changes brought about by generations of breeding are not the only factors that influence the behavior of domestic (vs. wild) animals (Price, 1999); behavioral and biological characteristics are also influenced by the management practices associated with domestic species (e.g., early weaning from parents and handling by humans). And even if genetic changes are responsible for changes in behavior, it is important to remember that genetic changes themselves can be influenced by mechanisms uncommon in the wild; in addition to artificial selection, domestic animals are subject to inbreeding, genetic drift, natural selection in captivity, and relaxed selection (Price, 1999). As can be seen from Table 1, a large number of studies have already been performed on farm animals and pets, so using domesticated species to test questions arising in personality psychology may largely be a matter of harnessing the methods and work already under way.

In short, researchers should continue to use evolutionary principles to guide their research. And, in accord with these principles, researchers should continue to study personality and its social, environmental, and developmental contexts in a wide variety of species.

Consider approaches that are not explicitly evolutionary. Even though all humans and animals have evolved, it does not follow that all of the important aspects of human and animal life need an evolutionary explanation. If it turned out that the theory of evolution by natural selection was false and creationism was true, many psychologists could continue to do their research without changing a thing. Stable individual differences play an important part in the lives of animals and humans, regardless of whether these differences have an evolutionary basis. Indeed, variation among individuals within a species is considered by some to be mere evolutionary noise (for further discussion of this issue, see D. M. Buss & Greiling, 1999; McCrae & Costa, 1999; Tooby & Cosmides, 1990).

Many questions about personality are not dependent on evolutionary processes and are important and interesting nevertheless. For example, even if a particular individual's level of aggression is considered evolutionarily irrelevant "noise," it still plays an important part in the life of the individual and those around her or him. Thus, for many questions (such as how personality develops), it may be sensible to relegate evolutionary theory to an implicit background assumption. Some questions in personality psychology can be addressed quite adequately without explicit reference to evolution, and a subset of these questions may benefit from animal research.

Take an ecological approach. When a human describes his or her dog as "protective," what does this tell us about the dog, and what does it tell us about the human providing the description? Until recently such questions were guided by one of two views: objectivism and relativism.

Objectivism is the view that the world has objective properties and that, when humans perceive something, they are perceiving these properties. Thus, the statement "Rover is protective" tells us something about Rover, an aspect of the objective world. Relativism challenges the objectivist notion of absolute truth and maintains that perceptions reveal more about the conceptual and perceptual systems of the perceiver than they reveal about objects in the world. According to this view, the owner's claim that "Rover is protective" tells us more about the owner than about Rover. Adopting relativism entails abandoning the goal of gaining absolute truth, whereas adopting objectivism entails abandoning the idea that our knowledge may be influenced by who we are. To many researchers, neither of these positions is particularly palatable, but until the emergence of the ecological approach there was no credible way to combine the merits of objectivism and relativism.

The ecological approach to perception (e.g., Neisser, 1984; Reed, 1994; Rosch, 1996; Varela et al., 1991) maintains that perception is influenced in part by what is out there in the world (the objectivist claim), in part by an organism's perceptual and conceptual capabilities (the relativist claim), and in part by the nature of the interaction between the objective world and the perceiver of it. According to the ecological approach, the distinctions an organism perceives are limited by the distinctions that exist, the distinctions the organism can detect, and the distinctions that are useful to it. Thus, the statement "Rover is protective" tells us something about Rover, something about the owner, and something about the nature of the interaction between Rover and its owner.

The ecological approach to perception views the way organisms perceive the world in terms of the important discriminations the organisms have evolved to make. A bee makes discriminations that a human does not, and vice versa. Thus, ecological principles are consistent with the evolutionary principles. Moreover, testable

hypotheses can be generated from an ecological approach. For example, we could hypothesize that the dimensional structure underlying personality ratings made by humans of dogs will vary as a function of the type of relationship humans have with dogs. In other words, the bases for distinguishing dogs will vary according to what humans are doing with the dogs. The structure underlying personality ratings of dogs by American pet owners, Tanzanian shepherds, and Vietnamese chefs should reflect the differences in the nature of these disparate human–dog relationships. This hypothesis is generated from the ecologically driven assumption that human–pet, human–tool, and human–food constitute different relationships, and different dimensions will be important for distinguishing individuals within these different relationships (e.g., cuddly, trainable, or succulent). Consequently, different dimensions will arise that best characterize individual differences along the relationship-relevant dimensions. Tests of these kinds of predictions will have important consequences for how psychologists conceptualize the processes underlying the formation of personality impressions.

I have suggested some guiding principles for integrating research on animal personality. I next turn to a number of key issues in personality that, in my view, have most to benefit from animal studies.

Empirical Implementation of a Comparative Approach to Personality Psychology

Although research on animals will not replace research on humans, the unique perspective provided by animal studies can enrich and augment human research. I suspect that a comparative approach to personality psychology will be particularly fruitful in the following interrelated areas.

Understanding the biological bases of personality. Since the second century AD, when Galen proposed that there were four personality types, each determined by an excess of one of four body fluids, links have been hypothesized between personality and biology (Rich, 1928; Stockard, 1931). Indeed, some of the earliest empirical work on personality was based on animals. Pavlov's seminal research on individual differences in dogs examined conditionability and susceptibility to experimental neurosis (Strelau, 1997). Pavlov classified individuals into the four types of temperament originally proposed by Galen (Melancholic, Choleric, Sanguine, and Phlegmatic), corresponding to four types of underlying nervous system (Weak, Unbalanced, Mobile, and Slow; Ruch, 1992). Although some animal researchers continued to investigate the neuroanatomical and neurochemical bases of personality (e.g., animals were the subjects in lesion studies of the effects of frontal leucotomies on personality; Freudenberg, Glees, Obrador, Foss, & Williams, 1950), most subsequent research on personality failed to maintain a strong link with biological studies of animals. However, there are signs that researchers are beginning to rebuild the neglected bridges between human and animal research (e.g., Castanon & Mormède, 1994; Clarke & Boinski, 1995; Depue, 1995; Gosling & Suomi, 1998; Higley & Suomi, 1989; Sapolsky, 1990; Suomi, 1987, 1991, 1999; Zuckerman, 1984, 1990, 1991). Researchers such as Gray and Zuckerman have made substantial and elaborate efforts to link human research on the dimensional structure of personality with animal-derived models of neurochemical function (see Budaev, 2000, for a review). In one recent integrative

effort, Depue and Collins (1999) elegantly combined findings from human and animal research to construct a comprehensive neurobiological model of the trait extraversion.

In their review of the primate literature, Clarke and Boinski (1995) highlighted many methodological advantages afforded by animal models for studies of the biological and genetic underpinnings of personality; in particular, they pointed to the experimental control that can be exercised and the biological measures that can be taken in animal studies that would be considered unethical or impractical in human studies. As Zuckerman (1984) has noted, "Using other species we have the full range of biological techniques available such as neurological and chemical lesioning and direct measures of brain levels (from autopsy) of crucial neurotransmitters and enzymes" (p. 414). Clearly, generalizations from animal biology to human biology should be made cautiously. However, the benefits conferred by this approach could be enormous, and I suspect that animal studies will soon facilitate major advances in our knowledge of the biological substrates of personality.

Understanding the genetic bases of personality. Another biological process that can be examined through a comparative approach is how genes affect personality. Human twin studies have pointed to genetic contributions for most personality traits (e.g., Bouchard, Lykken, McGue, Segal, & Tellegen, 1990; Floderus-Myrhed, Pederson, & Rasmuson, 1980; Loehlin, 1992). Although twin studies are immensely valuable, they can be very costly to perform, and they can present methodological challenges, such as cleanly disentangling genetic and environmental influences (Devlin, Daniels, & Roeder, 1997). And such natural experiments do not permit full experimental control of the environments to which the participants are exposed.

The potential contribution to be made by heritability studies in animals has long been recognized (Beach, 1953; Dawson, 1932; Gershenfeld et al., 1997; Hall, 1941; Scott, 1953; Scott, Fredericson, & Fuller, 1951). Early behavior-genetic analyses compared inbred strains of rats to determine the degree to which emotionality was heritable (Broadhurst, 1975; Stone, 1932). More recently, in a large study of farm mink, Hansen (1996) compared the heritability of exploration, fearfulness, and aggression, showing that after six generations of selective breeding, fearfulness was especially heritable. Other pioneering behavioral genetic work was Scott and Fuller's (1965) classic research on the genetic contribution to physical and behavioral traits in dogs. Using standard cross-breeding techniques, they analyzed the hereditary components of traits from five dog breeds. They found that behavioral traits could be measured reliably and analyzed just as well as hereditary differences in physical size, with traits such as timidity and aggressiveness having substantial genetic components (see also Dawson, 1932; Dickson, Barr, Johnson, & Wieckert, 1970; Lyons, Price, & Moberg, 1988). Recent work has gone on to examine the genetic mechanisms that account for such interbreed differences in behavior (Niimi, Inoue-Murayama, Murayama, Ito, & Iwasaki, 1999).

Animal-personality research provides an avenue of genetic research that is cheaper than research on humans and offers several important advantages (Gershenfeld et al., 1997; Gershenfeld & Paul, 1998). Plomin and Crabbe (2000) used the term *behavioral genomics* to refer to research that focuses on how genes and groups of interacting genes work to influence behavior, and they sug-

gested that animal models will play a vital role in this research. Mouse models are a particularly promising candidate, because so much quantitative and molecular genetic research has already been done on mice (Plomin & Crabbe, 2000), with the result that a great deal of genomic information for mice is now available (Blake, Eppig, Richardson, Davisson, & the Mouse Genome Database Group, 2000; *Mouse Genome Database*, 2000). In addition, modern gene-mapping technologies are allowing researchers to search for genes or multiple-gene systems (quantitative trait loci) for complex traits (e.g., Flint et al., 1995; Talbot et al., 1999), and some investigators have begun to use knock-out mice (in which a gene is artificially disabled to examine its function) to examine biological mechanisms hypothesized to underlie personality traits (e.g., Dulawa, Grandy, Low, Paulus, & Geyer, 1999). Transgenic methods and new cloning techniques (e.g., Wakayama, Perry, Zuccotti, Johnson, & Yanagimachi, 1998; Wilmut, Schnieke, Mc-Whir, Kind, & Campbell, 1997) could also provide novel opportunities for animal research to further our understanding of the genetic influences on personality. Among the many possibilities, one can foresee expanded twin studies in which, instead of using human identical twins, twenty genetically identical cloned animals are raised in systematically varied environments to examine genetic and environmental influences on personality. Until such cloning techniques are widely available, researchers can use naturally occurring clones such as armadillos, which give birth to four genetically identical offspring.

As noted earlier, experiments involving animals have been subject to fewer constraints than those involving humans (Higley & Suomi, 1989), such that more extensive and intrusive manipulations are possible in studies of genetically identical mice than would be permitted with human monozygotic twins. This relative flexibility means that animal studies can be used to replicate research from human studies and test specific hypotheses. For example, Weiss, King, and Figueredo (2000) used chimpanzees to replicate human research on the heritability of the FFM dimensions of personality. Suomi's (1987) cross-fostering study in rhesus monkeys suggested that infants' response to separation from their foster mothers is best predicted by their inherited levels of reactivity, not their foster mother's level of reactivity or caretaking style (see also Benus & Röndigs, 1997; Suomi, 1999). Of course, cross-fostering studies can also highlight the effects of nongenetic factors; studies of rats have emphasized the role of maternal care, rather than genetic transmission, in the transmittal of some traits (D. Francis, Diorio, Liu, & Meaney, 1999; E. W. Rasmussen, 1939). In short, animal studies will surely constitute one vital strand of research into the genetic bases of personality.

Understanding the environmental bases of personality. The ability to exercise control and carefully document individuals' personality development over time also facilitates research on how personality is influenced by the social and physical environments (e.g., MacDonald, 1983). Bard and her colleagues (see Bard & Gardner, 1996) have argued that much can be learned about social influences on human development by examining chimpanzee development. In their study of 29 chimpanzees, Bard and Gardner (1996) found that animals receiving extra species-appropriate maternal care developed into happier and less fearful individuals than those receiving minimal physical and social maternal care. Stevenson-Hinde, Stillwell-Barnes, and Zunz (1980a) found that the personality of male rhesus monkeys was less influenced than

that of females by an experimental manipulation of the social situation in which monkeys were removed from their groups in the main colony and put in a building with no other monkeys in it. In another study using rhesus monkeys, Capitanio (1984) demonstrated that infants reared by animate (dog) mothers developed better social abilities than did infants reared by inanimate mothers. Several other animal studies have shown how dynamic social processes can influence personality development (Mineka & Zinbarg, 1995, 1996). In short, animal studies provide a useful framework in which to examine how an individual's personality is influenced by his or her biology, genes, social and nonsocial environment, and the interaction among these factors (Castanon & Mormède, 1994; Stevenson-Hinde, 1983; Suomi, 1987, 1997).

Understanding personality change. The study of personality change or development has long occupied the efforts of psychological researchers (Caspi & Roberts, 1999). Typically, the most useful information on personality change is derived from longitudinal studies (Roberts & Friend-DelVecchio, 2000). As part of an exemplary study in humans, Helson and Roberts (1994) examined personality change in ego development in a cohort of graduates from Mills College in California. To do this, they assessed the participants at 21, 43, and 57 years of age. This study yielded many important findings but had to contend with the challenges facing all longitudinal research. For example, the Mills College study had its first assessment when the participants were graduating from college and, therefore, had to rely on fallible and potentially biased retrospective self-reports to obtain information about the first 20 years of life. As with all longitudinal research, there were gaps between assessments, there were no experimental manipulations (e.g., removing parents at an early age), and no biological measures were obtained. In short, a monumental and sustained effort is required to conduct longitudinal research effectively in human populations.

In some respects, animal studies provide an ideal situation in which to investigate personality development. Many captive animals are observed almost every day of their lives. Biological, psychological, and social events that are hypothesized to influence personality change can be recorded or experimentally manipulated, and hypotheses can be tested. Stevenson-Hinde and her colleagues examined consistency and changes in levels of Confidence, Excitability, and Sociability in a colony of rhesus monkeys over 4 years (Stevenson-Hinde et al., 1980b) and related these changes to specific events in the animal's life, such as early separation from mother and colony (Hinde et al., 1978; Stevenson-Hinde et al., 1980a). This study demonstrated another advantage of using animals in longitudinal research: The life span is often shorter for animals than for humans, which means developmental studies in animals can be performed in less time than they would in humans (Scott et al., 1951).

In addition to longitudinal designs, cross-sectional studies can be used to address questions about personality change. In human research, cross-sectional studies need to be interpreted cautiously because effects apparently due to aging may really be cohort effects driven by changes in the cultural and physical environments. In comparison with humans, most animals are subjected to relatively minor changes in their environments, so cross-sectional designs may be especially useful. Studies of animals rarely focus on a narrow age range and often include animals from across the life span. For example, McGuire et al. (1994) studied personality

in a colony of vervet monkeys ranging in age from 19 months to 14 years; they found that a personality factor tapping aspects of playfulness and curiosity was significantly higher in juveniles than in other animals. Such studies could become an important source of information about personality change and development.

Although practical and of great interest, studies of personality development and change in animals (e.g., MacDonald, 1983; Suomi, Novak, & Well, 1996) are rare. I believe much could be learned about personality change by turning our attention to this neglected source of information.

Examining the links between personality and health. In addition to elucidating the determinants of personality, animal research is well suited for investigating the impact of personality on real-world outcomes. I suspect that animal models will play an increasingly important role in research examining the connections between personality and health. We already know from studies of humans that personality is linked to disease susceptibility and adaptation to illness (Contrada, Cather, & O'Leary, 1999; Kemeny & Laudenslager, 1999). For example, a substantial body of research has identified hostility as a risk factor for coronary heart disease.

Now that connections between personality and health have been well established, what should the next step be? If we are to develop treatments and devise preventative strategies, we need to understand the mechanisms that link personality and health (Evenden, 1999). However, these mechanisms can best be examined with more invasive strategies and with more experimental control than has been possible with human populations, suggesting that animal models would be useful. For example, animal studies permit the use of a wide range of physiological interventions and the measurement of a wide range of physiological parameters, providing the type of data that are necessary to identify the mechanisms through which personality and health interact. Animals have been used in biomedical research for many years, so procedures for indexing health in nonhuman animals, particularly laboratory animals, are well developed. Progress in personality-assessment procedures for nonhumans opens the way for new interdisciplinary partnerships among personality–health researchers and researchers in immunology, animal behavior, and veterinary science.

Although quite rare, some animal studies have examined the links between personality and immunity (e.g., Capitanio et al., 1999; Laudenslager et al., 1999; Petitto et al., 1999) and have investigated the relations among personality and a number of health risk factors, such as high blood pressure (Vincent & Michell, 1996; for a review, see Rozanski, Blumenthal, & Kaplan, 1999) and excessive alcohol consumption (e.g., Higley & Bennett, 1999). These studies demonstrate the viability of animal models and hint at their potential for personality–health research.

Understanding personality perception processes. Many psychologists are interested in processes of person perception and would welcome any research, even animal research, if it shed light on how humans perceive one another. There are two ways in which animal-personality research can help illuminate how humans perceive personality in general. First, some studies directly compare humans' perceptions of animals with their perceptions of other humans. For example, J. L. Rasmussen and Rajecki (1995; Rasmussen et al., 1993) found that observers had similar implicit theories of mind (i.e., assumptions about an individual's mental processes) for both animals and human children. Their research

suggests that humans may have evolved a general predisposition to infer mental states such as emotions (Darwin, 1872/1998; Hebb, 1946) and intentions (Dennett, 1978) in other individuals. These theories of mind enable people to predict the behavior of both animals and humans (Eddy, Gallup, & Povinelli, 1993; J. L. Rasmussen & Rajecki, 1995; J. L. Rasmussen et al., 1993). Other researchers have begun to examine the processes by which individuals use behaviors of animals to form personality impressions (King, Rumbaugh, & Savage-Rumbaugh, 1999; Mitchell & Hamm, 1997).

The second and less direct way animal research can help provide an understanding of how humans perceive personality is to compare the structure of personality descriptions of animals with the structure of personality descriptions of humans. Gosling and John (1998) examined personality perceptions of humans, dogs, and cats and showed that human perceivers use a different set of personality dimensions when they think about the personality of humans than when they think about the personality of dogs and cats. Evidence such as this can be used to examine general issues in personality psychology. Consider Shweder's (1981) semantic-distortion hypothesis, according to which personality structure reflects how words are semantically related to each other rather than how personality traits covary in individuals. According to this hypothesis, we would expect to see semantically related words such as *kind* and *sympathetic* loading on the same personality dimension regardless of whether kind individuals also tend to be sympathetic; it follows that personality descriptions using the same set of descriptors to describe different individuals should produce the same personality structure irrespective of what those individuals are like. To test this claim, Gosling and John (1998) examined personality descriptions of humans, dogs, and cats using the same descriptors for all three species. They found that personality structure varied according to the species rated. These findings are contrary to Shweder's claim and instead suggest that the structure of personality ratings is based, at least partially, on aspects of the individuals being rated. Thus, animal studies provide two novel avenues of research that can be used to examine the processes underlying the formation of personality impressions.

Is There Anything We Cannot Learn About Personality From Animal Studies?

Are animal studies a panacea for the ills of personality research, able to solve all of the unanswered questions? Of course not. Many areas of personality psychology cannot be informed by research on animals, either because elements of personality are unique to humans or because the assessment methods cannot be adapted to nonhumans. Areas of personality that may be species specific because they require human consciousness, language, or culture include self-concept, identity, attitudes, and personal projects. Indeed, my review, summarized in Table 1, showed that personality studies of animals have largely been limited to studies of personality traits, with no studies focusing on self-concepts or identity. Moreover, methods that entail self-reports or any other use of language by the research participants cannot be used in animal studies. In short, animal research cannot solve all of the problems that face personality research, but this should not exclude animal studies from helping to solve some of them.

Conclusion

In the introduction of his presidential address to the American Society of Naturalists in 1938, the eminent primatologiest, Robert Yerkes underscored the idea that personality could be found in animals: "I am assuming that personality is the correct and adequate term for what is now known concerning the integrated behavior of the chimpanzee. Indeed, in my present thinking there is no question about the reality of chimpanzee mind, individuality, and personality" (Yerkes, 1939, p. 97). Yet in 1954, Hebb and Thompson described receiving looks of "open astonishment" (p. 532) when they presented the idea that animals should be of interest to psychologists interested in social behavior. Even today, the idea of "animal personality" is often treated with skepticism or even ridicule. However, as this article documents, the body of research on animal personality is growing. If properly implemented and interpreted, this research may be able to provide important insights into the genetic, biological, and environmental determinants of personality that could not be achieved by relying on human research alone. And the initial signs are good, with promising findings emerging from animal researchers who have used animal studies to tackle these long-standing issues (Suomi, 1999). I have suggested some general principles that can be used to guide an animal-based research agenda and outlined several areas that stand to benefit from animal research. When one considers the benefits afforded by a comparative approach, it is surprising that personality psychologists have, on the whole, neglected animal studies and the unique research opportunities they afford. By articulating a preliminary research agenda for a comparative approach to personality psychology, I hope this review will provide an impetus to resurrect the bridges between human and animal research envisioned long ago by pioneers such as Pavlov, Yerkes, and Hebb.

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