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The Janus-Faced Nature of Comparative Psychology - Strength or Weakness?

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Abstract: What is the nature of comparative psychology and how does or should it relate to evolutionary psychology? This is a time of reassessment of both fields and this article reviews the history of comparative psychology and its relationships with evolutionary psychology, ethology, and other approaches to behavior from the perspective of a former editor of the Journal of Comparative Psychology who has spent many decades engaged in research in animal behavior. Special attention is given to a reassessment of comparative psychology that was carried out in 1987. The various tensions and orientations that seem endemic to comparative psychology may, in fact, be both a strength and weakness as comparative psychology and evolutionary approaches to human psychology return to issues prominent in the late 19th Century, when both fields were just becoming established.

Keywords: evolutionary psychology, comparative psychology, ethology, animal behavior

Introduction

Evolutionary approaches in almost every area of biology and psychology have dual foci of interest - looking backward to the antecedents of the present and towards the future. Comparative psychology is no exception. There has been considerable discussion, over the years, as to what comparative psychology is and has been, it's current status, and where it is, or should be, going. An important exercise on these questions took place in 1987 that will be compared to recent attempts at refining, reorienting, and strengthening the field, along with its relationship with evolutionary psychology. An enduring tension is what should be the focus of our interest as we consider the evolutionary histories of the species we study and their diverse behavioral and cognitive capacities. This is expressed in the contrast between those intrinsically interested, like the ethologists, with understanding many aspects of animal behavior, and those who tend to see humans as the ultimate focus of interest and select their species, problems, and methods because of an overriding concern with what nonhuman animals can tell us about human behavior and mental abilities. These different foci of attention have consequences. I will, as immediate past-editor of the Journal of Comparative Psychology, reflect on the changes in the journal and the field over the decades, past debates on comparative psychology, recent developments in evolutionary psychology, and proposals for an integration of comparative and evolutionary psychology. Issues of methodology, concepts, and theory may change, but critical issues
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concerning what comparative psychology is, or should be, endure. This personal reflection is offered to stimulate discussion as well as research direction, is also based on my editorial positions at the journals Animal Learning and Behavior and Ethology, my presidential stints at the Animal Behavior Society and APA Division 6 (Behavioral Neuroscience and Comparative Psychology), my personal history working with a variety of species on quite a few topics, and a rich professional life during which I have been able to interact with, and sometimes debate, seminal and often colorful and controversial scientists. Though I hope my views are grounded and accurate, others may surely have different perspectives.

Is the New Old or Vice-versa?

For almost 70 years, the nature of comparative psychology (CP) has been debated. What is comparative about it? How does comparative psychology relate to other areas focused on understanding animal behavior? Should it be primarily allied with the interests of human-focused psychologists, helping them make progress with non-human animal models for addressing explicitly human mental and behavioral phenomena and disorders? Should it be primarily a field within animal behavior that focuses on cognition using the tools developed by psychologists to the exclusion of many other aspects of comparative behavior study? With the development of evolutionary psychology, there is now a proposal for a field to be called comparative evolutionary psychology (CEP), developed most thoroughly in Vonk and Shackelford (2012b). Is this essentially different than an evolutionary comparative psychology (ECP), an updated name for what Lorenz (1950) proposed in his critique of CP? On the surface, the recent proposal for a field termed phylogenetic comparative psychology (PCP) may appear similar to CEP (MacLean, et al., 2012). Are CEP and PCP best conceived of as subfields within comparative psychology, evolutionary psychology, both, or as replacements for them? Alternatively, is CP best viewed as a subfield of behavioral biology (Bateson, 2012; Burghardt, 2012)? Regardless of what name variant is used, does the mere presence of “psychology” in its name turn off evolutionary biologists and ecologists who should really be impressed with what psychology brings to the table? Has CP become a marginalized area within psychology and an orphan for funding in the biomedical, biological, and social science research communities? This latter point is not an idle one. A few years ago, leaders in the animal cognition and learning areas organized a write-in campaign to protect the field at NSF. This raises an additional question: Are CP, CEP, PCP fields mostly concentrated on comparative cognition to the exclusion of many other aspects of comparative behavior study? Is evolutionary psychology itself a viable substantive area that will endure, or is it primarily a current mixture of ideas and perspectives that can be applied to virtually every area within psychology and, once incorporated into them, cease to be a distinctive area for academic training and professionalism?

Persuasive arguments can be made on different sides of all the above, somewhat overlapping, questions; certainly I do not have the wisdom to resolve them, though I will unpack them a bit and focus on several. However, I think all raise important issues and should encourage additional discourse from a historical perspective as to what the field has been, how its adherents have viewed it, and what it may be able to accomplish. From a strategic perspective we need to appreciate that how a field develops is tied to its
institutional, professional, academic, funding, publication, and training linkages. With the growing international scope of science, geographic variation is a factor that also needs to be incorporated. Thus, the Janus illusion in my title highlights that to make effective progress ahead it may be useful to look back and see how earlier visions played out. But, the Janus motif runs deeper than the common anthropocentric/species-centric opposition I began with. As the other questions exemplify, the current field seems to be facing multiple directions, not just two. It is thus useful to be reminded of not so ancient history that has helped create the academic speciation occurring today.

**Looking Back At the First Century of Comparative Psychology**

An early focus of comparative psychologists, going back to Romanes (1883), was to construct a hierarchy of intelligence, emotion, and motivation (“will”) using a simplistic evolutionary ladder approach. C. Lloyd Morgan (1894) developed a more sophisticated comparative scheme (Burghardt, 1985a), though the view of intelligence as a progressive trait moving smoothly upward through the vertebrate classes, for example, was deeply ingrained. But, by the 1970s this was pretty much abandoned, even if a flurry of interest followed the development of learning set and reversal learning metrics developed by Harlow, Bitterman and others, that seemed to support the “levels of organization” approach, most prominently advocated by Schneirla (Burghardt, 1973). Today such attempts are again common in comparing intelligence, problem solving, social learning, and communication across taxa, especially comparing humans with the great apes and other non-human primates (e.g., MacLean et al., 2012; Vonk and Shackelford, 2012b). Old wine, new bottles? New wine, old bottles? This is one of the main shifts of interest animating much recent work in comparative cognition and the formation of an active Comparative Cognition Society, and seems to signal a return to the original agenda of a Romanesian CP. But before returning to this theme, some earlier shifts should be recalled.

Perhaps the first challenge to the image of comparative psychology as focused on learning processes, a largely American and English enterprise, was the rise of ethology. The derivation of ethology from natural history and zoology, and comparative psychology from post-Darwinian concerns with intelligence and mental life in humans and animals, has been explored in a number of historical treatments with sometimes differing conclusions (Boakes, 1984; Burghardt, 1973, 1985a,b; Burkhartd, 2005; Dewsbury, 1984a,b; Shettleworth, 2012; Vonk and Shackelford, 2012c). The *Journal of Comparative Psychology* (JCP) was founded in 1921 and, while initially focused on a mix of species and topics, the prestige areas became maze learning and conditioning in laboratory rats. This occurred in spite of the pioneering field studies on nonhuman primates by C. R. Carpenter and lizards by L. T. Evans that appeared its issues in the 1930s. It was the ethologists’ reassertion of the importance of evolutionary factors and instincts in animal behavior (e.g., Lorenz, 1950; Tinbergen, 1951) that was one factor leading, beginning in the late 1940s, to some re-evaluation as to the nature of comparative psychology, its methodological and conceptual assumptions, and its relationship to evolutionary approaches. The ethologists thought that the study of animal behavior should be based on looking at normal species-typical behavior in naturalistic contexts in a wide range of species and not just in a few highly domesticated animals. Furthermore, true phylogenetic comparison should be the
aim, which is virtually impossible when only a few species, largely unrelated, are studied. Lorenz laid down the gauntlet in his famous comment at the first meeting of psychologists, ethologists, and physiologists after WW2 when he said, typically hyperbolic, that he resented a journal being called the *Journal of Comparative Psychology* when to his knowledge there had never been a truly comparative paper published in it (Lorenz, 1950).

Strains were also appearing in the comparative psychology community. Both T.C. Schneirla (1946) and Frank Beach (1950) documented quantitatively that, indeed, most comparative psychology was the study of white rats. The Schneirla paper, though less well known, is the more astute. Beach, anticipating gambits now commonly employed to attract attention to scientific papers, used the Lewis Carroll poem about *The Hunting of the Snark* as his catchy metaphor. About this time, Howard Munn revised a standard comparative psychology textbook and decided to rename it *The Handbook of Psychological Research on the Rat* (Munn, 1950) to more accurately reflect its contents. At least he was honest, as contrasted with Hull (1943) and Skinner (1938), who named their rat-centric books *The Principles of Behavior* and *The Behavior of Organisms*, respectively. Perhaps this is being unfair at a great distance in time – they may actually have thought, being infused with naïve behaviorism, that species differences are irrelevant and, at best, a nuisance.

At this time, after WWII, physiological psychology, usually based on rat studies, was growing rapidly as new methods of surgery and endocrinology emerged on the scene and such research was appearing frequently in the JCP. Perhaps it was not surprising, then, that in 1947 the *Journal of Comparative Psychology* was renamed by the American Psychological Association the *Journal of Comparative and Physiological Psychology* (JCPP), reflecting the broadening interests of Division 6 of the APA. It stayed the JCPP until, in a major crisis for comparative psychology, the journal almost folded as physiological psychology, operant conditioning, and ethological research increased in prestige and funding and new journals in these areas were established. Should not the journal just focus on physiological psychology and neuroscience? Was comparative psychology different enough from other approaches to animal behavior to remain distinct? But comparative members of Division 6 prevailed and, 30 years ago in 1982, the JCPP split into *Behavioral Neuroscience* and a reborn *Journal of Comparative Psychology*. Jerry Hirsch, a behavior geneticist, was the first editor, from 1983 to 1988, followed by Gordon Gallup, Chuck Snowdon, Meredith West, myself, and now Josep Call, the first non-American editor. Attempts by some, including editors, to rename the journal, especially by dropping “psychology” from the title, were unsuccessful.

Nevertheless, none of the JCP editors were or are traditional comparative psychologists studying rats or pigeons; nor were they behaviorists accepting the proposition that elementary conditioning or associative processes were sufficient to explain diverse behavior in addition to learning and motivational phenomena. Hirsch, who had worked with Theodosius Dobzhansky, was known for his studies of genetics and taxis behavior in *Drosophila*. Gallup, early in his career, studied tonic immobility in a wide range of vertebrates, then self-recognition in apes, and later moved into “traditional” sexual selection topics in evolutionary psychology. Snowdon works on communication and sociality in New World primates. West studies vocalizations, development, and social behavior in birds, especially cowbirds, and I have focused on comparative studies of behavioral development and perception in snakes, lizards, turtles, and bears with a more
recent emphasis on comparative play. Call is known for his many studies on comparative cognition in apes, although he has also worked with dogs and other animals. Thus, none of the JCP editors ever reflected the old stereotype, true perhaps from the 1930s to 1950s, of CP as primarily the purvey of those studying rats, motivation and learning, leavened with pigeons and operant conditioning.

About the time that the JCP was reestablished, Don Dewsbury (Dewsbury, 1984a,b), after a detailed historical analysis, argued, contrary to the critics from the 40s and later (e.g., Hodos and Campbell, 1969; Lockard, 1971), that a “true” comparative psychology as a naturalistically oriented biological science with a strong evolutionary bent always existed, and was not that different in subjects and subject matter from European derived ethology, though perhaps more methodologically sophisticated. In addition to the Carpenter studies on primates, he pointed to the even earlier field studies on sooty terns by Karl Lashley and John B. Watson in the Caribbean before WW1 (e.g., Watson and Lashley, 1915) and the establishment in the following decade of the Yerkes Primate laboratory in Florida, the first institution devoted to primate behavior and biology (see also Dewsbury, 2006). According to Dewsbury, traditional research in comparative psychology was overshadowed by process oriented animal psychologists focused on general laws of behavior, and physiological psychologists focused on brains and hormones. Both these groups relied on a few domesticated lab species, rats in particular, and thus, according to Dewsbury, the papers by the critics such as Lorenz, Schneirla, and Beach were flawed because they did not differentiate among the various psychological fields using animals in research. This intriguing hypothesis suggests that there was always a core of naturalistic comparative psychologists, comfortable with field work, ecology, and evolution that were overshadowed by unrequitedly anthropocentric behaviorists of all stripes (radical, methodological, purposive). I remember attending conferences with Don about this time when he distributed large buttons for attendees to wear promoting Watson as a proto-ethologist!

Nonetheless, it is true that much of CP involved comparative studies of perception and sensory process in different species. What animals had color vision? Did early visual experience affect visual abilities in primates more than in cats or rats? Motivation, such as the salience of different foods or saltiness on runway performance, was assessed. But still, in most cases, learned behaviors were used to measure perceptual and motivational parameters.

By 1970 change was also occurring within ethology. The focus of the early ethologists on phylogenetic reconstruction of behavior, instinctive movements, sign stimuli and releasers, and motivational analysis became broadened, especially under the influence of Tinbergen. This shift was highlighted in his seminal paper that outlined the four aims of ethology that should be addressed in an integrative understanding of behavior: causation, ontogeny, adaptiveness, and evolution (Tinbergen, 1963). Robert Hinde explicitly attempted a synthesis of ethology and comparative psychology in his influential textbook (Hinde, 1966/1970). This book clearly showed how the focus within ethology had shifted from issues of traditional phylogenetic and instinctive mechanisms to questions seemingly more amenable to experimental analysis, with development an especially prominent focus. This synthesis minimized the differences between CP and ethology, leading some to question if the fields really were, or should remain distinct. At the same time, systematic
field studies became prominent around the globe; those of Jane Goodall and George Schaller being most well-known. These studies documented a level of complexity in wild animal behavior that even the ethologists could not have anticipated. The modern area of field primatology, often linked more with anthropology than psychology or biology, also took hold at this time.

Also during this period, the attempt to look at the evolution of specific behavioral and perceptual responses and mechanisms across taxonomic lines (behavioral homologies), in the spirit of Heinroth and Lorenz, among many others, was explicitly questioned by John H. Crook in a plenary lecture I attended at an International Ethological Conference (Crook, 1970b). Rather than look for the legacy of historical contingencies underlying the behavior of animals, we should focus, he argued, on the current or recent ecology of the animals we study in the field. Whether a species lives in the forest or open savanna is more important in understanding its behavior and social organization, for example, than its ancient evolutionary history. This social ethology (sometimes termed socio-ecology) movement had an impact in avian and primate ethology (e.g., Crook, 1970a) and, combined with Tinbergen’s move into studying the adaptive function of behavior and the development of optimal foraging and other models, helped set the stage for the field now known as behavioral ecology. This shift was facilitated by the gene-centered writings of Hamilton, Dawkins, Trivers, and E.O. Wilson that gave rise to sociobiology in the 1970s. Today we also have thriving areas with strong comparative themes such as behavioral neuroscience, primatology, comparative cognition, molecular behavioral genetics, Darwinian anthropology, as well as evolutionary psychology. These areas all reflect the continuing expansion of evolutionary ideas and methods. Yet names have consequences; sociobiology, a much more prominent label than socio-ecology, has faded rapidly from the scene due to relentless attacks and stereotyping by a motley assemblage of humanists, cultural anthropologists, Marxist biologists, and others. The Human Behavior and Evolution Society removed sociobiology from its journal’s name (Ethology and Sociobiology) to reflect more accurately the contents of the journal; but anyone familiar with the Zeitgeist of the 1980s is aware that those attracted to the then rapidly growing field of evolutionary psychology found it politically expedient to distance themselves from what was being heralded as a gene-centered science reminiscent of eugenics, racism, militarism, and other views associated, very unfairly, with sociobiology.

The 1987 Navel Gazing

All of these developments would clearly impact comparative psychology as both viewed and practiced. Jerry Hirsch, who was JCP editor during the initial renaissance of the JCP, organized a fascinating special issue for volume 101 (1987) of the journal titled “Comparative Psychology – Past, Present, and Future.” This issue provides a fascinating window to the thinking of the day, as Jerry solicited commentaries from a diverse swath of scientists studying animal behavior and who identified with comparative psychology to varying degrees. They were asked to address two specific questions: “(a) Substantively, what do we believe to be the subject matter of comparative psychology – what part of the world does or should it study and why? (b) Conceptually, what is or should be its relationship to the rest of psychology, to biology, or to the social-behavioral sciences and
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why?” (Hirsch, 1987, p. 219). Hirsch listed the following sources as relevant to critiques and defenses of comparative psychology: Beach (1950), Burghardt (1985b), Dewsbury (1984a,b), Lockard (1971), and Lorenz (1950). Many of the commentators are still active scientists or engaged retirees. In fact, several were consulting editors during my term as editor 20 years later and still are. I encourage readers to consult the originals (which I capsulize all too briefly) and ponder the wine-bottle analogy as new generations of authors enter the field. For example, how do these views compare with the visions expressed or implied 25 years later in various chapters in Vonk and Shackelford (2012b) or this issue? An additional question is how informed new researchers should or need to be about the past as they forge the future.

Disparate Visions of Comparative Psychology

In the 1987 issue there were two largely historical commentaries. Cadwallader (1987) recounted the background and accomplishments of Joseph Jastrow, who in 1888 was appointed to a professorship in “Experimental and Comparative Psychology” at the University of Wisconsin, perhaps the earliest such recognition of comparative psychology in the United States. While Jastrow did most of his research on other topics, his actual contributions to CP were teaching courses and writing popular articles. He became quite eminent and was elected the ninth president of the American Psychological Association in 1900. Of most interest for the topic of this essay is the influence he had at Johns Hopkins University where he engaged in graduate and postgraduate studies. G. Stanley Hall, a pioneer and entrepreneur of many areas of psychology, and especially child and adolescent psychology, had a strong evolutionary bent with a focus on “instinct” broadly conceived. Charles S. Pierce, a seminal figure in studies of logic and pragmatic philosophy, had published the first psychophysical experiment in the United States in 1877 and urged Jastrow to enter experimental psychology; they even published a paper together in 1884. But Cadwallader also notes that there were many zoologists interested in animal behavior and animal minds at Johns Hopkins at that time also. Thus, from the very beginning, CP in the USA involved cross disciplinary education involving psychology, biology, and philosophy.

Richard (Chip) Burkhardt (1987), who subsequently published the definitive history of ethology and its American forerunners (Burkhardt, 2005), masterfully reviewed the early history of the Journal of Animal Behavior, founded in 1911 by Robert M. Yerkes, probably the most truly comparative and productive of the first generation of self-identified comparative psychologists. This journal was the predecessor of the Journal of Comparative Psychology founded in 1921. Burkhardt (2005) argued that due to institutional factors and “professional uncertainty and insecurity,” the stereotype of comparative psychology as “the experimental study of animal behavior, performed primarily on mammals in the confines of the laboratory” (p. 229) rather quickly became a true representation of the early field of animal psychology and thus Burkhardt took strong exception to Dewsbury’s position discussed above.

The other commentaries, by working scientists, more explicitly discussed visions of what the field of CP should be in 1987 including methods, goals, and conceptual frameworks, raising issues largely unresolved today. Rather than save all my own reaction
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to the end I will add some editorial comments to the brief summaries at times. As the commentaries were published in alphabetical order I will largely do so as well, primarily emphasizing new positions expressed, rather than the redundancies.

Irwin Bernstein (1987) argued that, although comparative psychology began as the comparative study of mind, today it should be an eclectic field built around Tinbergen’s four questions or aims of causation, ontogeny, function, and evolution. It does not matter if one wants to focus on just one of these questions, focus on a single species or behavioral process, focus on comparing species-typical behavior of related species, employ animal models to understand human behavior, or focus on general principles transcending species. His was a call to get on with good work and pass on self-reflection. This may reflect a common view that, unfortunately, ignores the great influence that graduate programs, charismatic personalities, simplistic conceptions, and political influences play in supporting, transforming, or suppressing research programs.

Michael Domjan (1987), currently on the JCP editorial board, began, as did Bernstein, with comparative psychology being rooted in Darwinian concerns about the evolution of the mind, but firmly centers modern comparative psychology in updated versions of the study of mind as compared with Bernstein’s more general behavioral agenda. Thus, for Domjan, modern CP is centered on comparative cognition, and studies of learning placed in ecological, evolutionary, and functional contexts. Domjan centers comparative psychology in the study of animal learning and thus clearly disagrees with Don Dewsbury’s (1984a, b) attempts to divorce comparative psychology from laboratory studies of animal learning, even of the general process variety.

Doré and Kirouac (1987) responded to the critiques of comparative psychology, such as those noted above by ethologists and behavioral ecologists by unabashedly stating that comparative psychology is “not about behavior” at all. Like psychology in general, comparative psychology “is about mind” (p. 244). Behavior is only a tool to get at the way the mind works, and psychologists have much better tools to get at this, such as Piagetian methods, than do cognitive ethologists (e.g., Donald Griffin) or biologists in general. They do point out that comparative psychologists need to develop theory based on individual survival and flexibility rather than reproductive success as well as “complete current evolutionary interpretations by providing a process describing the ability to select one’s own selective pressures” and not just duplicate “the achievements of other animal behavior sciences or by continually reacting to their criticisms” (p. 246).

Epstein (1987) takes an even more radical approach, though equally certain that comparative psychology is about studying the mind. He claims that the mistake was in isolating psychology and biology at the very beginning of the field and advocates subsuming comparative psychology into a new field called praxiology, following a suggestion made by Zing Yang Kuo in 1937. The focus should be on establishing an interdisciplinary field emphasizing the “ontogenic and physiological aspects” (p. 251) of behavior, which will ultimately be described “in purely mathematical and physical terms.” Certainly these are worthy goals, and mathematical, computer simulation, and physical (e.g., robotics) models are becoming prevalent and are capable of dealing with increasingly complex behavior. Whether natural history and descriptive/experimental work on real animals will ever be completely replaced seems too far a stretch, however.

John Fentress (1987), known for his elegant work on the behavior of mice and
wolves, makes several points as he discusses adaptation as the pivotal issue in comparative psychology. But his is not the sociobiologist’s or geneticist’s view of adaptation, but one in which the critical task is to elucidate developmental and integrative aspects of behavioral differentiation across the lifespan and place them in an adaptive and comparative framework. He was perhaps prescient of current conceptions of general systems dynamic models in developmental psychology by calling for the study of the “dynamic properties of organization within any given species” (p. 258) through the multilevel study of differentiation and integration. His final section focuses specifically on comparative cognition where he states that “comparative psychologists try to ask how different organisms, at different stages in their development, arrange the world into separate and coherent packages” (p. 257) as in concept formation and multimodal perception.

Jeff Galef (1987), also a current member of the JCP board, agrees with Burkhardt that, contra Dewsbury, the critiques of comparative psychology by outsiders were, in fact, valid. However, comparative psychology has learned from them and is moving forward on two main fronts focusing on both general principles underlying behavior and species-typical behavioral adaptations. He writes “Exploitation by comparative psychologists of approaches they have ignored for decades is not a disgrace. It is an honest recognition of the fact that comparative psychologists have no monopoly on useful ideas” (p. 260). Galef claims that we should be proud of our heritage and forget about debating what comparative psychology is or should be. He takes an inclusive position quite similar to Bernstein and contra Dore and Kirouac.

Gilbert Gottlieb (1987) in his commentary advanced provocative ideas about evolution, development, and behavioral neophenotypes in a historical context, advocating a meshing of comparative developmental psychology with evolutionary biology. His model posited that a change in behavior would lead to changes in morphology and physiology leading to changes in genes. Although he could not have known the epigenetic mechanisms of environmental induction of genes switching on and off, with effects persisting for at least a few subsequent generations, his work is perhaps the most enduring legacy of the Schneirla-Lehrman school. I doubt that he would have been keen on comparative cognition as the leading template for CP.

Glen McBride (1987), a now retired Australian ethologist, began his behavioral work on social organization and behavior in chickens. He drew his inspiration for general theories of sociality from chickens, but was heavily inspired by Warder C. Allee at the University of Chicago. McBride feels strongly that natural environments are the touchstone for evaluating behavior and its functions as “it is in only the field that I expect to see the forces that contributed to that evolutionary process; only there do I expect to understand the significance of the behaviors observed” (p. 272). As McBride’s career developed he moved to a psychology department. He advocated that ethology and comparative psychology should be blended in psychology departments and that a key area of joint interest should be societal evolution. The recent work on social and cultural evolution in human and non-human animals supports his view and is reflected in growing numbers of articles in behavioral and biological journals including the JCP.

Médioni (1987), like Galef, accepts the criticisms that comparative psychology ignored natural behavior, species differences, and evolutionary biology, but then argues that this is all beside the point. The role of comparative psychology is, in fact, to reveal
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“general processes common to most animal groups.” In a rare defense of Bitterman’s 1960s studies of learning in the rat, the bird, the turtle, and the fish, he claims that the heart of comparative psychology is “a search for invariant psychological processes, taking a prominent part in human activities, as well as those of organisms sometimes far removed from mankind” (p. 275).

Nick Thompson (1987) boldly states that comparative psychology, per se, has no future as a free-standing discipline because it is tied to explanatory mentalism, an enterprise that can never succeed. What we need to do is focus on a descriptive mentalism that renders comprehensible descriptions of behavior and why we “apply mental predicates in the first place” (p. 285). What does this mean? Thompson notes that mentalistic language cannot be avoided even when scientists gather to discuss animal behavior, as avoiding such makes “conversation opaque and tortured.” He sees science as derived from contradictions and “The basic contradiction that generated ethology and comparative psychology was between the complex design of animal behavior and the biological explanations brought to bear on it” (p. 285). Whereas ethology has been largely successful in explaining design, a search for mentalistic explanations in CP “will continue to be relatively useless, because its mental entities are not the sort of things that can in principle explain other things” (p. 285). The best CP can do is to translate mental predicates into behavioral descriptions and construct a “new teleonomic behavioral science” (p. 285). In some respects, Thompson is reflecting the stance taken by Barrett (2012).

Moran (1987) was, regrettably, the only commentator to point to CP as critically important for applied studies of animal behavior. By this he means that those studying animal behavior and CP should do research on aiding nonhuman animals and not just try to understand them academically or view them as surrogates for human beings. He points out the value of CP for improving welfare of animals in zoos, aiding in the breeding and reintroduction of endangered species, helping to unravel behavioral processes in common companion animals and developing treatments for behavioral disorders in them, applying behavioral principles to agricultural animals, and using our skills and knowledge to contribute to discussions of animal ethics and alleviating suffering. This would seem to be an area of CP most relevant to those outside our field, but has received too little respect, in spite of journals such as Applied Animal Behaviour Science and The Journal of Applied Animal Welfare Science. Interestingly, the topic is also virtually absent from treatments of CEP (e.g., Vonk and Shackelford, 2012b).

Finally, Tolman (1987) claims that all psychology is comparative. “There is no studying animals ‘for their own sake.’ Animals are studied so as to shed light on the genesis of human psychic functioning.” And no field in psychology can “properly understand its subject matter except as informed by a theory of its evolutionary development.” (pp. 290-91). Thus, in this final vision in the special issue we see expressed the view that all psychology is, or should be both comparative and evolutionary. Yet the implication is clear that what drives comparative psychology is an anthropocentric preoccupation with looking for commonalities and differences between “man and animal.”

Looking over these commentaries I was impressed with another perspective that no one really developed in this set of essays. Is it possible that by attempting to understand animals on their own terms we will actually best gain knowledge for truly valid and useful extensions to humankind? Is unplanned serendipity key? How many of the most “useful”
kinds of scientific knowledge began with NO explicit promises or plans for human application? Thus the issue may be between the calls for “translational research” from funding agencies and political quarters, and impassioned pleas for a continued emphasis on “basic research.” But if the latter, what kinds of “basic research”? Is Janus looking bewildered these days?

Side-stepping to the Present

As editor of the *Journal of Comparative Psychology* from 2006-2011, I was confronted with these and other historical legacies of comparative behavior, the problems examined, the species studied, and the public and professional view of the field. In some respects, comparative psychology is greatly different from what went on under its name into the 1970s as normal paradigmatic science, or even in 1987 when the impacts of behavioral ecology and the seeds of evolutionary psychology had been planted and fertilized. In other respects, however, there remains a curious essentialist conservatism mingled with more sophisticated methodological considerations of evolutionary, ecological, and developmental processes.

In 1967 I submitted my first paper to the JCPP, derived from my dissertation on comparative chemosensory prey recognition in newborn snakes, years before the JCP was reborn. The JCCP associate editor for comparative psychology at the time was Daniel Lehrman, a comparative psychologist much influenced by European ethology, as was I, though he was very critical of Lorenz’s view of instinct and genetic substrates of behavior generally. Although the initial review took 7 months, the paper was accepted (Burghardt and Hess, 1968). My major professor at the University of Chicago was Eckhard H. Hess and in a class he taught we used an edited CP text with chapters by leading figures (Waters, Rethlingshafer, and Caldwell, 1960) which is still an interesting read for not only content but also for assessing what is different and what questions remain the same after over five decades. I became convinced that a naturalistically oriented comparative ethology was more scientifically viable than a comparative psychology studying non-human animals mainly to answer questions about behavior derived from human focused psychology. I felt this so strongly that I wrote an extensive historical/conceptual brief for a field to be known as Ethological Psychology (Burghardt, 1973). This field was to include evolution, but not to the exclusion of topics involving development, mechanisms, and adaptive function. I later added a fifth aim to Tinbergen’s four, the aim of attempting to comprehend, as much as possible, the personal world and private experiences of other species. This was greatly inspired by the writings of von Uexküll (Burghardt, 1997) and a somewhat critical response to the cognitive ethology of Donald Griffin (Burghardt, 1985a). I felt then, and still do, that such an additional aim was needed to accommodate growing advances in studies of neuroscience, brain imaging, perception, and emotion along with issues of animal welfare. As Shettleworth (2012) has also noted, Tinbergen was opposed to any studies that teetered on subjectivism, which also included play (Burghardt, 2005).

Returning to the question of what is comparative psychology today and how it is different from what it was 30 years ago, when the journal came home again, is a bit silly. Of course any scientific field is going to have many changes over 30 years if it is not moribund. Nonetheless, looking at the species and problems studied in the journals most
identifying with comparative psychology can help to show how some of the changes in the field occurred. In my inaugural JCP editorial in 2006 (Burghardt, 2006) I extended the analysis Gordon Gallup had published in his inaugural editorial of 1989 of the species composition in the JCP from 1983-1987 with the years 2000-2004. Basically, when comparing these two time periods, papers on rats and mice fell from 32.4% to 11% and studies on primates, including humans, rose from 14% to 40.4%. Studies of mammals other than rodents and primates increased from 5.8 to 14.4%. Birds remained fairly constant at a little less than 20% and the low representation of other vertebrates continued. Surprisingly, insect studies fell from 6% to less than 1%. During my editorship from 2006-11, the trends continued with rats and mice down to 4.5%, primates at 44.8%, birds holding steady, herps increasing to 6.5%, and insects almost up to 3%.

Sara Shettleworth (2009) did a comparative analysis of the species studied in the JCP, Animal Cognition, and Journal of Experimental Psychology: Animal Behavior Processes (JEP:ABP) for the years 2005-2007. Her results were comparable to mine for the JCP. While the pattern of decreases in rat studies and increases in representation of other mammals and vertebrates held for the JCP and Animal Cognition, the JEP:ABP showed less of a change in that rat and pigeon papers only slid from about 70% in 1991-93 to about 60% in the later period. Papers on primates, including humans, did show an increase from about 8 to 30%. The JEP:ABP focuses almost exclusively on animal learning and cognition and Dewsbury could be right that these three journals publish work by different species of scientists. Arguing against this proposition, however, is the observation that today many authors publishing in the JEP:ABP also publish in Animal Cognition and the JCP and many of their papers fit the editorial practices of them all. Shettleworth cogently reviews the various changes in the kinds of studies being carried out in comparative cognition today, the many additional venues for publication, and the increasing diversity of scientific fields drawing researchers. This alone would make the claims for a distinctive and proscribed approach to CP less tenable.

As noted, there have been shifts not only in species used but also in areas studied. Although the two are not unrelated, theoretically you can study most behavioral topics in any species, at least at some nontrivial level. In the 2000-2004 period, one third of JCP papers were on cognition and learning, 21% on communication, and 16% on social behavior, including social learning, and 16% on development. Other topics common in CP from the 1920s to 1980s declined in the JCP. Perception and sensory processes were down to 10%, foraging and feeding to 6%, reproduction at 4% and only a few papers appeared on behavior genetics, emotion, antipredator behavior, personality or temperament. Studies on motivation and early experience have withered. On the other hand explicitly comparative papers increased and were 10% of the total in this period. Nevertheless, in 2006-7 alone the JCP published papers on well over 50 different species and a third of these were explicitly comparative in that original data on more than one species are presented (this excludes papers that replicate in one species findings from another). This trend continues with the current editor who has explicitly called for studies formally comparing taxa with new empirical data in the same manuscript. In 2012 submissions to the JCP, 68 different species were represented and 17% involved multiple species. Of course, many papers already compare their findings with those reached in papers on other species. Still, as editor, I and reviewers often had to explicitly ask authors to place their findings in a wider comparative
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context. This is not the tradition in many neuroscience and animal learning studies.

Finally, Dewsbury (2012) has recently weighed in on historical trends in comparative psychology. He notes the following rather consistent trends in the JCP, which reflect the field in general. There has been a steady and dramatic increase in non US/Canadian authors of articles and a not so dramatic, but still marked, increase in international representation on editorial boards. Women are better represented on editorial boards as well. In terms of topics in the JCP, as Dewsbury calculates them, cognition/higher processes went from 0% in 1983 to 40% in 2010 and basic learning and memory declined from 38 to 7 % in that period with a slight decrease in other, often non-learning/cognition studies. So, changes in the field have occurred in recent decades. How does this relate to the prognoses of CP from the past? Do they give us confidence in our predictive abilities?

Janus Looks At Evolutionary Psychology and the Comparative Imperative

At the beginning of this essay I posed 11 questions about comparative psychology. I did not promise resolution or answers. The reader will surely recognize that I come down more on one side or the other on many of them. But, as I have followed the field for many decades, I am increasingly convinced that there always have been organic growth and shifting perspectives that dominate one era and may fade in the next, but nevertheless remain largely intact, even if dormant. This ambivalence is integral to my conclusions, in ways that I had not really recognized when I began this reflection. I will end with some partial answers to some of the 10 questions. But first some brief remarks on evolutionary psychology itself before commenting on CPs relation to it.

Before there was a move for an explicit evolutionary psychology, or human sociobiology, there was the movement to create a field of human ethology. The Human Ethology Society, with meetings and a newsletter, is still active and many of those associated with evolutionary psychology are members and were also involved in its early meetings, such as Barkow. The human ethology movement initially struggled with two tendencies. One was the movement to apply ethological methods of description and experimentation to human behavior, but to eschew any appropriation and testing of ethological and evolutionary concepts. The other tendency, supported by Tinbergen (e.g., 1951) and others, was to apply concepts of behavioral organization, ontogeny, and mechanisms derived from animal behavior studies to understanding our species. This latter tendency is where the controversies developed, as the idea that humans might have deep commonalities with other species was suspect by most academics, and certainly mainline psychologists. These were the days of controversies over Lorenz’s On Aggression, Desmond Morris’s Naked Ape, and Robert Ardrey’s Territorial Imperative. The social sciences in general, let alone psychology, were not ready to look beyond evolutionary continuity in basic learning, motivational, and affective processes. The human ethologists, however, did help fertilize these fields for the more positive growth of EP when it came on the scene.

Later, with the intellectual heft of E.O. Wilson building on the work of Hamilton, Trivers, and others in his integration of animal behavior and evolutionary biology, sociobiology came on the scene and inspired work by many social scientists, including
anthropologists, and behavioral ecologists searching for clear evidence for reproductive fitness benefits of various behavioral strategies. As previously noted, it has also faded from the scene as a label, though not as a body of science, largely because of opposition to evolutionary approaches to human behavior, some of Wilson’s specific claims, and a perceived lack of evidence on humans (Buss, 1999). Evolutionary psychology largely made its purvey not so much the proving of adaptive fitness as in trying to explain our behavior as a carryover of adaptations from our Pleistocene lifestyle prior to the agricultural revolution, large urban centers, writing, and much modern technology. When it first appeared on the scene, EP contrasted with Darwinian anthropology and related fields that, using methods of behavioral ecology, explicitly tested the reproductive fitness of different behaviors through studies of indigenous cultures and historical records. Studies such as those of Daly and Wilson (1988) on child homicide by biological and stepparents, for example, bridged the gap across these perspectives, but were somewhat outside the main thrust of early EP.

Although I emphasize that this does not reflect the diverse nature of current EP, it is informative to look at some founding documents of EP, including the first EP textbook (Buss, 1999). For example, in *The adapted mind* edited by Barkow, Cosmides, and Tooby (1992) the main concepts deployed were the EEA (environment of evolutionary adaptiveness) and mismatch theory. I was initially excited about the book and used it in a course (which has now transmuted into a graduate evolutionary psychology course). Many of the chapters were excellent and included empirical experiments on problem solving, spatial orientation, and perceptual preferences. Some of the chapters were by animal behavior researchers interested in looking at our species through a similar lens. However, there was, in retrospect, perhaps an overly enthusiastic focus on sex differences and sexual selection theory. This not only unnecessarily narrowed the field, but facilitated a parade of often sensationalistic popular books, on sex and gender differences, often by leading EP promoter scientists. Certainly sex is a topic of perennial interest, but was it too readily exploited?

Methodologically, the focus on describing and studying actual behavior and doing behavioral experiments was often replaced by surveys and questionnaires. In other words, EP methodologically became much more akin to traditional psychology and sociology, even when testing evolutionary theories and hypotheses (e.g., Buss, 1999). Another problem, which ironically seemed to underlie the perceived need for CEP, is that most of the early writers did not view nonhuman animals, other than perhaps some apes, as worthy of inclusion in evolutionary psychology, and when animal behavior was mentioned, the treatment was minimal and superficial if not misleading (e.g., Buss, 1999). In this I am reminded of an offhand comment Robert Hinde made to me when I visited Cambridge during the period when human ethology was developing as a distinct area of emphasis within ethology. Why should humans be selected out for special status? The danger, he presciently noted, was that the field would become isolated from the rest of ethology. This is something to ponder as evolutionary psychology graduate programs develop. How many explicitly require strong backgrounds in basic evolutionary biology and animal behavior? Fortunately many diverse strands, included rich comparative perspectives and current evolutionary theory, are now being incorporated into EP (e.g., Dunbar and Barrett, 2007). Will this inclusiveness last?
In the initial development of core EP (e.g., Barkow et al., 1992) individual differences, including genetic variation, not tied to sex were explicitly ignored. This, of course, was problematic since variation is the key factor in evolutionary change. The focus on our psychology being forged in the past and all human nature being similar (similar assortments of Swiss army knife tools) tended towards the typological thinking Ernst Mayr and many evolutionary biologists had been at pains to correct for decades. The idea that psychology was universal, just like our anatomy, was oft repeated. Additionally, modern understanding of neuroscience seemed to be unnecessary with the invocation of behavioral modules that worked like the aforementioned Swiss army knife. The paper by Panksepp and Panksepp (2000) laid out many such concerns, which now are being addressed (c.f., Dunbar and Barrett, 2007). However, the unfortunate upshot of these birthing pains is that many of those who should be natural allies in biology have a poor opinion of the evolutionary psychology label, as I discovered as JCP editor as well as through my extensive collaborations with biologists. Again, these points do not reflect the value of much present work in evolutionary psychology so much as perceptions established in the not so recent past. Thus, while social, developmental, personality, and cognitive psychologists may be amenable to the EP label, our allies in many of the natural sciences may be less so, even if they partake in interdisciplinary studies on phenomena of joint concern.

Now how does all this relate to comparative psychology? One of my conclusions from looking at the historical story is that comparative psychology is alive and well if we go back to the origins of our field in the late 19th century as the study of behavior and inferred mental abilities across taxonomic boundaries. Behaviorist and cognitive perspectives are both needed, as perhaps C. Lloyd Morgan recognized all too well in the first scholarly text of comparative psychology in 1894. Lloyd Morgan’s Canon is not an empty gun, though the ammunition has been updated (c.f. Barrett, 2012); skeptics often need to curb enthusiasm (Shettleworth, 2010).

Vonk and Shackelford (2012c) also addressed the relations of comparative psychology and evolutionary psychology. They raised many of the same tensions I have noted. For example, they noted that CP can be too anthropocentric and focused on work on single species. The role of field versus laboratory studies, ethotypic vs. arbitrary behavior measures, and others were delineated. It seems that they see CP as a largely eclectic enterprise that “has, at times, lost its focus... exploring the behaviors and capacities without placing those capacities in any sort of theoretical framework, evolutionary or otherwise” (2012c, p. 6). Actually, most of the papers do use some theory, but such theories may be of a “micro” sort and do not explicitly put the work in a more inclusive evolutionary or ethological context. For Vonk and Shackelford (2012c) evolutionary psychology is, paraphrasing Pinker, “an integrated set of hypotheses focused on gene-level selection, modularity, and adaptation, and an attempt to apply evolutionary theory to the mind” (p. 6). They also note “the current human-centric focus of evolutionary psychology” while expressing the hope that EP is the “overarching perspective from which all psychology can be understood and organized” (p. 6). Their solution is a call for a comparative evolutionary psychology that will become “a unified discipline for the study of evolved traits” (Vonk and Shackelford, 2012a, p. 547). Now, who among us would deny that ALL traits have an evolutionary history of some sort, a claim of long-standing (e.g., Lorenz, 1965) and even
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going back to the 19th Century? What seems to be the goal is for comparative psychologists to more explicitly frame their work in evolutionary (and ecological?) contexts and test hypotheses in a way comparable to modern biology. Their book (Vonk and Shackelford, 2012b) is an admirable compilation of various applications of this theme. Still, the methodological and theoretical diversity is great, with ample scope for heated debate, and not just at the comparative level. It is also very directed at cognition, to the neglect of other components of CP and evolved traits. For example, emotion is barely covered and motivation is not even in the index (while morality has many mentions). The future CEP should be broadened, though, of course, starting with the most active area of comparative cognition is tactically valuable.

The call for a Phylogenetic Comparative Psychology, at least as briefly presented in MacLean et al. (2012) is more problematic as it seems to be limited to an integration of comparative cognition and evolutionary biology. If we are going to return to the origins of CP in the agenda of Romanes (1883, 1888), we perhaps would do well to note that emotion and motivation were held to be on an equal standing with cognitive mental processes in understanding the animal mind. Finally, we want to be sure that the term evolution does not preclude research and concepts that explicitly go beyond a narrow evolutionary framework that is too often assumed when ‘evolution’ is asserted. Remember, that evolutionary dogmatists once denounced research questioning gene-focused selfish gene ideology and we want to avoid litmus tests of all stripes.

Finally, it is clearly beyond any doubt that exciting science is being done on many fronts that make evolution, comparative psychology, and related areas of animal behavior more essentially linked than ever before. Unanticipated discoveries await us. I have pointed out that names and labels matter, but the wonders of behavior all around us in field and lab, begging to be studied, matter far more. Labels should not be straitjackets, but entice us to go in whatever directions Janus is facing for each of us, though heading out in some directions may reach our destinations more quickly. But even Janus could not see the future.

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References

Barkow, J., Cosmides, L., and Tooby, J. (1992). *The adapted mind: Evolutionary psychology and the generation of culture.* New York: Oxford University Press.

Barrett, L. (2012). Why behaviorism isn’t Satanism. In J. Vonk and T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 17-38). Oxford: Oxford University Press.

Bateson, P. (2012). Behavioural biology: The past and a future. *Ethology*, 118, 216-221.

Beach, F. A. (1950). The snark was a boojum. *American Psychologist*, 5, 115-124.

Bernstein, I. S. (1987). Comparative psychology: The next 100 years. *Journal of Comparative Psychology, 101*, 221-222.

Boakes, R. (1984). *From Darwin to behaviourism.* Cambridge: Cambridge University Press.

Burghardt, G. M. (1973). Instinct and innate behavior: Toward an ethological psychology. In J. A. Nevin and G. S. Reynolds (Eds.), *The study of behavior: Learning, motivation, emotion, and instinct* (pp. 322-400). Glenview, IL: Scott, Foresman.

Burghardt, G. M. (1985a). Animal awareness: Current perceptions and historical perspective. *American Psychologist, 40*, 905-919.

Burghardt, G. M. (1985b). *Foundations of comparative ethology.* New York: Van Nostrand Reinhold.

Burghardt, G. M. (1997). Amending Tinbergen: A fifth aim for ethology. In R. W. Mitchell, N. S. Thompson, and H. L. Miles (Eds.), *Anthropomorphism, anecdotes, and animals* (pp. 254-276). Albany, NY: SUNY Press.

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits.* Cambridge, MA: MIT Press.

Burghardt, G. M. (2006). Editorial. *Journal of Comparative Psychology, 120*, 77-78.

Burghardt, G. M. (2012). A behavioral biology for the future (Commentary on Pat Bateson – Behavioural biology: The past and a future). *Ethology, 118*, 222-225.

Burghardt, G. M., and Hess, E. H. (1968). Factors influencing the chemical release of prey attack in newborn snakes. *Journal of Comparative and Physiological Psychology, 66*, 289-295.

Burkhardt, R. W., Jr. (1987). The *Journal of Animal Behavior* and the early history of animal behavior studies in America. *Journal of Comparative Psychology, 101*, 223-230.

Burkhardt, R. W., Jr. (2005). *Patterns of behavior.* Chicago: University of Chicago Press.

Buss, D. M. (1999). *Evolutionary psychology. The new science of the mind.* Boston: Allyn and Bacon.

Cadwallader, T. C. (1987). Origins and accomplishments of Joseph Jastrow’s 1888-founded Chair of Comparative Psychology at the University of Wisconsin. *Journal of Comparative Psychology, 101*, 231-236.

Crook, J. H. (Ed.) (1970a). *Social behavior in birds and mammals.* London: Academic Press.

Crook, J. H. (1970b). Social organization and the environment: Aspects of contemporary social ethology. *Animal Behaviour, 18*, 197-209.

Daly, M., and Wilson, M. (1988). *Homicide.* Hawthorne, NY: Aldine.
Dewsbury, D. A. (1984a). *Comparative psychology in the twentieth century*. Stroudsburg, PA: Hutchinson Ross.

Dewsbury, D. A. (1984b). *Foundations of comparative psychology*. New York: Van Nostrand Reinhold.

Dewsbury, D. A. (2006). *Monkey farm: A history of the Yerkes Laboratories of Primate Biology, Orange Park, Florida, 1930-1965*. Cranbury, NJ: Associated University Presses.

Dewsbury, D. A. (2012). Some historical trends in American comparative psychology. *The Behavioral Neuroscientist and Comparative Psychologist*, 27, 7-10.

Domjan, M. (1987). Comparative psychology and the study of animal learning. *Journal of Comparative Psychology, 101*, 237-241.

Doré, F. Y., and Kirouac, G. (1987). What comparative psychology is about: Back to the future. *Journal of Comparative Psychology, 101*, 242-248.

Dunbar, R. I. M., and Barrett, L. (2007). *The Oxford handbook of evolutionary psychology*. Oxford: Oxford University Press.

Epstein, R. (1987). Comparative psychology as the praxist views it. *Journal of Comparative Psychology, 101*, 249-243.

Fentress, J. C. (1987). Compartments and cohesions in adaptive behavior. *Journal of Comparative Psychology, 101*, 254-258.

Galef, B. G., Jr. (1987). Comparative psychology is dead! Long live comparative psychology. *Journal of Comparative Psychology, 101*, 259-261.

Gottlieb, G. (1987). The developmental basis of evolutionary change. *Journal of Comparative Psychology, 101*, 262-271.

Hinde, R. A. (1966/1970). *Animal behaviour: A synthesis of ethology and comparative psychology* (2nd ed. in 1970). New York: McGraw Hill.

Hirsch, J. (1987). Editor’s introduction. *Journal of Comparative Psychology, 101*, 219-220.

Hodos, W., and Campbell, C. B. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review, 76*, 337-350.

Hull, C. L. (1943). *Principles of behavior*. New York: Appleton-Century-Crofts.

Lockard, R. B. (1971). Reflections on the fall of comparative psychology: Is there a message for us all? *American Psychologist, 26*, 168-179.

Lorenz, K. (1950). The comparative method in the study of innate behavior patterns. *Symposia of the Society for Experimental Biology, 4*, 221-268.

Lorenz, K. (1965). *Evolution and modification of behavior*. Chicago: University of Chicago Press.

MacLean, E. I., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., . . . Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition, 15*, 223-238.

McBride, G. (1987). Ethology and comparative psychology. *Journal of Comparative Psychology, 101*, 272-274.

Médioni, J. (1987). Comparative psychology as a search for invariant rules. *Journal of Comparative Psychology, 101*, 275-276.

Moran, G. (1987). Applied dimensions of comparative psychology. *Journal of Comparative Psychology, 101*, 277-281.

Morgan, C. L. (1894). *An introduction to comparative psychology*. London: Walter Scott.
Munn, N. L. (1950). *Handbook of psychological research on the rat.* New York: Houghton Mifflin.
Panksepp, J., and Panksepp, J. B. (2000). The seven sins of evolutionary psychology. *Evolution and Cognition, 6,* 108-131.
Romanes, G. J. (1883). *Mental evolution in animals.* London: Kegan Paul, Trench, Trübner and Co.
Romanes, G. J. (1888). *Mental evolution in Man.* London: Kegan Paul, Trench, Trübner and Co.
Schneirla, T. C. (1946). Contemporary American animal psychology in perspective. In P. L. Harriman (Ed.), *Twentieth century psychology* (pp. 306-316). New York: Philosophical Library.
Shettleworth, S. J. (2009). The evolution of comparative cognition: Is the snark still a boojum? *Behavioural Processes, 80,* 210-217.
Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences, 14,* 477-481.
Shettleworth, S. J. (2012). Darwin, Tinbergen, and the evolution of comparative cognition. In J. Vonk and T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 529-546). Oxford: Oxford University Press.
Skinner, B. F. (1938). *The behavior of organisms.* New York: Appleton-Century-Crofts.
Thompson, N. S. (1987). Natural design and the future of comparative psychology. *Journal of Comparative Psychology, 101,* 282-286.
Tinbergen, N. (1951). *The study of instinct.* Oxford: Clarendon Press.
Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20,* 410-433.
Tolman, C. W. (1987). Comparative psychology: Is there any other kind? *Journal of Comparative Psychology, 101,* 287-291.
Vonk, J., and Shackelford, T. K. (2012a). Comparative evolutionary psychology: A united discipline for the study of evolved traits. In J. Vonk and T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 547-560). Oxford: Oxford University Press.
Vonk, J., and Shackelford, T. K. (Eds.) (2012b). *The Oxford handbook of comparative evolutionary psychology.* Oxford: Oxford University Press.
Vonk, J., and Shackelford, T. K. (2012c). Toward bridging gaps: Finding commonality between evolutionary and comparative psychology. In J. Vonk and T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 3-16). Oxford: Oxford University Press.
Waters, R. H., Rethlingshafer, D. A., and Caldwell, W. E. (Eds.). (1960). *Principles of comparative psychology.* New York: McGraw-Hill.
Watson, J. B., and Lashley, K. S. (1915). An experimental and historical study of homing. *Carnegie Institution Publication, 211,* 7-60.