

## Comparative Evolutionary Psychology: A United Discipline for the Study of Evolved Traits

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### Abstract

Several themes have emerged from the chapters in this volume. Some tensions exist between researchers seeking to answer questions concerning the adaptive purpose of human and nonhuman behaviors and capacities, and researchers seeking to shed light on the evolutionary forces giving rise to such traits. These tensions may be dissipated if several unnecessary dichotomies are avoided and researchers thereby embraced nonmutually exclusive stances to different methodological and theoretical approaches. We suggest that those studying humans and/or nonhumans—whether in the field or in the lab, with large numbers of participants or with few, from a behaviorist or nativist standpoint, asking questions about structure or function, stressing continuity or discontinuity—focus less on absolutes and existing dogma, and more on openness and objectivity. We suggest that, if all researchers with similar goals unite under the single unifying framework of evolutionary theory, many more advances can be made and a more focused field of study will emerge.

**Key Words:** evolutionary framework, dichotomy, unifying, tensions

Psychology has lagged behind the other natural sciences, which operate under a single unifying theoretical framework. Physicists accept the laws of quantum field theory and Einstein's theory of relativity without much question. Chemists have universally adopted the basic table of elements and atomic theory. Biologists unequivocally accept evolutionary theory as, rather than a theory, an all-encompassing explanation for the physiological and behavioral adaptations of all life on earth. Psychologists, in contrast, have seen schools of thought come and go in the discipline's relatively short history, without a single theoretical viewpoint dominating for any significant length of time.

Psychology divorced itself from philosophy by virtue of its focus on empirical methods, but also immediately adopted a focus on mechanistic

models of the human mind with the goal of dissecting human consciousness with Wundt's voluntarism (Schultz & Schultz, 2008). Titchener's structuralism was similarly focused and restrictive, disavowing the study of the mentally ill, human children, and nonhumans. The goal was to discover universal laws of human behavior similar to those that applied in chemistry and physics and other "hard sciences." By viewing man as a machine, given life by a great creator, scientists at the time could hope to uncover basic rules and operations by reducing man to his simplest elements; thus, they focused on physiology and anatomy in an attempt to understand the mind. With the rise of functionalism through the inspirational work of William James, Francis Galton, Charles Darwin, and others, psychologists appreciated the utility of more diverse methodology and

topics of study (Schultz & Schultz, 2008). Darwin's emphasis on mental and physical cross-species continuity also reawakened interest in the study of nonhuman behavior. Psychologists could move away from defining the elements of behavior and consciousness to attempting to explain the purpose and function of behavior. Watson's behaviorism provided the objectivity that was needed to study other organisms while adhering to rigorous scientific methods by eschewing reference to internal mental states that could only be inferred. Although behaviorism held sway for decades in the United States, other movements such as the gestalt movement, which retained an emphasis on consciousness, maintained prominence in Europe during the same time period (Schultz & Schultz, 2008). Watson's (1914) and Thorndike's (1911) reductionist approaches to the study of animal mental life have been critiqued for disavowing the principles of evolution (Tolman, 1987). Although evolutionary psychology has continued to exist as a discipline within psychology, evolution by natural selection has not achieved the status of an overarching framework with which we study all human mental life, in the same manner that it exists within biology for the study of animal behavior and morphology (Barkow, Cosmides & Tooby, 1992). Various other paradigms have continued to influence the methodology, topics of study, and theoretical frameworks of psychology. Although an evolutionary framework may never reach an all-encompassing status within psychology as a whole, this may be more likely within the study of animal behavior, or within the subfield now known as comparative psychology.

In the introductory chapter to this volume, we indicated that comparative psychology has sometimes lost its focus. Although it is the case that most comparative psychologists accept the principles of evolutionary theory, they remain divided on a number of other key fronts, some of which are clear when reading the chapters in this volume. We believe that merging the fields of comparative psychology and evolutionary psychology can provide that focus and move the new discipline of comparative evolutionary psychology forward (see also Lockard, 1971). It was a difficult task simply coming up with an appropriate title for this chapter. What should we label the study area of this new combined discipline? We could not restrict the focus of study to animal behavior; would that restrict us from focusing on cognitive processes or the study of animal minds? And we would not want to imply that humans should not be included within our focus. Should the focus be on

studies that make comparisons between nonhuman and human behavior or cognitive processes, or only those that situate any organism's evolved capacities within the context of its social and physical environment? We have opted for the latter focus. In what follows, we identify some challenges and goals that, when met, will allow current and future scholars to break new ground in unprecedented directions and provide the impetus for forging new collaborations that should produce further insights into the evolution of not only human psychology and behavior, but also the psychology and behavior of our closest and more distantly related animal relatives.

First, the divisions that have existed on a number of fronts need to be disassembled. Some of these divisions exist between: (1) researchers who work primarily with humans and those who work primarily with nonhumans, (2) field and laboratory researchers, (3) behaviorists and nativists or cognitivists, (4) the idiographic or "small-*n*" and the normative approach, and still (5) at some level between the functionalist and the structuralist approach, but perhaps most critically, (6) anthropocentric and "holy-grail" type pursuits and other more objective approaches.

Traditionally, comparative psychologists have focused on nonhuman species in an attempt to shed light on human evolution, but relatively fewer studied how human participants performed in analogous tests. However, this selectivity is dissipating, with more comparative psychologists including human participants in their experiments (see chapters 6, 14, 15, 20–25 of this volume). Sometimes presenting human participants with the same tests that have been presented to our animal counterparts has provided startling results. For instance, Silva and colleagues (Silva, Page, & Silva, 2005) discovered that humans fall prey to several of the same irrational perseverative strategies in the trap-tube problem as did the chimpanzee subjects in the Povinelli (2003) studies. In the original trap-tube problem, monkeys had to insert one tool into a narrow tube to push out a food reward, but there was a trap in the middle of the tube that caught the food if the animals attempted to push the food past the trap (Visalberghi & Limongelli, 1994). If they inserted the tool from the far side of the tube, over the trap and out the other end, they could succeed in obtaining the reward. However, if the trap is on top of the tube, it is causally irrelevant. Povinelli's chimpanzees learned to use a rule, "Always insert the tool in the end of the tube farthest away from the trap," which they continued to use even when the trap was not

functional and was at the top of the tube, instead of at the bottom of the tube, indicating that they did not understand the causal function of the trap. Silva and colleagues discovered that humans, surprisingly, often used the same strategy, even though it served no causal purpose. Humans also avoided the side of a table with an ineffective trap in a trap table version of the problem. In a different paradigm, Horner and Whiten (2005) discovered that children are more likely to copy causally irrelevant actions, compared to chimpanzees, who are more likely to emulate rather than imitate. Inoue and Matsuzawa (2007) found that chimpanzees sometimes performed more quickly and accurately in a memory task for sequential order of different numerosities compared to college students. As Lyn reviews (chapter 19), the well known bonobo, Kanzi, outperformed human children on certain measures of language (understanding of embedded clauses) in one set of tests (Savage Rumbaugh et al., 1993). Herbranson & Schroeder (2010) found that, even after extensive training, humans still failed to maximize choices in the well-known Monty Hall dilemma, whereas pigeons learned to adjust shift-and-stay strategies to maximize their rewards, leading the authors to ponder if pigeons were “smarter than mathematicians.” In the current volume, researchers have explored whether human children are indeed prosocial (chapter 20), although interestingly, adult humans have not been tested in paradigms equivalent to those presented to their nonhuman primate counterparts. Results with human children have been somewhat mixed, with children not always exhibiting prosocial tendencies as expected (Brownell, Svetlova & Nichols, 2009; chapter 20). In some cases, human children may, in fact, behave more spitefully than chimpanzees (chapter 20; Jensen, Hare, Call & Tomasello, 2006), although one might have predicted the opposite prior to having conducted the tests. In addition, more distantly related primates are more likely to give food in food-sharing tests of prosocial behavior, compared to our closest living relatives (chapter 20). Thus, testing nonhumans, both closely and distantly related species, and humans in conceptually identical tasks is far more illuminating than making assumptions about how humans and other species would perform in yet untested paradigms.

This point returns us to a point raised in the opening chapter about where the burden of proof should lie. Assumptions should always be tested before they are accepted as truths; to do otherwise is to fail to adhere to the principles of the scientific method. No theory is truth; it is only a framework

to use as a guide to develop hypotheses and methods and strategies for testing those hypotheses. Only when evidence has supported or dispelled these hypotheses can we begin to assume to write or speak with any certainty on whatever issue comes to bear. Experimental results and interpretations of such should also be questioned until alternative explanations for results have been exhaustively ruled out and replications have been conducted. An alternative viewpoint is that basic assumptions should be accepted as facts until such time as they are proven to be otherwise—but then where is the motive or impetus to test or challenge widely accepted notions, some of which become dogma and halt the progress of science? For instance, it was a long-held belief, in part due to Darwin’s variability hypothesis, that men were intellectually superior to women. Had Thompson-Woolley (Thompson, 1903) and Stetter-Hollingworth (Hollingworth, 1914), among others, not challenged and empirically tested such beliefs, other women, like themselves, may not be contributing to the sciences today because they would not have been provided such opportunities. One need only look at the list of contributors to this volume to consider the losses to our own discipline if women were restricted from contributing to academic pursuits because such a notion was accepted without challenge.

It was also long thought that evolution took place very slowly, over hundreds of thousands of years. A study based on the work of Peter and Rosemary Grant and their assistants (Weiner, 1994) with the famous finches on the Galapagos Islands, indicating that patterns of drought and rainstorm over a few generations could alter the survival rates and selection pressures on beak size and strength, altered that belief. As a more recent example, Subiaul has challenged long-held models of imitation, both by showing that monkeys, not just apes, can imitate, and that imitation may be differentiated by type: motor, cognitive, spatial, and so on (chapter 25). Science marches forward when investigators move against the current and have the courage to challenge ideas currently “in vogue.” Theories stagnate when they are no longer pitted against new ideas. Therefore, we should not accept ideas that have not been subjected to careful and rigorous testing, even if these are the most popular ideas at the time.

Popular ideas become particularly difficult to dispel because they are more prevalent; the more you see something the more credible it becomes. The more articles are published that express a particular viewpoint, the more difficult it becomes to publish

an opposing view, because it may be considered too far in opposition to the prevailing corpus of data. Scientists build careers based on compiling data that supports theories they have developed. They may be reluctant to publish findings that dispute their own theories and have now gained significant authority and power to suppress others who question their own views and findings. Results that are in line with the currently “popular” point of view is easier to publish, making it increasingly difficult to publish data that challenges such notions, even if the studies have been conducted with appropriate rigor. Although the scientific process is objective and fair over the long run, one need only think back to the monopoly that behaviorism held over psychology with John Watson as the editor of *Journal of Experimental Psychology* during the early twentieth century to recognize that the scientific process can be unfair in the short run. One can see the changing trends in the types of articles that are published depending on the theoretical preference of the most successful researchers in the field. A review of ape language research is one powerful example of changing views in our field (Lyn, chapter 19; see also Cartmill & Maestriperieri, chapter 10). Not so long ago, it was difficult to publish articles suggesting that even nonhuman primates had elements of theory of mind. It was next to impossible to publish articles suggesting that more distantly removed animals might share some components of the human theory of mind system. During the time when behaviorism held sway, topics such as theory of mind and meta-cognition would not have been extensively studied, much less found their way into the field’s top journals. Today, finding evidence for mental state attribution in other species seems to be “in vogue” and it is “unpopular” to challenge such notions (de Waal, 2009; Tomasello, Call & Hare, 2003b). It should go without saying that we should maintain objectivity in our tests. Bias can be a problem in research in all areas. It is particularly problematic in comparative research, somewhat ironically, because we must infer what the behaviors of our subjects tell us about their mental states. Furthermore, perhaps due to conservation issues and the prevailing notion that animals are of more value if they are more similar to humans, some researchers seem invested in specific patterns of results—those that support ideas of continuity between humans and other animals.

It is relatively easy to interpret the same pattern of results in different ways. Just one example can be seen in the recent exchange between Hare and colleagues on the one hand and Wynne and colleagues

on the other hand in *Animal Behaviour* (Dorey, Udell & Wynne, 2010; Hare et al., 2010; Udell, Dorey & Wynne, 2008; Wynne, Udell & Lord; 2008), regarding the role of ontogeny versus domestication in shaping domestic dogs’ response to human pointing gestures (Hare, Brown, Williamson & Tomasello, 2002). (See Miklosi and Topal, chapter 11, for an extensive exposition of these issues). Other examples abound in the literature on great ape causal understanding and theory of mind (Tomasello, Call, & Hare, 2003a, b; Povinelli & Vonk, 2003, 2004). For instance, Povinelli, Nelson, and Boysen (1992) first published results that they interpreted as suggestive that chimpanzees understood the intentions of others because they quickly learned to switch roles in a task in which they were allowed to observe and then play both roles. However, after a commentary by Heyes (1993), and a re-analysis of the results, it was suggested that the chimpanzees did not demonstrate understanding on the first trial of the original reversal, but instead learned rapidly once the roles had been reversed, demonstrating not evidence for “empathy,” as the original article suggested, but instead evidence of rapid learning (Heyes, 1994; Povinelli, 1994). A similar argument can be made for recent results reported by Manrique, Gross, and Call (2010) who report that great apes select tools on the basis of an understanding of rigidity, a physical property of objects that might play a causal role in performing certain tasks. However, when examining the results of a critical third experiment, one can interpret the results as indicating that the apes have simply learned to choose rigid tools in earlier experiments because they are more familiar and have been associated with success, and initially do not reverse their choices to more pliable tools when it becomes causally important to do so, based on a causal understanding of what works in different situations. Interestingly, while Manrique and colleagues (2010) generally present a balanced discussion and openly admit that most of the tools readily available to their apes are of rigid construction, thus potentially biasing them to choose such tools in their experiments, they still conclude that chimpanzees “spontaneously” select tools on the basis of rigidity after “gathering minimal observational information” (from abstract). Even more revealing, investigators from the same laboratory, also following a series of tool-related studies with great apes, conclude that:

Although our results show that apes succeeded in some problems spontaneously, their group

performance never exceeded 70% in the initial six trials. It is true that with additional trials performance increased, but it still remained quite low in most conditions. One possible explanation for this outcome is that their performance is not based on causal knowledge about the task. Another possibility is that they possess some causal knowledge, but that certain task features make it hard to express it consistently.

(Herrmann, Wobber, & Call, 2008, p. 229)

In other words, the performance of the apes was not consistent with the authors' preferred explanation, but they have chosen to maintain that preference anyway. Although researchers are burdened with the task of acknowledging alternative interpretations of our findings, we cannot stop there. We must also choose to support the conclusion that is most consistent with the results, or continue to test the hypotheses that result. Otherwise we are doing the scientific process a disservice. This process is particularly important in a field in which behaviors are observed but internal processes must be inferred. Smith and colleagues (chapter 15) present a rigorous review of the research on metacognition, discussing how findings have been interpreted as resulting from learned associations rather than from "higher order" cognitive processes such as metamemory or conscious planning, and the various ways in which researchers have ingeniously tried to tease apart these explanations, controlling for methodological confounds and implementing ever more creative and sophisticated experimental designs. Shettleworth also cautions us to consider how learning, rather than insight or inference, can account for similar patterns of results, sometimes highly touted as evidence for traits previously deemed only within the reach of humans (chapter 28). How researchers interpret their results may say more about biases in terms of whether they are seeking evidence for continuity or discontinuity, rather than whether such continuity or discontinuity exists.

A few of the authors in this volume cite the example given by Osvath (2009) of a chimpanzee in Furuvik Zoo in Sweden, who stashes stones in his enclosure for use later as weapons with which to hurl at zoo visitors. Osvath used the example as evidence of planning. Feeney and Roberts (chapter 13) and Raby and Clayton (chapter 12) find this anecdote compelling evidence of such, but Shettleworth (chapter 28) remains unconvinced and believes the anecdote can be explained by an associative learning account, without an appeal to higher order

processes such as metacognition and planning for the future. Barrett (chapter 2) points out that labeling the behavior (i.e., as planning) does nothing with regard to explaining it. Perhaps such differences of opinion cannot easily be resolved. What is important is that both explanations are considered equally in all accounts. Equal consideration is most likely to happen when researchers are open to viewpoints from those approaching findings from alternative perspectives and approaches. However, this openness does not always occur.

Such biases lead us to the discrepancy between the "Holy Grail" approach and what we suggest are more objective approaches to the study of both human and nonhuman psychology and behavior. As was pointed out earlier, sometimes assumptions are made about how humans will perform in various tasks that are not upheld when the requisite experiments are conducted. We should not be willing to ascribe abilities to humans without the appropriate tests to confirm such ascriptions any more than we should ascribe or fail to ascribe abilities to nonhumans without the appropriate objective tests and interpretations of those data. We should also consider that nonhumans may have evolved different capacities from those of humans for solving similar problems. Raby and Clayton (chapter 12) take pains to define episodic memory and discuss whether there might be precursors in nonhumans, even if the fully developed autozoetic conscious component that exists in humans is not fully present in nonhumans who maintain some aspects of episodic-like memory. These authors also reflect on why only some aspects would evolve in these species, and why a fully developed episodic memory would emerge in humans. As Feeney and Roberts point out (chapter 13), we may fail to find evidence for "mental time travel" in nonhumans if we are seeking evidence for only human traits when nonhumans may have evolved their own mechanisms for keeping track of past events—mechanisms that are best suited for the ecological niches in which they have evolved. Shettleworth (chapter 28) makes a similar point when she argues that it is unlikely that nonhumans would have evolved episodic memory to reflect back on their conscious experiences to tell stories and reminisce, but instead may have evolved such an ability to make predictions about future events, such as the likelihood of finding food or mates. Smith et al. (chapter 15) caution us against treating capacities such as metacognition as all-or-none capacities. This tendency might result in excluding *a priori* certain taxonomic groups from

further study. For example, in light of research findings such as the null results in Gallup's self-recognition tests for monkeys, making the assumption that monkeys lacking self-recognition would also lack metacognition, would have precluded the possibility of ever finding intriguing suggestive evidence for uncertainty monitoring in old world monkeys. We must consider that cognitive abilities, such as metacognition, theory of mind, and many others, might emerge in a manner more akin to a mosaic, rather than as modules. We certainly should not restrict our studies on the basis of *a priori* untested assumptions. Although we cannot prevent ourselves from entering our tests with certain hypotheses, we should be willing and open to all possible outcomes and ensure that we are interpreting the data in light of all readings of the data, not just the reading that is most consistent with our preferred outlook, or our own anthropocentric points of view. As scientists, we should not have "preferred" hypotheses. Our only preference should be for the hypothesis that is most consistent with the pattern of data.

Researchers have often cited Morgan's canon (Morgan, 1894) in such discussions, or the rule of parsimony, which have often been confused with each other (see also chapter 2 of this volume). Whereas the rule of parsimony is often expressed as the idea that the simplest explanation is often the correct one, and often treated as synonymous with Occam's (or Ockam's) razor (Karin-D'Arcy, 2005; Montminy, 2005; Newbury, 1954), there has been much philosophical discussion about the meaning of each and how they should be applied to scientific research (Fitzpatrick, 2008; Karin-D'Arcy, 2005; Montminy, 2005; Sober, 1998). One level of misunderstanding applies in thinking that the simplest explanation generally refers to what can be explained the most simply linguistically or pragmatically, rather than referring to what is the simplest explanatory mechanism for the phenomenon in question. This "simplest" mechanism in practice may not be the one that is easiest to explain. For instance, it may be simpler to explain that your dog was barking at the back door because he wanted you to know that he wanted to go outside. It requires a longer explanation to describe the history of learning in which the dog has been reinforced for standing at the door and barking and has then been let out into the back yard, and has also failed to be reinforced for not standing at the door or not barking, and thus has had to learn to connect the positive consequences to the combination of both behaviors, while also explaining why this level of

description does not require that the dog infers your thoughts, or even his own desires, but rather simply the causal relationship between your behaviors and the dog's behaviors. The first explanation may seem more parsimonious, or "simpler," but it requires an additional cognitive step: the dog must infer mental states based on behaviors at a causal level, even if these can be skipped over at the level of verbal explanation (see Povinelli & Vonk, 2004). Thus, the former explanation, while linguistically more parsimonious, is cognitively more sophisticated. Barrett presents another example (chapter 2) in which the authors confuse an argument that is easier for their intended audience to understand with an argument that is simpler from the standpoint of parsimony. Morgan himself cautioned that "...surely the simplicity of an explanation is no criterion of its truth" (Morgan, 1894, p. 54).

Thus, it is easy to see how the rule of parsimony or Occam's razor can be confused with Morgan's canon. Morgan's canon posits that, "In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan, 1903, p. 59). So here the distinction is clear; Morgan's canon refers to the level of explanation. Simplicity here refers to the degree of cognitive sophistication of the process required to explain the organism's behavior, not the number of steps required to explain it. That is, we should be cautious to exhaust all possible explanations for a behavior that may appear to provide evidence for a "higher-order" process, but may in fact be due to a "lower-level" process. This means that we should also guard against arguments by analogy, in which we are liable to accept any behavior that appears similar to human behavior to have arisen by the same mechanism by which it appears in humans. Although it should be noted that Morgan himself did not intend for his canon to be applied against arguments by analogy or anthropomorphism (see Costall, 1993; Fitzpatrick, 2008; Thomas, 1998, 2001). However, likewise, we should not simply accept a "lower-level" explanation for behavior in lieu of examining whether the behavior may have arisen as a result of a "higher-order" process. A similar point is made by Fitzpatrick (2008), who suggests that Morgan's canon be abandoned altogether. He points to the fact that authors have sometimes preferred "lower-level" explanations for animals' behavior over "higher level" explanations when, in fact, there is no objective criteria for doing so,

simply because of Morgan's canon (see also chapter 2, this volume). Barrett (chapter 2) reveals how mistakenly conflating Morgan's canon with the rule of parsimony allows researchers to justify preferring both mentalistic and associationistic accounts of the same behaviors or phenomena on no other (objective) basis. To be objective, we must apply our principles in all directions. Just as we should not accept "higher-order" explanations without considering all other possible explanations, we should not accept "lower-order" explanations without being equally critical. Indeed, it is sometimes the case that we are too liberal in assuming that humans make use of higher-order processes when they are, in fact, using what we deem lower-order processes to solve problems. Much of what humans do makes use of the same association-based learning that we attempt to reduce higher-order explanations to, when we feel researchers have "over ascribed" traits in other species. The reason that rats can be used as animal models for basic learning processes in humans is because many of the processes are, in fact, the same, or at least similar (see chapters 12 and 14, this volume). Indeed Sheskin and Santos note that researchers may want to reevaluate the work on "fairness" in primates, when considering that much of what we consider to be morality-based considerations of equity in humans may also be due to the same kinds of frustration effects we have attributed to nonhumans (chapter 23 of this volume). Likewise, Warneken and Melis (chapter 21 of this volume) discuss the difficulties in attributing altruistic motives to apparent altruistic behaviors in our closest living relatives, yet the same critiques could easily be applied to apparently altruistic behaviors in humans. For instance, humans who act kindly to assist others in need might be motivated to gain friendships or alliances that might later benefit themselves, or simply enhance their own self image. Lyn (chapter 19 of this volume) pointedly reminds us that critiques against the ape language research centered on accusations of operantly conditioned responses on the part of ape subjects might apply equally to much of the human language acquisition process.

The same argument should be made in terms of accepting "null" versus "positive" results. If we are to be exceedingly critical in accepting evidence for the existence of some trait or some behavior without exhaustively examining other possible explanations for how the behavior may have emerged by accident, by trial and error, or some other manner that does not attribute some ability in question to the organism of study, then we should be equally

critical of why a "negative" or "null" result has been obtained. Is it due to some methodological difficulty in the study or some experimental artifact, a failure of proper statistical analysis, and so on? We must be sure to apply our critical skills to all kinds of results; not just the results that we find harder to accept or those that challenge our expectations more strongly. We should also be skeptical of results that are in line with our expectations. Just because the results confirm our hypotheses does not mean that they were arrived at correctly or that they reflect reality or a lack of bias. Indeed, again, the very language that we use, describing results as "negative" or "null" and describing processes as "lower" versus "higher" level or order, indicates a problem with our objectivity as scientists—a problem we must be hypervigilant against.

Researchers have also questioned the validity of results based on the representativeness of the samples studied. Again here, though, we must be careful not to lodge this criticism, specifically when the studies yield results that contradict our "preferred" hypotheses and not when they are in line with those same hypotheses or theoretical viewpoints. For instance, researchers who work predominantly with wild animals sometimes call into question results from captive animals, citing a lack of external validity and cognitive deprivation as a major explanation for why captive apes may fail to "pass" certain experimental tasks. For instance in chapter 26 of this volume, Boesch calls into question results from Povinelli's laboratory with seven peer-raised chimpanzees, citing their lack of "typical" chimpanzee socialization and natural environment. He points to the fact that Povinelli's chimpanzees have often "failed" tasks that other chimpanzees "succeed" at. However, this is a commonly stated misinterpretation of the results from Povinelli and colleague's work, even if off the record, and ignores that fact that these chimpanzees have often been among the first to demonstrate evidence of natural chimpanzee behavior such as gaze following (Povinelli & Eddy, 1997), joint attention (Povinelli & Eddy, 1996b,c), discrimination between those with differing intentions (Povinelli, Perilloux, Reaux, & Bierschwale, 1998), successful use of tools (Povinelli, 2003), and other so-called "positive" findings. However, what differs between Povinelli's work and that of many others is in the interpretation of the results, not the results themselves. For instance, with regard to the findings that chimpanzees sometimes discriminated between those who intentionally versus accidentally spilled juice that they offered to the chimpanzees,

Povinelli and colleagues (1998) were more likely to interpret the chimpanzees as reading the behaviors rather than the mental states underlying those behaviors, whereas similar results in analogous paradigms were more likely to be interpreted in a manner more consistent with “higher-order” processes, such as recognizing the underlying intentions of the experimenters (e.g., Call, Hare, Carpenter & Tomasello, 2004; Call & Tomasello, 1998), even though a behavior-reading account leads to the same pattern of results (see Povinelli & Vonk, 2003, 2004). Likewise, results from the “see/not-see” paradigm (Povinelli & Eddy, 1996a) demonstrated that chimpanzees are astute from the first trial at differentiating between human experimenters who were facing them versus those who were facing away, and they could learn to discriminate between experimenters in other experimental conditions. Thus, Povinelli and colleagues (Reaux, Theall & Povinelli, 1999), following a series of careful control tests, concluded that the chimpanzees learned a series of behavioral rules and were not reasoning about underlying mental states. The results of others (Bulloch, Boysen, & Furlong, 2008; Kaminski, Call & Tomasello, 2004) are consistent with these interpretations but have been interpreted differently. A widely cited series of studies arguably responsible for turning the tide toward accepting continuity in mental-state attribution between humans and other apes showed that chimpanzees took competitors’ line of sight into account when competing for pieces of food that dominant animals could or couldn’t see (Hare, Call, Agnetta & Tomasello, 2000, Hare, Call & Tomasello, 2001). Hare and colleagues (Hare et al., 2000, 2001) argued that chimpanzees should be expected to demonstrate their understanding of others’ mental states in competitive paradigms, not cooperative paradigms, because these are the situations in which such abilities would have been most likely to evolve in their natural environments (Hare, 2001). Notwithstanding, the inherent difficulties with such an argument, which ignores the very reason that theory of mind might have evolved to begin with—to allow an organism flexibility in predicting the behaviors of others in a multitude of contexts and scenarios—the point we wish to raise at this juncture is as follows: a critical decision was made regarding the dependent measure in the Hare et al. studies. These researchers chose to measure which food item the subordinate individual managed to obtain on a given trial, not which food item they first attempted to obtain, which would have been the critical measure to determine their

understanding of which item the dominant animal could see. Of course, they were more likely to ultimately obtain the item that the dominant could not see (see also Karin-D’Arcy & Povinelli, 2002; Povinelli & Vonk, 2003, 2004). Thus, we must be cautious when concluding that the results differ between laboratories, when, in fact, it may be the interpretations and conclusions that differ, not the performance of the animals.

This is not to say that the question of rearing history is not an important issue. Certainly, animals deprived of the need to search for food and mates and the opportunity to socialize with their peers and perhaps parents from birth may be stripped of the chance to develop normal social behaviors. We know this from the early work of Harlow (Harlow, 1958). These results dovetail with what was learned about human children growing up in Romanian orphanages during World War I (Blum, 2002; Nelson et al., 2007), and related work has revealed profound implications for children growing up under various circumstances of abuse and neglect. Children deprived of normal social contact and affection display difficulty demonstrating affection and maintaining social and romantic relationships and attachments later in life (Cacioppo & Hawkley, 2003). Close physical contact in infancy can also improve later physical health (Cacioppo & Hawkley, 2003; Feldman & Eidelman, 1998). Various deprivation studies with animals and opportunistic studies of tragic human cases of neglect have revealed the disparate trajectories taken by those with abnormal histories. Although Sell (chapter 4 of this volume) makes a compelling case for why we should never treat nature/nurture as a dichotomy, and he is right—it is a false dichotomy—of course, all development is an interaction between the influences of heredity and the environment, it is still of interest to examine the relative contribution of each and the manner in which certain traits are plastic rather than canalized.

The relatively recent focus on enculturation in apes (Bering, 2004; Tomasello & Call, 2004) and domestication in canines (Dorey, et al., 2010; Hare, 2007; Hare et al., 2002, 2010; Udell, et al., 2008; Wynne, et al., 2008) emphasizes the importance of the role of plasticity in evolution. How much are we constrained by the biology of our species, and how much can our cognition be molded by the environment in which we are raised? Can this sculpting be altered within our own ontogeny, or does the shaping take place over generations (Dorey et al., 2010; Udell et al., 2008; Wynne et al, 2008)? Miklosi and

Topal (chapter 11) point out that interspecific comparisons of extant canid species have not been conducted to date, although these could be informative in terms of genome/environment interactions. These are hot topics in comparative evolutionary psychology today and ones that will be critical to defining questions about the role of genes and environment in shaping behavioral and cognitive traits.

Although few today identify themselves as strict behaviorists, many still operate under the same basic principles that it is not useful to refer to cognitive processes operating within the minds of the organism. These same individuals find it a detraction from the goals of science to study such topics as consciousness, metamemory (chapters 12–15), theory of mind, (chapters 3 and 27), morality (chapter 23), and so on, because they believe these topics will never be subject to the objective methods that are necessary to provide clarity to the subject matter. However, this seems to be a defeatist perspective. Titchener once believed that it was not possible to study human children or nonhumans or the mentally ill because they could not properly introspect (Schultz & Schultz, 2008). However, with the advance of methods other than introspection, psychology became much broader and psychologists have made progress in the study of human development and disorders, as well as in comparative psychology. Those who hold steadfast to the old behaviorist mantra may find themselves falling out of favor with the current trend toward cognitive topics in the study of animal behavior (see also chapter 2 of this volume).

An extreme nativist position is no more useful than an extreme behaviorist position. Ignoring the contribution of the environment and experience or the interaction between heredity and the environment is akin to assuming an alcoholic is destined to develop this disorder regardless of whether he ever takes a drink. In general, extreme positions have fallen out of favor because they succeed only in ignoring the contribution of other factors to the dependent variables in question.

The cognitive movement has taken over much of psychology, and it is consistent with an evolutionary framework (see chapters 2 and 4 of this volume, and Pinker, 1997). Cognitive psychologists tend to be, in part, both nativists and behaviorists. That is, they embrace both top-down and bottom-up processing accounts. They understand that all organisms may be biologically prepared to learn in certain ways about certain types of information and not others, and that information in some domains may be

acquired more readily than that in others (Dellarosa Cummins & Cummins, 1999; Garcia & Koelling, 1966), and this will likely depend on environmental input. They also understand that prior experience will affect the manner in which stimuli and events are interpreted and processed. We are not blank slates, but neither are we immune to the environment. Miklosi and Topal (chapter 11) place the discussion in context via an interesting contrast between the effects of human socialization on the domestic dog—a species selected for sharing the human social environment—and the “enculturated” ape—a species not selectively evolved for such an environment, and who may indeed be viewed as socially deprived when not raised in the wild (Suddendorf & Whiten, 2001). Barrett provides a lengthy exposition in her chapter (chapter 2) of the pitfalls one might encounter in attempting to resurrect a strong divide between behaviorist and nativist positions, particularly under the umbrella of current comparative and evolutionary research. Indeed, her thoughtful discussion may cause the reader to wonder if such a divide ever really existed in any practical sense.

To study the effects of the environment and the role of genetics on behavior, both idiographic and normative approaches can be illuminating. Again, it is not useful to adopt one approach completely at the expense of the other. Typically, comparative psychologists have been restricted to small-*n* studies because of limited access to the special populations they work with, or the expense of maintaining populations of their animals. Even Skinner, who worked with more accessible animals, such as rats and pigeons, was the most famous proponent of the small-*n* approach, believing that one should study small numbers of subjects in exquisite detail to fully appreciate their behaviors, rather than capturing small pieces of a problem in a large group of subjects, potentially losing the nuances of the larger picture. Issues of access may be less of a problem for evolutionary psychologists who primarily study human populations and may study large numbers in various cultures. Even for evolutionary psychologists, however, it is important to recognize how the individual is affected by the larger group, and how the group is affected by the larger cultural context (see Mesoudi & Jensen, chapter 22). Dunbar and Sutcliffe (chapter 6) note that a significant focus in evolutionary research has neglected to account for the fact that individuals of many species make the most important decisions in their lives as part of a social group. Both individual differences and the

larger group context, and the interactions between the two factors, must be considered.

Evolutionary comparative psychologists must move away from the study of few select species, such as the white rat, the pigeon, the rhesus macaque, and the chimpanzee. The last decade has witnessed an explosion of research with various fascinating species, some demonstrating surprising abilities in that they appear to resemble human capacities despite divergent evolutionary trajectories. Emery compares the abilities of apes and corvids (chapter 5) and discusses the possibility of convergent evolution as the driving mechanism giving rise to similar social cognitive skills. Others reveal surprising capacities for advanced cognitive skills in species as distant from humans as insects (Cocroft & Sullivan-Beckers, chapter 18), cephalopods (Mather, chapter 7), and reptiles (Wilkinson & Huber, chapter 8). As Jaakola (chapter 9) acknowledges, despite recent attempts to focus our efforts on these many interesting and diverse species, we have barely scratched the tip of the iceberg. As she reviews, although cetaceans have received a fair bit of interest, only bottlenose dolphins have been extensively studied, and even the data on this species is patchy, at best. Thus, for comparative psychologists, drawing conclusions about a species' capacities based on the performance of one, or few members, of that species can lead to misleading assumptions. One would not want to draw conclusions about the mental capacities of the human race based on an Einstein or a severely mentally disabled individual, any more than one would want to conclude that orangutans were mentally inferior to gorillas when comparing a single unmotivated socially isolated and cognitively deprived orangutan to a single socially enriched and well-trained, motivated young gorilla. Individual differences have not received wide attention in comparative studies, despite their profound implications for the field (see also Vonk & Povinelli, 2011). For instance, much of what was known about parrots was based on the work of a single individual with a single African grey parrot Alex (Pepperberg, chapter 16). Alex's cognitive feats lead many to deem parrots the "intelligent" birds. Only recently have corvids been deemed the "other intelligent" birds despite being the central figures in myths and folklore for centuries (Emery, chapter 5). However, many other bird species are relatively untested, and only fairly recently have other members of these families been tested in a variety of experimental paradigms.

Here it is also important to consider noteworthy examples of recent research. Warneken et al's

studies with juvenile chimpanzees indicated that these chimpanzees were willing and motivated to cooperate with human experimenters (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello; 2006; Warneken & Melis, chapter 21). Although it has been noted that these young chimpanzees had been raised and "enculturated" by the human experimenters, and thus may have behaved differently than other chimpanzees in different contexts, a follow up study showed similar results when chimpanzees interacted with less familiar humans (Warneken et al, 2007). Chimpanzees do not share food in studies of prosocial behavior (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008), but may do so when paired with offspring or individuals who display a particular need, such as individuals in poor health or who are food deprived. Studies that can track whether reciprocal exchanges take place may provide more insight into the motivations and histories of such individuals (see also Boesch, chapter 26; Silk & House, chapter 20). Such studies with few individuals may lead to conclusions that say more about individuals and their unique histories than about species' tendencies or traits as a whole. Miklosi and Topal also point out that:

The hunt for the "cleverest" species or a species that "outperforms" another one makes the field more similar to a horse race than a scientific enterprise. Scientists should be aware of the problems of comparing a few individuals of any species who may differ not only in their genetic constitution but with respect to many other factors. One key example for this is the naïve comparison of dog breeds, in which any difference is rapidly attributed to the specific "genes" disregarding nonspecific genetic effects (e.g., differences in size) or an array of environmental influence that may affect the two dog populations in different ways (chapter 11, pXXX-XXX.00).

We cannot ignore individual differences and factors other than species differences when working with small-*n* samples, and we cannot succumb to "Holy Grail" pursuits.

These issues we raise are not independent of each other. Whether individuals are studied in the wild or in the laboratory, have natural rearing histories, or have been affected by "alternative" rearing or testing environments, can have significant effects on the outcomes of our studies, and the conclusions we draw from them. No single approach will be perfect and will protect against all threats to internal or external validity. Both field and laboratory

approaches contribute different elements to our understanding of a species' behavior and cognition. Laboratory approaches sometimes have an advantage when they can control confounding variables and examine possible causes and motivations for individual subjects' behaviors or choices in a single experimental task (see also Silk & House, chapter 20). Of course, researchers studying a species in the wild can utilize experimental methods to rule out many confounding variables, an approach that has been demonstrated brilliantly by Cheney and Seyfarth over the years (chapter 27) and is exemplified in the work of their protégée (Zuberbühler, chapter 17). However, it is never as possible to be aware of the subjects' life histories and exposure to objects, events, and other individuals when they have been raised outside of the laboratory, making it more difficult to rule out explanations of learning outside the experimental context. However, others will argue that an ecological approach that places the animal in its natural social and physical environment is the only appropriate approach for the evolutionary study of mental continuity (chapters 3 and 26). Mesoudi and Jensen (chapter 22) reveal how topics such as cooperation and punishment have been examined in both experimental and field settings, in combination, giving a rich picture of the evolutionary forces giving rise to altruistic behaviors (or the lack thereof) in our own and closely related species. Hopper and Whiten (chapter 24) have also taken a combined approach, studying cultural learning in both the laboratory and in the field, and they argue that their two-pronged approach has revealed that humans are not alone in demonstrating culture—an assumption that was held for the greater part of the last century. Other topics, such as theory of mind, have simply not been studied extensively outside the laboratory, making it difficult to speculate about the adaptive function of such a mechanism and its selective pressures, as noted by Cheney and Seyfarth (chapter 27).

It is not just the methodology of choice that creates tension between researchers. The determination of what the central questions should be also causes friction. As in the early history of psychology, some researchers have structuralist leanings, believing that the critical goal should be to identify traits, capacities, and behaviors to describe and understand similarities and differences between species; in other words, to answer questions about *what is*. Others researchers have functionalist leanings and aim to answer questions about *what for*, and *why*. The latter position may seem more consistent with

an evolutionary perspective, but, again, a dichotomous take is not the most productive here. First, we must identify what dispositions are within the repertoires of species and only then can we ask why this would be so. Each type of question is the complement of the other; neither exists in isolation or operates in a vacuum. Barrett makes a cogent argument about why an organism's structure or physiology is often as vital as their brain for determining the manner in which they represent and process stimuli and events in their environments (chapter 2). That is, an organism's physiology, particularly with regard to its sensory systems, must also be sculpted for taking in information from the environment, sometimes in a manner that reduces the need for extensive cognitive processing and yet still leads to adaptive responding (see chapter 2 for a more detailed discussion). In any case, the brain, albeit an amazing computational device, does not operate in isolation from the other physiological adaptations of the organism. Miklosi and Topal (chapter 11) point to the emergence of cognitive ethology, as an attempt to explain functional behaviors at the level of their underlying mechanisms. As they so rationally declare,

From the functional viewpoint, no matter if dog-wolf differences and dog-human similarities lie in specific (qualitative) changes in the dogs' cognitive processing or far less specific (quantitative) changes in the attention and memory skills and associative learning capacities, and so forth, in reviewing parallels between human and dog behavior, it is better to refrain from premature interpretation of the cognitive processes that control the observed performance (chapter 11, p.xxx).

Again, one needs to understand wherein differences lie before one can speculate about why, or for what purpose, are the target traits or behaviors.

And perhaps that is the key message here: research should not pivot on false dichotomies or mutually exclusive endpoints that allow for no middle ground. Research does not exist in a vacuum, and it is least productive when researchers implicitly assume that it does. We have the benefit today of an ever-advancing wealth of technology in which we can easily use the Internet to download the latest article from journals or web sites, and we can e-mail authors or view video of experiments. There is no excuse for a failure to appreciate what goes on in a closely related discipline or to join the two to wed their strengths. Evolutionary psychology has taken advantage of advances in closely related fields such

as cognitive science, computational science, and neuroscience to further understanding of human and nonhuman cognitive processes. Dunbar and Sutcliffe's approach to the study of the evolution of the social brain is a good example of the melding of neuroscience, social psychology, and evolutionary theory (chapter 6). It is time that comparative psychologists similarly incorporate advances in closely aligned fields into their methodologies and approaches. Crystal's approach to the study of metacognition in the rat and its application to human memory failures is another clear example of such a movement (chapter 14).

This volume brings together a group of diverse researchers who sometimes hold opposing viewpoints on seminal issues in the study of human and nonhuman psychology and behavior. More important, what they share is an empirical approach to the study of behavior that cannot be characterized as purely behaviorist, nativist, or ethological. Rather, the approaches adopted by the contributors of this volume epitomize a new movement in the study of animal behavior—a movement that can merge comparative and evolutionary psychology into one field built on the principles of early ethology, behavioral ecology, and animal cognition. These approaches embrace the scientific method, but they place differential emphasis on tenets such as Morgan's canon, arguments by analogy, and false dichotomies such as nature versus nurture (see chapter 4 of this volume). Only when we see that these dichotomies are false and impede progress toward answering questions in the study of the evolution of psychology and behavior (human and nonhuman), can we chip away at the mysteries that nature has laid before us.

## References

- Barkow, J., Cosmides, L., & Tooby, J. (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- Bering, J. M. (2004). A critical review of the "enculturation hypothesis": The effects of human rearing on great ape social cognition. *Animal Cognition*, 7, 201–212.
- Blum, Deborah. (2002). *Love at Goon Park*. New York: Perseus Publishing.
- Brownell, Celia A., Svetlova, M. & Nichols, S. (2009). "To share or not to share: When do toddlers respond to another's needs?", *Infancy*, 14, 117–130.
- Bullock, M. J., Boysen, S. T., Furlong, E. E. (2008). Visual attention and its relation to knowledge states in chimpanzees. *Animal Behaviour*, 76, 1147–1155.
- Cacioppo, J. & Hawkey, L. (2003). Social isolation and health with an emphasis on underlying mechanisms. *Perspectives in Biology and Medicine*, 46, S39–S52.
- Call, J., Hare, B., Carpenter, M., Tomasello, M. (2004). 'Unwilling' versus 'unable': Chimpanzees' understanding of human intentional action. *Developmental Science*, 7, 488–498.
- Call, J., Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans, chimpanzees, and human children. *Journal of Comparative Psychology*, 112, 192–206.
- Costall, A. (1993). How Llyod Morgan's canon backfired. *Journal of the History of the Behavioral Sciences*, 29, 113–122.
- Dellarosa Cummins, D. & Cummins, R. (1999). Biological preparedness and evolutionary explanation. *Cognition*, 73, B37–B53.
- de Waal, F. B. M. (2009). Darwin's last laugh. *Nature*, 460, 175.
- Dorey, N. D., Udell, M. A. R., & Wynne, C. D. L. (2010). When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication? *Animal Behaviour*, 79, 37–41.
- Feldman, R., & Eidelman, A. (1998). Intervention programs for premature infants: How and do they affect development? *Clinics in Perinatology*, 25, 613–629.
- Fitzpatrick, S. (2008). Doing away with Morgan's canon. *Mind and Language*, 23, 224–246.
- Garcia, J., & Koelling, R. A., (1966). The relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123–124.
- Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, 4, 269–280.
- Hare, B. (2007). From nonhuman to human mind. *Current Directions in Psychological Science*, 16, 60–64.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298, 1636–1639.
- Hare, B., Call, J., Agnetta, B., Tomasello, M. (2000). 'Chimpanzees know what conspecifics do and do not see'. *Animal Behaviour*, 59, 771–785.
- Hare, B., Call, J., Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61, 139–151.
- Hare, B., Rosati, A., Kaminski, J., Brauer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: A response to Udell et al. (2008) and Wynne et al. (2008). *Animal Behaviour*, 79, e1–e6.
- Harlow, H. F. (1958). The nature of love. *American Psychologist*, 13, 673–685.
- Herbranson, W. T. & Shroeder, J. (2010). Are birds smarter than mathematicians? Pigeons (*Columba livia*) perform optimally on a version of the Monty Hall Dilemma. *Journal of Comparative Psychology*, 124, 1–13.
- Herrmann, E., Wobber, V., & Call, J. (2008). Great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, 122, 120–130.
- Heyes, C. (1993). Anecdotes, training, trapping and triangulating: Do animals attribute mental states? *Animal Behaviour*, 46, 177–188.
- Heyes, C. (1994). Cues, convergence and a curmudgeon: A reply to Povinelli. *Animal Behaviour*, 48, 242–244.
- Hollingworth, L. (1914). Variability as related to sex differences in achievement. *American Journal of Sociology*, 19, 510–530.

- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, 8, 164–181.
- Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, 17, R1004.
- Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London, Series B*, 273, 1013–1021.
- Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition*, 7, 216–223.
- Karin-D'Arcy, M. R. (2005). The modern role of Morgan's canon in comparative psychology. *International Journal of Comparative Psychology*, 18, 179–201.
- Karin-D'Arcy, M. R., & Povinelli, D. J. (2002). Do Chimpanzees Know What Each Other See? A Closer Look. *International Journal of Comparative Psychology*, 15, 21–54.
- Lockard, R. B. (1971). On the fall of comparative psychology: Is there a messages for us all? *American Scientist*, 26, 168–179.
- Manrique, H. M., Gross, A. N. M., & Call, J. (2010). Great apes select tools on the basis of their rigidity. *Journal of Experimental Psychology: Animal Behavior Processes*. Advance online publication. doi: 10.1037/a0019296.
- Montminy, M. (2005). What use is Morgan's canon? *Philosophical Psychology*, 18, 399–414.
- Morgan, C. L. (1894/1903) *An introduction to comparative psychology* (2nd ed.). Walter Scott.
- Nelson, C. A. III, Zeanah, C. H., Fox, N. A., Marshall, P. J., Smyke, A. S., & Guthrie, D. (2007). Cognitive recovery in socially deprived young children: The Bucharest early intervention project. *Science*, 21, 1937–1940.
- Newbury, E. (1954). Current interpretation and significance of Lloyd Morgan's canon. *The Psychological Bulletin*, 51, 70–74.
- Pinker, S. (1997). *How the mind works*. New York: W. W. Norton.
- Povinelli, D. J. (1994). Comparative studies of animal mental state attribution: A reply to Heyes. *Animal Behaviour*, 48, 239–241.
- Povinelli, D. J. (2003). *Folk physics for apes: The chimpanzee's theory of how the world works*. New York & Oxford: Oxford University Press.
- Povinelli, D. J. & Eddy, T. J. (1996a). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, 61(2).
- Povinelli, D. J., & Eddy, T. J. (1996b). Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *Journal of Comparative Psychology*, 110, 336–345.
- Povinelli, D. J., & Eddy, T. J. (1996c). Chimpanzees: Joint visual attention. *Psychological Science*, 7, 129–135.
- Povinelli, D. J., & Eddy, T. J. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, 15, 213–222.
- Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (1992). Comprehension of role reversal in chimpanzees: Evidence of empathy? *Animal Behaviour*, 43, 633–640.
- Povinelli, D., Perilloux, H., Reaux, J., Bierschwale, D. (1998). Young chimpanzees' reactions to intentional versus accidental and inadvertent actions. *Behavioral Processes*, 42, 205–218.
- Povinelli, D. J. & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Science*, 7, 157–160.
- Povinelli, D. J. & Vonk, J. (2004). We don't need a microscope to explore the chimpanzee's mind. Jointly published in *Mind and Language*, 19, 1–28, & S. Hurley & M. Nudds (Eds.) *Rational animals* (2006). Oxford, England: Oxford University Press.
- Reaux, J. E., Theall, L. A., & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, 70, 275–290.
- Savage-Rumbaugh, E. S., Murphy, J., Sevcik, R. A., Brakke, K. E., Williams, S. L., & Rumbaugh, D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, 58, v–221.
- Schultz, D. P. & Schultz, S. E. (2008). *A history of modern psychology* (9th ed.). Belmont, CA: Thomson & Wadsworth.
- Silk, J., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Shapiro, S., Richardson, A., Lambeth, S. P., & Mascaró, J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437, 1357–1359.
- Silva, F. J., Page, D. M., & Silva, K. M., (2005). Methodological-conceptual problems in the study of chimpanzees' folk physics: How studies with adult humans can help. *Learning & Behavior*, 33, 47–58.
- Sober, E. (1998). Morgan's canon. In D. Cummins & C. Allen (Eds.), *The evolution of mind*. Oxford, England: Oxford University Press.
- Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great apes and other animals. *Psychological Bulletin*, 127, 629–650.
- Thomas, R. K. (1998). Lloyd Morgan's canon. In G. Greenberg & M. M. Haraway (Eds.), *Comparative psychology: A handbook*. (pp. 156–163). New York: Garland Press.
- Thomas, R. K. (2001). Lloyd Morgan's canon: A history of misrepresentation. <http://htpprints.yorku.ca/archive/00000017/00/MCWeb.htm#Lloyd>.
- Thompson, H. (1903). *The mental traits of sex: An experimental investigation of the normal mind in men and women*. Chicago: University of Chicago Press.
- Thorndike, E. L. (1911). *Animal intelligence: Experimental studies*. New York: Macmillan.
- Tolman, C. W. (1987). Comparative psychology: Is there any other kind? *Journal of Comparative Psychology*, 101, 287–291.
- Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of apes revisited. *Animal Cognition*, 7, 213–215.
- Tomasello, M., Call, J., & Hare, B. (2003a). Chimpanzees understand psychological states: The question is which ones and to what extent. *Trends in Cognitive Science*, 7, 153–156.
- Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees versus humans: It's not that simple. *Trends in Cognitive Science*, 7, 239–240.
- Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76, 1767–1773.
- Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 108, 15–22.
- Vonk, J., Brosnan, S., Silk, J. B., Henrich, J., Schapiro, S., Richardson, A., Lambeth, S. P., & Povinelli, D. J. (2008). Chimpanzees do not take advantage of very low cost

- opportunities to deliver food to unrelated group members. *Animal Behaviour*, 75, 1757–1770.
- Vonk, J. & Povinelli, D.J. (2011). Individual differences in long-term cognitive testing in a group of captive chimpanzees. *International Journal of Comparative Psychology*, 24, 137–167.
- Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, 311, 1301–1303.
- Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *Public Library of Science, Biology*, 5, 1414–1420.
- Watson, J. B. (1914). *Behavior: An introduction to comparative psychology*. New York: Henry Holt.
- Weiner, J. (1994). *The beak of the finch: A story of evolution in our time*. New York; Alfred A. Knopf.
- Wynne, C. D. L., Udell, M. A. R., & Lord, K. A. (2008). Ontogeny's impacts on human-dog communication. *Animal Behaviour*, 76, e1–e4.