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Peer reviewed

Bottoms-up! Rejecting Top-down Human-centered Approaches in Comparative Psychology

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Although comparative psychologists have made considerable strides in the past several decades, expanding the breadth of species and questions examined, the field still suffers from an overemphasis on top-down approaches that begin and end with a focus on humans. This top-down perspective leads to biases and oversights that hamper the further development of the field. A bottom-up approach that considers species-specific abilities and behaviors in the context of theoretically relevant comparisons will be most useful in advancing knowledge of species-specific and shared abilities. This will allow a better determination of the extent to which continuities and discontinuities exist as a function of different ecological forces. In addition, a bottom-up approach will facilitate a shift in focus from using animals to better understand humans, to understanding animals themselves. This new approach will allow for an appreciation of how humans can benefit other species.

Comparative psychology has been defined as the study of the evolution and development of (all) animal behavior (Greenberg & Haraway, 2002). However, like many other psychology disciplines, the focus has often been on gaining a better understanding of human behavior and cognition, in this case, through comparisons to other species (e.g., Rumbaugh & Williams, 1992). The long held fascination with such comparisons is driven by a desire to understand how humans evolved and, in particular, the extent to which humans evolved cognitive capacities that are unique from those of other species. In the late 1800s, most notably through the works of Darwin (1871), it was proposed that the mental capabilities of humans and higher mammals share important continuities. This perspective, sometimes verging on anthropomorphic with a liberal top-down application of human traits or qualities to nonhumans, was in stark contrast to the previous reigning philosophy that humans were unique. This uniqueness was attributed in part to the fact that humans alone were believed to have consciousness (i.e., a soul) whereas nonhuman species were thought to be governed solely by primal instincts and basic drives (Descartes, 1637/1985). The extent to which humans are subject to many of the same basic instinctive patterns and biological drives has often been downplayed. In contrast, the extent to which animals may exhibit human-like qualities has often been exaggerated. Many comparative research programs have furthered the notion of continuity by applying top-down strategies and interpreting animal behavior through a human-centric lens. Important discontinuities, highlighting the uniqueness of nonhuman species, have received inadequate attention. Only recently has a more intermediate position been proposed to de-couple these extreme positions (Greenwood, 2016), which is a position we endorse.

Greenwood (2016) focuses discussion on two extreme positions. In strong continuity, researchers advocate for the notion that there is continuity between animal and human minds and that there is continuity between associative processes and so-called 'higher' cognitive processes. Alternatively, a strong discontinuity argument supposes a disconnect between animal and human minds, and a discontinuity between associative and cognitive processes. Greenwood suggests that the two relations within each of these positions can be de-coupled. That is, one can assume either that animal and human minds share important continuities or discontinuities without presupposing that associative and cognitive processes are continuous or discontinuous.

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Although we are sympathetic to the more intermediate position advanced by Greenwood, in this paper, we argue against strongly dichotomous thinking altogether and suggest that researchers reject the idea of placing animal minds and cognitive processes into discrete categories of "human-like" and "nonhuman-like." In rejecting points of comparisons to abstract notions of intelligent behaviors and processes, we advocate for a better understanding of the precise mechanisms underlying animal behavior with careful attention to the conditions necessary for the emergence of these mechanisms. We argue that comparisons between species are useful only in the extent to which they shed light on selective pressures giving rise to both similarities and differences between species. We provide a brief review of the extreme positions, with a commentary on how we believe such positions have disabled progress in the field. We focus attention on the types of comparisons that are critical for making progress in understanding animal minds, and we finish by highlighting growing areas of comparative psychology that shift the focus from using animals to understand humans and instead use animal-human interactions to better understand other species.

A Historical View of Comparative Psychology

The 19th century shift towards anthropomorphism was largely based on observation rather than through rigorous experimental testing. Darwin, for example, inferred a humble emotional state when a dog would prostrate into a 'humble' position. Through his observations of various species' behaviors, he conceived the notion that humans shared with the higher animals "…similar passions, affections, and emotions, even the more complex ones, such as jealousy, suspicion, emulation, gratitude, and magnanimity…" (Darwin, 1871, p. 79). One of Darwin's followers, George John Romanes (1883), who coined the term "comparative psychology" was in agreement that, if an animal expressed behaviors consistent with those seen in humans experiencing a particular emotion, few would doubt that the animal and human were experiencing analogous internal emotional states. Similarly, animals that solved complex problems were assumed to invoke insight (Kohler, 1924) and causal reasoning in order to do so, although lower level associative processes were later shown to be sufficient for explaining some of the same findings (e.g., Povinelli, Bering & Giambrone, 2000). Importantly, the same can be said of much of human behavior (e.g., Silva, Page & Silva, 2005), although this possibility is often ignored.

In the late 19th century, a desire for a more disciplined approach within comparative psychology was initiated by Conway Lloyd Morgan's (1894) canon, which espoused that higher-level mental states should not be attributed to an observed behavior if such a behavior could be explained by a lower-level mental ability. In other words, similar behaviors expressed by different species should not result in the inference of similar mental capacities. Further, Morgan appreciated that evolution embraces differences as well as similarities in cognitive processes, although this perspective is often neglected (Vonk & Povinelli, 2006). Morgan's perspective was the first step away from the fully anthropomorphic explanation of animal behavior. However, contrary to popular portrayal of Morgan's beliefs, he remained steadfast in his view that the only way researchers can investigate animal psychology is through the lens of human introspection, given that it is the only perspective to which humans have access (Morgan, 1894).

In critical response to Darwin and Romanes, the early 1900s was dominated by the strong behaviorist proposal to eschew any consideration of mental capabilities when studying animal behavior. In exploring how animals learn to escape from a puzzle box, Thorndike (1911) demonstrated that various species learned through trial and error. Further, such escape did not happen more quickly when the animal was able to watch a conspecific successfully escape, suggesting that animals did not have higher level 'insight' as was evinced in humans. Following such findings, Watson (1913), the father of behaviorism, completely rejected an

anthropomorphic approach to studying animals, indicating that it is absurd to invoke mental content to explain animal behavior. For many years, this dominant paradigm discouraged the pursuit of research into higher-order processes in nonhuman species. At the same time, truly comparative studies on a wide range of species were also discouraged given the focus on basic processes in simpler organisms and a shift away from a fascination with animal 'minds' in light of the behaviorist view that observable behavior alone was sufficient to explain animal behavior.

With the advent of cognitivism in the 1950s, there was a resurgence in research aiming to compare the cognitive abilities of nonhuman species to those of humans. Researchers focused attention in particular on higher level mental abilities, especially abilities previously considered unique to humans, such as causal reasoning, theory of mind, and metacognition. However, disagreement remains regarding the relationship between human and nonhuman cognitive abilities and the perspective one should take when investigating such questions (Dess & Chapman, 1998). A number of researchers suggest that, in line with Darwin's sentiments, humans and nonhumans share a number of mental capabilities but that differences lie in the degree to which a given species has a particular ability (e.g., de Waal & Tyack, 2003). This perspective is still largely an anthropomorphic one in which researchers strive to discover which known human attributes are shared with other species. Others suggest that nonhuman mental capabilities are functionally different from those of humans (Penn, Holyoak, & Povinelli, 2008). Furthermore, similarities should not be confused with equivalences, and, after determining outward similarities, the next question should always be to determine whether underlying mechanisms are similar or different. Without an overarching framework or agreed upon criteria for exploring animal cognition, researchers may become ensnared in the quagmire of intractable debates without ever reaching a productive middle ground.

The Problem with Top-Down Approaches

Although the last century of comparative psychology is replete with significant accomplishments, a number of pervasive problems continue to stunt the development of the field. These include; 1) a pattern of esoteric research findings driven by convenience rather than a clear theoretical framework, 2) a focus on artificial, as opposed to naturally occurring, or species-specific behaviors, 3) an emphasis on all-or-none human-like capacities rather than a search for relevant elements of a particular capacity, and 4) a lack of appropriate methodologies for making species comparisons. These issues can be attributed, at least in part, to a top-down approach to comparative psychology (see also de Waal & Ferrari, 2010). In the following paragraphs, we will detail these issues as well as provide suggestions to redirect the focus of comparative psychology given changing resources and theoretical advances. One direction for refocusing our efforts is to generate research that highlights the benefits of animal-human interactions for animals as well as for humans. In addition, we should investigate the extent to which human encroachment may be harmful for other species.

Lack of theory. Historically, comparative psychologists tested nonhuman animals for evidence of capacities once considered to demarcate uniquely human cognition, and focused, almost exclusively, on continuities between closely related species (Vonk & Shackelford, 2013). Top–down approaches begin with a concept of a capacity clearly defined and identified in a species, such as humans, and subsequently direct researchers to seek evidence for the same capacity in otherspecies. More recently, researchers have sought continuities between humans and even distantly related species that occupy distinct ecological niches (e.g., corvids, cetaceans). Researchers using top-down approaches do not always have adequate theoretical justification as to why the study species would produce similar patterns of results to that of previously tested

species (Vonk & Shackelford, 2013). Rather, researchers facing funding cuts and other roadblocks to research may be prone to adjusting research for available species rather than testing species that are best suited to answer an empirical question.

A bottom-up approach would be to assess natural behaviors in the given species and design experiments that further probe these natural behaviors or abilities, whereas a top-down approach sometimes seeks to extend findings from other species to this new species simply for the sake of generalizing, sometimes when it makes little sense to do so. For example, it might make little sense to extend studies of spatial memory to species whose food source is constantly available (e.g., grazers) or to study tool use in species that do not engage in extractive foraging. If the goal is simply to place animals into categories, such as "tool-users", "non-tool-users" to further demarcate boundaries between them, the top-down approach might suffice. But, if the goal is to understand why tool use has evolved in some species and not in others, then it makes sense to utilize a bottom-up approach - carefully examining components of behaviors related to tool use in a wide range of species that share or fail to share critical ecological factors. One might then examine the extent to which various bird species engage in extractive foraging, build nests, and explore novel objects as a function of their foraging ecology and environment. The goal would be to identify factors and behaviors that might be associated with the presence or absence of tool use rather than to simply label some species as more sophisticated than others.

When comparing 'apples to oranges' is fruitful. Researchers should selectively study topics and species based on hypotheses regarding the evolutionary factors that select for these abilities (Vonk & Shackelford, 2013). Evolutionary biologists and ethologists reap the advantage of a consensus within their fields that there is one overarching theoretical perspective that explains behavioral adaptations across species. Psychology, in contrast, is still struggling to find an overarching framework and has suffered through various paradigm shifts, as discussed above. Notably, evolutionary psychology is considered a sub discipline within psychology, rather than evolution being a framework from which all psychological questions can be explored (see also Vonk & Shackelford, 2012). Psychology is also hampered by its insistence on striving to explain human behavior, with humans positioned atop a pinnacle. Other species are of interest only as a source of comparison or a means to shed light on necessary criteria for uniquely human traits. Behavioral ecologists, ethologists, and biologists, in contrast, study species for their own sake, and situate each species in a larger ecological context, often examining the interactions between species. These disciplines are also characterized by well-grounded theoretical approaches to exploring the roots of animal behavior. Comparisons are selectively made based on elements of evolutionary or current environments that should predict different adaptations in modern species, and animals are typically observed in their natural environments.

Whereas comparative psychology could benefit from a similar theoretical grounding and a less anthropocentric approach to the study of nonhuman species, there are several strengths that comparative psychologists bring to the table. For example, comparative psychologists are typically well-trained in experimental design such that they can control and isolate factors in systematic experiments in both laboratory and field studies. Comparative psychology is also unique in its focus on cognitive processes, in comparison to a focus on directly observed behavior alone. Many experimental designs used by comparative psychologists are borrowed from other areas of psychology, especially developmental psychology. More methods could be adapted from social and cognitive psychology as researchers in those areas have focused exclusively on human behavior and cognition, but have studied many topics not yet widely applied to the study of animal minds. Comparative psychologists may thus be uniquely poised to develop tests of underlying mechanisms giving rise to the behaviors catalogued by ethologists, biologists and behavioral ecologists.

It is clear that a synthesis of the best attributes of these disciplines would produce the clearest insights into animal behavior. Elsewhere, Vonk and Shackelford (2012, 2013) advocated for a blending of comparative and evolutionary psychology approaches, but this proposal should be extended to advocate for a comparative psychology that pays tribute to its roots in ethology and behavioral ecology. As one example, if studies of cooperative behaviors are designed to examine specific predictors of cooperation, such as sociality (e.g., Gromov, 2017), researchers could target closely related species that vary primarily with regard to their natural social structure. In birds, for example, researchers could target species that exhibit, for example, communal nesting, pair-bonds, and cooperative groups or flocks. Studies of cooperative tendencies in humans have not arbitrarily compared societies but, rather, have focused on important distinctions such as agricultural versus hunter-gatherer societies or individualistic versus collectivist orientations (Henrich, Boyd, Bowles, Camerer, & Fehr, 2004). Comparative psychologists could also capitalize on behaviors observed in natural settings, and work to better understand the mechanisms underlying such behaviors, rather than presenting animals in laboratory environments with arbitrary tasks that have parallels in other distantly related species. We have been guilty of this approach ourselves, using food-provision tasks in unrelated chimpanzees (Silk et al., 2005; Vonk et al., 2008), when other types of cooperative behaviors may provide better demonstrations of prosocial sentiments in other apes. Warneken and colleagues, for example, have had success with instrumental helping paradigms (e.g.,Warneken, 2016). In bats, we have tried to replicate the food provisioning studies used with primates, and the escape paradigm used with rodents (e.g., Hoffmaster & Vonk, 2016) without much success, while Carter and colleagues have revealed important components of food sharing behaviors in vampire bats taking advantage of this species' natural blood-sharing behavior (e.g., Carter & Wilkinson, 2015; Carter, Wilkinson, & Page, 2017).

The cooperative string-pulling task, a version of the string-pulling paradigm in which two individuals must simultaneously pull on either end of a rope to access food is typically presented to social species, such as hyenas (Drea & Carter, 2009) elephants (Plotnik, Lair, Suphachoksahakun, & de Waal, 2011), parrots (Péron et al., 2011), ravens (Massen, Ritter, & Bugnyar, 2015), and chimpanzees (Hirata & Fuwa, 2007). Schmelz, Duguid, Bohn, and Völter (2017) used this paradigm to assess cooperative problem solving in two species of otters. One species – the giant otter - lives in social groups consisting of a breeding pair and various generations of offspring that help raise the young. Asian small-clawed otters also live in extended family groups, but unlike giant otters, forage individually. Thus, the study was designed to test the hypothesis that animals that forage together are more likely to solve the cooperative task compared to animals that forage independently. However, applying the task to, for example, snow leopards may make little sense unless the goal was to determine whether a relatively asocial species could learn to be cooperative in captive settings. All too often, in the past, such studies were justified with the sole rationale that a given species had not been previously tested in such a paradigm (e.g., giant pandas and mirror self-recognition, Ma et al., 2015).

Comparative psychology, by definition, is driven by the goal of making comparisons. It is tacitly assumed that the comparisons should occur between different species. Specifically, as outlined above, the field has often focused on comparing the cognitive abilities of other species to those of humans with the broad rationale of attempting to understand what evolutionary and environmental factors may support the emergence of particular human traits. Researchers are especially interested in those traits that are deemed potentially unique to humans, such as other-regarding preferences, theory of mind, and abstraction. However, it is also possible, and indeed, informative, to make comparisons between other species in order to understand how factors such as dietary habits (Byrne, 1997), sociality (Dunbar & Sutcliffe, 2012; Humphreys, 1976; Jolly, 1966) and exposure to varying environmental conditions (Sol, 2009) might influence cognitive development, and how various factors might support the emergence of traits not seen in humans, such as echolocation, infrared detection, and individual-specific vocalizations, to name a few. These are questions more typically

explored by biologists and ethologists, but, as mentioned above, psychologists are poised to make important contributions to these topics with their experimental design skills and ability to probe underlying mental mechanisms.

In addition, valuable comparisons can be made within members of the same species. Such intraspecies comparisons may be particularly valuable given the changing direction of comparative psychology and its increased focus on animal welfare and animal-human interactions. As just some examples, researchers might usefully compare captive to wild populations, sanctuary to lab animals, males to females, mother-reared to human-reared individuals, feral to companion animals, and so on. Although there has been a place in the literature for such intraspecific comparisons, this strategy has not been exploited to its full potential, perhaps due to researchers being hampered by small sample sizes and the confounding of variables when attempting to make critical comparisons. For instance, when comparing wild-caught to captive-born primates, the groups are necessarily confounded by age differences given that animals are no longer obtained from the wild. When comparing shelter dogs to companion dogs, it is impossible to know the true background of the shelter animals. Furthermore, other confounds may exist; shelter and pet dogs may also differ in measures of physical health, aggression and various other factors not critical to the main hypotheses.

Limited access could be due to the array of animal species available at zoos and sanctuaries. Some animals are not housed in captivity anywhere in the world (e.g., blue whales, mountain gorillas). Others (e.g., proboscis monkeys, uakari monkeys, quokkas, dugongs) are extremely rare. Although researchers are certainly not limited to studying captive animals, and indeed many studies are better suited for wild environments, some types of cognitive or physiological research may not be possible in the wild. For example, it would not be feasible to conduct long-term training studies with individuals, especially the type of studies that require the use of sensitive technology, such as touch-screens. Nor would it be possible to measure brain activity in response to different stimuli.

When accessibility dictates the direction of research, some species may be overrepresented in the scientific literature whereas others are neglected altogether, which could lead to mistaken assumptions about the prevalence of particular traits within orders or families. For example, lions are popular in captive settings and accessible for study in the wild, but more elusive clouded leopards are studied much less frequently. An overrepresentation of lions in cognitive studies might lead to an impression of feline cognition that is biased toward a species that is anomalous in terms of its social structure, with lions being the most social of the wild cats. Although there are currently over 300 primate species by some accounts, chimpanzees, rhesus macaques, and capuchins are overrepresented in the literature compared to, for example, saki, colobus, and proboscis monkeys, as well as gibbons. Researchers often use the term 'apes' to describe their subjects even when they have tested only chimpanzees and provide no data on the other ape species. Failure or inability to test various species in a range of experimental paradigms limits our ability to comprehend the extent of similarities and differences in cognitive capacities and the selective forces responsible for these differences.

Asking questions about the cognitive abilities of a domesticated species compared to its wild ancestor can shed light on what abilities have been lost or gained throughout evolution. Self -domestication in canines resulted in selection for the less aggressive individuals that took advantage of resources primarily provided by humans, For example, wolves approaching human settlements for scraps of food (i.e., garbage) resulted in decreased aggression, which manifested in reduced fearfulness of humans in domestic dogs (Hare, Wobber, & Wrangham, 2012; Hare & Tomasello, 2005). Domestic dogs have developed the ability to read communicative cues in humans such as; eye gaze (Udell, Giglio, & Wynne, 2008b), pointing (Udell et al., 2008; Hare et al., 2010), and verbal commands (Andics et al., 2016). If these capacities are due to domestication or to ontogenetic

influences, such as early social bonds with humans, we should not see the same abilities in wild dogs (e.g., Hastings, 2014) or feral dogs. Furthermore, if the effects of domestication are insufficient, and an evolutionary history of group-living and social complexity is important for understanding communicative skills, we might not expect to see the same abilities in other domesticated species, such as cats.

One caveat is that of course, one needs to consider that domestication may have led to changes in morphology and physiology in addition to cognitive changes (Hare et al., 2012), and that these processes will interact. Selective breeding that alters physiological traits, such as leg length, body shape and size, may interfere with the ability of the animal to engage in natural behaviors, such as hunting, which, when coupled with dietary changes, may either diminish or enhance behavioral flexibility and problem-solving. The approach that we advocate in which many factors are considered as possible predictors of cognitive differences, rather than comparing individuals as representatives of discrete species will better allow researchers to understand the selective pressures underlying various traits. The bottom line is that, when making inter-species comparisons, the selected species should be those for which comparisons will illuminate the key to a larger theoretical puzzle.

Artificial Tasks

Perhaps in part due to the top-down approach, comparative psychologists sometimes focus on training artificial behaviors rather than studying the mechanisms underlying naturally occurring behaviors; for example, asking primates to exhibit prosocial tendencies in the context of a food-sharing paradigm when few nonhuman primates actively engage in direct sharing. This situation may arise because researchers attempt to adapt paradigms used with humans, or other nonhuman species to more distantly related species (e.g., using the mirror mark test with dolphins, Mitchell, 1995). In doing so, researchers may be unintentionally forcing the animal to exhibit artificial behaviors that confound the ability to address functionally similar behaviors (Vonk & Shackelford, 2013). For example, nonhumans of many species have shown the ability to discriminate quantities (Agrillo & Beran, 2013), but the underlying mechanism that allows them to select the larger amount of food may be quite distinct from the human ability to count. Rather than imposing lengthy training sessions to attempt to teach animals to count (e.g., Beran, Rumbaugh, & Savage-Rumbaugh, 1998), it may be more useful to examine the extent to which animals rely on continuous factors such as magnitude as a cue to selecting the larger quantity using stimuli that they naturally discriminate between.

Another issue that we touched upon earlier, is that researchers often assume higher order processes in humans without subjecting human subjects to the same kind of tests to elucidate the mechanisms underlying their behavior. Comparative psychologists are in a unique position to draw comparisons to human behavior and cognition drawing on insights across many areas of psychology. When humans have been subjected to the same tests used to study mental processes in nonhumans, it is sometimes apparent that they are solving tasks in a manner that is distinct from the strategies used by other species (e.g., nonhuman primates and pigeons, Smith, Berg et al., 2012). Other times, it is clear that important continuities exist, such as in the categorization studies of Smith and colleagues (e.g., Smith, 2014). Yet, other studies have revealed that humans are sometimes subject to the same fallacies in reasoning that cause us to downgrade our descriptions of cognition in other species (e.g., Silva et al., 2005).

Comparative psychologists are also guilty of attributing dichotomous processes where actual processes may reflect a blend of various cognitive mechanisms. For example, psychologists are inclined to distinguish between associative processes and cognition as if cognition is not built upon associative learning (e.g.,

Greenwood, 2016). One area where this issue is pervasive is in the study of theory of mind. Researchers assume that the ability to attribute mental states involves an instantaneous recognition of underlying mental states in others. However, researchers often neglect to consider that mental states must be inferred from observable behavioral states. Thus, humans, like their animal counterparts, must first recognize the association between observable behaviors and traits and underlying mental states before they can draw inferences about mental states in others. This common oversight is discussed in more detail elsewhere (e.g., Vonk & Povinelli, 2006). The way that humans and nonhumans predict the behavior of other organisms may not be as distinct as it is often made out to be, but not because other animals are likely to have full blown theory of mind; rather, because humans are likely to rely extensively on observable behaviors when making predictions as well. Humans are also likely to rely frequently on intuitive processes despite the capacity for rational processes (e.g., Stark, Baldwin, Hertel, & Rothman, 2017). The fact that lower level processes may allow faster responding in contexts where conscious deliberation could delay the most adaptive response and cause harm to the actor, is often neglected when humans espouse the benefits of more advanced cognition.

All or none cognition. Related to these points, top-down approaches frequently pit one species against another, culminating in sharp dividing lines between species (de Waal & Ferrari, 2010). The idea that an ability is either present in its full capacity in a species (or completely absent) without consideration of a gradient of conceptual capacity greatly hinders the ability to detect continuity across phylogenetic lines. This type of all-or-none thinking can lead researchers to ignore potentially illuminating insights into animal cognition (Smith, Coutinho, Boomer, & Beran, 2012; Vonk & Shackelford, 2015). If one was seeking evidence of advanced mathematical cognition, for example, involving the partitioning of fractions, or the concept of zero, one might find that no other species exhibited abilities paralleling that of humans. However, examining mechanisms allowing for quantification of stimuli reveals important precursors to the more advanced mathematical abilities found in humans in many nonhuman species (Beran & Parrish, 2016). Similarly, attempts to find capacities such as metacognition in humans when using a humancentric definition may often fail to find confirmation of such abilities, when important components of the ability may be present (Smith, Coutinho et al., 2012). Focusing on the adaptive benefits of such an ability for the target species rather than focusing on the ways in which an ability may currently function in humans may help researchers to hone in on the necessary and sufficient conditions for the expression of elements of an ability. In the case of metacognition, it is most likely to have evolved when it allows an organism to predict important future events based on past experiences in predictable environments. It is not likely to have evolved explicitly to support the process of retrospection, although this is one way in which metacognition is expressed in humans (Shettleworth, 2012). Focusing on manifestations of a trait in humans may overshadow the utility of the trait for other species, and the fact that only elements of the human trait need be present to serve these functions. As another example, the ability to recognize oneself in reflective surfaces likely did not evolve so that humans could admire themselves in mirrors. Rather, it is likely that the ability to differentiate one's own movements from those of conspecifics or predators in shadows, or reflective water surfaces, was beneficial in reducing flight behavior when it was unnecessary.

Different levels of behavior in one species may be indicative of precursors to a cognitive ability present in its full form in another species (Vonk & Shackelford, 2013). Imitation provides another excellent example of this. Once defined as 'doing an act from seeing it done,' the definition of imitation now requires an understanding of the intention of another's actions (i.e., the other's goal and specific ways to achieve this goal; Whiten & Ham, 1992). With this definition, only humans were thought to have "true" imitative capabilities (de Waal & Ferrari, 2010). However, Mitchell (1987) argues that imitation can be broken down into five levels, which can be distinguished by the processes that bring about the imitation (first-level imitations are based on

evolution, selection, and morphogenesis; second-level, on perception and action; third-level, on learning; fourth-level, on self-awareness; and fifth-level, on planning and the awareness of another's awareness). When examined in terms of varying levels of complexity, forms of imitation can be seen in various bird species (Zentall, 2004), marmosets (*Callithrix jacchus*; Voelkl & Huber, 2007), capuchins (*Cebus apella*; Danforth, Thierry, de Waal, & Whiten, 2010), rhesus macaques (*Macaca mulatta*; Ferrari et al., 2006), and chimpanzees (*Pan troglodytes*, Whiten, Horner, & de Waal, 2005). Similarly, it is unlikely that other species have developed a full-blown capacity for theory of mind on par with what is expressed in humans, but many other species may express some component, such as an understanding of seeing, even if they do not pass false belief tests (Call & Tomasello, 2008), although the latter conclusion is currently under debate (Andrews, 2017).

Methodological shortcomings. Aside from issues of prevalence and availability, other aspects of captive environments may undermine the ability of researchers to conduct rigorous tests or draw accurate conclusions. For example, safety issues and enclosure design can present obstacles to ideal testing. An animal's habitat may not be conducive for observation or experimental set up. For instance, if the enclosure possesses a heavy metal mesh with limited view, recording and measuring a subject's behavior will be difficult. Moreover, the lack of space to separate individuals for testing could create artifacts whereby only dominant animals gain access to resources or interfere with the ability of subordinates to demonstrate learning. Some researchers have recently advocated for the benefits of group-testing and have provided some advice for dealing with the complexities of group-testing (Cronin, Jacobson, Bonnie, & Hopper, 2017), but there remain types of testing situations that are best done individually. Furthermore, when testing hypotheses about the importance of social complexity, captive tests are complicated by the fact that many naturally solitary animals are housed in groups in captivity (e.g., tigers, orangutans, bears), making it difficult to disentangle the species' natural lifestyle from the individual's ontogenetic history. Miklósi and Topál (2012) astutely point out that enculturation for domestic dogs is natural whereas - for apes - it is unnatural, rendering cross-species comparisons on the effects of enculturation somewhat inert.

Perhaps a more consistent problem in comparative psychology is that these top-down approaches involve the application of established methodologies to previously untested species, often without regard for species-specific behaviors, sensory capacities and motivations. The failure to properly account for important factors such as body plan (e.g., whether an animal can grasp an object or use a computer), preferred sensory modality (e.g., visual vs. olfactory vs. auditory), or ecology (which may lead to similar behaviors being expressed in different ways or contexts) when designing experimental tasks and apparatuses (Brosnan, Beran, Parrish, Price, & Wilson, 2013) can lead to incorrect conclusions regarding species capabilities. Furthermore, even animals with similar sensory foci may not perceive stimuli in exactly the same manner, for example, they may be sensitive to different ranges of auditory stimuli, or have different visual acuity. That is, researchers sometimes neglect to attend to whether the species has the physiological or perceptual capacity to detect the stimuli they are being asked to discriminate, or present stimuli in a manner that may be aversive to the animal. For example, presenting stimuli straight ahead of an animal whose eyes are located on the side of its head and not allowing the animal an opportunity to feel or rotate the stimuli, will lead to frustration and task failure. We ourselves have conducted many concept discrimination tasks in species for which there exists little data about visual acuity and color perception (e.g., Vonk & Galvan, 2014).

Asking primates to respond to experimenters' direct eye gaze may equate to presenting a direct threat, leading subjects to avoid approaching an experimenter who is looking ahead, and thus can see them, in favor of an experimenter who is looking away, for reasons other than, for example, a failure of theory of mind. Such intrinsic preferences can also partially account for superior performance in competitive versus cooperative

object choice tasks (Hare, 2001). Such results are then less informative about the ability being assessed and more reflective of species' natural tendencies. The proposal to use competitive versus cooperative paradigms in testing primate theory of mind, does, however, have the advantage that it reflects primates' natural ecology (Hare, 2001).

Of course, the question as to whether researchers should present the same or different tasks to different species is complicated by the need to draw comparisons of acquisition time and overall performance. Sometimes using different paradigms is a detriment to drawing useful comparisons. Even when different species are speculated to have comparable adaptations, researchers often fail to test them using similar paradigms, or neglect to suitably match the methodology (Vonk & Shackelford, 2013). Consequently, it becomes unclear whether abilities shown in one species are actually convergent to the abilities shown by another species or if those abilities are limited to specific, naturally occurring, contexts (Clary & Kelly, 2013). The challenge, which requires a fair bit of ingenuity, is to match the conceptual validity of the task and its functional meaning, while allowing the expression of behaviors within the different animals' natural repertoires. For example, one could compare time to learn visual discriminations in birds with comparable olfactory discriminations in rodents. A string-pulling cooperation paradigm could become a lever-stepping or token-choosing task in other species for which string-pulling would not be easily trained. Pattern recognition paradigms using nose-poke apparatuses for rats (e.g., Domenger & Schwarting, 2005) might not work well for horses, or chickens, which have instead been tested in the runway paradigm (Kundey, Strandell, Mathis, & Rowan, 2010), or for monkeys, which have been tested using a successive training task presented on a computer touchscreen (Chen, Swartz, & Terrace, 1997). Of course adapting paradigms to suit the propensities of different species may result in differential training periods to acquire the task, which presents another possible confound when comparing different species. This challenge highlights the advantage of presenting animals with more naturalistic tasks that require less training.

Although initial studies on the cognitive abilities of a given species should focus on naturally occurring behaviors, it is important to also consider the extent to which behaviors can be generalized to non-ecologically relevant contexts and tasks in order to test the constraints and limits of the ability. Examining behaviors outside of a limited context in which the behavior might be hard-wired will allow researchers to separate innate behaviors from flexible behaviors and to divulge the potential, as well as the confines, of a given species' cognitive abilities (Clary & Kelly, 2013; Vonk & Subiaul, 2009). If the goal is to understand how well chimpanzees can apply natural behaviors in novel contexts, it might be valid to present them with unnatural stimuli that they would not encounter in natural settings (Vonk & Subiaul, 2009). Researchers propose that theory of mind developed precisely to allow for a wide range of flexible responses to a suite of behaviors expressed in conspecifics. If the adaptive response emerges only in a narrow range of settings (e.g., competitive but not collaborative contexts) then the ability is more limited than that expressed in humans (Vonk & Povinelli, 2006).

A Bottom-up Approach

We have singled out several issues that we perceive to be instrumental in limiting the potential for comparative psychology to resolve some of its longstanding debates. We have attributed these challenges in part to the prevailing top-down approach to the study of animal cognition. We have made some explicit suggestions for how researchers could instead start from the bottom up to better understand the factors responsible for species-specific behaviors and shared behaviors without making discrete species comparisons. In what follows, we outline how a widely adopted bottom-up approach could move the field forward. This

proposition may seem at odds with our endorsement of theoretical rather than atheoretical justifications for research programs. However, our proposal dictates that theory informs the consideration of factors to examine in relation to each outcome variable. Once relevant factors are identified, representative species can be selected and tasks can be designed that are well suited for that species' natural behavioral repertoire. We reject the more general proposal to stack the deck in favor of particular theoretical explanations for behavior that pit processes or species against each other in a dichotomous fashion.

Bottom-up approaches should be used to establish "species-fair" controlled testing that ascertains the species' abilities and avoids a lack of theoretical justification. This starts from observing measurable behaviors that emerge from naturally evolved systems characteristic of the species, such as neurobiological systems (Uher, 2008). Furthermore, Brosnan et al. (2013) suggest designing studies that are as identical as possible across species, and then comparing responses from newly tested species to those of species whose outcomes are already known. Although using identical methods to test cognitive abilities across species would be ideal, the same methodology may evoke responses that have different meanings for different species. For example, tokens do not have the same meaning for nonhumans, who do not use currencies, as they do for humans. Because of this, one would not be able to use a methodology involving tokens for both humans and nonhumans and expect them to have the same motivations for completing the task. In such cases, it may then be preferable to use slightly different methodologies to test the same ability.

Additionally, similar outcomes in such tasks may not reflect similarity in the underlying mechanisms (Brosnan et al., 2013). For example, nonhuman primates may correctly choose to approach an experimenter who can see them versus one that cannot in a perspective-taking task, not because they appreciate the benefits of 'seeing' but, rather, because they may be intrinsically attracted to eye gaze. Other primates may find direct gaze aversive, and avoid the 'seeing' experimenters in favor of those looking away, not because they lack the capacity for perspective-taking, but rather because they are motivated to avoid an aversive stimulus. One of the prevailing challenges in the field of comparative cognition is to resist the urge to interpret human-like behaviors as reflecting human-like cognitive processes when alternative explanations are equally feasible. Furthermore, we must become aware of our own influence on the subjects that we observe and test.

To that end, studies of human/animal interactions from a basic science perspective have, until recently, been mostly restricted to studies of inter-specific competition and animal's understanding of human communicative cues and emotions. More recently, however, scientists have expanded the study of multi-species interactions, with a primary focus on animal-human interactions. The last point we wish to make is that comparative psychology can extend its reach by focusing not only on how animals can be used as models to understand human cognition, but on how humans can be used to understand animal cognition. Utilizing a bottom-up, rather than a top-down approach, will facilitate the shift to understanding animals for their own sake rather than using them as tools to investigate human centered issues or traits. Furthermore, the study of animals can, and should, be applied to the purpose of improving animal lives. Here is another area in which comparative psychology can distinguish itself from other related disciplines given the applied focus that is not found in fields other than psychology.

Animal Human Interactions

Comparative psychology is more than just the study of how individual species think or why they behave the way they do. The field has grown in recent decades to include an important emphasis on animal-human interactions. This includes a focus on conservation, animal-welfare and policy, and the anthropogenic

influences on wild animal populations. Further, it includes the applied science of animal medicine and husbandry. Perhaps in part due to the challenge of studying wild and captive species, many researchers have turned their focus to the study of domestic animals, such as farm or companion animals. As outlined above, such studies can illuminate effects of domestication on cognition, but they are also critical in informing our practices regarding animals that we depend upon for our own existence. As such, new areas of comparative psychology turn the subject matter on its head and examine the role of humans in understanding animals, rather than the other way around.

Training. The human desire to form relationships with nonhuman animals long predates the field of comparative psychology, as humans have been attempting to control or otherwise utilize nonhuman animals for thousands of years (Vila, et al., 1997). Indeed, from hunter-gatherers domesticating wolves to modern-day drug sniffing dogs, this relationship has proven beneficial for human societies (Mason, 1984). Ultimately, the attempts to understand the learning processes of animals at an empirical level arose in the late 19th and early 20th centuries with the work of Edward Thorndike (for history, see Young, 2002). Humans working with animals in a variety of contexts have benefitted from a better understanding of learning mechanisms and processes, which can allow for greater control by human trainers. The methodologies of training have changed drastically over the decades, largely informed by the work of comparative psychologists.

Until recently, animal training methodologies took a "carrot and stick" approach – an approach of rewarding desired behaviors and punishing undesired behaviors (Young, 2002). The thought was that training would be effective if trainers modelled natural dominance behaviors, and provided punishments that the animal would naturally receive (e.g., ear-biting or pinning in wolves). In a way, this method represented an attempt by humans to communicate with animals on their terms rather than our own. This methodology, however, assumes that animals respond to their trainers as conspecifics. Comparative psychologists at the time knew that this assumption may not be correct, as many nonhuman animals are capable of recognizing and differentiating species (Hemsworth & Barnett, 1987). Additionally, behavioral research had also suggested that punishment-based training was far less effective than reinforcement-based training (Chance, 1998). As the field of comparative psychology grew, this research received more public exposure, and training methodologies changed accordingly. Behavioral research on animal learning and cognition is now a primary resource for modern training techniques. This connection between comparative psychology and animal training allows for the understanding of nonhuman animal behavior to be the basis of the human-animal relationship.

By understanding nonhuman animal behaviors in more depth, the relationship between humans and nonhuman animals can be improved greatly. For example, stress has been shown to interfere with training (Sapolsky, 1996), and humans' ability to accurately assess the emotions of nonhuman animals is imperfect (e.g., Bloom & Friedman, 2013). Even among common household pets – dogs (*Canis familiaris*) – only happiness is readily recognized, whereas emotions like surprise and fear are confused for one another. Stressful situations such as reprimands or invasive grooming procedures elicit emotions that are not so easily recognized, even to experts. In order to maximize the results of training – and ultimately, our relationship with nonhuman animals – the subtle distinctions of stress-related emotions must be better understood. In naturally gregarious species such as humans and dogs, pack-bonding is a function of both verbal and nonverbal communication. Because most species lack the ability to communicate verbally, any interspecies interactions rely on nonverbal behaviors. Comparative psychology sometimes provides a basis for translating what animals are trying to communicate.

Animal roles in human lives. Animals are trained by humans for a variety of purposes in many contexts. Animals serve as entertainment, service, and companion animals, and are also consumed by humans. Companion animals have been utilized in therapy for a multitude of human conditions ranging from neuromusculoskeletal dysfunctions, such as cerebral palsy, traumatic brain injury, stroke and others (American Hippotherapy Association, 2010) to emotional issues (Earles, Vernon, & Yetz, 2015), and even academic engagement (Bassette & Taber-Doughty, 2013). Animal assisted therapy (AAT) is an increasingly popular technique, with formal education programs training individuals to practice AAT. One of the largest organizations responsible for therapy animals, the Delta Society, has defined animal assisted interventions as opportunities for motivational, educational, recreational, and/or therapeutic benefits to enhance quality of life (Stewart, 2016). Elementary students showed reduced aggression and hyperactivity and increased positive social interactions following exposure to a dog in their classroom (Kotrschal & Ortbauer, 2003). In addition, academic engagement behaviors increased in children with emotional and behavioral disabilities (Bassette & Taber-Doughty, 2013). Although many of these studies involve canines, are performed in the classroom, and emphasize improved behavior, other animals have also contributed in other contexts. For example, equine activities are known to help with psychological conditions in settings outside of the regular school curriculum. Earles et al. (2015) found that equine-assisted therapy effectively treated PTSD and other symptoms related to anxiety, which are often the root cause of behavioral problems. Previous research has shown an integrated approach between the horse and the rider in that horses' responses may provide immediate feedback about a person's nonverbal behavior (Maros, Gácsi, & Miklósi, 2008). This illustrates the concept that both humans and animals benefit from the interaction. Researchers have also recently turned their attention toward the study of impacts of human practices on equines within various kinds of work contexts (e.g., Lesimple, Fureix, Aubé & Hausberger, 2016). Further work is needed to assess the benefits for the animals involved in such programs.

Comparative psychology and zoo efforts. Humans have both positive and negative impacts on other species. While human population growth, agricultural and industrial practices have enormous detrimental impacts on animal environments, humans have also worked to aid in conservation efforts. Humans are also unique among animals in the desire to educate others about issues of biodiversity and conservation. This is one of the key functions of zoos - conservation through educating the public on animal and habitat welfare and through breeding programs. The success of these endeavors has been substantially informed by the findings of comparative psychology. For example, early research tied caretaker interaction to reproductive success in various felid species (Mellen, 1991), lower levels of stress hormones in clouded leopards (Wielebnowski, Fletchall, Carlstead, Busso, & Brown 2002), and more positive social interactions among nonhuman primate clans (Baker, 2004).

In addition to providing a vehicle for conservation efforts, positive keeper-animal relationships within zoo settings is critical for the welfare of captive animals. Arguably, the most important component of the human-animal relationship with regard to its effect on welfare is fear of humans (Carlstead, 2009). Fear is associated with chronic stress; living so close to humans can have a significant negative effect on an individual's welfare. For example, pigs' feeding behaviors and affiliative behaviors among conspecifics in petting zoos significantly decreased with high visitor presence while aggression amongst conspecifics increased (Farrand, Hosey, & Buchanan-Smith, 2014). Rates of aggression and abnormal behaviors (e.g., fighting, reduced feeding, and avoidance) increase, and affiliative behaviors (e.g., object interaction, playing, and grooming) are reported to typically decrease as visitor density increases (Farrand, et al., 2014; Hemsworth, Pedersen, Cox, Cronin, & Coleman, 1999; Kuhar, 2008; Lambeth, Bloomsmith, & Alford, 1997; Wood, 1998) in many species. For example, gorillas stayed in areas where they were out of sight to visitors when large crowds were present, (Kuhar, 2008), and pigs have been observed to avoid the areas closest to the fence of

their stalls when humans are present (Hemsworth, Verge, & Coleman, 1996). Facilitating positive keeper-animal relationships and ensuring appropriate habitats and enrichment can mitigate to some degree against these deleterious effects.

Positive keeper-animal relationships can be achieved not only through behavioral emotion recognition, but also through certain husbandry techniques. For example, Carlstead (2009) found that affinity was greater for keepers who interacted with their animals through a barrier than for those who entered the enclosure. Similarly, animals showed higher affinity for keepers who remained in sight than for those who were hidden at any time during the interaction. Additionally, recognizing the signs of acute and chronic stress would substantially increase the welfare of the animals by means of providing enrichment. Baker (2004) examined the notion that human play can help mitigate against the deleterious effects of stress. When unstructured play with humans was increased by only 10 minutes per chimpanzee, stressed, HIV positive chimpanzees were less tense and reactive, spent less time idle, and engaged in higher levels of affiliative behavior. Overall, their levels of abnormal behavior fell. Prior work has also shown that shelter dogs exhibit high levels of stress (Hiby, Rooney, & Bradshaw, 2006) and that this stress can be mitigated somewhat through interactions with humans (Shiverdecker, Schiml, & Hennessy, 2013). This pattern of findings indicates that using interactions with humans as enrichment has the potential for an increase in positive behavioral outcomes depending on the context in which humans interact with the animals. In addition, when the type of enrichment (unstructured human play) that promotes affiliative behaviors in chimpanzees was increased, the enrichment served to mitigate against aggressive behaviors caused by other stressors (HIV sickness, Baker, 2004). In summary, keeper practices as well as emotion recognition skills reduce the fear and stress on the animal, significantly affecting their welfare in captivity.

Zoos typically also work to educate the public on animal behavior, biology, and habitat, and in doing so, they seek to communicate the importance of conservation. Comparative psychologists have addressed the degree to which zoo education programs can affect conservation attitudes. Hacker and Miller (2016) found that conservation attitudes toward elephants were most affected by guests' up-close encounters with the animals and by seeing active, diverse natural behaviors. Zoos frequently offer behind-the-scenes tours, presentations with "animal ambassadors", or touch-pools, paired with their conservation message. Although commercializing such interactions comes hand in hand with certain ethical concerns (given the previously discussed patterns of findings that suggest a cost to the animal welfare in such up-close human interactions; see Carlstead, 2009; Farrand et al., 2014), it certainly seems to be a particularly effective way of influencing the public's attitudes toward conservation. Thus, animals should be diligently monitored and protected during interactions with the public to prevent undue stress. Additionally, those eligible for public interaction should be strictly limited to those who are not typically stressed by interaction, such as individuals previously kept as pets, or working animals. Briefly, in order to maximize the efficacy of conservation messages while simultaneously maximizing animal welfare, the work of comparative psychologists can be extremely valuable. Thus, a shift from the exclusive focus on what animals can do for us (e.g., animal models of human disease), to learning more about what we can do to benefit other animals, would be a welcome change of direction for comparative psychology.

Conclusions

Although we acknowledge that comparative psychologists have made numerous important discoveries over the years, the growth of the field has been constrained by some of the biases and shortcomings outlined here. For comparative psychology to grow, researchers need to shift focus from top-down approaches and all-

or-nothing thinking to a broader perspective that takes into account the natural behaviors and abilities of a wide range of species. Instead of asking which species has a particular cognitive ability, the question should be what are the necessary ingredients for that cognitive ability and how did these evolve (de Waal & Ferrari, 2010). Comparative psychologists should attempt to understand the basic processes and common denominators of a given cognitive ability before exploring species-typical specializations (de Waal & Ferrari, 2010). Breaking down cognitive abilities into levels of complexity will help determine the extent to which continuities, as well as discontinuities exist between various species, not just between humans and nonhumans, and is an important next step for comparative psychology. To be sure, comparative psychologists have already made tremendous strides in this direction. Lastly, with a growing social conscience regarding our treatment of nonhuman animals, comparative psychology must no longer examine each species in isolation, but should turn to an examination of the larger ecosystem with an emphasis on biodiversity and the important relationships between species. This includes, of course, our responsibility to care for other animals to prolong their existence on our shared planet, and to ensure that their stay is not subject to human abuse and misuse.

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