CHAPTER

1 Toward Bridging Gaps: Finding Commonality between Evolutionary and Comparative Psychology

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Abstract

This volume brings together an eclectic and provocative body of work from some of the brightest minds in comparative psychology and evolutionary psychology. The intent of this volume is to highlight the strengths and insights of each field and to bridge the gaps between them. Comparative psychology has sometimes lost the focus that evolutionary psychology wields to shed light on seminal questions in the study of human and nonhuman behavior. Although evolutionary psychology maintains an overarching framework with which to explore questions of ultimate or proximate causation—referring to mechanisms of natural selection, comparative psychologists sometimes study esoteric topics of interest, without placing these studies in a larger theoretical framework. However, the insights of comparative psychologists have often forged new ground, generating new theoretical debates and inspiring nonhuman studies in new directions. For instance, the recent explosion of work in canine cognition has been inspired to a large degree by hypotheses about the importance of domestication in sculpting canine cognitive skills, and these hypothesis have prompted much debate (Dorey, Udell, & Wynne, 2010; Hare, Brown, Williamson & Tomasello, 2002; Hare et al., 2010; Udell, Dorey & Wynne, 2008; Wynne, Udell & Lord; 2008). Bringing together comparative psychology and evolutionary psychology can strengthen the contributions of both. Rather than taking all or none approaches to scientific pursuits, our journey should allow the beacon of truth to guide us forward, even if the path is a middle ground. There need not be a divide between field researchers and laboratory scientists, between those who study humans and nonhumans, between behaviorists and cognitivists, or between comparative psychologists and evolutionary psychologists.

Key Words: comparative psychology; evolutionary psychology; ethology, field research; laboratory research

Introduction

> A human being should be able to change a diaper, plan an invasion, butcher a hog, conn a ship, design a building, write a sonnet, balance Accounts, build a wall, set a bone, comfort the dying, take orders, give orders, cooperate, act alone, solve equations, analyze a new problem, pitch manure, program a computer, cook a tasty meal, fight efficiently, die gallantly. Specialization is for insects.
> *Robert Heinlein* (1973, p. 123)

Heinlein eloquently summarizes one of the fundamental attributes of humanity: We are flexible, adaptable, and we are able to generalize what

we have learned to solve new problems. We tend to value these attributes as defining hallmarks of intelligent behavior, but that is an anthropocentric marker. Other species are specialists. All have evolved to survive and reproduce in the niches for which they are best adapted. Many who embark upon the fascinating study of nonhuman animals do so because of a similar quest to determine where these creatures depart from us in terms of their abilities, be they physiological, perceptual, or cognitive capacities that are the focus of study. Others take a less anthropocentric perspective and study animal behavior without explicit regard for its relationship to human behaviors or traits, focusing more on the relationships between the organisms in question and on their ecology. Sometimes researchers are seeking evidence of commonality between closely or distantly related species on the basis of their phylogeny or similar ecologies. Other times, they are seeking evidence of differences, for complementary reasons (i.e., because of distant relatedness and different ecologies). What most evolutionarily informed scholars of human and nonhuman behavior share is a curiosity about the evolutionary forces that gave rise to the emergence of different and similar traits. Why are we the way we are, and why are other animals the way they are? How are behaviors maintained in different populations? These fundamental questions bring together two fields of study: evolutionary psychology and comparative psychology.

At the heart of all of this research, past, present, and future, is commitment to the goals of the scientific method: objectivity, openness to scrutiny, self-correction, and careful control. We hope to uncover what is an honest reflection of reality and to appreciate the breadth and diversity of life on earth, for all of its wonder and splendor. Regardless of the degree to which species are similar or different, they are equally fascinating in their own right. The better we understand them, the better our abilities to draw inferences about the environmental forces and evolutionary pressures that sculpted them. We cannot lose sight of the fact that evolution is a branching bush, not a ladder leading to an ultimate creation in the image of man (Boakes, 1984; Hodos & Campbell, 1969). That is what we hope to accomplish, in small part, with this volume: a renewed appreciation for what two distinct fields of science—evolutionary psychology and comparative psychology—have to offer in terms of expanding our knowledge of the species with which we share this planet. We also hope to remind the reader that although the approaches of the two disciplines are quite different, the scholars in each have much to learn from each other.

At times, prominent thinkers in one field have raised issues that have been taken up by researchers in the other. For example, Cosmides' (1989) groundbreaking research suggested that humans have evolved a specialized capacity for reasoning within the social domain and that they solve problems more readily when framed as social contract problems rather than as equivalent logic problems. Evolutionary psychologists, along with cognitive and developmental psychologists, have proposed a number of other domain-specific "modules" or "expert systems" that may have evolved to deal adaptively with specific problems within relevant domains (Fiddick, Cosmides, & Tooby, 2000). For instance, Baron-Cohen (1995) and Leslie (1987) proposed a system for reasoning about mental states—the human theory of mind (TOM) system—a term coined by Premack and Woodruff (1978) who asked whether chimpanzees could reason about the intentions of humans. The question of whether humans have an expert system for dealing with social contract problems has been subjected to extensive empirical tests by evolutionary psychologists (reviewed in Cosmides & Tooby, 2005). The broader question of domain-specific versus domain-general intelligence and individual differences with regard to such skills has not been subjected to intensive study, however. Also, although Cosmides and Tooby did not explicitly study differences in reasoning within social and physical domains, broadly defined, Cosmides' (1989) groundbreaking work, sparking decades of research, can be said to have inspired such lines of inquiry.

Recently, comparative psychologists have taken up the challenge of extending such studies to other species, investigating whether nonhumans, perhaps because of TOM deficits, may be specialized to reason more proficiently within the physical rather than the social domain. However, only recently have investigators attempted to conduct analogous tests investigating whether typically developing and atypically developing humans, as well as nonhumans, reason about social (mental) and nonsocial (physical) stimuli with equal ease in a variety of paradigms, and within a variety of contexts. Brauer, Kaminski, Riedel, Call, and Tomasello (2006) were among the first comparative psychologists to set up direct tests of these hypotheses and suggested that dogs were more socially inclined than apes, who may be more attuned to the physical world—a suggestion that has exciting implications for both canid

and primate cognitive evolution. Such findings have sparked a wellspring of hypotheses concerning the selection pressures on canid evolution, ranging from domestication (Hare et al. 2002; Kubinyi, Virányi, & Miklósi, 2007), ontogenesis (Dorey et al., 2010; Udell et al., 2008; Wynne et al., 2008), or their natural social structure, which highlights cooperation among members of the pack (Mech & Boitani, 2003). Miklosi and Topal discuss these hypotheses in chapter 11. Tests comparing human children and other great apes on tasks designed to assess social and physical cognition revealed that the performance of apes differed more from that of human children in tests of social cognition versus physical cognition (Hermmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007), again suggesting that nonhuman primates may not share the same expert "system" or "module" for reasoning within the social domain. However, Lyn, Russell, and Hopkins (2010) later presented some of the same tasks, particularly focusing on communicative tasks, to chimpanzees and bonobos who had experienced different rearing conditions, and suggested that the proposed differences were more a function of environment than biology. The importance of attending to issues of both nurture and nature is addressed in several chapters in this volume (see especially, chapters 4 and 25). Sarah Barks and James Rilling, along with Lisa Parr have been investigating whether different parts of the primate brain are activated when processing social versus nonsocial stimuli (work in prep, but see Rilling et al., 2007). Thus, impressive advances have been made by comparative psychologists, presumably inspired by work in evolutionary psychology, whereas developmental psychologists have devoted less attention to the question of whether humans show a priority for social reasoning, despite intriguing differences in the abilities of typically developing children and children with autism, who cannot solve false belief tasks, but can reason about false photographs (Zaitchik, 1990).

All this is to make the point that investigators in one field or area can be inspired by topics, questions, methods, and approaches in another. In fact, the substantial body of research on theory of mind in children by developmental scientists was inspired by the 1978 article by Premack and Woodruff first asking "Does the Chimpanzee Have a Theory of Mind?" Trading favors, comparative psychologists often borrow methods used by developmental psychologists, particularly those working with preverbal infants, such as the looking-time or violation of expectation paradigms, often used to study false belief or physical causality understanding in nonverbal populations (Baillargeon, Scott, & He, 2010). Evolutionary psychologists provide a consistent theoretical framework, focus, and brilliance for placing questions in a broader evolutionary context, and comparative psychologists display ingenuity in experimental design and a willingness to embrace novel theoretical approaches. When the strengths of both are wedded, science might move forward in a way that neither field could accomplish without the talents of the best scholars in the other.

Definitions of comparative psychology and evolutionary psychology, and what it means to be a comparative psychologist or an evolutionary psychologist, have not always been clear. Sometimes comparative psychology is defined simply as the study of animal behavior. It has often been thought that, to be truly comparative, one must study a variety of species and/or must compare one of more species directly to humans. Sometimes the comparisons involve living species, in order to form inferences about evolutionary relationships; other times comparisons are drawn between living and extinct species in an effort to understand evolutionary processes. After extensive review, Dewsbury (1984) concluded that comparative psychology should be defined as involving generalities and dealing with both proximate and ultimate causation. This definition returns us to the fundamental questions referred to earlier: why do behaviors emerge in an organism's repertoire, that is, what functions do those behaviors serve? What adaptive purpose? These are questions of ultimate causation. What is causing the organism to engage in that behavior right now, at this given moment? What physiological, biological, or environmental mechanism(s) must be in place? These are questions of proximate causation. Others (Papini, 2003) suggest that the field should focus on the phylogenetic history and adaptive significance as well as the ontogenetic origins of an organism's behavior. With both Dewsbury's analysis and Papini's suggestion, it is easy to see Darwin's influence. How then does evolutionary psychology differ from comparative psychology?

In 1982, Robert Hinde suggested that, due to broadening interests in ethology and comparative psychology, few differences existed between the two. Hinde (1982) and Dewsbury (1984) sought to bridge what gap did exist between the two. Cartwright (2000) suggested that comparative psychology failed to fill in the divide between human and animal, whereas ecologists and sociobiologists were able to succeed. Evolutionary psychologists

investigate psychological mechanisms as adaptations produced by natural or sexual selection. Therefore, they focus on the ultimate cause of human behaviors and characteristics. Human nature is viewed as a set of psychological adaptations to problems that were recurrently faced in our ancestral history. According to Pinker (1999), evolutionary psychology is not a single theory but an integrated set of hypotheses focused on gene-level selection, modularity, and adaptation, and an attempt to apply evolutionary theory to the mind. Whereas the connection to Darwin is also evident, evolutionary psychology is linked more strongly to sociobiology and the biological sciences, in general, but also to cognitive psychology and behavioral genetics. Of course, we need not think of evolutionary psychology as a subdiscipline at all but rather as an overarching perspective from which all psychology can be understood and organized, much as evolutionary theory has done for biology or zoology (Barkow, Cosmides, & Tooby, 1992).

Historically, the two fields have operated fairly independently, as if their missions were separate, disregarding the common foundation, goals, and strengths that could move each field forward. Today, these separate paths are clearly reflected in the focus and methods of current research conducted in each discipline. Evolutionary psychologists have maintained their focus largely on questions concerning human psychology and evolution, and they fittingly frame human psychology in the context of evolutionary theory. The research questions are focused on issues of sex differences, mating strategies, spatial cognition, parental investment, aggression, affiliation, cooperation, and so on. One can explain human mate choice and strategies, and sex differences in such choices in both long-term and short-term relationships using an evolutionary framework (Buss, 1989, 1998, 2003; although see Haufe, 2008). As another example, one can examine paternal investment as a function of kin recognition from an evolutionary psychological perspective (Alvergne, Faurie, & Raymond, 2009). As a third example, in chapter 4, Sell discusses how humans estimate strength and fighting ability, that is, formidability, from human voice. The focus within evolutionary psychology is on parallels in all of animal behavior, (human and nonhuman) because some general laws of natural (and sexual) selection apply unequivocally.

Comparative psychology, in contrast, has, at times, lost its focus. Although comparative psychology maintains as one of its goals an interest in the evolutionary forces that built various capacities and morphologies in diverse species, research within this subfield has sometimes taken esoteric side trips, exploring the behaviors and capacities of a species without placing those capacities in any sort of theoretical framework, evolutionary or otherwise (see also Lockard, 1971; Tolman, 1987). In addition, although comparative psychologists are, by their very definition, comparative, many study only a single species and make little reference to how that species' abilities compare to others— even to humans. Others inappropriately compare nonhuman primates to developmentally delayed human children, as if they did not evolve their own unique suite of abilities and adaptations for their own ecological niche and lifestyle. On a related note, abilities are often not addressed within the context of a species' ecology. Thus, although comparative psychology is without the current human-centric focus of evolutionary psychology, it is also sometimes lacking the focus to guide it forward.

Anthropocentricism

How central should questions of human evolution be in the study of other species, particularly as psychologists? Should we study other species primarily because they provide clues to the origins of our own existence? Should we use ourselves and our own abilities as yardsticks against which all other species are measured? As just one example, should we design our tests of "intelligence" around capacities and feats we deem to be of value, because they are traits that serve *us* well in human societies? Should we investigate whether other species exhibit some of the same capacities that humans do, and to what extent, in our attempts to determine which other species are most "intelligent," "successful," and "adaptable"?

Heinlein (1973, p. 24) wrote "Never try to teach a pig to sing. It wastes your time and annoys the pig," capturing succinctly a fallacy of much of comparative research. That is, as humans, we are often determined to test nonhumans for the ability to perform some task or display some feat that would demonstrate that they share a capacity known to be within the range of human abilities. This human-centered approach has been deemed the "holy grail" approach to comparative research and poses serious problems for the study of animal behavior (Povinelli & Vonk, 2003, 2004). First, it may cause researchers to succumb to arguments by analogy. If nonhumans (or human infants, for that matter) behave in a manner similar to how fully developed humans behave in tests designed to assess those human abilities, the

researchers are particularly likely to assume that the outwardly similar behaviors are indicative of the same underlying abilities or mechanisms, rather than probing further. Sometimes when one probes further, one finds that subjects that appear to understand a task are solving it by means of quite different mechanisms than those originally investigated by the researcher. One of the best known instances of this phenomenon is the series of studies by Povinelli and Eddy (1996), originally designed to assess chimpanzees' ability to read the attentional states of humans. Povinelli and Eddy presented the chimpanzees with pairs of humans; one of whom could see them and one of whom could not. The chimpanzees were allowed to choose one of the two humans to beg from, using their species-typical begging gesture. Presumably if they understood who could see them and who could not, they would preferentially beg to that person from the first trial forward in each of the various trials. However, it was later determined that, even though the chimpanzees succeeded from the beginning on some of the configurations, such as the trials in which one experimenter sat facing the chimpanzee and the other experimenter sat with her back to the chimpanzee, success on those trials need not indicate that chimpanzees understood anything about mental states such as "seeing." Rather, chimpanzees could have succeeded on these trials by a different mechanism. Follow-up tests (Reaux, Theall, & Povinelli, 1999) indicated that the chimpanzees instead seemed to use a hierarchy of behavioral rules based on observable features of the tasks such as "gesture to the individual who is facing forward, then gesture to the individual whose face is visible, then gesture to the individual whose eyes are visible." What was not required was that the chimpanzees were operating on the basis of the same fully developed TOM system that humans might utilize in such a test. However, when tests are designed to test for the presence of known human abilities in nonhumans it is all too easy to interpret successful findings as indicative of "positive" findings of a particular attribute.

Second, adopting the "holy grail" approach leads to the strong possibility that one neglects or ignores other equally astounding and impressive traits and feats that other species exhibit but humans do not. For instance, bats and dolphins echolocate. We understand very little about how these abilities may have transformed the thoughts and perceptions of such species. perhaps because we are not capable of perceiving or conceiving of the world in the same manner, due to our own limitations. Researchers have only just begun to appreciate the intelligence of the cetaceans, assuming that they exhibit cognitive complexity because of their complex social lives, something that they share in common with human societies (Pack & Herman, 2006). However, again, cetaceans are usually tested for abilities that humans deem important, such as language, perspective taking, self-recognition, and numerosity (see Jaakola, chapter 9 this volume). However, even species closest to us phylogenetically may demonstrate surprising differences from us. Chimpanzees may respond more quickly and accurately in some tasks, like ordering numerosities, than college students do (Inoue & Matsuzawa, 2007). They may also be more sensitive than typically developing humans to local level patterns and changes in such patterns, rather than to global patterns and schemas (Fagot & Tomonaga, 1999). In terms of physiological and sensory adaptations, there are many along which humans could not compete with their nonhuman counterparts. Insects communicate by a vast array of chemical signals. Cocroft and Sullivan-Becker's chapter (chapter 18 in this volume) elaborates on the fascinating world of the social insects. Some fish and reptiles use electric/magnetic impulses to find prey. Yet we focus on research in which nonhumans attempt to pass tests that human children pass and most animals fail (see also Hermmann et al., 2007). That is, assuming they are motivated to attempt to pass the tests and understand what the test is even asking them to do. Many recent studies have emphasized cognitive continuities between humans and other apes, specifically chimpanzees, and deemphasized (or failed to address altogether) equally important cognitive *dis*continuities. However, to have a complete understanding of the animal mind evidence of discontinuities, usually portrayed as negative results, in addition to evidence of continuity, usually portrayed as positive results, must be reconciled.

As with any overarching theory, an all-or-none approach or viewpoint may not be fruitful. Other species may display important continuities with each other and with humans in some domains of both cognition and behavior, but not in others. Researchers, particularly those studying our closest relatives, the other primates, sometimes appear to be split into two diametrically opposed camps; those focusing on finding evidence for continuity in all aspects—TOM, metacognition, imitation, empathy, self-recognition, causal reasoning. and so on—versus those who have been accused of striving to demonstrate the uniqueness of the human mind

at the expense of appreciating intelligence in other apes (Bolhuis & Wynne, 2009; de Waal, 2005, 2009a, 2009b; Penn, Holyoak, & Povinelli, 2008). There is a middle ground. An objective approach would recognize that there are both continuities and discontinuities between even closely related species, such as chimpanzees and humans, and appreciating differences as well as similarities does nothing to denigrate the value of other species; rather, it informs us further about their uniqueness.

In that vein, it may be critical to note the pressures placed upon scientists by the publish- or-perish phenomenon. Of course, this dark cloud does not hover uniquely over comparative psychologists. However, it may be that comparative psychology is particularly susceptible to temptations and challenges given the lower rates of replication due to the smaller numbers of scientists working with exotic species and small numbers of individuals representing their entire species. When hard-to-come-by participants fail to produce good data or do not meet criterion on training tasks, allowing them to proceed to actual experiments, after weeks, perhaps months of time and financial investment, comparative researchers cannot quickly recruit more gorillas, parrots, or dolphins to test. What do you do, as a scientist, with a small number of subjects who are not producing publishable results, when you must produce papers to meet tenure and promotion criteria and maintain your position in the academic community? Of course, what one should do is find new questions, new experiments that take advantage of behaviors that are within the animals' natural repertoire, and strive to understand those phenomena.

A related phenomenon is the difficulty of publishing null results, which relates to the "holy grail" trend in comparative research. Much of the focus of research today is to demonstrate that the researcher's animal of choice is capable of some cognitive or behavioral trait, usually previously deemed unique to humans. If the researchers are "successful" in "demonstrating evidence" for such traits in their subjects, they are likely to be able to publish their results in high profile journals, such as *Nature* or *Science*. If the results are equivocal or, heaven forbid, "negative," they may never be published or they are publishable only in a lower-impact journal. When high-profile researchers at top-tier universities are found guilty of scientific misconduct, the media onslaught casts a dark shroud over the entire field.

Psychology, in general, has fought long and hard to reserve a slot among the sciences. Animal researchers, in particular, fight an uphill battle convincing reviewers and readers that interpretations of behaviors are objective. A potential positive outcome of these trying events is that the critical eye on comparative psychology will sway researchers in the field away from "holy grail" type pursuits toward more objective interpretations and a greater openness to both so-called "positive" and "negative" findings. The fact that results indicating that animals may not have the capacities we are testing them for are deemed as "negative" results reveals much about the goals and motives for conducting the research. Are comparative psychologists attempting to reveal the true state of affairs regarding the traits of our fellow species, or to set humans apart, or to show close kinships with the other creatures with whom we share this planet through perceived similarities? If we could strive to value differences as much as similarities, we may gain much both in our pursuit of truth and in scientific objectivity. After all, evolution is as much about differences as it is about similarities.

Of course, it is easy to say we should step outside of ourselves and frame problems from the perspective of the animals we are studying, and not just from an anthropocentric viewpoint, but that is easier said than done. Perhaps our own TOM is limited to minds like our own. There has been some suggestion that apes might perform better on experimental tasks when required to reason about, or imitate, conspecifics, rather than human experimenters, suggesting that, if they do reason about other minds, they may do so only with conspecifics. However, again, one has to be cautious because there are many purportedly "positive" findings whereby chimpanzees, as one example, were claimed to have reasoned about the mental states of human experimenters (Call, Hare, Carpenter, & Tomasello, 2004; Hare, Call, & Tomasello, 2006), as well as conspecifics (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001). Still, perhaps it is difficult, if not impossible, to envision what it is like to view the world in a dramatically different way with concepts we do not represent, or without concepts that have become so hegemonious in our own minds, such as those for mental states (see Povinelli & Vonk, 2004). Imagine what the world would be like if you did not wonder what others were thinking, that is, if you did not think about what they were thinking about *you*, whether they liked you, thought highly of you, wished to help you. It is next to impossible to imagine such a world once we develop the capacity to reason about the mental states of others, because

such thoughts become so prevalent in our minds and such a driving force in our own explanatory nature. The same is also true of language. Once we learn words, it is seemingly impossible to think without them. In fact, this is the prevailing explanation for infantile amnesia: our preverbal memories cannot be retrieved because they are stored in a different nonverbal code that is difficult to convert (Simcock & Hayne, 2003). It is difficult to describe anything once language is achieved without attempting to use words or labels of some kind. So the goal may be to understand the minds of other species, but if their minds are so different from our own, finding a way to design tasks that will tap into that knowledge and translate it for us into something that is meaningful and understandable may be much more challenging than it initially sounds. So, we return to our initial query. Is it, therefore, inappropriate to begin with tests standardized on a human-centered scale?

It seems reasonable to take into account the sorts of things an animal should be designed to reason about and the sorts of stimuli and experiences it is most comfortable confronting and go from there. Both comparative psychology and evolutionary psychology have their roots in early ethology and zoology. The early behavioral ethologists designed simple but elegant experiments that made use of an animal's natural environment. For example, Tinbergen's (1951) classic studies, which demonstrated the salience of releasing stimuli, and von Frisch's (1967) groundbreaking work with honeybees, which demonstrated the complexities of their communication system when forager bees returned to the hive and communicated the whereabouts of food sources to the rest of the hive, were conducted in natural settings examining the animals' natural behaviors.

Tensions

Since these seminal, provocative, and brilliant studies into what we now tend to think of as "lower" organisms, researchers working in field settings have often grown apart from those who have taken research questions into the laboratory, where more control can be exerted over extraneous and potentially confounding variables. Any good student of research methods in the behavioral sciences knows that there is a constant precarious balance between internal and external validity in any study. Should you allow a subject to behave naturally in its own environment, there is much external validity, and the results can easily be generalized to the real world because one is already studying the real world. However, internal validity has been compromised or never established to begin with. One is often unable to determine the true causes of the behavior one has observed because one has no control over all of the other variables at play: rearing history, exposure to other stimuli, learning experiences, reinforcement history and so on.

In the experimental laboratory, in contrast, one can exert control over such threats to internal validity. However, this control comes at the price of external validity; for example, one can no longer be sure that the animal is behaving the same way in the sterile laboratory environment, in the absence of the usual social and environmental stimulation and challenges, and normal rearing history, and, therefore, external validity is sacrificed (see also chapter 26 of this volume). These compromises explain the apparent disdain that field researchers sometimes seem to have for laboratory researchers, and vice versa, although each can see value in what the other is doing; each can focus on the weaknesses of the other approach and fail to take from the other what is most valuable and bring it into their own work to strengthen it. This is a shame, particularly in the fields of comparative psychology and evolutionary psychology, because each field has so much to offer the other. Field researchers observe what animals are doing naturally and learn about the natural environments: what challenges lie therein; what animals face on a daily basis; what priorities they must have, and what problems they must solve. Their work can produce insights to inform the questions we ask about their cognitive capacities and behavioral tendencies. However, the work should not stop there. Laboratory scientists can further probe the limits of their thinking under controlled conditions to elucidate the causes and contexts of behaviors and thoughts and attempt to answer cause-effect questions to more accurately identify species differences and individual differences.

Thus, one goal of this volume is to bring together researchers working on problems in the field and in the laboratory to reveal how complementary such approaches can be in the study of the animal mind. Indeed many contributors (see chapters 7, 17, 20, and 24 of this volume) already incorporate both approaches in their research program, and this is refreshing and inspiring. As one example, a prominent anthropologist, Joan Silk, known for her prolific field work largely with baboons (chapter 20) has recently forged collaborations with biologists and psychologists and conducted laboratory studies of prosocial behavior in chimpanzees and tamarins

AQ1 (Brosnan et al, 2009; Cronin, Silk, et al, 2005; Vonk et al., 2008). She and her colleagues have further extended this work to human children to study the ontogenetic and phylogenic roots of prosocial behavior (chapter 20 of this volume). Andy Whiten's program of research includes research conducted at African field sites in combination with studies of captive chimpanzees, capuchins, and squirrel monkeys, in conjunction with a complementary program of developmental studies with human children (see chapter 24 of this volume). In addition, Whiten coordinated several teams of field researchers studying the possible transmission of culture in chimpanzees (Whiten et al., 1999) and coordinated this effort with a similar research program studying wild orangutans (van Schaik et al., 2003). We believe this complementary approach is the future of both fields (more on this in the final chapter of this volume).

In fact, one of the most promising new directions of comparative research in the past decade has been a return to more ethological approaches to the study of animal behavior and cognition, even in laboratory studies. This approach has been championed by Sara Shettleworth (2009; see chapter 28 of this volume), among others, and is demonstrated brilliantly in the work of Emery (see chapter 5) and Clayton (see chapter 12) who work primarily in the lab but approach experimental questions with a keen eye to the types of problems their animal participants would face in the wild, constructing research tasks that are familiar, ecologically relevant problems. It is this approach that has revealed startling abilities in the corvid family for episodic-like memory (chapter 12), social cognition (chapter 5), and perhaps even planning (Correia, Alexis, Dickinson, & Clayton, 2007; Raby, Alexis, Dickinson, & Clayton, 2007) and perspective taking (Dally, Emery, & Clayton, 2006; Stulp, Emery, Verhulst, & Clayton, 2009). Then, there are researchers who work primarily in the field but who have adopted the experimental method, attempting to exert control over the surroundings and manipulate variables and stimuli to determine cause and effect and design true experiments, such as the brilliant team of Cheney and Seyfarth, whose groundbreaking book "How Monkeys See the World" (1990) changed our views of how another primate might view the world. This approach has influenced generations of scholars mentored in this tradition (see chapter 17 of this volume, for one example). Cheney and Seyfarth's own views on the directions of this field are elaborated on in chapter 27 of this volume.

Research Questions and Strategies

Different questions do sometimes rightfully deserve different methodological approaches. If the researcher is concerned with questions about what the animal does naturally, what the variability of the behavior is within the natural environment, and comparing those abilities to other species with different ecological backgrounds and phylogenetic histories, perhaps to explore the evolutionary roots of different traits, then a more ecological approach is likely warranted. If, however, the researcher is concerned with the limits of an animal's behavioral capabilities—not necessarily what it exhibits on an everyday basis, but what it is capable of achieving under unusual and varying circumstances—then perhaps it is justifiable to remove the animal from its natural setting and test its abilities in a controlled laboratory environment where one can present it with tests under diverse conditions and probe its responses outside the environment in which learning may have arisen due to instinctive responses or a long history of reinforcement. It is only in the laboratory that we can present animals with stimuli and events to which we can be relatively sure they have never been exposed and thus probe their ability to generalize prior learning to novel situations without the confounds of prior reinforcement or worry about whether genetics or evolution have merely sculpted the animal to respond in a canalized fashion to something that is prevalent in its natural habitat. So, although some critics are disparaging of laboratory approaches that present animals with tasks that are foreign to the animal and ask the animal to solve problems it would not face in its natural habitat (see chapter 26 of this volume), it can be precisely these kinds of tasks that tell us whether any other species shows the kind of behavioral flexibility and ability to generalize problem solving and reasoning to novel situations the way humans can and often do.

One might argue that it is necessary to remove a species from its natural environment to reveal flexible cognitive processing and problem solving rather than fixed responses in limited contexts. Vonk and Subiaul (2009) presented chimpanzees with a scenario that would be unfamiliar to them, but one that might reveal the ability to make inferences regarding possible outcomes based on a true causal understanding of the function of various limbs in performing tasks that were familiar to them. The chimpanzees were required to reason about whether humans with apparently missing arms and legs could deliver food rewards by passing food trays forward

that were initially positioned either in the humans' laps or on the floor at their feet (or where their feet would be). Although the chimpanzees may not have previously experienced humans without legs or with constrained arms or legs, they were nevertheless familiar with the manner in which humans typically perform certain tasks and, in the course of their development alongside humans, these apes had many opportunities to form hypotheses regarding the ability of humans to perform certain tasks if their limbs were not available. This assumption seems no different from the assumption of other researchers that chimpanzees can reason about who could and could not see them based on the visibility of the eyes and faces of humans (Hare et al., 2006; Kaminski, Call, & Tomasello, 2004; Povinelli & Eddy, 1996). Chimpanzees have had little or no experience with humans without eyes or faces or with faces completely invisible prior to participating in many cognitive tests of how they respond to humans with faces occluded. When results reveal that chimpanzees are successful on such tasks (e.g., the back/front condition of such experiments, Kaminski et al., 2004; Povinelli & Eddy, 1996), no one concludes that chimpanzees should not succeed because they should not be able to make inferences about bodily orientation of humans.

When nonhuman primates successfully use tools they would not encounter in their natural environment with equally unfamiliar apparatuses, the same concerns are not raised regarding the unfamiliarity of the testing environment. It is a mistake to apply such criticisms uniquely with regard to so-called negative findings. A study by Buttelmann, Call, and Tomasello (2008) indicated that apes were not more likely to respond to behavioral techniques that were familiar rather than unfamiliar to them. These researchers, among others, have often relied on arguments that experimental tasks often present chimpanzees with atypical situations that they would not likely encounter in their natural lives, thus questioning the validity of "negative" findings from experimental protocols. However, their own data (here and elsewhere) suggest that chimpanzees can reason about unnatural behaviors and tasks just as efficiently as they reason about highly familiar events. It is precisely such tasks that point to the highest levels of cognitive achievements in other species. Clearly, chimpanzees succeed at many tasks that would not be common or even possible in their natural environment. It is success in precisely these kinds of tasks that has allowed researchers to infer "superior" cognitive capacities in the species in question; otherwise it is difficult to differentiate between associative learning and causal reasoning explanations for performance. It is common for animals in the laboratory to be confronted with experimental tasks that are unfamiliar to them—water mazes and bar presses for rats and skinner boxes for pigeons, for example—and yet the use of these apparatuses have revealed much about animal learning. If experimenters simply test animals on questions related to a lifetime of experiences or situations so natural that the species may be innately prepared to respond to the situation in a particular way, we would not make progress in understanding their ability to reason about novel problems and would not be able to discriminate between cognitive mechanisms such as behaviorist associations and true inferential reasoning.

If chimpanzees perform well in competitive but not cooperative paradigms precisely because the former are more in line with situations they might naturally experience, then their abilities are more likely to be canalized and not indicative of the kinds of general inferential skills that humans utilize when solving novel, unnatural problems. We agree with Hare and colleagues that chimpanzees may solve competitive problems more readily than cooperative problems (Hare, 2001), but we disagree that one can conclude that the only fundamental difference in the reasoning abilities of humans and other apes is one based on prior experience. We argue that humans exhibit the ability to reason flexibly across domains that they are not biologically prepared to deal with—for instance, walking on the moon, a planetary object in which gravitational forces are vastly different from the world in which we evolved. Just because cooperation is not the natural state of interactions in the nonhuman primate social world does not imply that they would be incapable of reasoning about such activities. Rather than making the assumption that chimpanzees are unable to reason about things they have not directly experienced, one might design tests of this very assumption. One should not predicate experiments on assumptions, but it seems that others have made assumptions that chimpanzees would *not* be capable of reasoning about anything they have not directly experienced. If this assumption was true, how is it that chimpanzees can demonstrate the ability to learn the serial order of arbitrary photographs on a touch screen or complete match-to-sample tasks, neither of which are contexts that would have a place in their natural environments? Clearly, there is much we have to learn about the chimpanzee mind. In

some instances, we have underestimated their skills and intelligence, and perhaps in others we have enthusiastically overestimated them. Only through stretching the limits of our expectations can we compile an accurate depiction of their actual abilities. Of course, these principles hold true, not just for our closest relatives, but for all animal species we might study to further our understanding of the different forces giving rise to the vast array of animal capacities and behaviors.

Thus, there is certainly a place in comparative psychology for both laboratory and field approaches. In addition, there are differing perspectives about where the burden of proof must fall. For some, it is on the skeptics who must disprove the "positive" findings, rather than simply play the game of "nay saying." In other words, we can assume something to be the case unless it is proven not to be. For others, it is the affirmation of findings that must hold up to rigorous scrutiny. Again, if one appeals to the basic scientific method, one cannot prove the absence of something, but only the presence of something. However, you must construct hypotheses that are testable and refutable. One cannot claim something to be the case until it is proven otherwise. One must use the methods of science to show that it *is* the case. This is precisely why we have science and experiments to begin with: so that theories are not just theories and hypotheses are not just suspicions but that the data we accumulate can inch us closer to reality. Furthermore, both approaches of study are informative with regard to the evolution of capacities we often deem unique to humans. Here, we can see how both evolutionary psychologists and comparative psychologists must come together to embrace two approaches that have largely kept them at odds, both within and between their respective disciplines.

Hot Topics

Having established that many members of the disciplines that are the focus of this volume are coming together to forge new ground and break down barriers that were obstacles to such progress in the past, let us now turn to the topics that are the focus of their efforts. It is impossible to do justice to the vast number of exciting and diverse topics being studied by the growing fields of comparative psychology and evolutionary psychology in a single volume. We have chosen to spotlight a few areas of research that best reflect the breadth and depth of some of the brightest in our fields to exemplify the manner in which comparative psychology and evolutionary psychology can be brought together and bridge gaps between the two fields. Granted, the selection of topics will sound more typical of comparative psychology than of evolutionary psychology, but we hope to show how these topics can be studied by comparative psychologists, embracing an evolutionary framework.

Cognitive Specializations

In this section, we highlight several exciting advances that have been made with a diverse range of taxonomic groups, ranging from cephalopods and reptiles to humans. Jennifer Mather (chapter 7 of this volume) describes the perceptual systems of cephalopods. Anna Wilkinson and Ludwig Huber (chapter 8 of this volume) review what is known about cognition in reptiles, highlighting some exciting new developments in their own research. Emery and Clayton (chapter 5) discuss the parallels between the cognitive abilities of corvids and primates. Kelly Jaakola (chapter 9) summarizes some fascinating research on the bottlenose dolphin, as they are the only member of the cetacea so far that has been widely studied. Much is yet to be discovered about other cetaceans before we can know whether there are significant differences within this group. Indeed, we are just scratching the surface of our understanding of bottlenose dolphins. Dario Maestripieri writes on the social adaptations of primates in chapter 10. The recent years have witnessed an explosion of research into canine cognition, which is eloquently summarized by Miklosi and Topál in chapter 11; they also provide a theoretical framework for understanding the evolution of cognitive capacities in both domestic and wild dogs. Sell (chapter 4) discusses how an adaptionist program of research can be applied to the evolution of a particular human trait— the ability to discern fighting ability in both sexes. Sell also discusses how the nature/nurture debate has run its course in evolutionary psychology. Dunbar and Sutcliffe (chapter 6) discuss the social brain intelligence hypothesis to explain the unique abilities of humans to assess and prioritize social relationships, as a function of group size and complexity. Each chapter author or set of authors places the species or taxonomic group into ecological context to speculate about the evolutionary forces giving rise to the unique abilities held by that particular group, and the insights are at once groundbreaking and thought provoking.

Imitation and Culture

Imitation is somewhat of a controversial topic as it is so difficult to define (Galef, 1988; Heyes, 1996; Mesoudi, Whiten, & LaLand, 2006). However, it

is an important topic for several reasons. The broad area of social learning encompasses many traits often thought to be unique to humans, including imitation, teaching, and culture. Of course, it is a fundamental mechanism by which individuals might learn from others, and in which information might be passed down through generations and across regions and cultures. Until recently (Whiten et al, 1999; van Schaik et al. 2003), it was not known or expected that other animal societies contained elements of tradition or culture. It was also often considered that, if any other animals were capable of true imitation, it was only the great apes that had this capacity. Although, Subiaul, Cantlon, Holloway, and Terrace (2004) showed that monkeys imitated in a cognitive imitation paradigm, which removed some of the usual confounds of motor tasks (more in chapter 25 of this volume). Whiten and his colleagues have shown that cultural traditions may also be widespread among the primates (see Hopper & Whiten, chapter 24 of this volume).

Cooperation and Prosociality

Related to such issues are the questions of how cooperation and morality have evolved in human societies, and whether they exist in any other species. Are prosocial behaviors really altruistic or are they based on mutualism or reciprocity? Silk and House discuss the evidence for and against prosocial preferences in our closest relatives, and the development of such preferences in our own ontogeny in chapter 20 of this volume. Warneken and Melis also take up such issues in chapter 21, but with a focus on the phylogeny and ontogeny of cooperative behaviors specifically. Mesoudi and Jensen (chapter 21) get to the heart of the matter about why prosocial behaviors or cooperation would have evolved in our evolutionary past, and Sheskin and Santos revisit this topic by examining our distant cousins and the evolution of morality (chapter 23). Boesch (chapter 26 of this volume) reflects on social evolution, generally, and the importance of considering rearing environment when evaluating similarities and differences between ourselves and our closest relatives with regards to some of these weighty issues. These are popular topics in academia today because they reach to the heart of what it is that we think makes us human—and not just humans but "good humans." We value our morality and our desire to help others, sometimes at a cost to ourselves. When those traits are lacking in our counterparts, they are considered deviant, antisocial, and defective. To find such capacities in our closest or, especially, our more distant animal kin would surely close a fundamental gap. Thus, this work generates much controversy and excitement, and both comparative psychologists and evolutionary psychologists are conducting it.

Communication

Of course, to cooperate with each other, animals must communicate. Communication lies at the heart of many other aspects of behavior. Communication is used to signal aggression, mating, play, territorial defense, the presence of food, group cohesion, and belongingness, for example. Within the social insects alone, an entire volume could be written on the function of communication. Cocroft and Sullivan-Beckers (chapter 18 of this volume) have elected to focus on how communication functions to support mating in a few species of social insects. Sometimes, we do not think of insects as being highly communicative, which is why it is important to review the work on a range of species, because communication is crucial for all species who come in contact with others of their own and unrelated species. When we think of animal communication, however, we often think of primates and parrots. Pepperberg reviews her years of work with one very famous African Grey Parrot, Alex, in chapter 16, providing an overview of the insights that work has given into Alex's other cognitive capacities as well. Zuberbuhler reviews the work on vocal communication in primates in chapter 17. Lyn reviews the ape language research over a period of forty years, focusing more specifically on gestural and symbolic communication (chapter 19), a topic that is also reviewed by Cartmill and Mastripieri in chapter 10. Their reviews will provide some idea about the shifting methodological and theoretical focus in this area over just the last several decades. Of critical importance, as well, to the development of communication is the role of social environment, which is also considered by both Lyn (chapter 19) and Cartmill and Mastripieri (chapter 10). Pepperberg (chapter 16) also considers the importance of training methodologies in revealing the abilities of a species, which causes one to consider the importance individual differences and the role of nature and nurture in the manifestation of behaviors—natural or otherwise.

Memory

Memory is another capacity that must underlie many other cognitive capacities. Without memory, an organism could not retain the meaning behind

communicative signals. An organism could not find food or discriminate between mates or navigate the environment. Memory is one of the most critical cognitive capacities because it serves as a foundation for all learning. One can study memory in a variety of contexts: metamemory, episodic memory, prospective memory, spatial memory, foraging, learning, serial learning, and so on. In this volume we hone in on episodic-like or metamemory research because it is one of the most exciting areas of research in comparative psychology today, and one in which investigators are working with a variety of species, using ecologically valid paradigms and procedures. Crystal (chapter 14) reviews his work on metacognition in the rat and discusses how the results of these studies inform our understanding of human memory and disorders of memory. Raby and Clayton (chapter 12) and Roberts and Feeney (chapter 13) provide different overviews of memory and planning. Smith and colleagues (chapter 15) provide an extensive review and critique of the work on metamemory and provide suggestions for how to move that work in a new direction.

Summaries and Conclusions

Although it was not possible to do justice to the wide array of fascinating topics that fall under the broad umbrellas of evolutionary psychology or comparative psychology, and we are sure to have missed some very exciting topics, authors of the introductory and concluding chapters have done the volume justice by providing keen insights into the larger issues at play in the fields today. Barrett (chapter 2) provides a sharp view of comparative psychology's approach to the study of social cognition—its strengths and flaws. Andrews and Radenovic (chapter 3) write from the perspective of philosophers with an eye to a new direction researchers might take to study such hot topics as TOM, and they also provide a stellar overview of the debate about concepts, what it means to have a concept or a representation, and how one might even gather meaningful evidence for such a thing. Cheney and Seyfarth (chapter 27) ponder how and why "social minds" evolve and how we have arrived at evidence for "social" minds in other species. Shettleworth (chapter 28) reminds us of the value of considering the adaptive purpose of a behavior and placing our experiments in ecologically relevant contexts,that is, not just our experiments, but also our mindsets. And Vonk & Shackelford (chapter 29) have attempted to bridge the gaps that we see between these leaders in our disciplines and bring them together so that we can move forward together and break new ground.

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