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Original Article

An Introduction to Comparative Evolutionary Psychology

Jennifer Vonk, Oakland University, Department of Psychology, Rochester MI, U.S. Email: vonk@oakland.edu (Corresponding author).

Todd K. Shackelford, Oakland University, Department of Psychology, Rochester MI, U.S.

Abstract: Previously we (Vonk and Shackelford, 2012, in press) proposed an integration of comparative psychology and evolutionary psychology into a new field of "comparative evolutionary psychology." This integrative discipline incorporates principles from ethology, ecology, biology, anthropology, and psychology, broadly defined. We present in this special issue a collection of original empirical and theoretical review articles in which leading researchers propose ways to successfully integrate comparative and evolutionary approaches within their particular areas of study. We showcase the key contributions of these articles and highlight several empirical and theoretical challenges, as well as key future directions, for comparative evolutionary psychology.

Keywords: comparative psychology, evolutionary psychology, comparative evolutionary psychology

A Unified Comparative Evolutionary Psychology

Recently, Vonk and Shackelford (2012) proposed a unification of comparative psychology and evolutionary psychology into a new field, comparative evolutionary psychology. Although this was not the first of such proposals, Vonk and Shackelford's was more integrative than prior proposals (see Burghardt, this issue). Our primary emphasis was to bridge some of the gaps between researchers with disparate goals and approaches. For instance, we proposed that a focus on evolutionary theory with a comparative approach can help to integrate the work of field researchers and laboratory researchers, human-centered researchers and researchers of animals, behaviorists and cognitivists, and nomothetic researchers and ideographic researchers. We noted that both comparative psychologists and evolutionary psychologists sometimes adopt too narrow a focus; either neglecting interesting differences between species in the search for continuity (comparative psychology) or neglecting other species altogether (evolutionary psychology), sometimes with a blind eye to the phylogenetic history of our own and other species.

Narrow Focus

Both comparative psychologists and evolutionary psychologists have been guilty of focusing solely on continuities, especially between closely related species, although this narrow focus has been both motivated by different goals and manifested in different shortcomings. Within comparative psychology, researchers have attempted to demonstrate, in particular, mental continuity (in the spirit of Darwin) among various species, whether closely related or not. For example, researchers have found that fish attribute reputations (Brosnan, Earley, and Dugatkin, 2003), that honeybees are capable of sophisticated categorization (Menzel and Giurfa, 2001), that canines understand some mental states (Udell, Dorey, and Wynne, 2011), and that birds use and modify tools and understand their causal properties (Emery and Clayton, 2004). At times, such findings are not couched in terms of the likely selective forces giving rise to such traits. Additionally, researchers sometimes neglect to consider whether similar traits and behaviors may have arisen as a result of different selection pressures or are manifestations of different underlying processes or mechanisms. Comparative psychologists historically have sought evidence for capacities in non-humans once considered unique to humans. One potential solution to this focus on all or none human-like capacities is to focus on relating different forms of behavior for a given species into "levels of complexity," acknowledging that various levels of a behavior may indicate precursors to a trait present in its full form in another species. Such an approach within the context of language is outlined by Uriagereka, Reggia, and Wilkinson (this issue), and can be useful for exploring other apparently unique traits across a range of species that differ on some key aspect of morphology or environment.

We outlined various reasons for the focus on all-or-none human-like capacities in non-humans (Vonk and Shackelford, 2012), including the difficulties inherent in publishing null results. We also drew attention to the negative consequences of such a focus, such as the potential for data massaging and fabrication. Furthermore, we alluded to the costs associated with the emphasis on human-like traits in determining the value of other species from an "animal rights" perspective. Animal welfare has been a neglected topic within comparative psychology, perhaps because of the overwhelming focus on species that display human-like features, such as empathy and mental state attribution, rather than an overarching appreciation for the diversity of life on this planet. We hope that when animals are viewed in light of the role that they play in the diverse ecosystem that comprises our planet, hierarchies that place animals with more human-like qualities at the top will fall by the wayside.

Evolutionary psychologists have sometimes focused on human uniqueness, with the outcome that only closely-related species are examined as a means to elucidate the history and emergence of traits deemed unique to humans. Consequently, other interesting adaptations not shared with humans can be overlooked. For instance, cetaceans and chiroptera echolocate, honeybees see only four colors, including ultraviolet (Kuhn, 1927), and fish breathe through gills and exhibit external fertilization. Whereas evolutionary biologists have long examined such unique traits, teasing apart commonalities and differences between distantly-related species and closely-related species to identify selective pressures that produce these traits, evolutionary psychologists have been more

concerned with establishing human nature, using comparisons to non-humans only sparingly as a way to determine when such traits might have emerged in our own evolutionary history.

Both comparative psychologists and evolutionary psychologists are concerned with human uniqueness. Comparative psychologists have attempted to break down these Cartesian barriers and emphasize the discovery of outward similarities. Unfortunately, they have not always worked as hard to uncover differences in internal motivations and mechanisms. Evolutionary psychologists may be less goal-driven with regard to highlighting human uniqueness, but have been less concerned with traits in other species that can be equally illuminating in uncovering the types of environmental factors responsible for these adaptations. We propose that an equal emphasis on convergent evolution and divergent evolution, and less concern with elucidating human nature specifically, may be beneficial to the integration possible with the new field of comparative evolutionary psychology. We do not wish to imply that all comparative psychologists and evolutionary psychologists are guilty of the critiques we have outlined; rather, that these problems are prevalent, due to both longstanding and recent trends in both disciplines (see also Burghardt, this issue).

The Goal of Comparative Evolutionary Psychology

In our 2012 volume, we gathered contributions from exemplary scholars that embodied the spirit of our proposal. The majority of the contributions came from those who self-identify as comparative psychologists. We selected those who work with a variety of species and anchor their explorations within an evolutionary perspective. Too often, comparative psychologists become caught up in what we deemed "Holy Grail" pursuits, attempting to find evidence for surprising traits (particularly those unexpectedly human-like) in species that may not illicit a strong rationale for exhibiting such traits from an evolutionary perspective. The researchers that contributed to our volume were mindful of framing their studies within the context of better understanding the roots of human behavior by making careful comparisons to relevant species that share important morphological or environmental variables with human ancestors. In the current special issue, Forbes makes the important point that it is not always our closest ancestors that make the best comparison group for a given topic. For example, when examining non-shared factors within a family, it may make more sense to look at altricial bird species that simultaneously raise different broods, rather than non-human primates that raise one offspring at a time. However, Forbes and others in this issue make clear the relevance of comparing human behavior to that of other species to better understand the factors underlying the emergence of specific traits and behaviors. Comparative evolutionary psychologists could take heed from such careful comparisons.

The primary goal for compiling this collection of reviews and empirical articles was to expose the readership of *Evolutionary Psychology* to some of the cutting-edge work in both fields, but especially within comparative psychology, with the hope of further opening the lines of communication and exposing evolutionary psychologists to novel perspectives and approaches. We asked our "comparative" contributors to consider how their research

informs questions of evolutionary significance. We asked our "evolutionary" contributors to consider how their research might be better integrated with comparative research addressing similar questions. In so doing, we believe that our contributors, and our readers as a result, will extricate the parallels between work historically conducted within one field and not the other.

One of the problems we identified recently (Vonk and Shackelford, in press) was that psychologists feel the need to identify themselves as belonging to a particular subfield within the larger discipline. Reznikova and Dorosheva (this issue) also note the many "divided" sub-disciplines of psychology, and that it is only recently that these sub-disciplines have begun to incorporate evolutionary principles into their programs of research. It is our hope that we can begin to avoid such "pigeon-holing" and embrace multidisciplinary breadth within an evolutionary framework. Although we've chosen the moniker "comparative evolutionary psychology" to denote the proposed integrative field, our expectation is that the new field will be inclusive of ethological, ecological, cognitive, and developmental frameworks as well.

Overarching Themes

Phylogenetic and functional questions

Several themes emerge from the contributions to this special issue. Waller, Liebal, Burrows, and Slocombe (this issue) address the integration of functional and phylogenetic questions in the study of the evolution of communication. Integrating such research questions is a useful exercise for the study of behavior and cognition, in general. These authors suggest that "…comparative psychologists are often interested in identifying similarities and differences between related species, and evolutionary psychologists are often interested in identifying the adaptive reasons for these differences (p. 541)." Although comparative psychologists are tasked with identifying the factors that predict differences and similarities between species, and attempt to frame their research questions accordingly, it sometimes occurs that researchers study a new species on a previously established task to determine whether the new species shows a similar pattern of results to species previously tested, without sufficient theoretical justification. For example, one might question why elephants should be expected to demonstrate mirror self-recognition (Plotnik, de Waal, and Reiss, 2006), or bats should follow human pointing cues (Hall, Udell, Dorey, Walsh, and Wynne, 2011). Hall et al.'s research illuminated the effect of exposure to humans – an important ontogenetic factor in determining sensitivity to human cues – in a non-domestic species, and the species in question may be irrelevant. However, our point is that researchers should selectively study topics and species based on hypotheses regarding the factors behind the specific constellation of traits and behaviors. Researchers engaged in exploratory analyses expose themselves to the criticism that they are seeking only to show how "smart" a particular animal is. Arguments such as these are irrelevant and detract from the mission of comparative evolutionary psychology, which seeks to understand all adaptations, regardless of whether the adaptation maps on to a human-centered scale of intelligent behavior.

Skerry, Lambert, Powell, and McAuliffe (this issue) suggest that evolutionary

biologists have "…traditionally been concerned with ultimate rather than proximate levels of analysis, [but that] understanding the cognitive processes that underlie behavioral phenomena will be crucial to understanding their phylogenetic origins (Chittka, Rossiter, Skorupski, and Fernando, 2012; MacLean et al., 2011)" (p. 558). Thus, both comparative psychologists and evolutionary psychologists have sometimes failed to integrate functional/ultimate explanations with proximate explanations in their analyses. In addition, Chittka et al. (2012) suggest that understanding the underlying mechanism – how a trait has evolved – may be as important as understanding what function a trait serves. Waller et al. (this issue) correctly note that identifying current fitness consequences does not imply that these consequences were the reasons for the trait evolving. This is the danger of *post hoc* analyses and the inability to perfectly recreate the conditions under which organisms evolved, but it is a limitation that is sometimes neglected when researchers propose hypotheses purporting to explain unlikely behaviors and traits.

Zentall (this issue) asks us to reconsider the nature of the questions posed in a given area of research; in this case – episodic memory. For example, researchers typically ask whether animals have the capacity for episodic memory, while neglecting what purpose such a capacity would serve for that species. As Shettleworth (2012) notes, it is unlikely that the ability to reflect on past experiences arose in animals to allow them to ruminate over the meaning of life's experiences, as would an autobiographer reflecting on the events of their own life. It is more likely that the capacity would arise to allow animals to learn from past experiences and inform future decisions in the context of foraging and mating decisions. Thus, Zentall offers that we should ask what it would mean if animals did *not* have any form of episodic memory. These types of questions can be posed with regard to any aspect of comparative evolutionary psychology that focuses on the existence of particular abilities.

Species-relevant behaviors

Related to the issue of demonstrating the existence of traits in species for which there is no clear rationale for doing so, is the issue of focusing on artificial rather than naturally occurring behaviors. Both Gerlai (this issue) and Brosnan, Beran, Parrish, Price, and Wilson (this issue) stress the need to design experiments in which the natural behavior of organisms is adapted to the experimental paradigm, rather than forcing the display of artificial behaviors that confuse the ability to address functionally homologous behaviors. Reznikova and Dorosheva (this issue) note that:

> It is a challenging problem for comparative psychologists to understand to what extent these cognitive adaptations can be attributed to flexible learning abilities, versus innateness. To solve this problem, different forms of learning should be investigated in natural situations in which animals can perform their innate behavioral repertoire, together with flexible components of their behaviors (p. 514).

Brosnan et al. (this issue) and Clary and Kelly (this issue) also address the issue that, even when different species are speculated to possess similar adaptations, researchers often fail

to test for them in similar paradigms, or fail to appropriately match the methodology. For example, corvids have been hailed as "feathered apes" (Emery, 2004; Pepperberg, 2013) due to proposed cognitive parallels between corvids and apes. However, Clary and Kelly point out that these animals are seldom tested using similar procedures. Whereas tests of social cognition in corvids have been largely restricted to caching paradigms, tests of social cognition in primates have been more diverse and have focused on both natural (food competition) and artificial (guesser/knower, see/not see) paradigms. Clary and Kelly attempt a first step in remedying this shortcoming by testing corvids in a paradigm widely used with primates to assess perspective-taking and understanding of human cues.

Although testing corvids in non-caching paradigms removes them from their species-specific natural behavior, Clary and Kelly make the argument that doing so allows the researcher to determine whether the skills are domain-general and adapted for a non-context-specific flexibility – a point that Vonk and Subiaul (2009) argued previously (see also Reznikova and Dorosheva, this issue). As Clary and Kelly state:

> …examining species in both ecologically relevant and non-ecologically relevant contexts can reveal the potential, and equally as important, the limits of a given species' cognitive abilities. Furthermore, when used with multiple species, this approach can elucidate how the underlying mechanism responsible for the animal's behavior (i.e., associative and/or cognitive processes) vary in relation to phylogeny, and thus, how cognitive abilities may have developed over evolutionary time. (p. 641)

It is important to balance both considerations – the naturalness of the behavior, and the extent to which it can be used to disentangle behavioral flexibility versus innate behaviors in explanations of animals' behaviors. If one is drawing parallels to human abilities like theory of mind (the ability to interpret and represent underlying mental states in others), then one must allow for the behavior to exist outside of a narrowly construed context in which the behavior might be hard-wired, rather than the flexible sort of mind-reading that allows for making predictions in novel contexts (see also Vonk and Povinelli, 2012).

Brosnan et al. (this issue) take up the challenge of designing studies that are species-appropriate or "fair," in addition to allowing valid comparisons across species with different adaptations. They focus on studies modeled in experimental economics, designed specifically to identify parallels in decision-making processes between humans and other primates, such as capuchins and chimpanzees. They question the assumption that tasks established for non-humans should be understood in a comparable manner to tasks given to humans complete with verbal instruction. As they point out, human performance is often radically altered by the removal of such instructions, thus calling into question the relevance of cross-species comparisons both with and without the inclusion of instructions for human participants. They have proposed that one way to address this challenge is to test new methodologies in species for which typical patterns of response are already established to test whether the novel procedure generates expected results. They argue that the best approach is to establish as much similarity as possible across testing procedures, while also comparing responses within species based on known and unknown outcomes. Forbes (this

issue) addresses the likelihood that individuals vary in the extent to which they are affected by the same environmental factors. He makes a compelling case for such individual differences within the context of family relationships. The same parenting style, for instance, may exert profoundly different effects on a gregarious, outgoing child than it would on an introverted child. Given that we cannot ensure similar effects of the same environments on members of the same species, we must be cautious when assuming that similar conditions affect different species in the same manner and to the same degree.

With any comparative study, one cannot assume similar underlying mechanisms on the basis of similar manifest behaviors. As Brosnan et al. (this issue) summarize:

> Aside from function, comparative work is also essential for understanding the mechanisms that drive behavior. Even in situations in which the same outcomes are reached by different species, the cognitive (or other) mechanisms that are used to do so may be very different… if a behavior is beneficial it will evolve in whatever way is possible, given the cognitive and behavioral architecture already in place … it is useful to understand the relative strength of the selection pressure. For instance, was a trait so critical that multiple species evolved it independently (e.g., sight)? Second, it helps us to understand how selective pressures may have differed, particularly if species that are otherwise quite similar in cognitive architecture do *not* evolve similar behaviors. Third, differences in cognitive mechanisms may highlight situations in which behaviors do differ from one another, despite what appeared to be similarity on an initial investigation. Fourth, understanding what mechanisms underlie decision making may highlight the way in which a trait unique to a single species may affect its choice behavior. (p. 621)

This passage helps to identify the importance of comparative studies in answering questions of adaptation across a range of species, but also specifically with regard to human traits. Psychologists can no longer focus on humans alone, speculating about causes for the emergence of particular aspects of human nature, without an investigation into whether such aspects exist in closely-related and distantly-related species and in species that do and do not exhibit similar behaviors.

This challenge is also addressed by Hollis and Nowbahari (this issue), who focus on defining and explaining the emergence of "empathy" in organisms as "simple" as ants. The view of empathy endorsed by these authors acknowledges the result of convergent and divergent selection processes as reflected in the similarities and differences in the means through which both human and non-human animals attend to another's distress. They also emphasize that "…just because ants' and rats' rescue behavior appears similar, doesn't mean that it comes about via the same mechanism...the ability to truly understand and react to another's distress most likely evolved from simpler forms" (p. 660). This inability to be certain of underlying mechanisms is a limitation that deserves more space in the thought processes and products of comparative evolutionary psychologists.

Broad approaches

Brosnan et al. (this issue) make a compelling argument that it is not possible to

elucidate an evolutionary function of a behavior when one has data from only a single species. Many empirical studies focus on the behavior of a single species, despite the goal of better understanding factors responsible for the emergence of specific traits. This shortcoming is evident in the work of comparative psychologists who focus on single species, and in the work of evolutionary psychologists, who focus predominantly on humans (see also Burghardt, this issue). One excellent strategy is to compare the behavior of closely-related species that differ on key aspects of their social or physical environments, as exemplified in the work of Taylor, Visvadar, Nowbahari, and Hollis (this issue), who examine rescue behavior in two ant species that differ in colonial structure and aggression toward non-nest-mates. This approach is also taken by Brosnan et al. (this issue), who compare the decision-making strategies of humans, chimpanzees, and capuchins in analogous economic "games." In their studies, they emphasize the importance of testing social animals in groups as well as individually. Too often researchers study a social phenomenon, such as cooperation, in light of the behavior of individuals, although such processes presumably act at the group level. A cooperative individual will not improve its own fitness without a system within its social ecology whereby cooperation is rewarded and defection is punished.

A separate point regarding the importance of broadening the scope of comparative investigations of human adaptations is made by Georgiev, Klimczuk, Traficonte, and Maestripieri (this issue). These authors emphasize the importance of studying similar traits in a range of closely-related and distantly-related species to obtain "phylogenetic 'mapping' of human psychological and behavioral traits" (p. 680). A proposal for a phylogenetic comparative psychology also has been offered by MacLean et al. (2011). Such a process should contribute vastly to an understanding of the evolution of various apparently adaptive aspects of human nature.

Costs and benefits

In a recent special issue of Philosophical Transactions of the Royal Society B titled "New Thinking: The Evolution of Human Cognition", Heyes and Frith (2012) discuss the importance of evaluating the fitness costs and benefits of traits in consideration of their likelihood to have evolved in a variety of species and contexts. What Heyes refers to as "super cognitive processes" are less likely to have evolved in many species when the added benefits (relative to associative learning) are marginal, given the energy cost to developing the brain required to produce such processes. This argument highlights the need to carefully consider arguments of parsimony when applied to cognitive processes (Barrett, 2012). It is not always the case that a purportedly more sophisticated mechanism is more parsimonious in terms of the number of processes involved (or the energy required to support them). It is important to consider the benefits derived from adding complexity to a model in terms of efficiency and resources.

The cost/benefit model is useful when considering the evolution of behavior, more generally. Georgiev et al. (this issue) also stress the utility of cost/benefit analyses in understanding sex, individual, and species differences. Kaighobadi and Stevens (this issue) address risk-taking in women as a function of their ovulatory cycle status, predicting that risk may be more likely nearer ovulation, as it will have greater benefit when there is

potential for a reproductive pay-off. Their approach to studying human psychology and behavior is informed by a substantial literature within comparative psychology. Welling (this issue) takes the opposite approach, discussing the effects of hormones and contraceptives on human behavior and using this literature to speculate about similar effects in non-human behavior. Like Brosnan et al. (this issue), Kaighobadi and Stevens utilize paradigms from behavioral economics to test predictions concerning risky decision-making; however, instead of explicitly comparing different species, they have extracted information from data on species ranging from insects to non-human primates in foraging contexts, to devise a test for human females in a mating context. Heinrich (this issue) also alludes to cost/benefit analyses when introducing a fascinating new context for considering the potential uniqueness of human art. He places art and aesthetics into a comparative framework – examining whether behaviors exhibited by non-humans in the context of attraction to mates, nesting materials, and habitat might also reflect adaptations. This contribution signals a new field of study, as aesthetic sense has not been rigorously examined in the animal kingdom, but may have implications for the traditional view of such preferences as unique to human cultural life. Perhaps aesthetics are more deeply rooted in the animal kingdom, and should be explored more broadly. We hope that this, and other contributions, in the current special issue will stimulate additional productive thinking and research on a variety of topics relevant to comparative evolutionary psychology.

Concluding Comment

The topics addressed in this special issue and in our previous volume (Vonk and Shackelford, 2012) are not meant to be an exhaustive list of relevant topics, but instead might be considered exemplars of the theory and empirical work that will lead to better integration of comparative psychology and evolutionary psychology.

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