Comparative Evolutionary Psychology: Current Status and a Proposal for a More Integrated Future

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Abstract

Taking into account the shortcomings and strengths of the related fields of comparative psychology and evolutionary psychology, we propose merging these subfields into Comparative Evolutionary Psychology. This new field will encompass the study of cognitive continuities and discontinuities across species, with the goal of understanding both ultimate and proximal causes for the emergence of various traits. Importantly, comparative evolutionary psychologists will embrace both field and laboratory approaches and shed the shackles of an exclusive focus on uniquely human traits. This new field will exemplify an appreciation for a diversity of traits in both closely related and distantly related species that an understanding of evolution demands.

Defining Terms

Every field of scientific inquiry has its problems. The subdisciplines within psychology are no exception. Perhaps one of the greatest stumbling blocks to progress is the perceived need of psychologists to self-identify as belonging to one particular area within psychology to the exclusion of others. This need is, at its foundation, antithetical to an integrative science and to interdisciplinary work. We see this problem expressed in the long-standing debate about what it is to be a comparative psychologist or an evolutionary psychologist, perhaps most exhaustively examined in a special issue of the *Journal of Comparative Psychology* published over two decades ago (Burghardt, in press). Papini (2003) suggested that the field of comparative psychology should focus on the phylogenetic history and adaptive significance as well as the ontogenetic origins of an organism's behavior. Cartwright (2000) suggested that comparative psychologists failed to bridge the divide between human and nonhuman, more successfully bridged by ecologists and sociobiologists. Evolutionary psychology has built upon these fields by focusing on the investigation of psychological mechanisms as adaptations produced by natural or sexual selection to solve the problems faced in our ancestral history. The focus of evolutionary psychology is thus on the ultimate cause of human behaviors and characteristics. Evolutionary psychology represents an integrated set of hypotheses focused on selection, modularity, and adaptation, and is particularly interested in applying evolutionary principles to the mind (Pinker, 1999; *see* Evolution of Cognition: An Adaptationist Perspective). Evolutionary psychology is linked more strongly to sociobiology and the biological sciences, in general, and to cognitive psychology and behavioral genetics, as well (*see* Sociobiology: Overview). Comparative psychology is tightly linked to primatology, behaviorism, ethology, and, often, cognitive science. There have been various proposals to unite the two fields (most recently, Vonk and Shackelford, 2012). Vonk and Shackelford (2012) focused on specific problems within each field and attempted to identify barriers to a more open foray into something akin to cognitive behavioral ethological psychology with a focus on studying evolved traits in a wide range of species. Our proposal, which we elaborate upon here, is to unite these areas of research into Comparative Evolutionary Psychology, with the goal of removing barriers between (1) those who work in the field and those who work in the laboratory, (2) those who work with different species with a nomothetic or ideographic approach, and, especially, (3) those with a human-centered perspective and those who study individual species that are of interest in their own right.

Goals and Limitations

Comparative Psychology: Focus on Continuity

We believe that both comparative psychologists and evolutionary psychologists have sometimes fallen into the trap of endorsing goals that are both narrowly focused and ultimately stand in defiance of evolutionary theory. For instance, we focused on the tendency of comparative psychologists to focus on continuity and similarity between species, to the neglect of equally interesting differences and species' unique adaptations (Vonk and Shackelford, 2012; *see* Comparative Method in Evolutionary Studies). Although we applaud recent efforts to expand the species of study and the questions and topics under investigation, we suggest that much would be gained by returning to the lessons of methodological behaviorists and logical positivists, who fought to place psychology among the sciences. We see the trend in animal research, particularly with regard to cognitive research, as highlighting similarities with human traits and abilities, but at the expense of objectivity. That is, the focus has been on cognitive continuity, and equally interesting discontinuities have sometimes been discounted in favor of arguing for contexts that may have interfered with the ability to express humanlike traits (Girndt et al., 2008; Vonk and Povinelli, 2006). Sometimes alternative outcomes are obtained and researchers still hold steadfast to 'preferred' hypotheses that center on similarities between humans and their closest relatives, rather than giving equal weight to equally plausible, or even more plausible, alternative explanations for their findings. As just one recent example, in a recent study of tool use in apes, Herrmann et al. (2008, p. 229) write: "Although our results show that apes

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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." These authors insist that the apes have knowledge even when that knowledge is not clearly demonstrated in the tasks at hand rather than allowing the data to speak for itself and relinquishing their preferred hypothesis to accept a more conservative conclusion that perhaps the apes do not possess causal knowledge at all, and instead show the ability to learn by trial and error or reason about observable features.

This approach of seeking evidence for humanlike traits in nonhuman species has sometimes been deemed the 'Holy Grail' approach to comparative psychology (Povinelli and Vonk, 2004). We propose that, instead, investigators focus on traits that are expressed within a species' ecological and social environments and examine factors that may have led to the expression of these traits. Such an approach need not exclude laboratory studies that seek to explore the generalizability of behaviors to novel contexts under controlled conditions. Further, studying both captive and wild animals has the potential to illuminate the role of ontogenetic factors and the role of plasticity in development. This is not a novel argument, but when combined with a broadly comparative perspective and an evolutionary framework, this approach has the potential to unify the study of comparative psychology and evolutionary psychology in a manner that has clearly not been accomplished in recent years. The fact that this unification has not yet been achieved is evidenced by the recent number of proposals seeking greater integration. Along with our own volume (Vonk and Shackelford, 2012), see also special issues of *Philosophical Transactions of the Royal Proceedings B*, edited by Grodzinski, Clayton, and Thornton (2012) and Heyes and Frith (2012) focusing on the evolution of the animal and human mind, respectively.

Researchers should certainly be encouraged to consider whether existing capacities are similar to or different from those in both closely related and distantly related species. It is precisely such considerations that allow us to speculate about the evolutionary forces behind the emergence of these traits. However, we suggest that researchers should not be motivated by the desire to seek evidence for particular patterns of behavior simply because those behaviors exist in humans (Shettleworth, 2007), particularly if there is no ecologically relevant reason to find such a trait in the species in question. We should examine behaviors and abilities that the animal exhibits in its natural environment rather than design tasks with a predetermined goal or 'stack the deck' to find evidence for traits that have not yet appeared in natural environments. For instance, research should be motivated by an interest in adding to our understanding of capacities in species with particular behavioral ecologies, rather than attempting to demonstrate how 'intelligent' a particular species is. Thus, explorations of differences in spatial memory as a function of whether species cache food or must find patchily distributed food resources over large ranges are particularly fruitful (Shettleworth, 2010). Perdue et al.'s (2011) recent examination of sex differences in carnivore search strategies as a function of mating strategies and range size is another excellent example of such research. An unbiased approach is more likely to illuminate both parallel and convergent evolutionary processes.

The allure of Holy Grail pursuits (Povinelli and Vonk, 2004) has attracted many researchers. Rather than designing experimental tasks to uncover the cognitive capacities of a species with consideration of the ecological and social forces likely to have given rise to particular traits in particular populations, some researchers seem especially focused on seeking evidence for humanlike abilities in nonhumans, regardless of that species' ecological niche or phylogenetic distance from humans. This anthropocentric focus can be seen in book titles such as *Kanzi: The Ape at the Brink of the Human Mind* (Savage-Rumbaugh and Lewin, 1994), *Next of Kin* (Fouts and Mills, 1997), *Our Inner Ape* (de Waal, 2005), *Chimpanzee Politics* (de Waal, 1982), and *The Smartest Animals on the Planet* (Boysen & Custance, 2009). Although humans are naturally drawn to species that share certain humanlike characteristics such as the ability to read human social cues, the role of the scientist should be to laud other equally impressive abilities that various species have evolved to solve problems in their unique physical and social environments. Together, comparative evolutionary psychologists are best equipped to do so.

Evolutionary Psychology: Focus on Human Uniqueness

Some evolutionary psychologists have been similarly focused on the traits that define what it is to be human, such as cooperation and prosocial behavior (Fehr et al., 2002; Fehr and Fischbacher, 2004; Fehr and Gintis, 2007). Such a focus may result in a reversal of the Holy Grail pursuits by comparative psychologists in that researchers may focus on traits that they assume are not shared with other species, in the absence of evidence for these assumptions (Matsuzawa, 2012; Saxe, 2006; Tomasello, 1998). In actuality, evolutionary psychologists are poised to demonstrate continuities, with much work focused on sex differences in mating strategies that closely parallel sex differences in other species (Birkhead et al., 1987; Buss, 1995; Buunk et al., 1996; Schmitt, 2005; *see* Human Mate Choice, Evolution of). However, this work has been historically controversial within psychology. If psychologists were concerned with identifying both similarities and differences across broad taxonomic groups, with the goal of elucidating rather than assuming the cross-species links, comparative psychology and evolutionary psychology may find themselves less under attack and more often in the driver's seat when it comes to unifying the subfields within psychology.

Diverse Topics: The Need for Evolutionary Framework

On a positive note, examples of recent research abound with forays into previously discouraged topics for comparative research, such as consciousness and metacognition. Not only are such topics fervently studied nowadays, but their study is no longer restricted to primates; they have been extended to species as evolutionarily distant from humans as cephalopods (Mather, 2008), pigeons (Sutton and Shettleworth, 2008), and

rats (Foote and Crystal, 2007). However, seldom are such examples couched in terms of why such abilities might exist in such distantly related species. Even when such attempts are made, they seem like post hoc justifications for the research. For example, why should elephants exhibit mirror self-recognition (Plotnik et al., 2006)? Elephants live in relatively large and complex social groups and display extraordinary memory, but so do most canine species, and birds such as psittacines and corvids, and there is no evidence as of yet for mirror self-recognition in these latter species (although see Prior et al., 2008). One cannot simply suggest that a single factor, such as developing within a complex social environment, may have given rise to any particular 'higher order' cognitive trait, such as mirror self-recognition, without a logical exposition of why that factor would have led to the emergence of that particular trait, and why in this species or this population and not in others that share this factor. We would hope to encounter discussions of parallel or convergent evolutionary processes focused on life in complex social groups, or challenging physical environments necessitating the need for advanced causal reasoning to extract food, not as a post hoc suggestion, but as a driving impetus to conduct the research with multiple species and populations to begin with. In fact, one of us has recently been motivated to explore the cognitive abilities of a large-brained relatively nonsocial mammal with a nod to the importance of testing the 'social intelligence' hypothesis in nonsocial species (Vonk and Beran, 2012; Vonk et al., 2012). The social intelligence hypothesis (Humphrey, 1976; Jolly, 1966) states that species that have evolved to live in large, complex social groups will display superior social cognitive abilities (and perhaps more sophisticated cognition, in general) relative to less social species. Thus, we need to test this hypothesis by comparing social and nonsocial species that are otherwise similar (such as comparing lions with tigers or bears with wild dogs). We have also recently embarked upon a program of research to compare the cognitive abilities of various species of bats that differ both in sociality and in diet. All too often research seems instead to proceed more like a traditional Mardi Gras hunt – a search for all of the random ingredients to make a great gumbo. Once some piecemeal evidence for humanlike capacities in other species is uncovered, an exciting story is then woven together and submitted for publication in a high-profile journal where it will likely attract much publicity. This approach may tell us more about our own biases than about the minds or capacities of the species we so painstakingly study (Povinelli and Vonk, 2004; Shettleworth, 2007).

Biases: False Dichotomies

A biased approach is problematic for several reasons, not just because it flies in the face of the scientific process, but also because it may set the researcher up to fail. Creating scenarios in which the desired outcome must be an all-or-none result ignores the possibility of discovering many other results. Scientific reasoning should encourage researchers to acknowledge possible outcomes that they may not anticipate. When we do not leave ourselves open to such discoveries we may not discover them. If the only options we were open to interpreting consisted of 'humanlike'/'nonhumanlike,' we would miss out on 'chimpanzee-like' or 'elephant-like' behaviors and cognitions that we may not have imagined prior to our investigation. Before Povinelli (2012) began his extensive study of chimpanzees' understanding of weight, we may not have anticipated that the chimpanzee concept of weight was so tied to kinesthetic impressions on the body and so removed from the objects that they were lifting. The studies discussed by Povinelli (2012) demonstrate an attempt to understand how chimpanzees perceive weight – not just whether it maps onto the human concept of weight. Admittedly, it is more difficult to work from a nonanthropocentric frame as it may not be possible to experience the world through a sensory system we do not ourselves embody.

Approaching research with the idea that results will pivot on a false dichotomy such as humanlike/non humanlike, innate/learned, or conscious/automatic is bound to lead to pressure to interpret results in line with a particular strong viewpoint, when plausible alternatives might exist. The difficulty in publishing 'null' results has likely contributed to such a drive in our field. Scientists are rewarded by the public's enthusiasm for demonstrations of humanlike behaviors in even distantly related species. When rooks were discovered to drop rocks in water to raise the water levels so that they could retrieve previously inaccessible worms (Bird and Emery, 2009), the findings were touted as evidence for causal reasoning and insight, even 'tool use' – something that was once attributed only to humans. Thus, the results garnered much attention both in the scientific community and in the public. The same was true when Betty, a new Caledonian crow, another member of the corvid family, was seen to bend a piece of straight wire into a hook to retrieve a food reward from the bottom of a pipe (Weir et al., 2002), even though birds presumably bend wires and similar objects naturally when nest building. Betty may have arrived accidently at the solution to the task at hand, rather than by cognitive insight. If the birds were never to modify the objects, or use the tools at all, the results would likely not be published, or relegated to a lower impact journal, and would not garner any excitement either within or outside of the research community. Thus, one can see the motivation to seek empirical findings that stress continuity with human traits – particularly those that have been set as benchmarks of human uniqueness. Such traits are dangled like carrots tempting researchers to knock them from that status, just as 'tool use' and 'theory of mind (ToM)' have now forever been wrenched from the fists of Cartesians who would claim a strong divide between man and beast, with animals deemed incapable of any form of thought or feeling.

If there should be any lesson from the Cartesian dichotomy of the past, which allowed for decades of inhumane animal experimentation, it is that we should not create such strong divisions and set up false dichotomies when we design scientific studies. Although we have argued that researchers should not be blinded by desires to seek evidence for continuity in cognitive processes, abandoning equally strong evidence for cognitive discontinuities, it is important to stress that both continuity and discontinuity exist in nature; these complementary processes are together central tenets of evolutionary theory. In our recent volume on Comparative Evolutionary Psychology (Vonk and Shackelford, 2012), we stressed the value of casting aside such dichotomies and divisions between

those approaching research from different perspectives, frameworks, and methodologies. We advocated a release from the lack of objectivity that resonates in Holy Grail pursuits, and we advocated a return to the lessons of the logical positivists and the methodological behaviorists, who stressed the objectivity of the scientific method. We cannot move forward with credibility as a science if we do not do so. We cannot accept theories without extensive tests and we must revise hypotheses when the data do not fit, or are consistent with multiple hypotheses.

When investigators are overly invested in existing theory or preferred hypotheses, however, they sometimes manufacture middle ground hypotheses to satisfy their theoretical framework and fit the data. Thus, one might see researchers arguing that, first, chimpanzees do not share human ToM abilities (Tomasello et al., 1993), then that chimpanzees do share some ToM abilities (Tomasello et al., 2003), later that these abilities might be exhibited only within certain restricted contexts, such as in competitive contexts (Hare, 2001). These types of arguments, although interesting, do not address the very reason ToM is likely to have evolved in the first place – to enable an organism's behavioral flexibility in anticipating another organism's responses in a variety of novel circumstances. If one can reason about another's mental states in only a very constrained set of situations – those that have driven that species' fitness through imposing mating or feeding advantages (i.e., by allowing one to compete for food) – then it seems more likely a mechanism that is innate and inflexible, and precisely not what ToM is designed to do. By maintaining a clear evolutionary perspective, comparative psychologists will be better able to reject implausible hypotheses or explanations that are driven by biases to discover commonalities regardless of evidence for divergence.

The 'Problem' of 'Null' Results

Few people are excited by 'negative' findings or 'null' results, or the absence of humanlike traits in our nonhuman counterparts. The fact that we label the absence of evidence for such abilities as 'negative results' says more about our anthropocentric biases than it says about the value of the results. Such findings can be just as illuminating as 'positive' results. They tell us just as much about the animals' abilities and the way that they reason. Or at least they could, were the tests and experiments properly constructed in such a manner as to highlight what the subjects could do, and how they think, rather than being fashioned in a dichotomous manner: Do they do what humans do, or do they not? In one example, Vonk and Subiaul (2009) explored chimpanzees' ability to reason about humans' capability to perform a simple task – offering a food tray to the ape subjects. The humans' ability was constrained on the basis of whether their arms or legs were visible and available to perform the physical actions required. These results (and other similar findings) are often interpreted as failures on the part of the chimpanzees, because they did not evidence causal reasoning. However, what the researchers showed was that chimpanzees were reasoning – they just were not reasoning about the causally relevant variables in the task – even though those variables were directly observable. However, rather than showing what the chimpanzees could not do, Vonk and Subiaul, in a series of follow-up studies, attempted to show what features of the task the chimpanzees were attending to, and what features allowed them to perform successfully on some trials. And this is the bottom line in many similar studies – chimpanzees (and other animals) may or may not 'succeed' at the tasks we present to them; what matters for illuminating the cognitive processes underlying their performance is how they succeed (or fail) at the tasks. And the same should be said for determining how humans succeed in experimental tasks. We should not take for granted that humans use particular mechanisms for solving problems, until we have tested these hypotheses (Silva et al., 2005, 2008).

A closely related point is that researchers often suggest that chimpanzees 'fail' particular tasks when they do not perform in a manner consistent with how humans might be expected to perform (sometimes in the absence of having any available human data to bear on the issue). Such claims have led to suggestions that captive chimpanzees are unable to perform well in cognitive experiments because they have been cognitively deprived, removed from the socially rich lives they would have led in the wild, without the challenges of finding food, mates and shelter, and navigating social conflicts, forging alliances within large groups, and so on (Boesch, 2008). These arguments neglect the fact that experimentally experienced chimpanzees have a wealth of experiences that wild chimpanzees do not. They also live in social groups. But, in addition to that, they have extensive experience with human caretakers, human-made objects and artifacts, and contrived situations and contingencies that they would not face in the wild. Furthermore, it is precisely when you take an animal out of the environment in which evolution has sculpted them to survive that you can best determine their ability to generalize knowledge to unfamiliar and novel circumstances, as humans often do. Still, these critics also fail to acknowledge that chimpanzees that sometimes do not reach criterion or perfect performance on experimental tasks are not 'failing' our tasks. Rather, they are illuminating for us how the chimpanzee sees the world; and it is often quite different from our human-centered biases have led us to see. It is only through thoughtful probing of their responses in carefully constructed post hoc tests that we are able to learn more about their thoughts. The chimpanzees that have participated in dozens or hundreds of experiments designed by psychologists do not 'fail to be human.' Rather, they succeed at being chimpanzees, and as primatologists and objective scientists, it is our mission to learn what that means. Where results appear to differ between laboratories, it is often not the results that differ, but the interpretation of the results.

We should not claim continuity or discontinuity, or 'high' or 'low' order explanations, for either humans or nonhumans until we have examined alternative explanations for performance in our tests. Only when we fashion our experiments in an unbiased, nonhuman-centered way with an open mind as to how other species might approach problems with a consideration of the sorts of problems, they have evolved to face will we be enlightened as to the kinds of minds with which we share this planet. We will not find a human mind in another species, not even those species most closely related to humans. Those species have evolved their own traits, capacities, and thought

processes – some of which are equally impressive, astounding, and perhaps beyond our capacity to comprehend. We must embrace the nature of evolution – an appreciation for both continuity and discontinuity – even in closely related species such as humans and other great apes. In doing so, we may have to abandon Holy Grail pursuits and be open to finding evidence for abilities that our closest relatives have that we do not, and vice versa. We may also find evidence for humanlike abilities in distantly related species. We need not attempt to turn chimpanzees into some kind of half-human hybrid to appreciate their cognitive accomplishments. Our study of their minds should not be guided by such a missive.

Bridging Gaps

On that note, comparative evolutionary psychologists could take heed from the early ethologists who remained focused on the goals of determining mechanisms underlying both human and nonhuman behaviors at both the ultimate and proximate levels. To their credit, evolutionary psychologists have incorporated advances in cognitive science, behavioral economics, developmental psychology, linguistics, cultural anthropology, sociobiology, and ethology, and yet work from an overarching theoretical framework. The basic mechanisms of natural selection and sexual selection can explain both human and nonhuman mating practices (Buss, 1989, 1994), sex differences in spatial abilities (Voyer, Voyer & Bryden, 1995), attractiveness (Burke and Sulikowski, 2010), investment in offspring (Alvergne et al., 2009), and so on. Comparative psychologists, while unequivocally but sometimes only implicitly accepting evolutionary theory, have not always placed their work within the same overarching framework, and sometimes take esoteric side trips, investigating questions that, although interesting, do little to explain the forces giving rise to various traits in different populations.

This is not to say that comparative psychology is fundamentally flawed relative to evolutionary psychology, or that evolutionary psychology is beyond reproach. We have been critical of the focus of comparative psychologists to seek out commonalities between humans and other species at the expense of exploring many fascinating adaptations that humans do not share (echolocation in distantly related cetaceans and Chiroptera for instance). We have also been critical of evolutionary psychology for its tendency to focus exclusively on what other species can tell us about human evolution. Indeed, we recently attended a talk where an evolutionary psychologist defined evolutionary psychology as the study of human behavior and the human mind. This unitary focus on humans was surprising. There will be those who will staunchly defend their fields against such criticisms and point to the many counterexamples that defy our critiques. For example, there are researchers studying mate guarding in birds (Birkhead, 1988) that parallels work in humans. This work may be less prototypical of either comparative or evolutionary psychology. Should it be labeled as one or the other? Or should such work fall under the umbrella of Comparative Evolutionary Psychology, as it is both comparative in its nature and evolutionary in its focus? We would say yes – that is, exactly the kind of work that this new field would embrace. But the results of such investigations will shed light not only on human psychology but also on reasons for the emergence of this behavior in other species.

Although both comparative psychologists and evolutionary psychologists are interested in the mechanisms underlying behaviors exhibited by various species and specific human and nonhuman populations, as well as the evolutionary forces that gave rise to such traits and behaviors, these two fields have taken somewhat disparate trajectories, rather than culminating in a single field of study. We propose that much would be gained if the fields were merged into a new science of Comparative Evolutionary Psychology. The goals would remain – the new science would aim to explore the ultimate and proximate causes of behavior in humans and their close and distant relatives – and the relatively newfound appreciation for an eclectic approach to empirical questions and methodologies would be retained. We must adopt more open-minded approaches to our studies, in which we do not grasp firmly onto 'preferred hypotheses,' but are willing to formulate new theories and hypotheses that emerge from a consideration of the contexts that shape an animal's evolutionary history.

One of the solutions to removing these barriers is to increase communication and advocate for collaborations among researchers with different perspectives and specialized expertise. In order to best accomplish this open-minded perspective, we suggest dissembling the barriers that arose when creating false dichotomies between nature/nurture, behaviorism/nativism, field/laboratory, ideographic/nomothetic, and human/nonhuman research, and, most importantly, a willingness to let go of the idea that other species are most valuable when they most closely approximate humans (cf. Savage-Rumbaugh and Lewin, 1994). By doing so, we will allow ourselves to appreciate the diversity that exists on this planet, and to better understand the process of evolution – as it applies to both the behavior and psychology of organisms. Thus Comparative Evolutionary Psychology can be a single unified field for the study of evolved traits in all species.

See also: Cognition, Evolution of; Comparative Method in Evolutionary Studies; Human Mate Choice, Evolution of; Sociobiology: Overview.

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